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Species interactions involving cushion plants in high-elevation environments under a changing climate

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Species interactions involving cushion plants in high-elevation environments under a changing climate

Resumen: The effects of global warming are stronger in high-elevation environments than elsewhere. Here, we review recent advances in alpine plant ecology with a focus on dry mountain ranges, mainly in Mediterranean-type climate, with a global change perspective. Raising temperatures and changes in precipitation influence both plant growth and reproduction, and therefore the spatial distribution of species. Research in high-elevation systems evidenced that plant–plant interactions involving cushion plants play a crucial role in the assembly of plant communities, influencing species richness, genetic and phylogenetic diversity, and species persistence. By buffering environmental extremes and ameliorating biophysical conditions, cushion plant species acting as ecosystem engineers are fundamental in the response of alpine ecosystems to global warming, mitigating negative impacts on different plant species with narrow niche and small distribution range.

Keywords: alpine ecosystems; climate change; gradient analysis; plant interactions; plant traits

Interacciones entre especies y el papel de las plantas cojín en ecosistemas de alta montaña bajo un clima cambiante

Abstract: Los efectos del calentamiento global son más notables en entornos de gran altitud que en otros ecosistemas. Aquí revisamos avances recientes en ecología de plantas alpinas centrándonos en cadenas montañosas secas, principalmente bajo clima de tipo mediterráneo, y con una perspectiva de cambio global. El aumento de temperatura y los cambios de precipitación influyen tanto en el crecimiento y reproducción de las plantas como en la distribución espacial de las distintas especies. La investigación en sistemas de alta montaña ha puesto de manifiesto que las interacciones planta-planta implicando plantas cojín desempeñan un papel fundamental en la formación de las comunidades vegetales, influyendo en la riqueza de especies, la diversidad genética y filogenética y la persistencia de las especies. Amortiguando extremos ambientales, algunas especies que actúan como ingenieros del ecosistema, como muchas especies de plantas almohadilladas, pueden ser clave en la respuesta de los ecosistemas alpinos al calentamiento global, mitigando los impactos negativos sobre muchas especies que tienen un nicho limitado y una distribución espacial restringida.

Palabras clave: análisis de gradientes; cambio climático; ecosistemas alpinos; interacciones entre plantas; rasgos de plantas

Introduction

The alpine environment has attracted increasing attention of ecologists, as reflected by the increasing number of papers published on this topic during the last 20 years. This renewed research interest focused mostly on plant interactions, and publications on this topic almost tripled in one decade (according to Clarivate-ISI database accessed on Jan 2021 with the queries “alpine” and “plant interactions”). The surge in such publications was also prompted by the strong effects of global change on mountain ecosystems, which are quite sensitive to changing environmental conditions. In fact, climate change is having more pronounced effects in high-elevation habitats than elsewhere (Giorgi and Lionello 2008; Lenoir and Svenning 2015), potentially causing biodiversity loss in plant communities (Losapio et al. 2021a). Research mainly focused on the negative effects of raising temperatures (Thuiller et al. 2005; Chelli

et al. 2017) and nitrogen deposition (Bobbink et al. 2010) on plant species distribution, but also on the importance of plant–plant interactions for the diversity of alpine communities (Callaway et al. 2002) and their potential role in mediating species responses to climate change (Cavieres et al. 2014). Here, we review and synthesize recent advances in alpine plant ecology with a focus on dry mountain ranges, mostly in Mediterranean-type climate, under a global change perspective. Global change is threatening the biodiversity of high-elevation environments (Lamprecht et al. 2021). We put particular emphasis on the role of cushion plants in mediating the effects of climate change on alpine biodiversity. The generally positive effect of many cushion plants in high elevation environments makes them notable facilitator species (Cavieres and Badano 2009; Cavieres et al. 2014; Gavini et al. 2020) (Fig. 1). Cushion plants have served as testing ground for many ecological concepts, contributing in the last years to a wealth of knowledge pertaining a wide

range of fields, from community assembly (Schöb et al. 2012), physiological ecology and global change responses (Reid et al. 2010, Boucher et al. 2016) to ecological network theory (Losapio et al. 2019). Cushion plants are quite variable in form and function, and one such species, *Azorella compacta* (yareta or llareta), found at the edge of the Atacama Desert between 3800 and 5200 m elevation, can reach much over 6 m in diameter with a mat-like shape. This is one of the woody plant species occurring at highest elevations in the world and, since they can be older than 3000 years, have to deal with disturbance and herbivory many times throughout their lifetime, for which they are heavily protected by chemical compounds (Pugnaire et al. 2020a).

The abiotic environment

The elevation gradient along mountain slopes involves changes in multiple environmental variables such as rainfall, temperature or pressure of atmospheric gases (e.g. O₂, H₂O, and CO₂), which considerably affect other environmental conditions like soil pH, organic matter, and nutrient availability (Körner 2003). These variables do not change in a similar manner with elevation, nor in moist and dry mountains, and are evolutionary selective agents that shape plant form and function, ultimately determining community composition. Environmental conditions affect plant morphology and physiology, influencing traits such as specific leaf area, intrinsic water use efficiency (García-Cervigón et al. 2015) or stomatal density. The adaptation of plants to harsh, high-elevation conditions ensure optimal CO₂ supply during the relatively short periods of favourable weather conditions in the alpine belt (Kammer et al. 2015).

Elevation gradients have often been used as a space-for-time approach to study the impact of climate change. Lower elevation sites are experiencing less precipitation and higher temperatures, i.e. climatic conditions expected in many alpine areas of the world in the future. In temperate climates such as the Alps or the Rocky Mountains, where most of alpine plant ecology developed, low-elevation ecosystems provide generally more benign conditions for plant growth, while abiotic stress increases with elevation. This is



Figure 1. *Androsace tapete* hosting beneficiary species in a gravel area at 5000 m elevation in the Tibetan Plateau, Qinghai, China (Photo: F.I. Pugnaire).

Figura 1. *Androsace tapete*, albergando especies beneficiarias en una zona de gravas a 5000 m de altitud en la meseta tibetana, Qinghai, China (Foto: F.I. Pugnaire).

due to the decrease of temperature with elevation, leading to little-developed soils and poor nutrient supply. In contrast, mountain ranges in dry environments like the Sierra Nevada in Spain and California, parts of the Andes or the Karakoram and Himalaya mountains, do not only experience increasing environmental stress towards high elevations as in temperate systems but also towards low elevations due to increasing aridity (Schöb et al. 2013; Pescador et al. 2016). Therefore, plant growth in dry mountains is environmentally limited both at high and low elevations (Fig. 2). This effect is quite evident when looking at species in dry mountains with a relatively large elevational distribution.

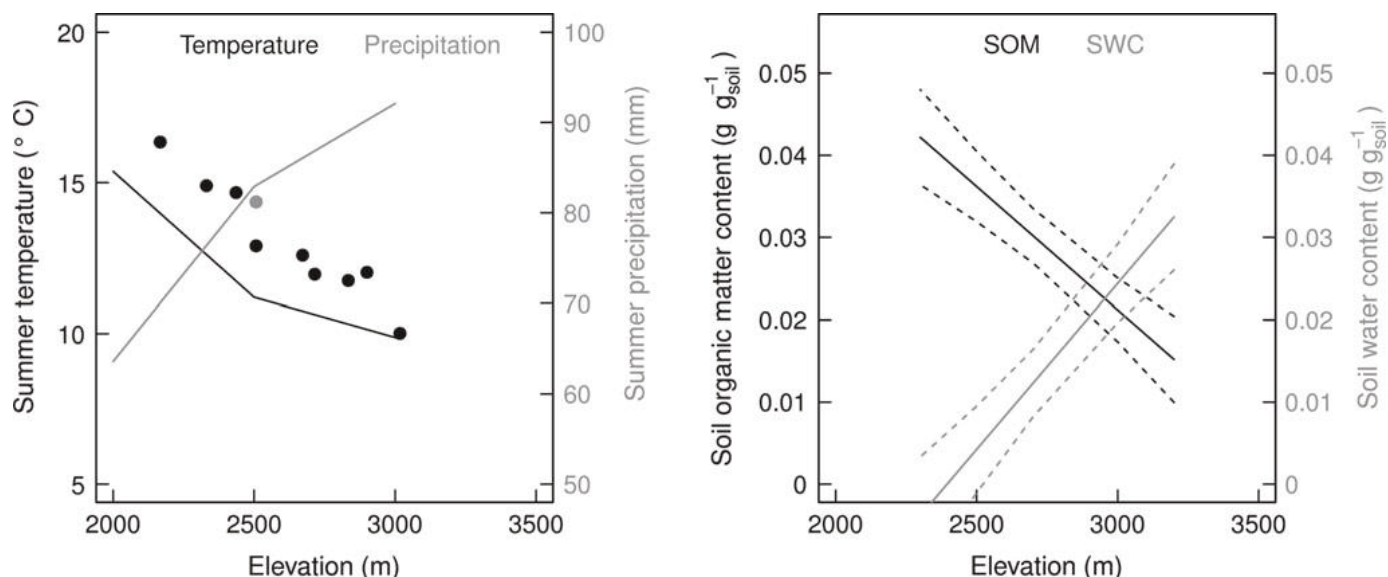


Figure 2. The two opposing climatic gradients in dry mountains (left) consisting of summer (June-September) mean temperature (black) and summer mean precipitation (grey; Delgado Calvo-Flores et al. 1988) running in parallel to two opposing resource gradients (right) consisting of soil organic matter (SOM; black) and soil water content (SWC; grey) in open areas. Lines in the right panel for SOM and SWC are model-predicted means (solid lines) and 95% CIs (dashed lines) of generalized linear regression models with log link function ($n = 38$). Dots in the left panel are mean summer temperature (black) and summer precipitation (grey; only one value available) (From Schöb et al. 2012)

Figura 2. Gradientes climáticos opuestos en las montañas secas que consisten, en el panel izquierdo, en la temperatura media del verano (junio-septiembre) (en negro) y la precipitación media del verano (en gris; Delgado Calvo-Flores et al. 1988) que van en paralelo a dos gradientes opuestos de recursos (panel derecho) consistentes en materia orgánica del suelo (SOM; en negro) y contenido de agua del suelo (SWC; en gris) en zonas abiertas. Las líneas en el panel derecho SWC son medias predichas (líneas continuas) e intervalos de confianza del 95% (líneas discontinuas) de modelos de regresión lineal generalizada con función de enlace logarítmico ($n = 38$). Los puntos en el panel izquierdo representan la temperatura media de verano (en negro) y la precipitación de verano (en gris; sólo un valor disponible) (tomado de Schöb et al. 2012).

Changes in physiological and morphological traits of *Arenaria tetraquetra*, a cushion plant species endemic to Sierra Nevada in Spain, reflect these different environmental constraints at both ends of the elevation gradient. Cushion plants are life forms with a hemispherical or mat-like, prostrate canopy well adapted to the extreme conditions of cold regions that have appealed to scientists for their ability to cope with extreme environments in most mountains, arctic, and subantarctic regions of the world (Aubert et al. 2014). Functional traits in *Arenaria tetraquetra* varied differentially in response to the two main opposing stress gradients, temperature and aridity (Schöb et al. 2013). Plants at high elevation showed good physiological status, with compact and large canopies, and understory soil stored more water and organic matter than open areas away from cushions. On the contrary, at low elevation, *A. tetraquetra* formed loose and small cushions, with understory soil properties more similar to open areas, overall suggesting stressful abiotic conditions for this species compared with high elevation habitats. Under these particular conditions of dry mountains, the middle point along the elevation gradient always shows better conditions than the two extremes, where either one or the other stress factors strongly limits plant life. This explains the unsuitability of elevation gradients in dry mountains as unidirectional stress gradients (Schöb et al. 2013; Pugnaire et al. 2015).

As an alternative to the space-for-time approach along elevation gradients for climate change research, both temperature and rainfall can be manipulated through so called open-top chambers (OTC), i.e. acrylic truncated pyramids with an open top that reduce rainfall and increase temperature compared to control areas without chamber (Fig. 3). Manipulations with OTCs have been used to explore climate change effects on plant growth and gas exchange in several high-mountain environments like the Andes (e.g., Cavieres and Sierra-Almeida 2012; Hernández-Fuentes et al. 2015) and the Spanish Sierra Nevada Mountains (Pugnaire et al. 2020b). In the latter study, higher temperatures enhanced photosynthesis and respiration of the target species, *Arenaria tetraquetra*, leading to larger cushions with thinner leaves, but did not change other cushion traits such as branch length and leaf size or reproductive parameters. Some traits, however, responded to inter-annual climate variability, suggesting that global warming and specifically the expected increases in temperature and drought will change cushion plant physiology in the long-term through an increase in respiration and a decrease in CO₂ fixation. This process will likely exhaust plant reserves and the plants' ability to address events of herbivory or disturbance like fire, with threatening consequences for plant survival and community structure (Pugnaire et al. 2020b).

Plant survival and species diversity are strongly and positively linked to soil water content (Schöb et al. 2009; Kammer et al. 2013), which in alpine regions is decreasing as a consequence of climate change (Pauli et al. 2012; Nogués Bravo et al. 2008; Sillmann et al. 2013; Lenoir and Svenning 2015). The capacity of soils to retain water will be an important factor for plant persistence as climate variables related to water balance correlate to species richness in alpine plant communities worldwide (Cavieres et al. 2014).

Alpine plants minimize physiological risks derived from drought and frost by adjusting their hydraulic system, coordinating responses at the xylem level with responses in plant architecture and leaf traits (Schreiber et al. 2015; Olano et al. 2017; García-Cervigón et al. 2020), and decreasing vessel size to increase xylem hydraulic efficiency without compromising the safety of the hydraulic system (Sperry et al. 2008). In *A. tetraquetra*, intra-specific variation and coordination of stem xylem anatomy, leaf functional traits, and plant architecture responded to elevation, aspect, and the presence of beneficiary species (García-Cervigón et al. 2021). Xylem traits and plant architecture were the most responsive to environmental conditions, showing high coordination (García-Cervigón et al. 2021). Cushions were more compact and had smaller, more grouped conductive vessels in the southern than in the northern aspect. These 'adjustments' allow minimizing the negative impacts of more intense drought in the south than in the north. No single traits responded to

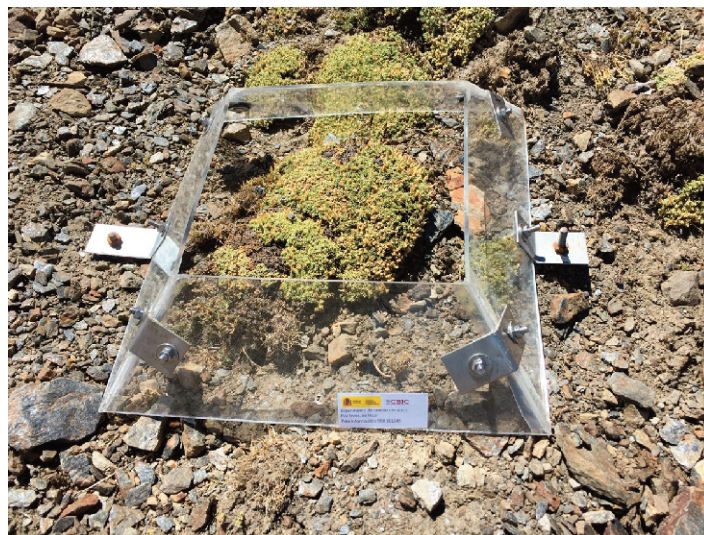


Figure 3. Open-top chamber on an *Arenaria tetraquetra* cushion at 2800 m elevation in the San Juan Valley, in the northern aspect of Sierra Nevada, Granada, Spain (Photo: F.I. Pugnaire).

Figura 3. Cámara a cielo abierto sobre la planta cojín *Arenaria tetraquetra* a 2800 m de altura en el Valle de San Juan, en la vertiente norte de Sierra Nevada, Granada, España (Foto: F.I. Pugnaire).

elevation, probably due to the complex nature of environmental gradients in dry mountains (Schöb et al. 2013). Individual cushion plants hosting beneficiary species coordinated plant architecture and xylem traits better than non-hosting individuals. As mentioned before, cushion plants hosting beneficiary species had higher canopy compactness, less leaves per branch and less, more isolated vessels than cushions not hosting other species, which reflects the negative feedback of beneficiaries on the nurse water status. In non-nursing cushions, plant architecture coordinated with leaf traits instead. Water-related traits show that stress by frost at high elevation constrained xylem anatomy in the northern aspect, whereas stress by drought had the same effect in the southern aspect, pointing to the harshest sites for *A. tetraquetra* (García-Cervigón et al. 2021).

Water, however, may not be the only limiting factor in high mountains (Kikvidze et al. 2011), and for instance, in the Central Tibetan Plateau interaction intensity among plants responded more to temperature than to rainfall. In these dry, high-elevation environments the cushion plant *Androsace tapete* expanded the realized niche of some beneficiary species growing within its canopy (Fig. 1), countering adverse environmental conditions mostly by buffering temperature extremes (Pugnaire et al. 2015). In a similar way, densely packed communities protect plants from strong, cold winds frequent in alpine environments, highlighting the role of facilitation in maintaining species richness in high-elevation systems (Callaway et al. 2002).

Cushion plants, interactions, and species distribution

Climate warming is driving plant species upward (Lenoir et al. 2008; Evangelista et al. 2016; Rumpf et al. 2019), moving the alpine treeline up in a process mediated by ecological interactions. Transplant experiments at the alpine treeline in southwest China showed that the shrub *Rhododendron rupicola* modifies its physical and biotic environment in such a way that favours the establishment and performance of two other treeline species, *Larix potaninii* and *Picea likiangensis*, through increased soil moisture and nutrient content, and by buffering soil temperature fluctuations (Chen et al. 2020). As a consequence, tree seedlings under *R. rupicola* shrubs had significantly higher survival, growth rates and nutrient accumulations than those in open areas, as shown earlier in cold systems elsewhere (e.g. le Roux and McGeoch 2010; Macek et al. 2016). Shrubs thus

act as 'stepping stones' for the establishment and range shift of other species beyond their current distribution, potentially facilitating the upward migration of entire communities (Chen et al. 2020).

There is increasing evidence that biotic interactions can shape species' distributions through their impact on the realized niche (Alexander et al. 2016), potentially constraining or expanding the range of conditions under which a species can occur (O'Brien et al. 2019). In sub-Antarctic Marion Island, the cushion plant *Azorella selago* influences the distribution of associated species with the result that some species occur beyond their basic range (i.e. in open areas). This is the case for instance of *Acaena magellanica*, which was found 26 m higher up under *A. selago* than in open areas; of *Colobanthus kerguelensis*, found 37 m higher, or *Lycopodium saururus*, 19 m higher (Raath-Krueger et al. 2019). The reported upward migrations are quite significant in the context of Arctic regions, as differences in elevation have relatively more impact given

the flat topography and the high latitude. Similar effects have been shown in dry, low-elevation systems elsewhere (O'Brien et al. 2019), evidencing the potential of plant–plant interactions to expand the distribution limit of species by increasing the niche space, although the effects are species-specific (Raath-Krueger et al. 2019).

Although species interactions determine local-scale diversity, they may also have critical effects at larger biogeographical patterns (Harrison and Cornell 2008). The effects of plant interactions on diversity and community structure may be relatively smaller than those of climate *per se*, but their contribution is still substantial (Cavieres et al. 2014). Cushion plants enhance species richness especially in systems with low local diversity (Fig. 4), acting as climate change modulators (Cavieres et al. 2014) and as a safety net sustaining diversity under harsh conditions. Thus, positive species interactions enable recruitment of relatively stress-intolerant species that otherwise would not establish under increasing stressful conditions.

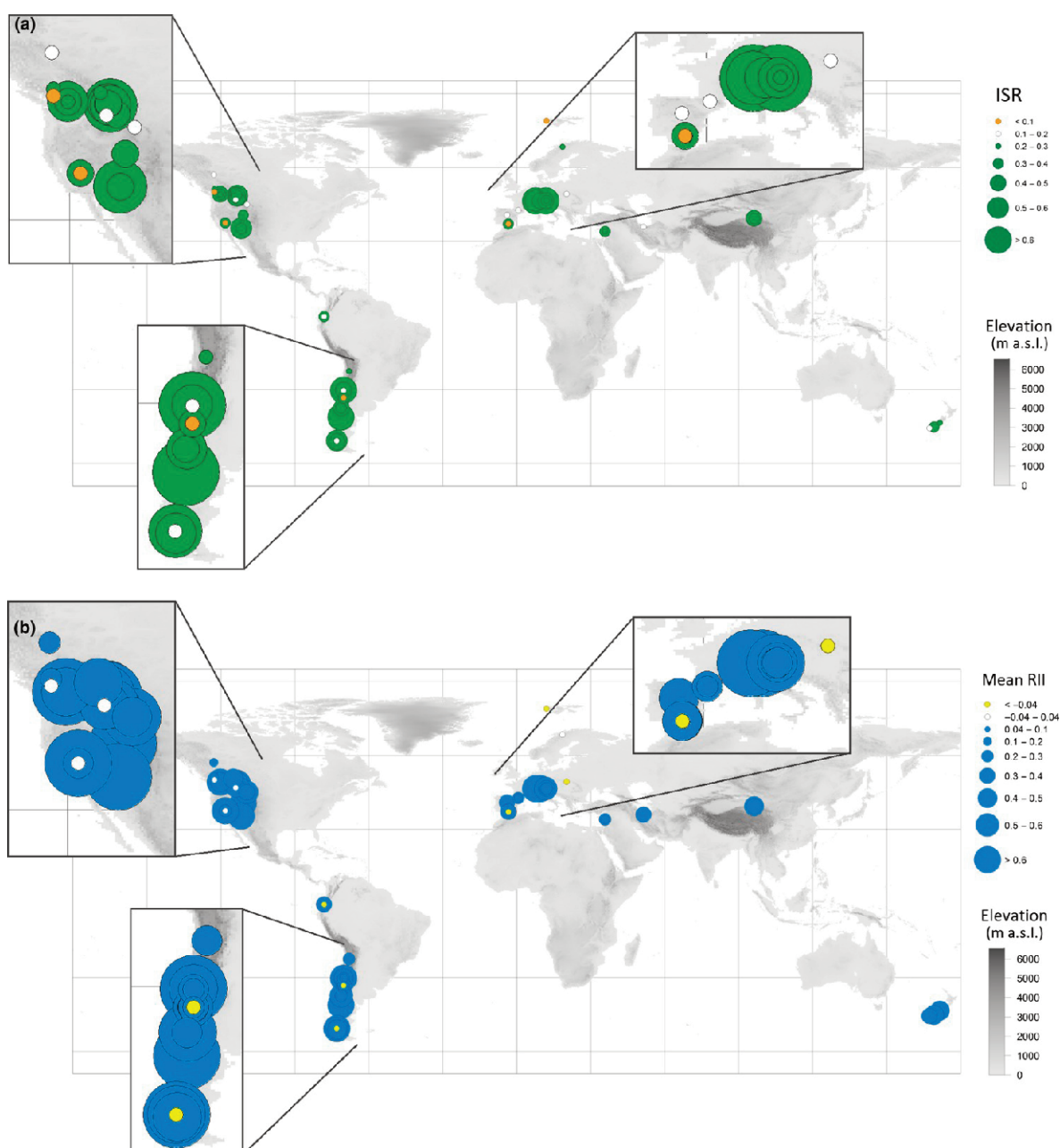


Figure 4. World map showing the sign (colour scale) and magnitude (size scale) of (a) the proportional increase in species richness due to the presence of nurse cushion species (ISR) and (b) the mean interaction (calculated using the mean Relative Interaction Index, RII) between cushion species and the rest of the plant community at our studied alpine sites (From Cavieres et al. 2014).

Figura 4. Mapa global que muestra el signo (escala de color) y la magnitud (escala de tamaño) de (a) el aumento proporcional en la riqueza de especies debido a la presencia de plantas cojín (ISR) y (b) la interacción media (calculada utilizando el índice RII) entre las especies cojín y el resto de la comunidad vegetal en sitios alpinos (tomado de Cavieres et al. 2014).

However, the niche space constructed by cushion plants supports a more homogeneous composition of species than the niche space found beyond the cushion's influence; i.e. cushion plants host a community of beneficiary species whose similarity is higher than the community in open microhabitats (Kikvidze et al. 2015). This process leads to differences among shrubs in the structure of the subordinate plant community (Anthelme et al. 2017), each species showing a unique composition which generally depends on soil humidity (Piston et al. 2016), but also has evolutionary consequences. A recent report shows how plants genetically differentiate into more stress-adapted ecotypes prevalent in open areas and more competitive ecotypes prevalent in association with shrubs (O'Brien et al. 2021), which demonstrates that cushion plants, as ecosystem engineers, act as selective forces along the stress tolerance–competitive ability trade-off and promote genetic diversity of alpine species (see also Gavini et al. 2019). These modulating effects are critical for the persistence of species outside their optimal range and contribute to increase community-level genetic diversity, species richness and phylogenetic diversity. There is, therefore, strong evidence that cushion plants in alpine systems commonly act as foundation species, strongly affecting species recruitment and driving the relationships between local and regional species diversity (Kikvidze et al. 2015).

Community assembly and interaction mechanisms

Plant–plant interactions are now firmly established among the most important drivers of plant community assembly in alpine systems due to the relevant role of stress-tolerant species (Pescador et al. 2014; Losapio et al. 2018) and their buffering of extreme conditions while building up soil resources and decreasing disturbance (Cavieres y Badano 2009; Sklenář 2009; Schöb et al. 2012, 2013; Malatesta et al. 2016; Pistón et al. 2016; Mihoč et al. 2016). Species interactions also influence the overall phylogenetic structure of plant communities. The phylogenetic limiting similarity hypothesis (MacArthur and Levins 1967; Blomberg et al. 2003; Wiens and Graham 2005) states that closely-related species tend to compete stronger than distantly-related species because their requirements are similar (but see Cahill et al. 2008; Mayfield and Levine 2010). In *Arenaria tetraquetra* in Sierra Nevada, the effects of cushion plants on closely related species changed from negative to positive as environmental conditions became more severe, while the interaction with distantly related species did not change along the gradient, evidencing context-dependence in patterns of phylogenetic similarity (Piston et al. 2015) that shape phylogenetic community structure (PCS). In a study that assessed PCS in alpine plant communities around the world, both within cushion species and in adjacent open ground, Butterfield et al. (2013) compared the effects of cushion species and climate on phylogenetic alpha (i.e., within microsite), beta (between open and cushion) and gamma (open and cushion combined) diversity. In the open, phylogenetic alpha diversity shifted from highly related to distantly related with increasing productivity. However, there were no relationships between phylogenetic gamma diversity and climate, due to divergence in phylogenetic composition between cushion and open sub-communities in severe environments, as demonstrated by increasing phylogenetic beta diversity. Without accounting for this important biotic interaction, the global plant primary productivity–phylogenetic diversity relationship would go undetected (Butterfield et al. 2013).

The impact of cushion plants on community assembly takes place through two mechanisms, namely changes in environmental filtering and niche differentiation (Schöb et al. 2012). The first process determines the limits and range of trait distribution in a community, whereas niche differentiation affects the trait distribution within the limits set by the environmental filter (Webb et al. 2002). Filtering effects (in particular range shifts) created by cushion plants increase with environmental severity at higher elevations. Under harsh conditions, the filtering effect of cushions can be in magnitude equivalent to a change of 500 m in elevation (Schöb et al. 2012).

Once again, facilitation appears as strongly context-dependent and modifies the taxonomic and functional diversity of ecological communities in the alpine belt (Schöb et al. 2012). Since plants can have positive effects on each other through accumulation of nutrients, provision of shade, or protection from herbivores (Callaway 2007), the assumption that the distribution and abundances of plant species are independent of other species may be inadequate as a theoretical underpinning for understanding species coexistence and diversity (Callaway 2007).

Plant interaction responses to the abiotic environment

Spatial patterns in plant communities are controlled by the interplay between species interactions and environmental constraints, and the outcome of such relationship is strongly dependent on the abiotic environment (Callaway et al. 2002). For example, in a comparison of the effect of plant–plant interaction type in shaping plant communities, a stressful alpine system in Spanish Sierra Nevada showed both positive and negative association among plant species. By contrast, in semiarid sites in Spain and sand plains in the Gran Sabana in Venezuela, there was a high degree of positive species association. Finally, negative associations predominated in Altos de Pipe, a site of high plant productivity in northern Venezuela (Tirado and Pugnaire 2005). The spatial association between plants was highly correlated with the frequency of species interactions, so that aggregation pointed to positive interactions and segregation to competitive or interference effects that, in absence of soil heterogeneities of hidden microsite effects, provide a link between spatial patterns and species interactions (Tirado and Pugnaire 2005; Pescador et al. 2014).

Yet, establishing the relationships among patterns, processes, and properties of plant communities is crucial for developing meaningful conceptual models in community ecology. Addressing such relationships in 18 plant communities spread throughout nine Northern Hemisphere high-mountain systems, Kikvidze et al. (2005) found both linear and non-linear correlative links among temperature, precipitation, productivity, plant interactions, spatial patterns, and species richness (Kikvidze et al. 2005). For example, sites with comparatively mild climates had greater plant biomass, with strong competition leading to overdispersed species distribution that reduced intraspecific patchiness but increased local richness. By contrast, sites with cold climates had less biomass, but a higher proportion of species benefited from strong facilitative effects of neighbors, leading to an aggregated distribution of plants. Sites with intermediate or relatively moderate climates were intermediate in biomass too, and net interaction outcomes were neutral (i.e., competition was countered by facilitation). This corresponded to a nearly random distribution of plants and lower-than-average species richness. The relationship between interspecific spatial patterns and community richness thus reflects niche differentiation and/or construction, which allows for the coexistence of more species than would be possible with random, unstructured spatial distributions (Kikvidze et al. 2005).

In a pioneer paper, Callaway et al. (2002) reported a large-scale experiment in 11 alpine plant communities in different mountain ranges with 115 species designed to examine the generality of positive interactions in plant communities and their importance relative to competition. They reported that biomass, growth and reproduction of alpine plant species were higher when other plants were nearby, showing that competition generally, but not exclusively, dominates interactions at lower elevations where conditions are less physically stressful. By contrast, at high elevations, where abiotic stress is high, plant interactions are predominantly positive (Callaway et al. 2002). Similar results have been reported multiple times afterwards (e.g., Schöb et al. 2012; Anthelme et al. 2014). Linking spatial patterns to ecological processes is a needed step to understand and leverage the central role of plant interactions in alpine ecosystems (Tirado and Pugnaire 2005; Losapio et al. 2021b).

Snowbeds are a particular alpine ecosystem where soil conditions are reasonably good and water is available throughout the whole growing and reproductive season. Here, the major limiting factors for plant growth are herbivory and a short growing season. Snowbed patches usually form a dense carpet of palatable species (known as *borreguiles* in Sierra Nevada) where facilitation and competition are modulated by growing season length and herbivory. In a removal experiment, Schöb et al. (2010) altered community composition showing the effects of neighbour removal were weak but generally consistent among species and snowmelt dates. The removal treatment showed that plants competed for nutrients, water, and light. However, the presence of neighbours reduced herbivory and facilitated species presence in the patch. Protection against herbivores in this system thus countered competition for resources (Schöb et al. 2010).

Facilitator species with different phenotypes modify the microhabitat in different ways, affecting the environmental engineering effect and, in turn, influencing subordinate community composition and the feedback effects between them. For example, the shrub species *Cytisus galianoi* has either tight or loose canopies that differ in their effects on the microhabitat and on the beneficiary plant community in a dry subalpine system. The presence of a particular phenotype may depend on the local environmental conditions and reflect ecotypic differentiation (Michalet et al. 2011) or simply be a matter of ontogeny (Pistón et al. 2018). Observational and manipulative experiments allowed assessing the influence of the different canopy types, which differed in mean values of functional traits (like stem density or plant height) and how they modified their microenvironment. The different phenotypes therefore hosted distinct subordinate communities (Pistón et al. 2018). The loose phenotype hosted higher species richness than the tight phenotype, highlighting the importance of phenotypic variation for plant interactions and community-level diversity.

As in other nurse-plant systems (Rodríguez-Echeverría et al. 2013, 2016), micro-climatic effects of facilitator species regulate the diversity and composition of beneficiary plant species, but also affect soil microbial communities, which are major drivers of soil processes influencing nutrient availability. For example, soil microbial communities associated to *Azorella* cushion species in the southern Andes changed along a gradient of abiotic conditions such as aridity, UV-B radiation, and air temperature. The presence of *Azorella*, along with aridity, was the most important predictor of soil microbial community structure, followed by UV-B radiation, which affected mostly soil fungi (Rodríguez-Echeverría et al. 2021).

Bidirectional interactions among facilitators and beneficiaries

Although the unidirectional effects of nurse plants on beneficiary species has received considerable interest, nurse-mediated interactions among beneficiary species (so-called indirect interactions) are less known. Community composition in nurse plant systems is generally considered as a simple consequence of the facilitative effect of the nurse, when in fact this may not be the exclusive factor. In an observational study including four *A. tetraquetra* communities differing in aspect and elevation in dry gravel habitats in Spanish Sierra Nevada, there were predominantly positive effects of the nurse plant on beneficiary species and negative effects of beneficiary species on the nurse plant. Yet, the magnitude of the facilitative effects of nurses was significantly higher than the negative effects of beneficiary species (Schöb et al. 2013; Raath-Kruger et al. 2021). However, the negative effects of beneficiary species on its benefactor can result in reduced fitness of the benefactor.

Using a global dataset on alpine cushion plants, Schöb et al. (2014b) assessed the context-dependence of small- and large-scale drivers on the feedback effects of beneficiary species on their cushion benefactors. Beneficiary species became more neg-

ative for the benefactor when beneficiary plant diversity was higher and facilitation more intense. In high-productivity sites, the negative feedback effects of beneficiaries on the benefactor were weaker, showing a limited impact of beneficiary feedback effects on benefactor cushions and strong context dependence, which may help to explain the ecological and evolutionary persistence of this widespread facilitative system (Schöb et al. 2014b). Further studies unveiled the bidirectional nature of these interactions and in particular the consequences on the physiology and fitness of both beneficiaries and benefactors. In a cushion plant species systems, *Arenaria tetraquetra* ssp. *amabilis* and three other beneficiary forb species (*Eryngium glaciale*, *Lotus corniculatus* ssp. *glacialis* and *Plantago nivalis*) in the Spanish Sierra Nevada, results showed that all three forbs improved their water status when associated with the cushion, and that *Lotus* and *Plantago* significantly increased their seed set (Schöb et al. 2014a). By contrast, *A. tetraquetra* showed poorer water status and reduced flower density and seed set with increasing cover of beneficiary species. Cushion plants without beneficiary species showed increased seed set and higher seed mass, most likely linked to increased photosynthetic and water use efficiencies and higher leaf nitrogen content. These results show the predominantly antagonistic interaction between beneficiary and benefactor species, which could be termed parasitic (Schöb et al. 2014b).

Such bidirectional interactions could be accompanied by other indirect interactions including pollinator-mediated benefits for the cushion, as they are visited by more diverse and abundant pollinators when blooming with associated plants than when blooming alone (Losapio and Schöb 2020). In *Arenaria tetraquetra*, fruit and seed sets were negatively affected by the presence of beneficiary species, whereas in *Hormatophylla spinosa*, another facilitator species in Sierra Nevada, fruit and seed set were higher or unaffected when hosting beneficiary species. These data suggest that, besides suffering direct costs most likely associated to plant resource competition, cushion species can benefit from hosting other species in their canopy by increasing their own visibility to pollinators. The outcome of direct plant-plant interactions might be mediated by indirect interactions including third players (Losapio and Schöb 2020), evidencing that biological diversity depends on multiple, co-occurring interactions where the outcome is not always evident.

Using a large dataset from mountain ecosystems across the globe, Losapio et al. (2021a) analysed the prevalence and importance of both facilitative and competitive associations among plants for species diversity, showing that facilitative and competitive interactions must be addressed together in order to explain biodiversity patterns. Data show that ecological networks that leverage the interplay of both competition and facilitation can be a valuable solution for supporting community persistence and mitigating species loss (Fig. 5). Above all, local species richness depends on many interacting species with changing hierarchies, and whether the effects are transitive or not have multiple consequences for coexistence (Soliveres et al. 2015; Godoy et al. 2017).

In summary, recent research in high-elevation systems evidences that species interactions play a crucial role in the shaping of plant communities, influencing species richness, genetic and phylogenetic diversity, species distribution, and the persistence of alpine plant species. Through their usual role in buffering environmental extremes, some species acting as ecosystem engineers - and among them many cushion plant species- should be instrumental in the response of alpine ecosystems to global warming, mitigating its negative impact on beneficiary species and, overall, alpine ecosystems. Therefore, if affected by disturbance or habitat loss, the dismissal of these species can also exacerbate the consequences of warming. Future studies shall address how interactions vary over time, incorporating observational and manipulative designs to capture long-term responses of species assemblages to a changing climate.

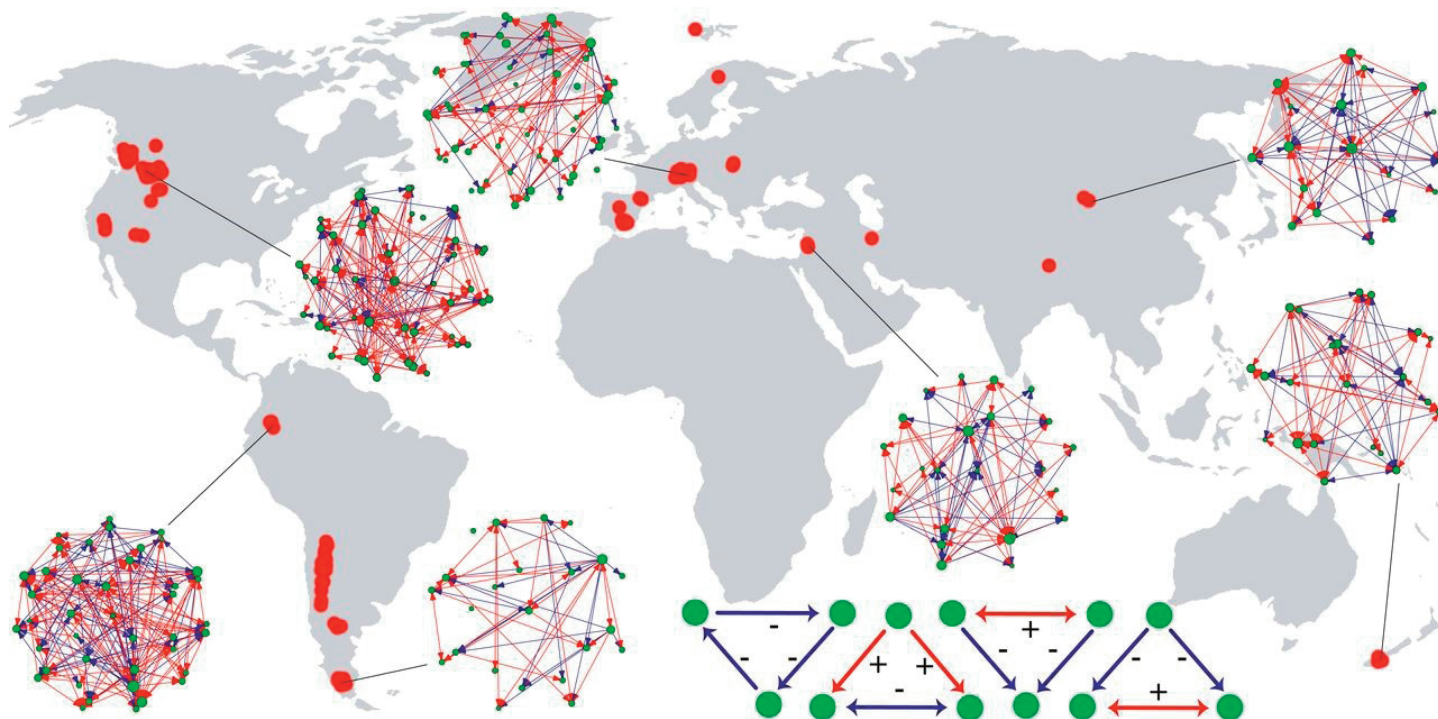


Figure 5. Global map of alpine plant networks studied in Losapio et al. (2021a). Red dots on the map indicate the spatial location of the networks, with a few networks plotted for reference. In the networks, green dots represent plant species, and blue and red arrows represent negative and positive species associations, respectively. Dot size is proportional to species abundance. The four network modules analysed here are represented at the bottom of the figure, from left to right: intransitive competition, facilitation-driven competition, and competition-driven facilitation (From Losapio et al. 2021a).

Figura 5. Mapa global de las redes de comunidades alpinas estudiadas en Losapio et al. (2021a). Los puntos rojos indican la ubicación espacial de las redes, con algunas de ellas trazadas como referencia. En las redes, los puntos verdes representan especies de plantas y las flechas azul y roja representan asociaciones negativas y positivas entre especies, respectivamente. El tamaño de los puntos es proporcional a la abundancia de especies. Los cuatro módulos de red analizados están representados en la parte inferior de la figura, de izquierda a derecha: competencia intransitiva, competencia impulsada por la facilitación y facilitación impulsada por la competencia (tomado de Losapio et al. 2021a).

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Author contributions

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