

Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes

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Abstract. It has been proposed that in the harsh arctic and alpine climate zones, small microtopographic variations that can generate more benign conditions than in the surrounding environment could be perceived as safe sites for seedling recruitment. Cushion plants can modify wind pattern, temperature and water availability. Such modifications imply that cushion plants could act as 'nurse plants' facilitating the recruitment of other species in the community. This effect should be more evident under stressful conditions. We tested these hypotheses comparing the number of species that grow inside and outside *Bolax gummifera* cushions at two elevations (700 and 900 m a.s.l.) in the Patagonian Andes of Chile (50°S). At both elevations, and in equivalent areas, the number of species was registered within and outside cushions. A total of 36 and 27 plant species were recorded either within or outside *B. gummifera* cushions at 700 and 900 m a.s.l., respectively. At 700 m a.s.l., 33 species were recorded growing within cushions and 29 outside them, while at 900 m a.s.l. these numbers were 24 and 13 respectively. At both elevations there were significantly more species growing within than outside cushions, and the proportion of species growing within cushions increased with elevation. Thus there is a nurse effect of cushion plants and it is more evident at higher elevations. Shelter from wind and increased soil water availability seem to be the factors that increase plant recruitment within cushions.

Keywords: Alpine ecology; *Apiaceae*; Facilitation; Shelter.

Nomenclature: Marticorena & Quezada (1985).

Introduction

Several studies have recently re-examined the importance of positive interactions in plant communities (e.g. Bertness & Callaway 1994; Callaway 1995; Callaway & Walker 1997; Holmgren et al. 1997; Olofsson et al. 1999; Kikvidze et al. 2001). Positive interactions typically occur with the presence of 'nurse plant' species, that is species which ameliorate the abiotic environment for other species and facilitate establishment beneath their canopies (Callaway & Walker 1997). Commonly reported ameliorative influences of the nurse plant canopy include: cooler temperatures and lower evaporative stress, increased soil moisture, protection against herbivores, and greater availability of nutrients (Callaway & Pugnaire 1999). Several authors (e.g., Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998) have proposed that positive effects between species are more likely to be seen in disturbed or stressful environments. The reasoning was that harsh environments 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. Brooker & Callaghan (1998) concluded that positive interactions are particularly likely in arctic/alpine habitats, since they contain a variety of stresses and disturbances, and the abiotic environment is the primary limitation on plant growth.

Although nurse plants have been described for a wide range of ecosystem types, they are particularly common in arid and semi-arid environments (Jordan & Nobel 1979; Franco & Nobel 1988, 1989; Valiente-Banuet & Ezcurra 1991; Aguiar et al. 1992; Pugnaire et al. 1996; Raffaele & Veblen 1998). However, recent studies have also reported this phenomenon in alpine plant communities (Cavieres et al. 1998; Nuñez et al. 1999; Molina-Montenegro et al. 2000).

Alpine habitats, like arid environments, are well known for their severe life conditions. Here plants are

confronted by low temperatures, short growing seasons, excessive radiation and unstable substrates (Billings & Mooney 1968; Billings 1972; Bliss 1985; Körner 1999, 2000). Cushion plants represent one of the life forms best adapted to the extreme alpine environment (Armesto et al. 1980; Alliende & Hoffman 1985; Pyšek & Lyska 1991). Because of their low stature and compact form, cushion plants favour the development of particular micro-environments within their canopy (Körner & de Moraes 1979; Körner & Cochrane 1983). Several studies report the presence of other species growing inside cushions from many alpine habitats (Griggs 1956; Alliende & Hoffmann 1985; Pyšek & Lyska 1991; Cavieres et al. 1998; Nuñez et al. 1999; Molina-Montenegro et al. 2000) suggesting that cushions are nurse plants. For example, Nuñez et al. (1999) reported that in the high Andes of southern Argentina (41 °S) the cushion plants *Mulinum leptacanthum* and *Oreopolus glacialis* are effective nurse plants, and that the ameliorative environmental effect of these species could be explained by cushions being more efficient in producing and retaining organic matter as well as conserving nutrients and soil moisture. Moreover, these authors reported an absence of replacement of species or species exclusion suggesting that negative interactions are absent from this kind of habitat, supporting the stress hypothesis (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker and Callaghan 1998). However, other studies from high alpine habitats have shown that negative interactions occur and are important in determining the community structure (Moen 1993; Theodose & Bowman 1997; Olofsson et al. 1999).

A useful approach to elucidate how the relative importance of positive and negative interactions change with abiotic stress in alpine habitats is the study of the interactions in a single cushion plant species along an environmental gradient. Thus, if, according to the environmental stress hypothesis, a cushion plant species offers conditions more favourable for the establishment of other species which act as a nurse plant, it would be expected that cushions growing in more stressful habitats should harbour, proportionally greater numbers of species in comparison with cushions growing in more benign habitats. Given that in alpine zones, habitat severity increases with elevation (Billings 1972), we tested this hypothesis comparing the number of species that grow inside and outside *Bolax gummifera* cushions at two elevations in the Patagonian Andes of Chile (50 °S). If cushions at higher elevations harbour more species, then a series of questions related to other community parameters arise: are species abundance and diversity greater within than outside cushions at two different elevations and are the floristic similarities between species assemblages within and outside cushions more similar at lower elevations than at higher?

Study site and target species

This study was conducted at two elevations at Cerro Diente, Torres del Paine National Park (50°48'S, 73°10'W), an International Biosphere Reserve located in southern Patagonia (Fig. 1). Cerro Diente is 12 km east of the Southern Patagonian Icefield, the third largest sub-polar icefield in the world. The Torres del Paine

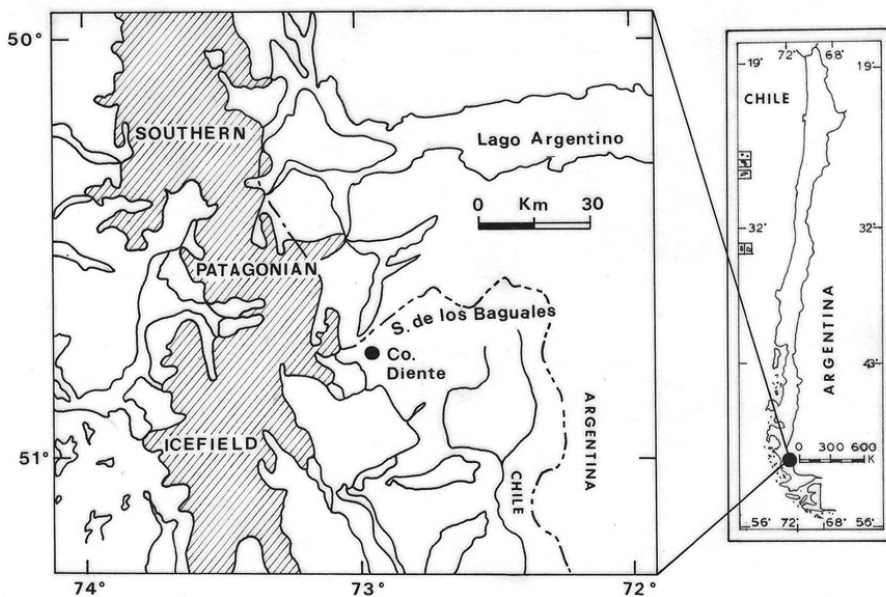


Fig. 1. Map of the study area, showing the location of Cerro Diente, patagonian Andes, Chile.

National Park lies in the path of the westerlies that are associated with storm passages throughout the year (Pisano 1974). The high alpine zone lies immediately above the *Nothofagus pumilio* tree line found at 650 - 700 m a.s.l., and receives precipitation throughout winter and summer (Squeo 1991). During winter, precipitation occurs as snow, with snow persisting above the tree line from the beginning of March to the end of November; summer precipitation occurs in the form of sleet, hail or snow. Annual precipitation at the edge of the icefield is ca. 900-1000 mm (Pisano 1974). The most conspicuous feature of summer weather patterns are powerful winds originating on the Southern Patagonian Icefield, which are generally stronger during daylight hours, with velocities exceeding 60 km.hr⁻¹ many days during summer (Arroyo & Squeo 1987). The mean daily temperature in the high alpine Cerro Diente is around 5 °C, with a mean relative humidity of 67% (Squeo 1991).

The target species, *Bolax gummifera* (*Apiaceae*), is a flat, tightly knit cushion species occurring widely throughout the alpine Cerro Diente. Individual cushions may reach 20-60 cm in diameter. Other physiognomically important compact cushion species occurring on Cerro Diente include *Azorella monantha* (*Apiaceae*) and *Oreopolus glacialis* (*Rubiaceae*).

Methods

Two plant communities on east facing slopes dominated by *Bolax gummifera* were selected, one at 700 m a.s.l., just above the tree line, and another at 900 m, at the upper limit of the cushion belt (Squeo 1991). At the lower elevation, the community is co-dominated by prostrate shrubs such as *Gaultheria mucronata* (*Ericaceae*) and *Empetrum rubrum* (*Empetraceae*) while the higher elevation is co-dominated by perennial herbs such as *Nassauvia pygmaea* (*Asteraceae*) and *Hamadryas kingii* (*Ranunculaceae*; Squeo 1991). Cover analyses estimated by 50-m linear transects (unpubl. data) showed that at 700 m a.s.l. the absolute cover of *B. gummifera* cushions was 35%, while open ground represented 51%; at 900 m cushion cover declined to 30%, while open ground increased to 59%.

At each elevation, 50 *B. gummifera* cushions were selected at random. This was performed with the aid of a compass and a pocket calculator that generated random numbers between 0 and 1 which were converted to hexadecimal degrees. The random number generated indicated the direction (degrees from the magnetic North) and the first cushion intercepted by an imaginary straight line was selected. Metal hoops of 20, 30, 40, 50 and 60 cm diameter were placed over the surface of the

cushion, hoop size being chosen to be similar in diameter to the cushion. All plant species found inside the hoop were identified and recorded. In a similar fashion, a hoop of identical size was located at random outside the cushion, where again all species included in the hoop were recorded. The random location of the hoop outside the cushion was determined by a procedure similar to that used in the selection of the cushions. At 700 m a.s.l., 16 cushions of 20 cm diameter, 22 of 30 cm, 6 of 40 cm and 6 of 50 cm were studied. At 900 m these numbers were 18, 21, 5, 3 and 3 for cushions of 20, 30, 40, 50 and 60 cm diameter, respectively. This results in total sampled areas of 399 and 411 dm² per microhabitat (within and outside cushions) at 700 and 900 m a.s.l., respectively. Number of species within and outside cushions were compared by ANCOVA with elevation and position (within or outside cushion) as factors and the area of the used hoop (in dm² as suggested by Nuñez et al. 1999) as the co-variable.

In order to detect the preferences of individual species for a particular microhabitat, we investigated the differences between the frequency with which a species was found within or outside cushions with randomization tests (Slade & Hall 1999) using the software Resampling Stats (Simon et al. 1990-1995). From the total frequency of a species at one elevation we generated 1000 random values of that species within and outside cushions. Then, we calculated the probability of the observed frequency within cushions being generated by chance.

For each microhabitat at each elevation, total species richness, total frequency as a measure of abundance, reciprocal of the Simpson's index of diversity, and evenness based on this index (Krebs 1999) were determined. Significance of differences between the two microhabitats for each parameter at each elevation were assessed with randomization tests (Slade & Hall 1999). In these cases we generated random assignments of the observed frequency values to the two microhabitats and calculated the difference of each parameter between the microhabitats. This procedure was repeated 1000×.

Results

A total of 36 and 27 plant species were recorded either within or outside *Bolax gummifera* cushions at 700 and 900 m a.s.l., respectively. At 700 m a.s.l., 33 species were registered growing within cushions and 29 outside them, while at 900 m a.s.l. these numbers were 24 and 13, respectively (Table 1). Although a large number of the species occurring within cushions was also found outside, proportionately more species were shared between the two microhabitats at 700 m a.s.l. than at 900 m a.s.l. (Table 1).

Both elevation and position within or outside cushion had significant effects on species density ($F_{1,196} = 73.7, p < 0.01$; $F_{1,196} = 66.4, p < 0.01$, for elevation and position, respectively). Both within or outside cushions, the number of species was significantly lower at the highest elevation, while at the two elevations there were significantly more species growing within cushions (Fig. 2). However, the difference in species density between elevations was greater for species within cushions (0.45 species.dm⁻²) than for species outside (0.29 species.dm⁻²). The ratio of the number of species found within cushions to those outside at altitudes of 700 and 900 m a.s.l. were 2.28 and 4.23, respectively. These numbers suggest that proportionally there were more species within cushions at 900 than at 700 m a.s.l. This can also be clearly shown by plotting the logarithm of the number of species against the logarithm of the sampled area (Fig. 3). At 700 m, linear regressions were significant for both microhabitats ($F_{1,48} = 26.6; p < 0.01$; $R^2 = 0.25$ and $F_{1,48} = 31.3; p < 0.01$; $R^2 = 0.40$ for within and outside cushions, respectively) and the outside-cushion regression slope was significantly greater than the within-cushion regression slope ($t = -2.58$, d.f. = 96, $p < 0.05$), suggesting that nurse effect is only evident at small sampling areas (Fig. 3). In contrast, at 900 m a.s.l. linear regressions were also significant for both microhabitat ($F_{1,48} = 13.6; p < 0.01$; $R^2 = 0.22$ and $F_{1,48} = 20.6; p < 0.01$; $R^2 = 0.30$ for within and outside cushions, respectively) but the within cushion regression slope was significantly steeper than the outside cushion regression slope ($t = -5.5$, d.f. = 96, $p < 0.01$). Thus there were more species growing within cushions than outside them (Fig. 3) at all sampled areas at this altitude.

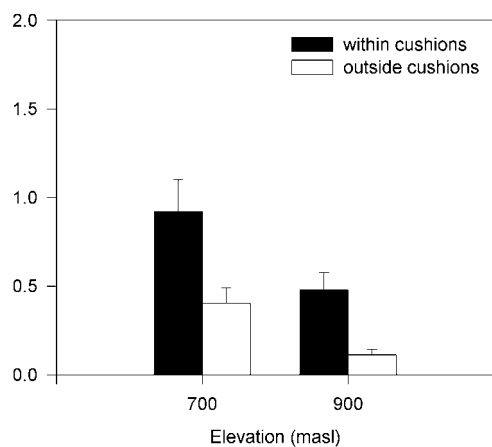


Fig. 2. Number of species (± 2 SE) per dm² growing within and outside *Bolax gummifera* cushions at two altitudes at Cerro Diente, Patagonian Andes, Chile.

Table 1. Frequencies of species growing within (In) and outside (Out) *Bolax gummifera* cushions at two altitudes (700 and 900 m a.s.l.) at Cerro Diente in the Patagonian Andes, Chile (50° S); p -values are from randomization tests (see text). Asterisks indicate p -values < 0.05 .

Species	700 m a.s.l.			900 m a.s.l.		
	In	Out	p	In	Out	p
<i>Abrotanella emarginata</i>				22	0	$< 0.01^*$
<i>Acaena antarctica</i>	2	1	0.511	1	0	0.510
<i>Acaena magellanica</i>	1	0	0.498			
<i>Acaena pinnatifida</i>	8	5	0.279	2	0	0.257
<i>Adesmia lotoides</i>	14	1	$< 0.01^*$			
<i>Adesmia parvifolia</i>	2	0	0.257			
<i>Adesmia pumila</i>	7	0	0.005*			
<i>Adesmia solicornioides</i>	1	1	0.483			
<i>Astragalus nivicola</i>	16	5	0.021*	2	0	0.236
<i>Azorella fuegiana</i>	5	8	0.267	4	0	0.042*
<i>Azorella lycopodioides</i>	4	0	0.058	9	0	0.004*
<i>Azorella monantha</i>	13	15	0.720	2	1	0.520
<i>Calceolaria uniflora</i>	3	2	0.503	1	1	0.758
<i>Cerastium arvense</i>	1	2	0.502	4	1	0.210
<i>Colobanthus subulatus</i>	1	1	0.746	2	0	0.264
<i>Draba funiculosa</i>	0	1	0.512			
<i>Draba magellanica</i>	5	7	0.394	1	0	0.512
<i>Elymus glaucescens</i>				1	3	0.293
<i>Empetrum rubrum</i>	23	1	$< 0.001^*$	3	0	0.132
<i>Erigeron leptopetalus</i>	8	8	0.601	7	0	0.006*
<i>Festuca magellanica</i>	32	20	0.052	13	3	0.007*
<i>Gaultheria pumila</i>	14	14	0.559	18	3	$< 0.001^*$
<i>Hamadryas kingii</i>				0	12	$< 0.001^*$
<i>Hypochoeris incana</i>	7	4	0.289			
<i>Leucheria leontopodioides</i>	3	0	0.133			
<i>Luzula alopecurus</i>	13	6	0.077	16	3	0.003*
<i>Luzula chilensis</i>	5	2	0.230	3	0	0.132
<i>Nassauvia aculeata</i>	0	5	0.027*	5	1	0.097
<i>Nassauvia revoluta</i>	0	1	0.535	0	1	0.489
<i>Oxalis enneaphylla</i>	3	5	0.344			
<i>Perezia megalantha</i>				0	3	0.107
<i>Perezia pilifera</i>	27	15	0.04*	5	0	0.031*
<i>Phleum alpinum</i>	1	0	0.507			
<i>Plantago uniglumis</i>	6	4	0.378	1	0	0.497
<i>Poa alopecurus</i>	3	0	0.107			
<i>Poa pratensis</i>	7	8	0.488	3	0	0.137
<i>Poa spec.</i>	7	3	0.151	5	3	0.362
<i>Senecio magellanicus</i>	1	5	0.113	2	0	0.262
<i>Trisetum spec.</i>	21	12	0.076	16	2	0.001*
<i>Vicia bijuga</i>	4	1	0.181			

Morisita-Horn's similarity index showed that species composition within and outside cushions had greater similarity at 700 m than at 900 m, while similarity between elevations was greater for the species established within cushions than outside (Table 2). At 700 m only five species (*Adesmia lotoides*, *A. pumila*, *Astragalus nivicola*, *Empetrum rubrum* and *Perezia pilifera*; 14% of the total found at this elevation) were found significantly more frequently within cushions and one (*Nassauvia aculeata*) significantly more frequently outside (Table 1). At 900 m, 10 species showed significant differences (Table 1), nine of which (33% of the total found at this elevation) were found significantly more frequently within cushion, and one (*Hamadryas kingii*) significantly outside. Seven of the 24 species that grew within cushions at both elevations changed the nature of

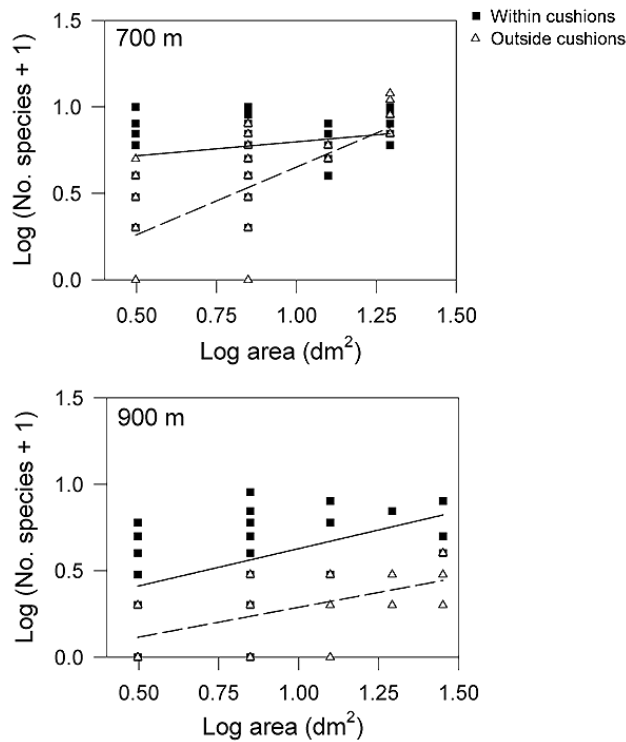


Fig. 3. Linear regressions between log of sampled area and log of number of species found within (■ and solid line) and outside (△ and dashed line) *Bolax gummifera* cushions at 700 and 900 m a.s.l. at Cerro Diente, Patagonian Andes, Chile. Adjusted linear equations were: $y = 0.16x + 0.64$; $R^2 = 0.32$ for 700 m within; $y = 0.78x - 0.13$; $R^2 = 0.39$ for 700 m-outside; $y = 0.43x + 0.19$; $R^2 = 0.22$ for 900 m within; and $y = 0.25x + 0.18$; $R^2 = 0.30$ for 900 m outside.

the interaction with *B. gummifera*, having no preference for cushions at 700 m a.s.l., to being significantly more frequent within cushions at the highest elevation. These were *Azorella fuegiana*, *A. lycopodioides*, *Erigeron leptopetalus*, *Festuca magellanica*, *Gaultheria pumila*, *Luzula alopecurus* and *Trisetum* spec. Notably, the species *Nassauvia aculeata* that established negative interactions with *B. gummifera* at 700 m grew more frequently within cushions at higher elevations.

Differences between species richness, diversity and evenness between within and outside cushions at the two

Table 2. Morisita-Horn's index of floristic similarity for the assemblages of species found within and outside *Bolax gummifera* cushions from two altitudes (700 and 900 m) at Cerro Diente, Patagonian Andes, Chile.

	Within		Outside	
	700 m	900 m	700 m	900 m
Within - 700 m	-	-	-	-
Outside - 700 m	0.846	-	-	-
Within - 900 m	0.611	0.648	-	-
Outside - 900 m	0.247	0.277	0.319	-

elevations showed that there were no significant differences in these parameters at 700 m. At 900 m, however, while diversity did not differ significantly between within cushions and outside, abundance did, suggesting that cushions strongly improve the performance of beneficiary species, but not community diversity (Table 3).

Discussion

As has been shown for other alpine cushion species (Alliende & Hoffmann 1985; Lough et al. 1987; Pyšek & Lyska 1991; Cavieres et al. 1998; Nuñez et al. 1999; Molina-Montenegro et al. 2000), evidence of a nurse effect in *Bolax gummifera* was found. Additionally, the strength of the nurse effect varied with elevation: the higher ratio of species growing within/outside cushions at 900 m suggesting that the nurse effect is more important at higher elevations. At the lower elevation, although many species grew within cushions, evidence of a true nurse effect was limited to five species being preferentially sheltered (14% of the species found at this elevation). Moreover, the species-area relationship indicates that at the lowest elevation, given that the bare ground accumulated species faster than cushions, the nurse effect is evident only for small cushion sizes. This suggests that if the sampling area increases there could be more species growing outside cushions. In contrast, at the higher elevation cushions contained and accumulated species faster than the bare ground, suggesting that they contained species absent from the open ground. At this elevation

Table 3. Diversity of species assemblages within and outside *Bolax gummifera* cushions from two altitudes at Cerro Diente, Patagonian Andes, Chile. *p*-values are from randomization tests. Asterisk shows values significantly higher than expected by chance.

	700 m				900 m			
	Within	Outside	Difference	<i>p</i>	Within	Outside	Difference	<i>p</i>
Richness	33	29	4	0.35	25	13	12	0.07
Abundance	268	163	105	0.06	148	37	111*	<0.01
Reciprocal of Simpson's index	16.99	16.07	0.92	0.43	12.32	6.61	5.71	0.20
Evenness	0.52	0.55	-0.04	0.32	0.49	0.51	-0.02	0.47

more than 30% of the plant species from equal sampling areas grew more frequently in cushions than outside cushions with eight species being restricted to that microhabitat and seven changing the nature of their interaction with *B. gummifera* in relation to 700 m a.s.l. Such changes in the nature of the interactions between species with environmental abiotic stress have been observed in other systems (Callaway et al. 1991; Greenlee & Callaway 1996; Callaway 1998a; Pugnaire & Luque 2001). For instance, Pugnaire & Luque (2001) showed that interactions between the shrub *Retama sphaerocarpa* and its associate understorey species changed from neutral and negative to positive when the environment became more stressful (see also Haase 2001).

Nevertheless, a wide variety of responses of species with respect to establishment on cushions was observed. For example, at 900 m 17 species showed a preference for cushions whereas 18 did not. Such variation has been reported previously by Alliende & Hoffman (1985) and Cavieres et al. (1998) who suggested that the nurse effect of alpine cushions is a species-specific phenomenon (cf. Callaway 1998b). *B. gummifera* forms tight cushions which could limit the growth of some species, especially those that require conditions for quick growth (e.g. annual species) or those that require free spaces (e.g. suffruticose or woody species). At each elevation there was one species which occurred significantly more frequently outside cushions and two other species that were found only on the open ground, suggesting that there was a negative association with these species and *B. gummifera*. At 700 m the three species showing negative association were rhizomatous (*Draba funiculosa*, *Nassauvia aculeata*, and *N. revoluta*) a fact that suggests that there could be some kind of interference at the root level with the cushion; additionally *N. aculeata* is a suffruticose perennial herb, a fact that suggests that there could also be interference at the secondary growth level. At 900 m a.s.l. the three species found growing only outside cushions were also rhizomatous (*H. kingii*, *N. aculeata* and *Perezia megalantha*). The majority of the species that grew more frequently within cushions were small perennial herbs. Thus, in spite of the fact that cushions establish positive interactions with some species, for others interactions are neutral or even negative.

Although differences in species richness, diversity, and evenness between cushions and the bare ground were not significant, differences were greater at the higher elevation. The fact that at 900 m abundance was significantly higher within cushions than outside suggests that at higher elevations cushions form a more preferred environment for species recruitment than the surrounding open ground, improving significantly the performance of nursed species.

In alpine habitats the benefits for cushion intruding

species are mainly shelter from wind, increased temperature, provision of moisture and availability of nutrients (Griggs 1956; Callaghan & Emanuelsson 1985; Pyšek & Lyska 1991; Cavieres et al. 1998; Nuñez et al. 1999). In Patagonian ecosystems wind plays a major role (Aguiar et al. 1992), especially at higher elevations where the most critical effects are soil erosion and surface drying (Squeo 1991). Wind has been seen to generate huge dust clouds along the tops of Cerro Diente during the summer, and local lifting of finer substrates is commonplace throughout summer (Squeo 1991), a phenomenon that, in turn, could produce denuded soil surfaces composed mainly of stones and rock debris, dry and poor in nutrients. Wind also increases the loss of heat and water (Nobel 1988). Hager & Faggi (1990) reported that *Mulinum spinosum* (a lowland Patagonian cushion) reduced wind velocity by 89% and formed an effective shelter for other species that grow in association (Aguiar et al. 1992). Sheltered plants can increase their temperature 1 - 2 °C above air temperature (Carlsson & Callaghan 1991) and this small rise in temperature may nevertheless be of crucial importance when the plant is existing close to its lower temperature limit (Körner & Larcher 1988). Additionally, it has been shown that soil beneath cushions maintains higher humidities than the surrounding soil (Cavieres et al. 1998), and certain species can store up to several times their own weight in water (Walter & Breckle 1989). Cushions could trap their own litter and intercept other windblown litter which, in addition with the higher availability of water and the increase in temperature, could result in locally increased concentration of nutrients (Carlsson & Callaghan 1991; Nuñez et al. 1999). This suggests that cushions offer a more favourable habitat for seed germination and seedling recruitment than the open ground. Alternatively, cushion plants could accelerate species recruitment by representing more effective seed traps than any other growth form in this community. This is a common phenomenon in lowland Patagonia, where prostrate shrubs (e.g. *M. spinosum*) trap more wind-blown seeds than other life forms (Aguiar et al. 1992). Thus, by either offering a more benign microhabitat or trapping seeds or a combination of both, *B. gummifera* cushions may play a key role in determining the structure of these alpine communities, especially at higher elevations.

Direct positive interactions, such as the nurse effect, can increase species diversity by facilitating species that might not normally survive under very high physical disturbance or stress (cf. Hacker & Gaines 1997). This last effect is clearly manifest at Cerro Diente. While the number of species outside cushions decreased significantly with elevation, the number of species within cushions remained fairly constant. As a result of cushions sheltering many species found otherwise outside cushions only at

lower elevations, total species richness failed to decrease with elevation, as it typically does along altitudinal gradients. This can be appreciated with the Morisita-Horn's index of similarity, which showed that floristic similarity between elevations is higher within cushions than outside. Similar results have been reported by Nuñez et al. (1999) who showed that patches containing cushion plants in the Patagonian Andes in Argentina sustained a much richer flora than patches lacking cushion species.

In conclusion, our results support the idea that when the environment becomes stressful, positive interactions increase in importance. A debate is currently under way about the nature of interactions between plant species in extreme habitats. While some studies suggest that positive interactions are the main interspecific interactions in alpine habitats (e.g. Kikvidze 1996; Kikvidze & Nakhutshvili 1998; Nuñez et al. 1999), others conclude that positive interactions are not the general rule, with competition also being an important structuring element (e.g., Moen 1993; Theodose & Bowman 1997, Olofsson et al. 1999). *Bolax gummifera* established neutral, negative, and positive interactions with the other species, with prevalence of the latter at higher elevations. It should be borne in mind that of all major biomes, the alpine spans the widest latitudinal range. While the common denominator of the alpine environment is low temperature, alpine communities vary enormously with respect to precipitation, radiation, and wind conditions, reflected in wide physiognomic and cover variations. Only as studies encompassing such variation become available, will it be possible to evaluate the global importance of positive interactions and the nurse effect in alpine habitats.

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