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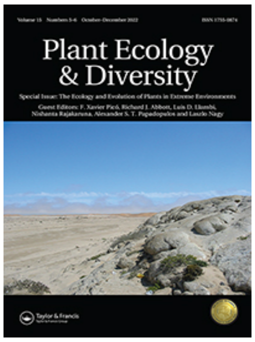

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Introduction to special issue: the ecology and evolution of plants in extreme environments

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ABSTRACT
In plant ecology, extreme environments are those that pose physiological or other limitations to plant growth, especially for non-adapted taxa. In these environments, the severity of climate conditions and/or the limitations imposed by particular soil substrates represent major selective pressures for plants, leading to the evolution of a wide array of functional traits, specific strategies and adapted taxa. In this special issue, we present a collection of papers that focuses on plants in various extreme environments, including the Arctic and Antarctic, regions with serpentine and gypsum soils, high mountain areas and deserts. The papers include a broad array of methods to study the ecology and evolution of plants in extreme environments, such as field surveys, greenhouse and field experiments, molecular phylogenetic analyses and/or physiological measurements. Overall, this special issue showcases research on how plants thrive in extreme environments which, in turn, may provide pointers to how plant communities might respond to living in increasingly challenging environments resulting from unprecedented land-use changes and climate warming at the present time and in the future.

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Introduction

Since their appearance during the Ordovician period about 460 Mya, land plants have adapted to a wide array of extreme environments. Such environments are characterised by severe climatic conditions in different ecological settings (e.g. semi- and hyper-arid deserts, high elevations, polar regions) and/or specific local characteristics, such as substrate types (e.g. saline, serpentine, gypsum). To cope with the physiological challenges of these environments, plants have developed multiple strategies, involving various morphological, anatomical and/or physiological traits, by modifying existing genetic and molecular regulatory pathways. Furthermore, as extreme environments exert strong selection pressures on plant populations, the adaptive challenges imposed by extreme conditions have been major drivers of evolutionary diversity of plant assemblages through population differentiation and speciation at local, regional and even continental scales.

The unprecedented rapid transformation of environments during the Anthropocene has further increased levels of environmental stress experienced by plants across a wide range of biomes. Longer lasting, more frequent and intense droughts, heat waves in polar regions, increase in aridity due to land-use intensification and global warming, and environmental pollution have affected many plant communities. Because of the uncertainty regarding the response of plants to global change (e.g. tipping point *vs.* linear responses), effective conservation and restoration actions are required to maintain unique plant ecotypes, species and communities that occupy extreme environments. Consequently, further studies are needed to comprehend the ecological requirements, physiological mechanisms and evolutionary processes operating on plants in extreme environments. Such studies will both enrich our current knowledge of the ecology and evolution of plants in extreme environments and help foresee future plant communities subjected to increased levels of environmental change.

The collection of papers that comprise this special issue on *The Ecology and Evolution of Plants in Extreme Environments* provides insightful examples of how plants respond to environmental drivers in

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some of the most extreme environments on the planet. These environments include some of the coldest polar regions, high mountain areas, extreme soil types and arid deserts. Overall, this special issue explores the ecology and evolution of plants in extreme environments merging detailed field observations, sophisticated experiments in controlled conditions and natural settings, molecular phylogenetic analyses and/or physiological measurements in a wide array of plant species and plant communities (some also including biotic interactions with animals and microorganisms).

A total of 38 research groups, including 57 authors from 16 countries from The Americas (Argentina, Canada, Chile, Colombia, Ecuador, Mexico, Panama and the United States), Europe (Austria, France, Greece, Spain, the Netherlands and the United Kingdom), Africa (South Africa) and Oceania (Australia), contributed to this special issue.

The ecology and evolution of plants in extreme environments

The issue begins with three papers dealing with polar regions, including maritime Antarctica, Antarctica and the Canadian High Arctic, all of which are currently affected by rapid climate warming. In a first paper, Sindel et al. (2022) provide an overview of factors to consider with regard to the impact, ecology and management of non-native plants in sub-Antarctic and Antarctic regions, such as prevention of further spread of non-native plants combined with low-impact control and eradication programmes. One conclusion is that predicting the invasive behaviour of non-native species in these environments is not a straightforward task, although such behaviour may represent an excellent indicator for tracking ecosystem change in polar regions. In a related paper, Ballesteros et al. (2022) examine a potential driver of plant invasiveness in maritime Antarctica, namely seed fungal endophytes as a promoter of establishment and invasion of the non-native grass, *Poa annua*. The presence and inheritance of seed endophytes in *P. annua* individuals that colonised this region are shown to have likely made this species more competitive in its interactions with native plants, thus promoting its invasiveness. In the third paper of this group, Panchen (2022) reports on the advance of major phenological traits in seed plants, such as flowering and dispersal times, at the warmest study sites for up to seven conspecific species from six different plant families characteristic of the Canadian High Arctic. Although it is stressed that further studies are needed to estimate the long-term effects of observed phenological changes on population viability and plant assemblages, plants from the Canadian High Arctic are experiencing important alterations in their environments that already affect their phenology.

A second group of papers focuses on the performance of plants growing on extreme soil types, such as those with ultramafic and gypsum substrates. Ultramafic (also known as serpentine) soils contain high concentrations of certain heavy metals, low levels of essential plant nutrients and may have a low water-holding capacity. Consequently, plants that grow on these soils exhibit specialised adaptations to ensure survival and reproduction. In a first paper, Gotty et al. (2022) examine the persistence of relict lineages of Alseuosmineae (Asterales) that occur on ultramafic substrates in Oceania. They find that adaptation to ultramafic substrates and metal accumulation, measured in herbarium specimens with X-ray fluorescence spectrometry, may have contributed to the survival of these lineages until the present time with low net diversification rates. In addition, Samojedny et al. (2022) estimate variation in specific leaf area (SLA) of dominant species on paired ultramafic and non-ultramafic soils in five biogeographically distinct regions (i.e. Puerto Rico, Costa Rica, South Africa, California and the island of Lesbos in Greece). In this case, the authors find lower SLA values in plants on ultramafic than on non-ultramafic soils in practically all regions, except Puerto Rico, highlighting the strong selection for stress resistance strategies in plants occurring on ultramafic soils. Interestingly, this study detects some of the lowest SLA values ever recorded in plants, indicating the existence of very rare ecotypes in these extreme environments that are worth considering in future research.

Turning to gypsum soils, these represent extreme environments due to their high concentrations of calcium sulphate dihydroxide combined with low nutrient retention and availability. In a first paper, Cera et al. (2022) explore the active role that herbivory may play in the evolution of gypsum soil specialist plants in Spain. Plants growing on gypsum soils are found to accumulate sulphur in response to grazing, providing an illustrative example of how biotic agents interact with edaphic properties to understand plant ecology and evolution in these particular extreme environments. In a second paper, Vargas-Colin et al. (2022) determine the effects of varying timings and amounts of rainfall on the taxonomic, functional and phylogenetic components of an entire gypsophilous plant community from the Mexican Chihuahua Desert. The authors conduct an experiment in which they apply different rainfall treatments to soil monoliths, i.e. intact soil portions containing the natural soil seed bank of plant communities translocated from the field into controlled conditions. They find that late rainfall buffers the negative effect of water shortage on species richness and diversity in gypsophilous plant communities. This finding highlights the important interplay between the amount and the timing of rainfall for the persistence of plant communities in climatically and edaphically extreme environments.

A third group of papers deals with high mountain areas as representative of extreme environments. Although such areas may differ substantially with respect to latitude, high elevation always implies broad temperature fluctuations on a daily basis, high solar and intense ultraviolet radiation and strong winds. In a first paper, Ayarza-Páez et al. (2022) investigate the interplay between environmental factors and spatial distribution of three common *Hypericum* species in the Colombian Páramo at 3250 m a.s.l. The crucial role of physiological mechanisms to cope with water deficit, particularly vulnerability to cavitation, are pinpointed as major drivers of the spatial distribution of these species. In addition, the authors hypothesise how variation in duration and intensity of drought episodes in a warmer world, may affect plant distribution in the demanding Páramo. In a second paper, Sumner and Venn (2022) examine how reductions in soil moisture, using rain-out shelters to impose a drought treatment *in situ*, affect the capacity of plants to tolerate extreme fluctuations in temperature in plant communities of the Australian Alps at 1800 m a.s.l. They find that these plant communities (composed of evergreen shrubs, graminoids and perennial forbs) are relatively robust in terms of tolerance to both high and low temperatures as well as to chronic reductions in soil moisture, which represent a certain degree of protection against the consequences of climate change in this region. In a third paper, Vélez-Mora et al. (2022) evaluate experimentally the effects of climate, grazing and nutrient input on life-history traits of *Croton* shrubs, a complex of interbreeding hybrids taxonomically unresolved, in tropical dryland ecosystems in inter-Andean dry valleys in Ecuador at intermediate elevations (1400–1700 m a.s.l.). It is suggested that extensive grazing (cows and goats), addition of nutrients (N and P) and increased herbaceous plant density may account for the observed reduction of *Croton* abundance in the study area. This is important because *Croton* facilitates recruitment of both *Croton* and other species of the plant community in this particular ecosystem. The authors emphasise the value of their results for the development of more environmentally compatible human use of resources in inter-Andean dry valleys.

Finally, this special issue touches on the ecology and evolution of plants in arid deserts. In addition to the study already mentioned on gypsophilous plant communities in the Mexican Chihuahua Desert by Vargas-Colin et al. (2022), Milton et al. (2022) examine parapatric (or 'budding') speciation (i.e. the appearance of a derivative species near the edge of a progenitor's range, leaving the latter almost unchanged) in the Namib Desert of south-west Africa. They show by means of phylogenetic, morphometric and experimental-genetic approaches that the widespread, diploid, self-fertilising Southwest-North African disjunct, *Senecio flavus*, is most likely a derivative of self-incompatible *S. englerianus*, a Namib Desert endemic. Remarkably, hybridisation between *S. flavus* and a related diploid *Senecio* species in the deserts of North Africa, subsequently resulted in the origin of an allotetraploid which has spread to both the Mojave Desert in North America and the Thar Desert in the northwestern part of the Indian subcontinent.

The way forward

The pace and intensity of global change now affecting the planet is presenting challenges to the survival and reproduction of many plant species across diverse ecosystems. Hence, all extreme environments harbouring plants are perfect natural laboratories to learn how plants endure in environments with harsh climatic and/or edaphic conditions. Here, we gathered a collection of papers showing some evolutionary patterns, ecological processes and physiological mechanisms by which plant species and communities thrive in extreme environments. Based on these studies, we outline two major future research avenues. First, biotic interactions (e.g. plant–plant, plant–herbivore, plant–microorganism) emerge as a fundamental aspect to understanding the ecological complexity of plant growth and dynamics in extreme environments (Ballesteros et al. 2022; Cera et al. 2022; Vélez-Mora et al. 2022). Hence, further studies need to consider plants in relation to the interactions that they establish with other organisms as they all eventually compete for limited resources under harsh conditions. Second, the climatic idiosyncrasy of extreme environments represents a major driver of plant evolution (Gotty et al. 2022; Milton et al. 2022). However, soil type, and the interaction between extreme climate conditions and soil substrate, can be as important as climate to comprehend plant evolutionary patterns in extreme environments (Gotty et al. 2022; Samojedny et al. 2022; Vargas-Colin et al. 2022). Thus, further studies also need to include the interaction between climate and soil type to broaden the concept of extreme environments beyond harsh weather conditions.

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