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Alpine and arctic plant communities: A worldwide perspective[☆]



1. Background and context

High-elevation and high-latitude ecosystems experience among the most severe climates on Earth where plant and animal life can thrive (Körner, 2003). Termed arctic and alpine regions, they represent 8% of the global land area and occur on all continents (Chapin and Körner, 1995). Despite their extreme environmental harshness, these ecosystems harbour relatively important biodiversity and endemism, with high diversity turnover along steepest environmental gradients. Some of these ecosystems have long been the focus of ecological studies and captured the attention of some of the most popular naturalists and biologists during the last few centuries (reviewed by Billings and Mooney, 1968; Körner, 2003). The reasons for such a scientific interest are multiple. From a strictly conceptual viewpoint, alpine and arctic ecosystems exhibit relatively simple vegetation patterns, with little vertical stratification, making it easier to characterize stress and disturbance effects on community and ecosystem functioning (Chapin and Körner, 1995). They provide “unsurpassed possibilities for comparative ecological research” because of steep elevation and topographical gradients (Körner, 2003). Their relative isolation allows studying ecological systems at diverse spatial scales, such as local scale communities, along environmental gradients, or entire mountain ranges (e.g. Chalmandrier et al., 2017; Marx et al., 2017). This isolation combined with the common historical setting of most mountain ranges also allows exploring questions related to the origins of biodiversity patterns, local speciation and endemism (Molina-Venegas et al., 2015, 2017). Alpine and arctic ecosystems are key providers and regulators of water resources to human societies (e.g., *water towers*; Körner, 2003), and also serve as biomass reserve for livestock grazing (Jacobsen and Dangles, 2017). Finally, the exceptionally high capacity of some arctic and alpine ecosystems to stock carbon makes them efficient carbon pools (Segnini et al., 2010; Tarnocai et al., 2009).

Although the accumulated knowledge on arctic and alpine environments is now substantial, there remains some unexplored alpine areas, hence current knowledge on alpine systems is geographically unbalanced (Fig. 1). While some important efforts have been devoted to studying arctic and temperate alpine ecosystems, mainly in the northern hemisphere, some important alpine areas such as the Himalayas and the Andes have long remained understudied. Tropical alpine regions are probably the most diverse alpine regions of the world, with unparalleled rates of speciation and resulting high local endemism (Anthelme et al., 2014; Madriñán et al., 2013), but have been particularly overlooked by researchers (Fig. 1). Such a discrepancy would be of minor importance if all arctic and alpine ecosystems were facing similar constraints in comparable climatic and edaphic environments. In fact, despite important common features such as cold temperature, infertile soils and frequent drought (Körner, 2003), a close examination shows strong dissimilarities between alpine regions of the world, mainly in relation to latitudinal position and topography (Nagy and Grabherr, 2009). For instance, prevailing climates in tropical alpine areas are much less seasonal, with daily variations in temperatures exceeding annual variations. As a consequence, winter snow cover, which is considered as a major driver of alpine and arctic vegetation structure (Carlson et al., 2015; Rixen et al., 2014) is almost absent in the tropics, thus affecting freezing and drought frequency. In addition, the inversion of precipitation gradients above 3000–3500 m in most tropical alpine systems generates tropical alpine deserts while annual precipitation increases with elevation in most extra-tropical alpine environments (Anthelme and Dangles 2012). In view of these differences, bridging this latitudinal knowledge gap between alpine regions is an important challenge, for both understanding how climate shape biodiversity patterns in alpine regions and drawing scenarios for the future of alpine and arctic biodiversity.

An important modern challenge for the study of alpine and arctic regions is obviously to understand and predict the consequences of the current high pace and expected high magnitude of global changes on ecosystem properties. A large body of evidence demonstrated that arctic environments are disproportionately impacted by climate warming, a phenomenon known as *arctic amplification* (Pachauri et al., 2014; IPCC report). A less known but now increasingly documented phenomenon is also the expected higher warming at higher elevations (MRI – Mountain Research Initiative EDW Working Group, 2015; Wang et al., 2016). Accordingly, the impact of warming should be exacerbated in tropical alpine systems, which are mostly located above 4000 m a.s.l. These issues are particularly alarming for the conservation of biodiversity and ecosystem functioning. The majority of alpine regions are highly fragmented, isolated and restricted to a very small portion of land surface, thus threatening most species adapted to the narrow environmental conditions of high elevations and high latitudes. Also, climate warming may induce a release of carbon and methane captured in permafrosts, with expected large feedbacks to global climate. This calls for more research about how climatic changes (both past and

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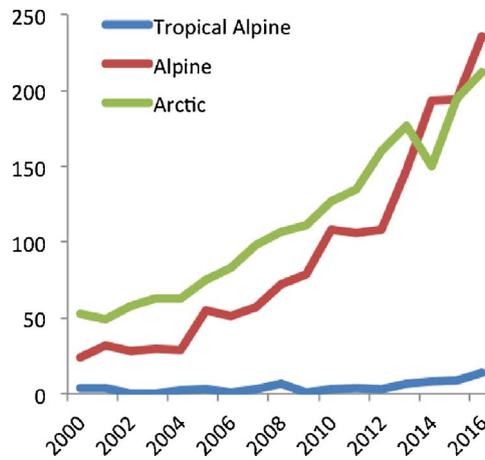


Fig. 1. Number of publications focusing on arctic/alpine ecology between the years 2000 and 2016 (Web of Science). Research strings used for alpine: alpine OR high-elevation OR high-altitude (title) AND ecosystem* (topic). Research strings used for arctic: arctic OR high-latitude OR Antarctic (title) AND ecosystem* NOT marine (topic), excluding field “oceanography”. Research strings used for tropical alpine: tropical alpine OR tropical and high elevation OR tropical and high-latitude (title) AND ecosystem* (topic). Results have later been refined manually, excluding papers out of scope. Analysis made on the 29 of June 2017.

contemporary) affect the biodiversity and functioning of alpine and arctic ecosystems. These thus constitute important sentinel ecosystems where much fundamental research is motivated by the need to understand and anticipate the effects of global changes.

Apart from modern societal challenges, alpine and arctic ecosystems raise a number of fundamental questions. The scope of these questions is very large, spanning the entire spectrum of ecological and evolutionary theory, and certainly cannot be tackled within a sole journal special issue, not even a single book. These key fundamental questions concern: (i) the evolutionary origins and historical build-up of species rich biomes and biodiversity hotspots, (ii) the effect of quaternary climatic oscillations on species distributions and biodiversity patterns, (iii) the ecological and micro-evolutionary drivers of species distributions and species range shifts in changing environments, (iv) the mechanisms of community assembly and species coexistence at local spatial scales, and the nature of biotic interactions (both plant–plant and plant–animal interactions). High elevation and latitude ecosystems provide very suitable settings for teasing apart these different mechanisms at varied temporal and spatial scales, and the conceptual contributions of arctic and alpine studies clearly goes beyond the sole study of these biomes.

2. Objectives and themes of this special issue

This special issue presents a selection of papers exploring some of the aforementioned key topics, following a symposium entitled ‘High-elevation ecosystems’, held at the Ecosummit conference, Montpellier, August 29th – September 1st 2016. The selected papers present cutting-edge research on arctic and alpine plant communities along a double latitudinal and altitudinal gradient, thus reflecting the biogeographic continuum between arctic and alpine ecosystems (see Fig. 2a). These regions include arctic areas in Norway, high alpine areas of Europe, New Zealand, Himalayas, but also high tropical alpine areas. These studies have been selected because they provide significant advances to current ecological theories and improve our understanding of global change effects on plant communities. They also describe a number of original methods, which might be inspiring for future research.

Based on authors’ extensive experience in alpine ecology, some papers of the special issue offer conceptual contributions centred on key climatic parameters critical to understanding arctic-alpine ecosystems. By reviewing up to 90 ways to measure temperature, Körner and Hiltbrunner (2018) highlight important pitfalls and propose a narrow selection of indices to depict the effects of temperature on plant distributions. They argue that mean annual temperature may be one of the less pertinent measurements because it does not consider the effects of snow cover and seasonal/diurnal

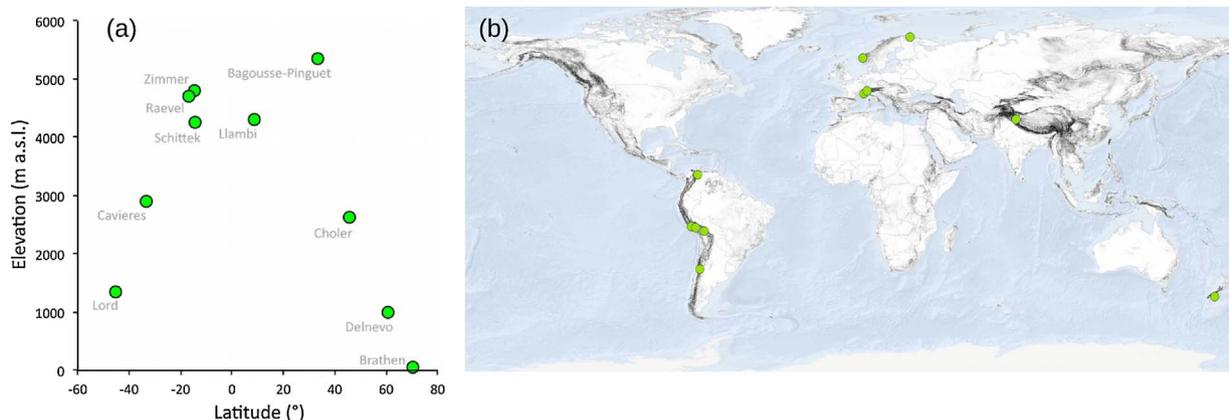


Fig. 2. Biogeographic situation of different empirical contributions to this special issue. (a) Diagram showing the continuous distribution of different study areas along latitude (x-axis) and elevation (y-axis) gradients worldwide. (b) Map depicting different alpine areas of the world according to a ruggedness scale (from light grey to black), following Körner et al. (2011) and the geographic position of all empirical papers included in this special issue. Note that the position of the two conceptual papers of this special issue, namely Körner and Hiltbrunner (2018); Graae et al. (2018), are not depicted in these two figures.

variations in temperature. Given the singularity of each site, the inherent complexity of alpine topography and the frequent occurrence of biotic thermal refuges, the authors recommend researchers to not rely on temperature extracted from extrapolated databases but rather measuring microclimate directly in their own target environments. Along the same line but with a purpose more focused on the structure of alpine vegetation under a warming climate, [Choler \(2018\)](#) demonstrates the need to measure temperature at a finer scale to account for the considerable local-scale environmental heterogeneity of alpine ecosystems. Focusing on the root zone temperature of temperate alpine plants, the author proposes that the combination of two temperature indices, namely growing degree days (GDD) and freezing degree days (FDD), represents a so-far undocumented “leading axis of habitat differentiation in the alpine zone”, which allows drawing very realistic scenarios of plant community change in relation to snow cover duration. In a conceptual contribution aiming at characterizing the main survival options for plants in a changing environment (“stay or go”), [Graae et al. \(2018\)](#) combine macro and micro-climatic variables during the growing season and winter. They propose that plant communities in more heterogeneous landscapes are less prone to species range shifts under global warming than communities occurring in homogeneous landscapes. In turn, communities in homogeneous landscapes may face high extinction rates, resulting in unsaturated communities. This is expected by the authors to leave more opportunities for other species to immigrate locally due to lower interspecific competition. Interestingly, these three contributions agree on the fact that local environmental heterogeneity is a major driver of plant distribution and community assembly in a changing world. Because each of the three contributions focuses on alpine and arctic environments periodically covered by snowpack, the authors insist that confronting these models to the reality of tropical environments or dry steppes, where snow cover is very limited in time, is an important challenge for future research in alpine ecology ([Choler, 2018](#)).

Along with [Choler \(2018\)](#) and [Graae et al. \(2018\)](#), three other contributions focus on the effects of snow cover dynamics on plant communities. First, [Lord et al. \(2018\)](#) present a 14-year transplant experiment of vegetation curves across a natural snow cover gradient in the mountains of South Island, New Zealand. One interesting result, among others, was that communities were strongly altered by this environmental shift, both by reduced fitness of initial species and by colonization from surrounding vegetation. The authors conclude that biotic interactions and species-specific traits are key drivers of alpine vegetation change following the alteration of snow cover regimes. Second, assuming that changes in temperature and precipitation will impact the timing of snow cover, [Delnevo et al. \(2018\)](#) tested to what extent warmer and wetter conditions (according to IPCC scenarios) impact the phenology and growth of *Ranunculus acris* (Ranunculaceae) through changes in snow cover duration. To do so, they also performed a transplant experiment along environmental gradients in the mountains of southern Norway. Advanced snowmelt resulted in accelerated reproductive phenology, hence a greater exposure of reproductive organs to the risk of frost damage. Interestingly, those phenological changes experienced by the study species were both due to phenotypic plasticity and genetic changes, and were less pronounced at higher elevation (i.e. in the most limiting environment). This second result is echoed by another contribution to this issue by [Cavieres and Sierra-Almeida \(2018\)](#), who study seed germination of fifty Andean alpine plants from Chile. They find that the importance of cold stratification for seed germination was more pronounced for lower elevation species, suggesting that modifications of snow cover duration could affect disproportionately germination phenology of lower alpine species than the ones growing at higher elevations. These latter two studies together suggest that plants facing the harshest conditions at higher elevations may exhibit little phenological responses to global changes. Further research is therefore needed to assess whether this lack of phenological adjustment reflects a greater plasticity or rather an absence of adaptive potential due to strong conservatism in phenological features, and how these potential plastic and genetic responses are potentially mediated by biotic interactions.

Alpine and arctic plants are adapted to high levels of environmental stress with a set of specific traits, well known as stress tolerance syndromes ([Cerabolini et al., 2010](#); [Grime, 2006](#)) such as slow growth rate, reduced stature, high individual longevity and varied protective traits. The rapidly changing climate combined with abrupt land use changes may now start favouring different adaptive traits in plants. In this issue, [Zimmer et al. \(2018\)](#) use a 38-year post-glacial chronosequences in the tropical Andes, matching a known period of accelerated climate warming. They observed that most plants having colonized recently unglaciated areas were anemochorous and rapidly growing ruderal species whereas slow-growing, stress-tolerant species were far less abundant. This suggests that the rapidly shrinking glacier cover may favour plants with opportunistic ecological strategies over slow-growing, stress tolerant, plants typical of high alpine environments, likely generating unexpected and likely novel plant communities at such elevations. However, this may not mean that slow growing, stress tolerant plants are immediate candidate to extinction in high alpine and arctic environments. [Schitteck et al. \(2018\)](#) examine the longevity of a cushion-forming plant in the dry Andes of Peru. Radiocarbon dating on the peat formed by the cushion identified a chronosequence of 1050 years and permitted reconstructing past plant communities during humid/dry climatic oscillations. The cushion plant was able to cope with extended droughts, demonstrating that stress tolerant species can also support the effects of environmental oscillations in the long term. Nevertheless, the authors indicate that the capacity of the cushion to survive in a changing climate is conditioned by the maintenance of its protective plant surface. It is possible, then, that the intensification of land use will generate higher mortality of this type of plants, resulting in a regression of patrimonial habitats, but also loss of valuable data on past climate and vegetation.

Positive interactions among organisms are a crucial driver of plant community organization in arctic and alpine environments ([Cavieres et al., 2014](#)). One major challenge of ecological research is to infer how these interactions will change in response to global changes ([Bulleri et al., 2016](#); [HilleRisLambers et al., 2013](#); [Olsen et al., 2016](#)). Several contributions in this special issue have devoted some efforts to answering this question. [Lord et al. \(2018\)](#) demonstrate that plant–plant interactions and plant–invertebrate interactions were very strong drivers of community changes in response to an alteration of snow cover regimes. [Zimmer et al. \(2018\)](#) suggest that the reduced capacity of stress-tolerant nurse plants to colonize recently unglaciated alpine areas might have cascading effects on vegetation structure, by not allowing lower elevation species to colonize these sites, as they would normally do thanks to facilitative effects. [Llambí et al. \(2018\)](#) identify in the Venezuelan Andes a complex network of plant reciprocal interactions where nurses facilitated the presence of a native community and an exotic species. The exotic species had no reciprocal effect on nurse plants but had a negative effect on the rest of community members. By facilitating the presence of an exotic species, the nurse plant hence impact negatively the native community through indirect interactions. In a macro scale study in the Norwegian tundra, [Bråthen et al. \(2018\)](#) characterize an extended network of interactions involving plants and a large herbivore (*Rangifer tarandus*), along a temperature gradient. They show the overwhelming influence of the allelopathic shrub *Empetrum nigrum* on the distribution and abundance of other plant species and demonstrate that this shrub is currently spreading due to a combination of climate warming and lack of herbivory, announcing a scenario of local biodiversity loss in the next decades. Such a scenario would not have been detected by studying only interactions among pairs of plant species only. Focusing on alpine communities dominated by cushion-forming nurse plants, [Raavel et al. \(2018\)](#) examine variations in the functional traits of subordinate plants, which may provide insights into the ecological processes shaping species niches ([Albert et al., 2011](#)). They show that graminoids developed a stress avoidance strategy whereas forbs shifted from stress avoidance to stress resistance along an increasing stress gradient. They also demonstrate that cushion plants were able to buffer the effects of biotic and abiotic stresses on subordinate plant traits. Given that stress levels are expected to increase under global changes, these positive effects of nurse plants in the high Andean peatlands may preserve important ecosystem services such as water

resource and biomass production.

An outstanding component of alpine biodiversity is constituted by its high rate of endemism. Smyčka et al. (2018) tested two alternative hypotheses to understand the origins of endemic plant species in the European Alps. Through a spatially-explicit bayesian analysis of phylogenetic structure of the high alpine flora, they observe that high endemism occurs in potential glacial refugia, but mainly on calcareous bedrock, and also at high elevations. Plant assemblages in calcareous refugia showed a signature of phylogenetic overdispersion – suggesting non-selective persistence of different lineages during ice ages, whereas those located in high mountain areas showed phylogenetic clustering – indicating repeated recent speciation and environmental filtering. From a conservation viewpoint, the authors conclude that calcareous glacial refugia are more important to conserve, as they host many range restricted species and more diverse evolutionary lineages. It is interesting to note that the primary drivers of mountain endemism cited by these authors, elevation and glacial refugia, are exacerbated in tropic alpine areas (Crawford, 2008; Sklenář and Laegaard, 2003). These regions have been cited to exhibit remarkable rates of endemism in plants and animals, especially in the Andes (Anthelme et al., 2014). A nice research challenge following the approach of Smyčka et al. (2018) would then consist in inferring endemism patterns in the high tropical mountains of the Andes. In another study conducted in the *trans*-Himalayas, Le Bagousse-Pinguet et al. (2018) hypothesized that more constraints at higher elevation should lead to higher phylogenetic clustering of local plant communities. They instead observed that plants at higher elevation displayed random phylogenetic patterns, and that no particular mechanism of niche-based species coexistence process could therefore be inferred from the phylogenetic structure of these plant communities. This study echoes a recent one conducted in nival communities of higher summits of western European Alps, where the authors could not reject neutral mechanisms of community assembly by comparing community phylogenetic structure to neutral based simulations of community assembly (Marx et al., 2017).

3. Conclusion and perspectives

The discovery and study of unknown ecosystems and biodiversity have often provided novel knowledge and explicative models in biology (e.g. Rothschild and Mancinelli, 2001). So the position of arctic and alpine ecosystems at the climatic extreme of plant and animal life suggests that their study bears unique findings regarding the ecology and evolution of natural communities. We hope that the paper selection included in this special issue provides a first demonstration of the importance of studying arctic and alpine systems, both for advancing ecological and evolutionary theories, but also for understanding the future of cold-adapted ecosystems under contemporary global changes. A noteworthy progress in arctic-alpine studies reflected in this special issue is the increasing integration with research techniques and concepts typically associated with physical sciences (glaciology, paleogeomorphology, cosmogenic nuclide and carbon isotopic dating, micro-climatic monitoring etc...). Also notable is a number of empirical approaches that will need to be undertaken by networked researchers across different mountain ranges of the globe; these are long term monitoring of multi-trophic community changes and whole-community transplant experiments (meadow turves) along key climatic gradients. We thus hope that this special issue will serve inspiring future research in the field of arctic-alpine ecology and beyond.

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References

- Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G., Violle, C., 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspect. Plant Ecol. Evol. Syst.* 13, 217–225.
- Anthelme, F., Dangles, O., 2012. Plant–plant interactions in tropical alpine environments. *Perspect. Plant Ecol. Evol. Syst.* 14, 363–372.
- Anthelme, F., Jacobsen, D., Macek, P., Meneses, R.I., Moret, P., Beck, S., Dangles, O., 2014. Biodiversity patterns and continental insularity in the tropical high Andes. *Arctic Antarctic Alp. Res.* 46, 811–828.
- Billings, W., Mooney, H.A., 1968. The ecology of arctic and alpine plants. *Biol. Rev.* 43, 481–529.
- Bråthen, K.A., Gonzalez, V.T., Yoccoz, N.G., 2018. Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.06.005>.
- Bulleri, F., Bruno, J.F., Silliman, B.R., Stachowicz, J.J., 2016. Facilitation and the niche: implications for coexistence: range shifts and ecosystem functioning. *Functional Ecol.* 30, 70–78.
- Carlson, B.Z., Choler, P., Renaud, J., Dedieu, J.P., Thuiller, W., 2015. Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities. *Annals Bot.* 116, 1023–1034.
- Cavieres, L.A., Sierra-Almeida, A., 2018. Assessing the importance of cold-stratification for seed germination in alpine plant species of the high-Andes of central Chile. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.09.005>.
- Cavieres, L.A., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C.J., Xiao, S., Al Hayek, P., Anthelme, F., Cranston, B., Garcia, M.C., le Bagousse-Pinguet, Y., Reid, A.M., le Roux, P., Lingua, E., Nyakatyá, M., Touzard, B., Zhao, L., Callaway, R.M., 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecol. Lett.* 17, 193–202.
- Cerabolini, B.E., Brusa, G., Ceriani, R.M., De Andreis, R., Luzzaro, A., Pierce, S., 2010. Can CSR classification be generally applied outside Britain? *Plant Ecol.* 210, 253–261.
- Chalmandrier, L., Münkemüller, T., Colace, M.-P., Renaud, J., Aubert, S., Carlson, B.Z., Clément, J.-C., Legay, N., Pellet, G., Saillard, A., Lavergne, S., Thuiller, W., 2017. Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. *J. Ecol.* 105, 277–287.
- Chapin, F.S.I., Körner, C., 1995. *Arctic and Alpine Biodiversity: Patterns Causes and Ecosystem Consequences*, vol. 113 Springer Science.
- Choler, P., 2018. Winter soil temperature dependence of alpine plant distribution: implications for anticipating vegetation changes under a warming climate. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.11.002>.
- Crawford, R.M.M., 2008. *Plants at the Margin: Ecological Limits and Climate Change*. Cambridge Univ. Press.
- Delnevo, N., Petraglia, A., Carbonegani, M., Vandvik, V., Halbritter, A.H., 2018. Plastic and genetic responses to shifts in snowmelt time affects the reproductive phenology and growth of *Ranunculus acris*. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.07.005>.
- Graae, B.J., Vandvik, V., Armbruster, W.S., Eiserhardt, W.L., Svenning, J.C., Hylander, K., Ehrlén, J., Speed, J.D.M., Klanderud, K., Bråthen, K.A., Milbau, A., Opedal, Ø.H., Alsos, I.G., Ejrnaes, R., Bruun, H.H., Birks, H.J.B., Westergaard, K.B., Birks, H.H., Lenoir, J., 2018. Stay or go? How topographic complexity influences alpine plant population and community responses to climate change. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.09.008>.
- Grime, J.P., 2006. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons.
- HilleRisLambers, J., Harsch, M.A., Ettinger, A.K., Ford, K.R., Theobald, E.J., 2013. How will biotic interactions influence climate change-induced range shifts? *Ann. New York Acad. Sci.* 1297, 112–125.

- Jacobsen, D., Dangles, O., 2017. Ecology of high altitude waters. Oxford University Press.
- Körner, C., Hiltbrunner, E., 2018. The 90 ways to describe plant temperature. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.04.004>.
- Körner, C., Paulsen, J., Spehn, E.M., 2011. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alp. Bot.* 121, 73–78.
- Körner, C., 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer Science.
- Le Bagousse-Pinguet, Y., Liancourt, P., Götzenberger, L., de Bello, F., Altman, J., Brozova, V., Rehakova, K., 2018. A multi-scale approach reveals random phylogenetic patterns at the edge of vascular plant life. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.10.002>.
- Llambí, L.D., Hupp, N., Saez, A., Callaway, R., 2018. Reciprocal interactions between a facilitator, natives, and exotics in tropical alpine plant communities. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.05.002>.
- Lord, J.M., Mark, A.F., Humar-Maegli, T., Halloy, S.R., Bannister, P., Knight, A., Dickinson, K.J., 2018. Slow community responses but rapid species responses 14 years after alpine turf transplantation among snow cover zones, south-central New Zealand. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.07.004>.
- MRI – Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Change* 5, 424–430.
- Madriñán, S., Cortés, A.J., Richardson, J.E., 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers Genet.* 4, 192.
- Marx, H.E., Dentant, C., Renaud, J., Delunel, R., Tank, D.C., Lavergne, S., 2017. Riders in the sky (islands): using a mega-phylogenetic approach to understand plant species distribution and coexistence at the altitudinal limits of angiosperm plant life. *J. Biogeogr.* 44, 2618–2630.
- Molina-Venegas, R., Aparicio, A., Slingsby, J.A., Lavergne, S., Arroyo, J., 2015. Investigating the evolutionary assembly of a Mediterranean biodiversity hotspot: deep phylogenetic signal in the distribution of eudicots across elevational belts. *J. Biogeogr.* 42, 507–518.
- Molina-Venegas, R., Aparicio, A., Lavergne, S., Arroyo, J., 2017. Climatic and topographical correlates of plant palaeo- and neoendemism in a Mediterranean biodiversity hotspot. *Annals Bot.* 119, 229–238.
- Nagy, L., Grabherr, G., 2009. *The Biology of Alpine Habitats*. Oxford University Press.
- Olsen, S.L., Töpfer, J.P., Skarpaas, O., Vandvik, V., Klanderud, K., 2016. From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biol.* 22, 1915–1926.
- Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., et al., 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC.
- Raevel, V., Anthelme, F., Meneses, R.L., Munoz, F., 2018. Cushion-plant protection determines guild-dependent plant strategies in high-elevation peatlands of the Cordillera Real, Bolivian Andes. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.09.006>.
- Rixen, C., Wipf, S., Frei, E., Stöckli, V., 2014. Faster, higher, more? Past, present and future dynamics of alpine and arctic flora under climate change. *Alp. Bot.* 124, 77–79.
- Rothschild, L.J., Mancinelli, R.L., 2001. Life in extreme environments. *Nature* 409, 1092–1101.
- Schitteck, K., Forbriger, M., Berg, D., Hense, J., Schäbitz, F., Eitel, B., 2018. Last millennial environmental dynamics in the western Peruvian Andes inferred from the development of a cushion-plant peat hillock. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.09.002>.
- Segnini, A., Posadas, A., Quiroz, R., Milori, D.M.B.P., Saab, S.C., Neto, L.M., Vaz, C.M.P., 2010. Spectroscopic assessment of soil organic matter in wetlands from the high Andes. *Soil Sci. Soc. Am. J.* 74, 2246–2253.
- Sklenář, P., Laegaard, S., 2003. Rain-shadow in the high Andes of Ecuador evidenced by paramo vegetation. *Arctic Antarctic Alp. Res.* 35, 8–17.
- Smyčka, J., Roquet, C., Renaud, J., Thuiller, W., Zimmermann, N.E., Lavergne, S., 2018. Disentangling drivers of plant endemism and diversification in the European Alps—A phylogenetic and spatially explicit approach. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.08.003>.
- Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G., Zimov, S., 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles* 23, GB2023.
- Wang, Q., Fan, X., Wang, M., 2016. Evidence of high-elevation amplification versus Arctic amplification. *Sci. Reports* 6. <http://dx.doi.org/10.1038/srep19219>.
- Zimmer, A., Meneses, R.L., Rabatel, A., Soruco, A., Dangles, O., Anthelme, F., 2018. Time lag between glacial retreat and upward migration alters tropical alpine communities. *Perspect. Plant Ecol. Evol. Syst.* <http://dx.doi.org/10.1016/j.ppees.2017.05.003>.

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