

MECHANISMS AND CONSEQUENCES OF FACILITATION IN PLANT COMMUNITIES

Facilitation among plants as an insurance policy for diversity in Alpine communities

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Summary

1. Positive interactions have started to gain a place as important drivers of community structure and biological diversity. Defined as non-trophic interspecific interactions that increase the average individual fitness of one species, by definition, the presence of one plant species enhances the chances that another species co-occur in the same place, indicating that positive interactions may determine biological diversity. However, this has been poorly explored.

2. The majority of the studies addressing community-level consequences of facilitation have compared the diversity of the plant assemblages growing within nurses vs. those growing outside them, reporting contrasting results among them. Nonetheless, nurses and their alternative microhabitats (open areas among nurses) are part of the same community. Thus, if nurses allow for the persistence of species that otherwise would be excluded from the community, a net increase in the species diversity at the entire community level will be generated even though nurse plants contained fewer species than open areas.

3. Here, we conducted a bibliographic search using the ISI Web of Knowledge data base and reviewed the literature conducted on alpine plant communities where assessments of the diversity of plants growing within and outside a nurse species were available. In most cases nurse species substantially increased species richness at the community level, despite the fact that in some cases, they contained lower species numbers than open areas. Nurse species enhanced species richness more in systems with impoverished local diversity, suggesting that facilitative interactions in alpine habitats act as an insurance policy that sustains diversity under very harsh conditions.

Key-words: alpine, cushion plants, facilitation, nurse species, positive interactions, species richness

Introduction

Determination of the processes that maintain biological diversity is one of the primary aims of community ecology (Morin 2011; Mittlebach 2012). Although early research focused on negative interactions such as competition and predation as the main biotic factors structuring plant communities and regulating biological diversity (e.g. Grime 1973; Connell 1978; Tilman 1982), nowadays ecologists have demonstrated that species diversity is governed not only by local interactions among coexisting species, but also by large-scale biogeographic and historical processes

(Ricklefs 2004, 2008; Harrison & Cornell 2008). Nonetheless, some authors promote the perspective that biotic interactions play a minor role, the climate and historical processes being the major drivers of local species diversity (Ricklefs 2008; Harmon & Harrison 2015). These views do not conform well with the evidence that interactions among species are key to local-scale diversity (e.g. Tilman 1997; Brooker *et al.* 2009; Allesina & Levine 2011; Rabosky & Hurlbert 2015) and that in some cases appear to sustain large-scale diversity patterns (Valiente-Banuet *et al.* 2006; Harrison & Cornell 2008; Rabosky & Hurlbert 2015).

Although negative interactions still play a central role on some explanations for plant diversity at local scales

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(Silvertown 2004; Wilson 2011), positive interactions have started to gain a place as important drivers of community structure and biological diversity (Bruno, Stachowicz & Bertness 2003; Michalet *et al.* 2006; McIntire & Fajardo 2014; Soliveres, Smit & Maestre 2015). Positive interactions are defined as non-trophic interspecific interactions that increase the average individual fitness of one species (Bertness & Callaway 1994; Callaway 1995, 2007; Bruno, Stachowicz & Bertness 2003). Thus, by definition, the presence of one plant species enhances the chances that another species co-occur in the same place, indicating that positive interactions may determine biological diversity.

One of the most commonly recognized plant–plant positive interactions is the facilitation by nurse or foundation species, in which one species (the facilitator, foundation species or nurse plant) provides shelter from physical stress or herbivory to other plant species (Callaway 2007). It has been suggested that facilitative interactions may have strong impacts in harsh environments, where the mitigation of extreme conditions by facilitator species can be beneficial to many other species (Bertness & Callaway 1994; Brooker & Callaghan 1998). Although most of the examples of facilitative interactions among plants are from harsh, unproductive habitats such as deserts, cold alpine and arctic tundra (Callaway 1995, 2007), they have also been reported in more productive environments, such as tropical and subtropical habitats (e.g. Powers, Haggard & Fisher 1997; Anthelme, Gómez-Aparicio & Montúfar 2014), where the concept of relative stress or disturbance experienced by a focus plant is relevant (Holmgren & Scheffer 2010; Le Bagousse-Piguet *et al.* 2014). In environmentally severe habitats, harsh abiotic conditions may restrict plants from acquiring resources, and any amelioration of these conditions will favour growth to the extent that it outweighs the negative, competitive impact of growing in close associations (Hacker & Gaines 1997). Depending on the physical stress limiting the survival in a particular habitat, the mechanisms involved in the facilitation by a nurse plant species differ between habitats (for an extensive review of mechanisms see Callaway 2007).

Alpine habitats are well known for their severe abiotic conditions, where plants are confronted by low temperatures, short growing seasons, excessive radiation and unstable substrates (Körner 2003). Indeed, one of the most explored environments to demonstrate the existence and importance of facilitative interactions is alpine habitats (Kikvidze 1993; Kikvidze & Nakhutsrishvili 1998; Choler, Michalet & Callaway 2001; Callaway *et al.* 2002; Cavieres *et al.* 2002, 2006; Kikvidze *et al.* 2005, 2011). In addition, because many of these stressful abiotic conditions change along elevation, alpine habitats have been widely used to test how facilitative interactions change across severity gradients (Choler, Michalet & Callaway 2001; Callaway *et al.* 2002; LeRoux & McGeoch 2008; Kikvidze *et al.* 2011). However, despite the well-documented facilitative effects at individual and population levels in alpine habitats, the consequences of these effects for diversity at the

community level (i.e. considering all the species present in the community) have received much less attention (but see Cavieres & Badano 2009; Michalet *et al.* 2015). While some studies indicate that they are relevant for diversity (Cavieres *et al.* 2014), others indicated that facilitative interactions are not important and are unrelated with richness and community structure in subarctic alpine plant communities (Mitchell, Cahill & Hik 2009).

To assess the importance of facilitative interactions on community structure and richness is important to distinguish among two, not mutually exclusive, potential effects. On one hand, as nurse species provide shelter from physical stress or herbivory to other plant species, the number of species associated with the nurse might differ to that found in the open areas out of influence of the nurse plants. Usually, it is expected that nurse species patches contain higher richness than open areas. On the other hand, nurses and their alternative microhabitats (open areas among nurses) are part of the same community. Thus, if nurses allow for the persistence of species that otherwise would be excluded from the community, a net increase in the species diversity at the entire community level will be generated even though nurse plants contained fewer species than open areas. However, the simple question of how many species are added to a community due to the presence of a facilitator species has been rarely addressed (Cavieres & Badano 2009).

Cushion-forming plants are one of the most conspicuous plants found in exposed alpine habitats, and several studies have reported plant species growing inside of cushion plants suggesting a facilitative role for them (e.g. Nuñez, Aizen & Ezcurra 1999; Cavieres *et al.* 2002, 2006; Arroyo *et al.* 2003; LeRoux & McGeoch 2008). The low stature and compact form of cushion plants attenuate the effect of extreme environmental conditions, allowing the persistence of other species inside them (Cavieres *et al.* 2006, 2007). Hence, alpine habitats dominated by cushion plants are ideal systems to assess the community-level effects of facilitative interactions. Here, a search was conducted using ISI Web of Knowledge data base for articles associated with cushion plants' facilitation in alpine habitats, and using the information of these articles, we assessed whether nurse cushion species contain cushion-dependent species (i.e. species that are only found growing within cushions, hence would be absent from the community if cushions were not present), producing an increase in species richness at the entire community level. The assessment of these effects on more than a single community is important to tackle the generality of the community-level consequences of facilitation.

Study selection process

On 1 April 2015, a search was conducted using the ISI Web of Knowledge data base where the following search terms were used: cushion plant OR nurse plant AND facilitat* AND alpine. This search resulted in 64 articles. This

search was refined by screening all these publications to determine whether they evaluated either effects of facilitation on diversity or species richness. This final refinement generated 35 studies that were used to evaluate the community-level consequences of facilitation (Table S1, Supporting information).

The problem of quantifying the effect of cushions on species richness of a community

The effect of cushions (or other nurse or foundation species) on the species diversity in a given community is often assessed by looking at the number of species associated with cushions and comparing it with the richness of species in the open area out of influence of the cushion plants. As nurses (i.e. cushions) and open areas are patch types, we will refer to this as patch scale comparisons. Thus, at the patch level, we can simply compare species numbers between the two microhabitats (e.g. Cavieres *et al.* 2002; Dvorský *et al.* 2013) or use indices such as the Relative Interaction Index (RII, Armas *et al.* 2004), which is a ratio and can measure the effect of cushions on species richness as:

$$\text{RII} = (\alpha_{\text{cushion}} - \alpha_{\text{open}}) / (\alpha_{\text{cushion}} + \alpha_{\text{open}}),$$

where α_{cushion} is species richness found in the cushions and α_{open} is the richness of open area patches (e.g. Anthelme *et al.* 2012).

Nonetheless, to assess the effect of cushions of the diversity at the entire community level, we need to distinguish between the diversity at two scales: local = patch = plot (α -richness, mean values per cushion or patch of the same size in the open area) and entire community (γ -richness, all species found in plots of a given microhabitat, or the species pool). These two levels of richness are connected by β -diversity: $\beta = \gamma/\alpha$, where β represents differentiation diversity or the variation of species composition across the sampled patches or plots (Whittaker *et al.* 2001). If $\alpha_{\text{cushion}} > \alpha_{\text{open}}$ or positive values of RII occur, then cushions increase species richness in average at local (patch) scale. However, this does not warrants that at the community level, the number of species associated with cushions is more than that found in the open area plots. Because the sampling design compares two different microhabitats (cushions vs. open area), it produces two species pools that usually overlap: (γ_{cushion} and γ_{open} , see Fig. 1, left panel Venn diagrams as a conceptual representation). The size of γ_{cushion} and γ_{open} can vary so that along the cases where $\gamma_{\text{cushion}} > \gamma_{\text{open}}$, there could be also cases where $\gamma_{\text{cushion}} < \gamma_{\text{open}}$ and $\gamma_{\text{cushion}} = \gamma_{\text{open}}$. The latter cases do not seem to conform well to the widely accepted facilitative role of cushions. Yet, this is an illusory mismatch as the model $\beta = \gamma/\alpha$ can explain it: it is possible that $\gamma_{\text{cushion}} < \gamma_{\text{open}}$ if $\beta_{\text{cushion}} < \beta_{\text{open}}$ (species composition varies more strongly across open area patches than that in the cushions), even though $\alpha_{\text{cushion}} > \alpha_{\text{open}}$. To our knowledge, this type of analyses has not been undertaken yet with empirical data and so can be a target for further

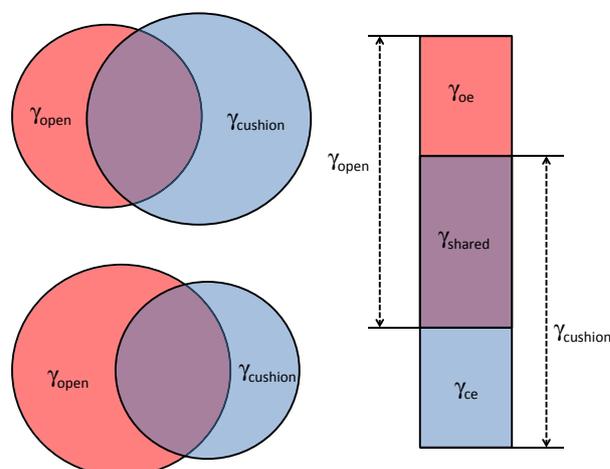


Fig. 1. Presentation of community species pool (all species recorded in patches of two microhabitats – within the cushions and outside them in open area) represented as two overlapping sets of species – one associated with the cushions (γ_{cushions}) and another constituted by species found in open area outside of cushions (γ_{open}); these two sets of species can vary in size (left panel, compare upper and lower Venn diagrams). The combined species pool can thus be partitioned into three non-overlapping subpools (right panel): γ_{cc} represents the species found in the cushions exclusively; γ_{oe} is the subset of species found exclusively in open area patches; γ_{shared} are the species found both in the cushion and open area patches.

studies on the effects of cushions or other foundation species on biodiversity patterns.

To see the problem quantitatively, the total species pool of a community (all species found both in the cushions and in the open area plots included) can be presented as three non-overlapping subsets: γ_{cc} = species found exclusively in the cushions, γ_{oe} = species found exclusively in open area patches and γ_{shared} = species found in both microhabitats (Fig. 1, right panel). It is easy to see that both γ_{cushion} and γ_{open} can contain a (variable) proportion of shared species: $\gamma_{\text{cushion}} = \gamma_{\text{cc}} + \gamma_{\text{shared}}$ and $\gamma_{\text{open}} = \gamma_{\text{oe}} + \gamma_{\text{shared}}$, so that the direct comparisons γ_{cushion} vs. γ_{open} cannot not be entirely informative. Instead, the proportional increment of species richness brought about by the cushions as $\gamma_{\text{cc}}/(\gamma_{\text{cc}} + \gamma_{\text{shared}} + \gamma_{\text{oe}})$ can be a simple and more correct way for quantifying the real effect of cushions on the total species pool of a given community. A practical and simple estimation of this proportional increment of species richness brought about by the cushions is the Increment in Species Richness (ISR) Index suggested in Cavieres *et al.* (2014) and estimated as follow:

$$\text{ISR} = (S_{\text{Total}} - S_{\text{Open}}) / S_{\text{Total}}$$

where S_{Total} is the number of non-cushion species present in the entire community at a given site ($\gamma_{\text{cc}} + \gamma_{\text{shared}} + \gamma_{\text{oe}}$ in Fig. 1) and S_{Open} corresponded to the number of species found in open area samples (i.e. outside cushions: $\gamma_{\text{oe}} + \gamma_{\text{shared}}$ in Fig. 1). This index gives a qualitative idea of the magnitude of the effect of cushion species on species richness at the scale of the entire local community (Cavieres

et al. 2014). Unless $\gamma_{ce} = 0$, the presence of cushions will *always* add species to the community species pool.

With this conceptual framework in mind, in the following sections, we illustrate the effect of alpine cushion plants on richness at the entire community level. However, as usually employed as an indicator of the existence (or absence) of facilitative interactions, we will start by looking at the effects of nurse cushion species at the patch level.

Facilitation and species richness at patch scale

The great majority of the studies addressing some consequences of facilitation on species diversity in alpine habitats have compared the species richness and species composition of the plant assemblages growing within nurses vs. plant assemblages growing outside nurses. While some studies reported higher species richness within nurses compared to open areas ($\alpha_{\text{cushion}} > \alpha_{\text{open}}$: Badano *et al.* 2002; Cavieres *et al.* 2002; Cranston *et al.* 2012; Schöb *et al.* 2013), others found either no differences ($\alpha_{\text{cushion}} = \alpha_{\text{open}}$: Pyšek & Liska 1991; Totland, Grytnes & Heegaard 2004; Pugnaire *et al.* 2015) or higher species richness outside the nurses ($\alpha_{\text{cushion}} < \alpha_{\text{open}}$: Cavieres *et al.* 1998; de Bello *et al.* 2011; Dvorský *et al.* 2013). For example, Cranston *et al.* (2012) studied the number of beneficiary species associated with *Silene acaulis* in the alpine tundra systems of the northern Rocky Mountains, USA, and consistently found that *S. acaulis* cushions contained higher number of species per unit of area than open areas (see also Cavieres *et al.* 2002; Arroyo *et al.* 2003; Michalet *et al.* 2011 for similar effects). In contrast, Pugnaire *et al.* (2015) recently reported that the number of species associated with the cushion species *Androsace tapete* in the Himalayas is not higher than that found in open areas; indeed, they reported that at a lower elevation site, the number of species growing inside *A. tapete* cushions is lower than those found outside cushions (see de Bello *et al.* 2011; Dvorský *et al.* 2013 for similar results).

Although the majority of the studies indicate positive effect of cushions at the patch level, there is no unequivocal support for the idea that species richness is higher within patches created by nurses (de Bello *et al.* 2011; Dvorský *et al.* 2013), suggesting idiosyncratic effects of nurses (Badano & Cavieres 2006). However, many of these idiosyncratic responses depend on the intensity of abiotic stress experienced by the plants in the microhabitats away from nurses, and on the ability of nurses in mitigate such stressful conditions. For instance, Antonsson, Björk & Molau (2009) calculated the difference in the number of species found inside and outside *S. acaulis* cushions in the alpine zone of northern Sweden and showed that this difference changed from negative (more species in the open areas compared to cushions) to positive as elevation increased. This is in line with several other studies that have shown that the difference between the numbers of species found inside cushions with that outside them is

higher as elevation, or environmental severity, increases (Cavieres *et al.* 2002, 2006; Arroyo *et al.* 2003; Badano & Cavieres 2006; Yang *et al.* 2010; Cranston *et al.* 2012). As already mentioned, the particular architecture and compact form of cushion plants help generate microclimatic conditions that differ from their surrounding environment (e.g. Cavieres *et al.* 2007; LeRoux & McGeoch 2008; Haussmann, Boelhouwer & McGeoch 2009; Schöb, Butterfield & Pugnaire 2012; Schöb *et al.* 2013), thus allowing the persistence of other species inside the cushions. Depending on the cushion species, the magnitude of these differences from the surrounding environment seems to become higher as the environmental conditions overall become more severe (Arroyo *et al.* 2003; Cavieres *et al.* 2006; Yang *et al.* 2010), which may explain the stronger nurse effect of cushion in harsher abiotic environments. When cushions do not provide microenvironmental conditions different from the surrounding environment, no associations with cushions might be expected as it has been shown by Dvorský *et al.* (2013). Therefore, the idiosyncratic effects of cushions on species richness at the patch scale might be related to both the provision of a microenvironment different from their surrounding and the magnitude of this mitigation effect. In addition, the concept of the relative stress experienced by the different species of the same community (Holmgren & Scheffer 2010; Le Bagousse-Piguet *et al.* 2014) might help to understand these idiosyncratic effects. Future studies using this approach (i.e. focused on patch level effects) to assess facilitative interactions should take into account these variables as they might explain the existence (or absence) of effects on species richness at the patch level.

Facilitation and species richness at the entire community level

To assess the effects of the presence of facilitator species on richness at the entire community level, we must simultaneously consider all microhabitats, including those created by nurses and those out of their influence. Although the species richness associated with nurses can be lower than that found in open areas ($\gamma_{\text{cushion}} < \gamma_{\text{open}}$, Fig. 1), the pivotal question is whether certain number of species are added to the community owing to the presence of the nurse. However, this important question often escaped the attention in previous studies on facilitation. For example, Schöb *et al.* (2013) studied the facilitative effects of the alpine cushion plant *Arenaria tetraquetra* across an elevation gradient in the Sierra Nevada of Spain and found that this cushion species contained more species than the bare ground only at the two highest elevations (3010 and 3240 m elevation); there were no significant differences in species richness per microhabitat at the lowest elevation (2315 m). However, a thorough examination of their data shows that at the highest elevation (3240 m), only one (*Festuca pseudeskia*), out of the 13 species found at this elevation, occurred exclusively within cushions. This sharply

contrasts with the three species that grow exclusively within cushions (*Erysimum nevadense*, *Sedum gypsicola* and *Plantago holosteum*) out of 11 species found at the lowest elevation site (2315 m). Overall, while the cushions increase the total community diversity by *c.* 7% at the highest elevation, this effect reaches 27% at the lowest elevation. It is known that in alpine habitats of Mediterranean-type climate zones, environmental severity can be very high at lower elevations due to summer drought (Cavieres *et al.* 2006). Cushion plants at these lower elevations have been shown to provide higher soil moisture than bare ground areas, which is vital to surviving the summer drought (Cavieres *et al.* 2006, 2007; Schöb *et al.* 2013). Thus, it is not surprising that the positive effect of alpine cushions on species richness at this lower elevation was stronger than that at higher elevations.

Using a different sampling approach, Sklenář (2009) studying the páramo of Iliniza volcano in Ecuador found that, in general, plots containing cushion plants had higher species richness than plots with no cushions. Actually, from the 25 species found in their samples, seven were found only within cushions, indicating that 28% of the entire community diversity was related to the presence of cushions. In the Patagonian Andes of Argentina, Nuñez, Aizen & Ezcurra (1999) found that the patches (20 × 20 m) with nurse cushion species contained higher species richness than the patches where cushions were absent (see also Badano & Cavieres 2006). In a similar vein, Antonsson, Björk & Molau (2009) sampled the vegetation associated with *S. acaulis* cushions in northern Sweden between 1150 and 1447 m elevation and showed that out of the 48 species found along this gradient, 35 occurred inside cushion, 42 in open areas and 30 on both microhabitats. Nonetheless, five species were found exclusively inside cushions, indicating that *c.* 10% of the diversity of this zone was dependent of the presence of this cushion species. de Bello *et al.* (2011) and Dvorský *et al.* (2013) studied the effect of the cushion plant *Thylacospermum caespitosum* on the diversity of alpine plants at different sites in the trans-Himalayas. Both studies found that *T. caespitosum* cushions never contained more species than the open areas. However, in the study of Dvorský *et al.* (2013), it can be observed that while at lower elevations cushions contained significantly lower number of species than open areas, this difference disappeared at higher elevations where cushions and open areas contained similar number of species. More importantly, however, at the highest elevation (5250 m) in Nubra, out of the 23 species found in this site by Dvorský *et al.* (2013), four (*Elymus schrenkianus*, *Trisetum spicatum*, *Saussurea gnaphalodes* and *Kobresia schoenoides*) were found only inside cushions, indicating that *c.* 17% of the diversity of this very high elevation site in the trans-Himalaya depended on the presence of this cushion species. This contrasts with the conclusion of Dvorský *et al.* (2013) that facilitation is negligible in this system. Likewise, de Bello *et al.* (2011) reported a total of 13 species at 5900 m in the Chalung Mountains

(Himalayas), of which seven can be found growing inside *T. caespitosum* cushions and 12 outside. Nonetheless, as in Dvorský *et al.* (2013), the species *S. gnaphalodes* was only found inside the cushions. Similarly, Yang *et al.* (2010) reported 26 and 29 species growing within and outside *Arenaria polytrichoides* cushions in the Himalayas at 4700 m, respectively. Nonetheless, three species were found exclusively growing within the cushions, indicating a 9% increase in richness at the entire community level due to the presence of cushions. All these examples illustrate that despite some studies reported higher species richness in open areas outside of the nurses, a careful reconsideration of their data shows that there are species restricted to the nurse microhabitat, and hence, without the presence of nurses, these species cannot persist in the community. Therefore, as long as the persistence of a particular group of species in a given community depends on the presence of a nurse species, the effect of the facilitation by nurses will increase species richness at the entire community level.

Recently, Cavieres *et al.* (2014) using a data set spanning 78 alpine sites dominated by cushion plants over the five continents assessed the relative importance of positive interactions and climate in determining plant diversity in alpine plant communities. They found that climate variables related to water balance showed the highest correlation with richness at the global scale. Strikingly, although the effect of cushion species on diversity was lower than that of climate, its contribution was still substantial. In particular, at 92% of the studied sites, nurse cushion species enhanced species richness at the whole community level, with several cases where the increase in species richness was higher than 50% (Cavieres *et al.* 2014). That is, half of the species found in the community were dependent of the presence of the nurse cushions species. Interestingly, the effect of cushion species on species richness at the entire community level was *inversely* correlated with surrogates of productivity as cover and species density in open areas, indicating that the facilitative role of cushion species was greater in unproductive environments (Cavieres *et al.* 2014).

To further explore the effect of nurse cushions on species richness at the entire community level, and how this can vary along environmental gradients, from Table S1, we used published studies conducted at different latitudes along the Andes in South America where it was possible to calculate the contribution of cushions to the entire community level through the ISR Index. To take into account data collected along the same mountain range along a large latitudinal gradient (0°–50°S) provides more comparable data. The studies considered in this analysis were as follows: Cavieres *et al.* (2002, 2006, 2014), Arroyo *et al.* (2003), Badano & Cavieres (2006) and Anthelme *et al.* (2012). It can be observed that, similarly to Cavieres *et al.* (2014), the effect of nurse cushions on species richness at the entire community level (ISR) was negatively correlated with either cover or the total number of species in the community (i.e. species pool) (Fig. 2). Thus, the impact of the facilitative effect of cushion species on richness at the entire community

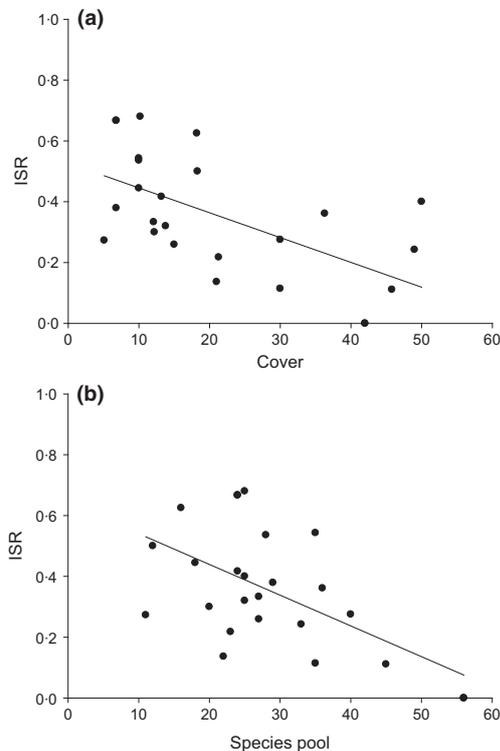


Fig. 2. Relationships between nurse species effects on richness (increment in species richness, ISR) with total site cover (a) and the size of the species pool (b) using data collected at the different sites along the Andes in South America. Linear regression results are as follows: panel (a): $r^2 = 0.36$, $P < 0.01$; panel (b): $r^2 = 0.34$, $P < 0.01$. Data sources are as follows: Cavieres *et al.* (2002, 2006, 2014), Arroyo *et al.* (2003), Badano & Cavieres (2006) and Anthelme *et al.* (2012).

level was greater in habitats with low cover and species poor. These results agree well with general predictions of the stress gradient hypothesis (SGH) that increasing in environmental severity is associated with a shift from competitive to facilitative interactions (Bertness & Callaway 1994), and add that the facilitative interactions with the nurse species had more important effects on maintaining higher local diversity in systems with an inherently low number of species than in systems that were species rich (Cavieres *et al.* 2014). Although the generality of the relationships proposed by the SGH has been debated (e.g. Maestre *et al.* 2009), the predictions of the SGH appear to be well supported by recent meta-analyses (He, Bertness & Altieri 2013) where it is clearly shown a general pattern of decreasing competition and/or increasing facilitation with increasing environmental severity, irrespective of the climate type, experimental approach and a wide range of other factors. However, this meta-analysis excluded studies which involved species turnover along the stress gradient as we considered in our exploration of the alpine cushion literature. Certainly, the relationships between severity, interaction effects and species richness found in our study fit with the patterns found in many other studies (e.g. Choler, Michalet & Callaway 2001; Callaway *et al.* 2002; Kikvidze *et al.* 2011), and although cushion plant systems are particularly suited to assessing the effects of facilitators, our

results are highly likely to be applicable across temperature-limited environments in general.

Recent theoretical studies indicate that positive interactions among resource competitors can produce species-rich communities supported by a single limiting resource (Gross 2008). Indeed, in meta-community models, it has been observed that positive interactions among species can rapidly evolve in communities with reduced regional pools of species and/or with low environmental quality, thereby generating higher richness than predicted from competitive or neutral processes (Filotas *et al.* 2010). Interestingly, meta-community models also show that even if local–regional species richness relationships point to relatively high contributions of regional species pool to the richness of local communities, supporting neutral processes, positive interactions still are likely to play important roles in determining local species diversity by generating local–regional richness relationships with the alternative stable states of mean local richness at intermediate to high levels of regional richness (Takimoto 2011; Michalet *et al.* 2015). Thus, both from the theory and from the empirical evidence, facilitative interactions play a role in determining diversity at different spatial scales, especially in alpine plant communities.

Concluding remarks

Community ecologists recognize that many factors affect the species composition of a given community, with no single factor providing a complete explanation for observed patterns (Lortie *et al.* 2004). Moreover, different factors can interact in a complex hierarchical fashion. Regional species pool provides the potential members of a community; dispersal ability set the identity of those species available to colonize a given community where local interspecific interactions and niche-filtering processes will play a fundamental role in the success or failure of species as community members. We have seen that the presence of facilitator species in alpine habitats can add to species richness at the whole community level. This effect emerges even in those studied that denied the presence and importance of facilitative interactions with cushions because they contained lower species diversity than open areas (e.g. de Bello *et al.* 2011; Dvorský *et al.* 2013). Further, the facilitative interactions with the nurse species had more important effects on maintaining higher local diversity in systems with an inherently low number of species than in systems that were species rich (Cavieres *et al.* 2014). Butterfield *et al.* (2013) showed that facilitation by cushion species has an important effect on the phylogenetic diversity at the community level, with the beneficial effects of cushion species on phylogenetic diversity being stronger in more extreme and species-poor sites. Thus, facilitative interactions appear to buffer the negative effects on diversity from changing environment, and in the particular case of alpine cushion plants, they act essentially as an ‘insurance policy’ that sustains diversity under very harsh conditions.

Although alpine habitats are inherently species poor compared to some more benign habitats, they contain very

high levels of endemism and provide important ecosystem services as the provision of pure water (Körner 2003). Thus, facilitative interactions seem to play an important role in preserving the particular diversity of alpine habitats and the ecosystems services that they provide. Alpine habitats are particularly sensitive to major anthropogenic drivers of ecosystem change, including climate change, land use change and introduced species. Thus, for a proper management and conservation of these environments, it is vital to increase our understanding of the importance of facilitative interactions among plants in the regulation of alpine biodiversity as it can act as an insurance policy for future environmental changes.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Articles found after a bibliographic search conducted using ISI-Web of Knowledge database using the following search terms: cushion plant OR nurse plant AND facilitat* AND alpine.