
Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile

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Summary

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- In alpine habitats, positive interactions among plants tend to increase with elevation as a result of altitudinal increase in environmental harshness. However, in mountains located in arid zones, lower elevations are also stressful because of scarce availability of water, suggesting that positive interactions may not necessarily increase with elevation.
- Here we analysed the spatial association of plant species with the nurse cushion plant *Laretia acaulis* at two contrasting elevations, and monitored the survival of seedlings of two species experimentally planted within and outside cushions in the semiarid Andes of central Chile.
- Positive spatial associations with cushions were more frequent at lower elevations. Species growing at the two elevations changed the nature of their association with cushions from neutral or negative at higher elevations to positive at lower elevations. Survival of seedlings was higher within cushions, particularly at lower elevations.
- The increased facilitation by cushions at lower elevations seems to be related to provision of moisture. This result suggests that cushion plants play a critical role in structuring alpine plant communities at lower elevations, and that climatic changes in rainfall could be very relevant for persistence of plant communities.

Key words: alpine ecology, cushion plants, facilitation, microclimate, positive spatial associations, seedling survival, semiarid mountains.

Introduction

Positive interactions are defined as nontrophic interactions between species that increase the average individual fitness of at least one of the species involved (Callaway, 1995; Bruno *et al.*, 2003). Studies that have examined the relative importance of positive and negative interactions in plant communities along environmental gradients suggest that the relative importance of facilitation increases with environmental harshness (Bertness & Callaway, 1994; Callaway & Walker, 1997; Brooker & Callaghan, 1998; Bruno *et al.*, 2003). The rationale behind this is that given that harsh environments may restrict plants from acquiring resources, any amelioration of these

conditions by the presence of a neighbour will favour growth to the extent that it outweighs the negative, competitive impact of growing in close associations (Brooker & Callaghan, 1998; Bruno *et al.*, 2003).

Alpine habitats have been particularly useful for evaluating the relative importance of positive and negative interactions along environmental stress gradients because they present easily quantifiable changes in various stressors and disturbances (Choler *et al.*, 2001; Callaway *et al.*, 2002). For example, elevation gradients combine decreasing temperature, growing season length, and substrate stability, and increasing radiation and wind (Körner, 2003). At a global-scale, Callaway *et al.* (2002) reported results of neighbour removal experiments

carried out in 11 different mountain ranges around the world, and concluded that at lower elevations, where conditions tend to be less stressful, negative interactions (competition) generally dominated interspecific interactions. By contrast, at higher elevations, where abiotic stress is high, interactions among plants were predominantly positive (see also Choler *et al.*, 2001). Further, other studies based on spatial associations of species have also found evidence that positive interactions increase with elevation (Kikvidze, 1993, 1996; Kikvidze & Nakhutsrishvili, 1998; Cavieres *et al.*, 2002; Arroyo *et al.*, 2003). All these studies suggested that the main mechanism behind the facilitative process in the alpine is the thermal amelioration and protection from strong desiccant winds provided by the neighbours, which are crucial for survival in these cold environments.

In most alpine habitats plants probably do not experience shortages in water availability (Körner, 2003). However, studies conducted in arid mountains, particularly at low elevations, suggest that water deficits can have important effects (Mooney *et al.*, 1965; Rada *et al.*, 1999; Rundel *et al.*, 2003). For example, in the alpine of Sierra Nevada, CA, USA, Mooney *et al.* (1965) reported that while soil moisture increases with elevation, transpiration rates in *Polygonum bistortoides* decreased, suggesting that at low elevations transpiration can exceed water absorption from the soil, limiting the survival of this species. Other studies performed in alpine sites, where periods of drought are frequent during the growing season, also showed that water availability limits plant growth and ecosystem productivity (Billings & Bliss, 1959; Scott & Billings, 1964; Klikoff, 1965; Walker *et al.*, 1994; Fisk *et al.*, 1998).

It is well known that in mountains located in temperate zones, total precipitation increases with elevation (Chabot & Billings, 1972; Barry, 1973; Flohn, 1974; Körner, 2003). This, together with the lower evaporative demands produced by the low air temperature at higher elevations (Körner, 2003), results in an altitudinal decrease in conditions leading to water stress. Hence, altitudinal gradients in arid zones may be exceptionally complex, with water stress moving in the opposite direction to temperature stress. Thus, moisture stress would be expected to increase with decreasing altitude, suggesting that positive interactions would not necessarily increase with elevation in mountains located in arid zones.

Cushion plants are one of the growth-forms best adapted to the alpine habitat, and are typical of temperate and subpolar regions (Körner, 1995). Because of their low stature and compact form, cushion plants are particularly efficient heat-traps, decoupling their temperature from the surrounding air and generating thermal differences between leaves and the air as high as 20°C (Körner, 2003). Several studies have reported disproportionately greater abundance of other plant species inside cushions than outside (Cavieres *et al.*, 2002) and most studies suggest that cushions are good nurse plants because they provide thermal refuges (Arroyo *et al.*, 2003). However, cushion plants also enhance moisture and availability of water

(Griggs, 1956; Pysek & Lyska, 1991; Körner, 2003), suggesting an alternative, but not mutually exclusive, facilitative mechanism. For example, Körner & De Moraes (1979) showed that moisture loss per unit of cushion surface area is small, even during bright midsummer days because of the intrinsically low leaf area index of this growth form. Cavieres *et al.* (1998) reported greater gravimetric water content of the soil beneath cushions than that of the bare ground, with these differences being higher at lower elevations. This has been explained by greater evaporation rates in bare ground compared with that below cushions (Cavieres *et al.*, 1998).

While thermal stress increases with elevation in many alpine environments, there are others where low moisture availability is a more important factor than low temperature. Thus, if cushion plants improve water availability in arid alpine systems, generating microhabitats that facilitate the recruitment of other species, more species may be expected to be positively associated with cushions at lower elevations than at higher elevations. Further, greater survival of seedlings may be expected within cushions than outside them, particularly at lower elevations where differences in water availability between microhabitats could be more important than the differences in temperature of higher elevations. In this study we tested these hypotheses by comparing the number of species establishing positive associations with cushions of *Laretia acaulis* and monitoring the survival of seedlings planted within and outside cushions at two contrasting elevations in the Andes of central Chile. In addition, we monitored some abiotic conditions (substrate temperature, soil humidity and nutrient content of soil) found within and outside cushions.

Materials and Methods

Study site and target species

Our study site was located in the central Chilean Andes (33° S), in the surroundings of the Valle Nevado ski complex (33°20' S 70°16' W) located *c.* 50 km east to the city of Santiago.

Central Chile possesses a Mediterranean-type climate (di Castri & Hajek, 1976), which is characterized by cool rainy winters and long dry summers spanning *c.* 6–7 months. According to Santibáñez & Uribe, (1990) mean total annual precipitation at 2500 m elevation is *c.* 445 mm (Fig. 1), falling predominantly as snow between May and September, with snow always occurring between June and August. By contrast, at 3200 m mean annual precipitation has been estimated to be 943 mm (Fig. 1) with snow present from May to late October, and occasionally as early as April and as late as December (Santibáñez & Uribe, 1990). Although rainfall events may occur during summer months, these are more frequent at higher elevations (Fig. 1). Mean monthly air temperature during the growing season ranges from 7°C in April to 12°C in February at 2600 m, while at 3150 m it ranges from 3°C in April to 7.6°C in February (Cavieres & Arroyo, 1999).

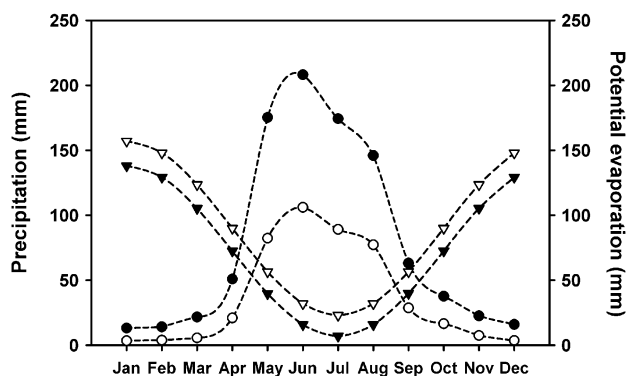


Fig. 1 Monthly precipitation (circles) and potential evaporation (triangles) at 2500 m (open symbols) and 3200 m (closed symbols) in the Andes of central Chile. Data taken from Santibáñez & Uribe (1990).

Above the *Kageneckia angustifolia* (Rosaceae) treeline located at 2200 m above sea level, we selected two slopes of different exposure and with presence of cushion plants along a continuous elevational gradient. One of these slopes was north-west facing, while the other was west facing. At each slope we selected two sites differing in elevation, with each dominated by the cushion plant *Laretia acaulis*. Elevations were 2800 m and 3200 m, which corresponded to the lower and upper altitudinal limit of the cushion vegetation belt, respectively (Cavieres *et al.*, 2000). At each site, a sampling area of *c.* 5000 m² was defined. Cover of cushion plants was *c.* 22% and 30% at the low and high elevation sites, respectively (E. I. Badano *et al.* unpublished). Apart from *L. acaulis*, which is the only tightly knit cushion species present, vegetation at the lower elevation sites was comprised of prostrate shrubs (e.g. *Chuquiraga oppositifolia*, *Berberis empetrifolia*) and perennial herbs such as *Nassauvia aculeata*, *Euphorbia collina*, *Quinchamalium chilense* and *Tristagma* spp. The upper site was characterized by rosette forming perennial herbs such as *Nastanthus agglomeratus*, *Pozoa coriacea*, *Barneoudia major* and *Viola philippii* (Cavieres *et al.*, 2000).

The target species, *L. acaulis* (Apiaceae), is a very flat and tightly knit dioecious cushion species, occurring widely throughout the alpine zone of central Chile. Vegetative growth commences as soon as the ground thaws, and flowering occurs in mid January, with its leaves dying at the end of the growing season (Alliende & Hoffmann, 1985). According to Armesto *et al.* (1980), the size of individual cushions of *L. acaulis* at our study area ranges from 10 to > 100 cm diameter, with mean size increasing with elevation. This increase is due to large-size cushions (> 1 m diameter) being more frequent at the high altitude, as the frequency of cushions < 1 m diameter does not significantly change with elevation (Armesto *et al.*, 1980). Spatial pattern analyses using Ripley's K function performed for the north-west facing slope indicated that cushions of *L. acaulis* are randomly distributed at both elevations (E. I. Badano *et al.*, unpublished).

Microclimatic measurements

To characterize the microclimatic changes induced by the presence of *Laretia acaulis* cushions, substrate temperature, and soil moisture and nutrient content within and outside cushions were measured at the two elevations. At each elevation, precipitation and incoming radiation were assumed to be the same on north-west- and west-facing slopes (cf. Rozzi *et al.*, 1989), and thus microclimatic conditions were characterized only on the north-west-facing slope.

Temperature At each elevation, four cushions were randomly selected. Using a random number table, we selected four pairs of two consecutive numbers between 0 and 1. For each pair, the first number was multiplied by 100 and indicated a distance in meters to walk from the centre of our sampling site. The second number was converted to hexadecimal degrees, and indicated the direction in degrees from magnetic north to walk, where the first *c.* 50 cm diameter cushion found was selected. For each selected cushion a point on the bare ground was also selected, spaced at least 1 m away in a random direction. At each selected cushion one temperature sensor connected to a mini-logger (HOBO-H8; Onset Corp., Bourne, MA, USA) was placed at the centre of the cushion, within its tight 'canopy', at 2 cm depth from the canopy surface. Sensors on the bare ground were also placed at 2 cm depth from soil surface. The mini-loggers were programmed to record temperature once every hour for the duration of the growing season, starting on November 28, 2003 and finishing on March 30, 2004. For each pair of sensors located within and outside cushions we calculated the difference in temperature at each hour during the entire growing season. An ANCOVA with the difference in temperature as the dependent variable, elevation as the factor and ground temperature outside cushions as the covariable was performed to assess the magnitude of the decoupling in temperature between cushions and the bare ground at both elevations.

Soil moisture The matric potential of the soil was used to compare the soil moisture beneath and outside cushions. Soil moisture was measured at two different times during the growing season: early summer (December–January) and the end of summer (March), and during two consecutive growing seasons: 2003 and 2004. In the growing season of 2003, measurements for early summer were taken on January 16 and 17 at the low and high site, respectively; measurements at the end of the austral summer were taken on March 6 and 7, 2003, at the low and high site, respectively. For the 2004 growing season, snow-pack melted earlier than the previous year hence measurements were taken on December 20 and 19, and March 17 and 16, at the low and high sites, respectively. On each date, five cushions of similar size (*c.* 50 cm diameter) and five points on the bare ground were randomly selected at each elevation. At each cushion and bare ground

point a soil-tensiometer (2725 Series Jet Fill Tensiometer; Soilmoisture Equipment Corp., Santa Barbara, CA, USA) was dug into the soil at a depth of 10 cm. Tensiometers were placed at 00 : 10 h, and after a stabilization period of 4 h, the matric potential of the soil was recorded. For each year data were analysed with factorial ANOVAS, where altitude, periods (early and late summer), and position (within and outside cushions) were the independent factors.

Nutrient content of the soil In the 2004 growing season, at each elevation, *c.* 100 g soil samples were collected from beneath five randomly selected cushions and five randomly selected points on the bare ground. Samples were placed in sealed plastic bags, and sent to the Laboratory for Soil Analyses, Agronomy Faculty, University of Concepción, where availability of nitrogen (NO_3^- and NH_4^+), phosphorous and potassium was estimated. Data were compared with a factorial two-way ANOVA with elevation and position as factors.

Vegetation sampling and data analyses

Vegetation sampling was done on both north-west- and west-facing slopes. At each elevation, 50 50–60-cm diameter cushions were selected. Selection was done 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 magnetic north) in which the first cushion that met our size criteria was selected. We selected this cushion size because it is the most abundant size class along the entire altitudinal gradient (Armesto *et al.*, 1980), thus allowing comparisons without introducing confounding factors such as cushion size and cushion size distribution at different elevations.

For each sampled cushion, a 50-cm diameter metallic hoop was centred over the surface of the cushion, and all plant species found inside the hoop were identified and recorded. At the same time, 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 hoops outside cushions was determined with a procedure similar to that used in the selection of cushions, although the selected point outside had to be at least 50 cm away from the nearest cushion. Vegetation sampling was done during February 2004, in the middle of the growing season, and when the majority of the species were in flower, thus facilitating the identification of specimens to species level.

In order to statistically detect positive associations of individual species for a particular microhabitat (i.e. cushion or bare ground) we performed randomization tests (Slade & Hall, 1999; Kikvidze *et al.*, 2001) with the software RESAMPLING STATS (Resampling Stats, Inc., Arlington, VA, USA, 1990–95). First, from the total frequency of incidence of a particular species, we randomly redistributed the total number of presence recordings between the within and outside cushion habitats.

For each species we performed 1000 runs of random redistributions and calculated the probability of the observed frequency within cushions being generated by chance (see also Cavieres *et al.*, 2002).

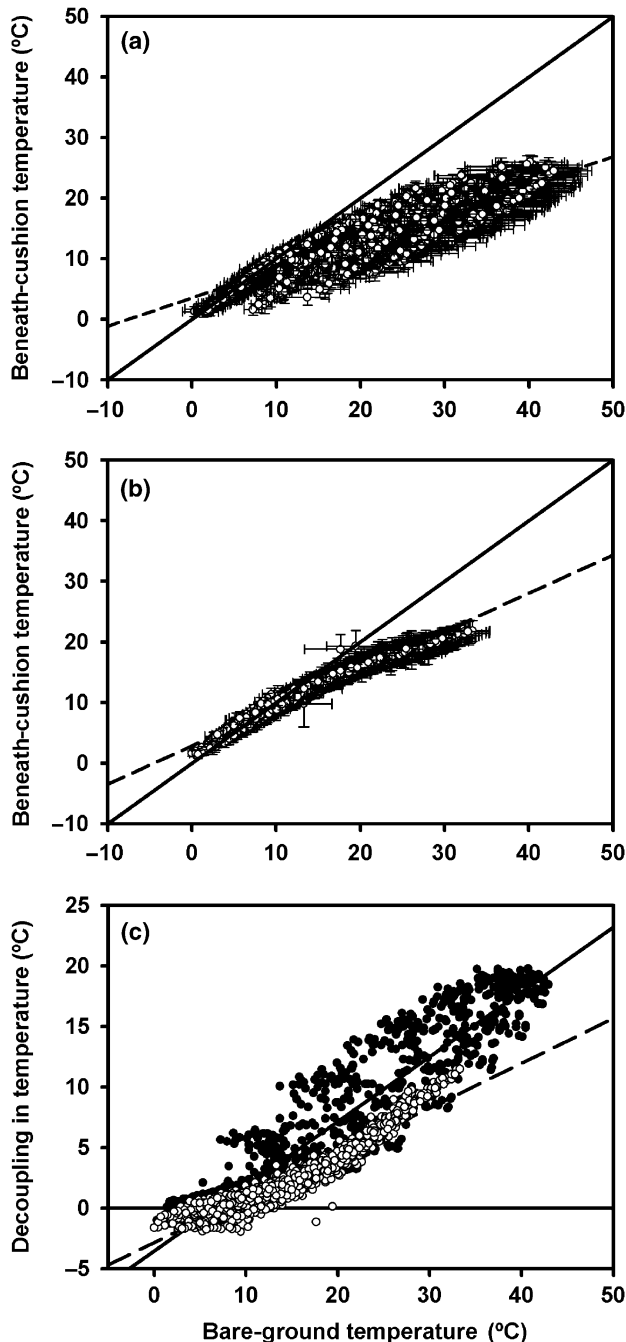


Fig. 2 Temperatures registered during the entire growing season within cushions of *Laretia acaulis* and bare ground points in the Andes of central Chile. (a,b) Temperatures recorded at 2800 m (open circles) and 3200 m (closed circles), respectively. Error bars indicate 2 SE. (c) Thermal difference between cushions and the bare ground at each elevation during the entire growing season.

Seedling survival

Seedling survival experiments were performed at the two elevations of the north-west-facing slope. Seeds of the species *Cerastium arvense* and *Hordeum comosum*, collected during March 2003, were germinated in growth chambers at controlled temperature conditions (20°/10°C day/night) during October 2003. These species were selected because they produce large number of viable seeds, thus facilitating the generation of seedlings, and because they exhibited altitudinal changes in the spatial association with cushions (see Results). Emerged seedlings were planted in small plastic bags, and were maintained in a growth-chamber at 10°/5°C (day/night) for 1 month. The 1-month-old seedlings of both species were taken to the field where they were extracted from the plastic bags. At each elevation, and for each species, one group of 10 individuals each was planted inside of each of six previously random-selected cushions and in each of six randomly selected points on the bare ground. Seedlings were planted on November 28, 2003, at both elevations, and seedling survival was monitored every 2 wk from December 2003 to March 2004. Survival curves of seedlings for each species at each elevation and position were estimated by means of the Kaplan–Meier method and statistical differences were assessed with the Cox–Mantel test (Fox, 1993).

Results

Microclimate

Temperature Overall, at 2800 m, there was a wider variation in temperature on the bare ground than within cushions (Fig. 2a). While surface soil temperature on the bare ground reached 45°C, temperatures within cushions never exceeded 25°C. By contrast, at 3200 m these differences were smaller (Fig. 2b);

while bare ground temperature ranged from 0° to 30°C, temperature within cushions fluctuated from 0° to 22°C. Temperature decoupling between cushions and bare ground was greater at low elevation (ANCOVA $F_{1,3430} = 5.7$; $P < 0.05$), and the degree of decoupling increased more with ground temperatures at 2800 m than at 3200 m ($F_{2,3430} = 8841.3$; $P < 0.001$; Fig. 2c).

Soil moisture In both years, date (early or late summer), position (within or outside cushions) and all the interaction factors significantly effected soil moisture (Table 1). Elevation only had significant effects on the measurements of 2003 (Table 1). In early summer, at both elevations, soil moisture beneath cushions and the bare ground did not differ (Fig. 3). This pattern was consistent during the two growing seasons analysed. By contrast, in the more xeric late summer, soil moisture was much higher inside cushions than in the open ground surrounding them (Fig. 3). The magnitude of this difference between the soil beneath cushions and bare ground during late summer was markedly greater at 2800 than at 3200 m, in both years (Fig. 3).

Nutrient content of soils Although soil NO₃ and NH₄ content at both elevations tended to be higher in the soil beneath cushions, these differences were significant only at the lower site (Table 2). A similar pattern was observed with respect to phosphorous content (Table 2). By contrast, cushions only increased soil K content at the 3200 m site (Table 2). There were no significant effects of the interaction between position and elevation in any of nutrients evaluated.

Species association patterns

At 2800 m a total of 26 and 19 plant species were registered either within or outside *Laretia acaulis* cushions at the

Table 1 Results of factorial ANOVAS performed to assess the effects of elevation (2800 m and 3200 m) and date (early or late summer) on the soil moisture beneath *Laretia acaulis* cushions and beneath the bare ground in the Andes of central Chile

Source of variation	SS	df	MS	F	P
2003					
Elevation	67.6	1	67.6	13.3	0.0009
Date	756.9	1	756.9	148.8	< 0.0001
Position	883.6	1	883.6	173.7	< 0.0001
Elevation × date	324.9	1	324.9	63.9	< 0.0001
Elevation × position	129.6	1	129.6	25.5	< 0.0001
Date × position	324.9	1	324.9	63.9	< 0.0001
Elevation × date × position	152.1	1	152.1	29.9	< 0.0001
Error	162.8	32	5.1		
2004					
Elevation	18.2	1	18.2	1.4	0.2395
Date	1600.2	1	1600.2	126.1	< 0.0001
Position	1729.2	1	1729.2	136.3	< 0.0001
Elevation × date	93.0	1	93.0	7.3	0.0108
Elevation × position	55.2	1	55.2	4.4	0.0450
Date × position	697.2	1	697.2	54.9	< 0.0001
Elevation × date × position	140.6	1	140.6	11.1	0.0022
Error	406.0	32	12.7		

SS, sum of squares; MS, mean square.

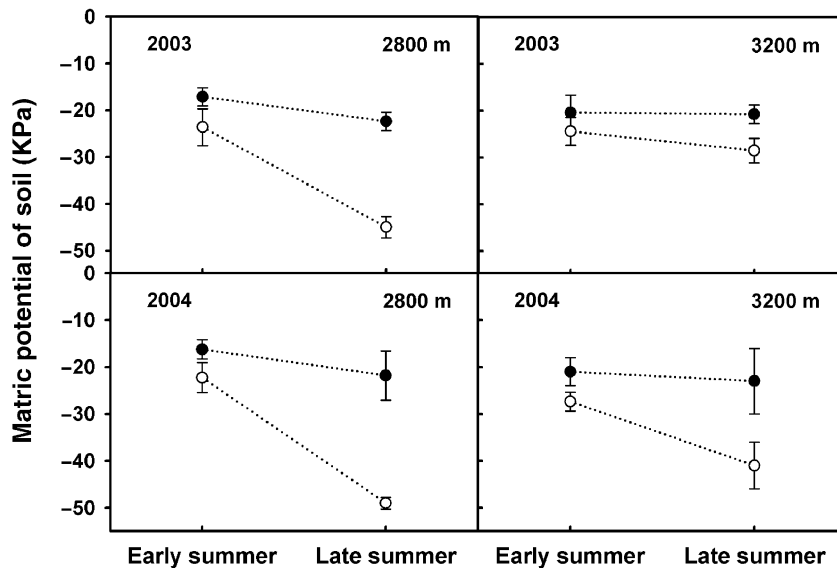


Fig. 3 Soil moisture assessed by the matric potential of soils beneath and outside *Laretia acaulis* cushions in early and late summer during two consecutive growing seasons (2003 and 2004) at 2800 m and 3200 m elevation in the Andes of central Chile. Closed circles, beneath *L. acaulis*; open circles, outside *L. acaulis*; error bars indicate 2 SE.

Nutrients (mg kg ⁻¹)	Elevation			
	2800 m		3200 m	
	Beneath	Outside	Beneath	Outside
NO ₃	7.8 (4.1) ^a	1.7 (0.8) ^b	3.7 (3.6) ^{ab}	0.8 (0.2) ^b
NH ₄	1.2 (0.6) ^a	0.2 (0.04) ^b	0.9 (0.8) ^{ab}	0.2 (0.1) ^b
P	69.9 (38.5) ^a	52.6 (19.2) ^{ab}	35.2 (6.8) ^{ab}	26.9 (15.9) ^b
K	1180.7 (417.3) ^a	612.6 (161.6) ^{ac}	1024.2 (464.2) ^a	195.7 (78.1) ^{bc}

Numbers in parentheses are 2 SE. Different superscript letters indicate significant differences (Two-way ANOVA; $P < 0.05$).

north-west- and west-facing slope, respectively (Table 3). For 3200 m these numbers were 19 and 23 for north-west- and west-facing slope, respectively.

At 2800 m, on the north-west-facing slope, nine species (35% of the total found at this site) were found to be positively associated with cushions, whereas only one (5%) was found more frequently outside (Table 3). On the west-facing slope, eight species (42%) were found to be significantly associated with cushions, whereas two (9%) were found significantly more frequent outside (Table 3). By contrast, at 3200 m on the north-west-facing slope, only two species (10% of the total found at this elevation) were found to be associated with cushions, whereas five (24%) grew more frequently outside (Table 3). While only two species (9%) were found significantly associated with cushions on the west-facing slope at 3200 m, four species (17%) grew more frequently outside (Table 3). Therefore, on both slope aspects, we found more species associated with *L. acaulis* cushions at the lower elevation than at the higher elevation.

Five species changed the nature of their spatial association with *L. acaulis* with decreasing elevation. On both slopes, *C. arvense*, *H. comosum*, *Poa* sp., *Senecio polygaloides* and *Thlaspi magellanicum* changed from having no preference for

cushions at 3200 m, to being significantly more frequent within cushions at the lower elevation (Table 3). *Taraxacum officinale* also changed the nature of its interactions with cushions from neutral at higher elevations to significantly positive at lower elevations, but only on the north-west-facing slope. On the west-facing slope, the pattern shown by this species was similar. However, and although all individuals of *T. officinale* at the lower sites were found within cushions, its low frequency made the presence of significant association with cushions undetectable. In addition, *Nassauvia aculeate*, which established negative relationships with cushions on the north-west-facing slope at 3200 m, changed to neutral associations at the lower elevation (Table 3).

Seedling survival

At 2800 m, survival of planted seedlings of *C. arvense* and *H. comosum* was significantly higher within cushions than on the bare ground (Table 4; Fig. 4). At 3200 m, there were no differences between positions in survival of *C. arvense* (Table 4; Fig. 4). At this elevation, survival of *H. comosum* was significantly higher within cushions than in open spaces (Table 4), which was probably related to a higher survival of this species

Table 3 Frequencies of species within and outside *Laretia acaulis* cushions at two elevations in two slopes of the Andes of central Chile (33° S)

Species	Life-form	North-west				West			
		2800		3200		2800		3200	
		Within	Outside	Within	Outside	Within	Outside	Within	Outside
<i>Adesmia exillis</i>	HP	4	2				1		
<i>Berberis empetrifolia</i>	SHR	1	3			2	2		
<i>Barneoudia major</i>	HP-R				8	-			
<i>Bromus</i> sp.	HP-G	11	3	+			7	+	12
<i>Carex</i> sp.	HP				4				
<i>Cerastium arvense*</i>	HP	24	4	+	7	6	5	+	4
<i>Chaetanthera apiculata</i>	ANN								5
<i>Chaetanthera euphrasioides</i>	ANN		31	-		26	-		3
<i>Chaetanthera pusilla</i>	ANN		7	-		12	-		8
<i>Chaetanthera planiseta</i>	ANN						1		
<i>Chuquiraga oppositifolia</i>	SHR	3	8				7	7	
<i>Erigeron andicola</i>	HP				3	1			2
<i>Euphorbia collina</i>	HP	8	8				5	4	
<i>Galium araucanum</i>	HP	5		+					
<i>Haplopappus anthylloides</i>	SHR						2		
<i>Haplopappus scrobiculatus</i>	SHR	4	1						
<i>Hordeum comosum</i>	HP-G	11	3	+	3	5	9	1	+
<i>Hypochaeris tenuifolia</i>	HP								1
<i>Loasa</i> sp.	HP								1
<i>Microsteris gracilis</i>	ANN	2	4						
<i>Montiopsis andicola</i>	HP				10	3	+		2
<i>Montiopsis potentilloides</i>	HP					1			
<i>Nassauvia aculeata</i>	HP						13	10	
<i>Nassauvia lagascae</i>	HP					1			
<i>Nassauvia pyramidalis</i>	SHR	16	17			9	-		4
<i>Nassauvia uniflora</i>	SHR						1	9	-
<i>Nastanthus agglomeratus</i>	HP				2	3			4
<i>Oxalis squamata</i>	HP	2	7						1
<i>Perezia carthamoides</i>	HP	4	7				1	1	
<i>Perezia pilifera</i>	HP						12	4	+
<i>Phacelia secunda</i>	HP							9	-
<i>Poa</i> sp.	HP-G	25	8	+	28	21	26	7	+
<i>Polygala salasiana</i>	HP	2				1			
<i>Pozoa coriacea</i>	HP					2			5
<i>Quinchamalium chilense</i>	ANN	8	10			2			
<i>Rodophiala andicola</i>	HP-B	5	3						
<i>Rytidosperma pictu</i>	HP-G	6		+					1
<i>Senecio polygaloides</i>	HP	19	9	+	5	4	17	3	+
<i>Senecio pentaphyllus</i>	HP	2			1				
<i>Olsynium scirpoideum</i>	HP	2	1						
<i>Taraxacum officinale*</i>	HP	8	1	+	8	6	4		3
<i>Thlaspi magellanicum</i>	HP	7		+	5	3	5		+
<i>Trisetum preslei</i>	HP-G						5		+
<i>Tristagma nivale</i>	HP-B	5	6						
<i>Tropaeolum polyphyllum</i>	HP								6
<i>Viola philippi</i>	ANN				1	12	-		3

ANN, Annual species; PH, perennial herb; PH-B, bulbous perennial herb; PH-R, rhizomatous perennial herb; PH-G, perennial grass; SHR, shrub; SUFF, suffruticose. Asterisks indicate alien species. *P*-values are from randomization test (see text). +, Significant positive association with cushions ($\alpha = 0.05$); -, significant negative association.

within cushions during the first 135 d; after that, survival within cushions did not differ from outside (Fig. 4). Interestingly, survival of both species within cushions was significantly higher at 2800 m than at 3200 m (Table 4).

Discussion

Previous studies in alpine habitats have provided evidence for positive associations of plants with cushion species (Griggs,

Table 4 Results of the Cox–Mantel test for comparisons of the survival of seedlings planted within and outside *Laretia acaulis* cushions at two elevations in the Andes of central Chile

Planted species	2800 m		3200 m	
	Within	Outside	Within	Outside
<i>Cerastium arvense</i>				
2800 m	Within	–		
	Outside	7.1 ($P < 0.01$)		–
3200 m	Within	4.3 ($P < 0.01$)		–8.2 ($P < 0.01$)
	Outside	–2.8 ($P < 0.01$)		–7.7 ($P < 0.01$)
<i>Hordeum comosum</i>				
2800 m	Within	–		
	Outside	13.4 ($P < 0.01$)		–
3200 m	Within	–2.2 ($P < 0.05$)		–11.5 ($P < 0.01$)
	Outside	8.7 ($P < 0.01$)		–1.6 ns
			–8.9 ($P < 0.01$)	–

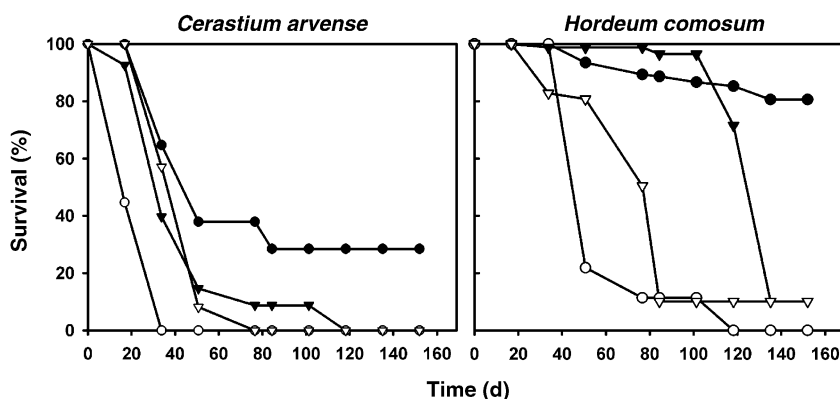


Fig. 4 Kaplan-Meier estimated survival of seedlings of *Cerastium arvense* and *Hordeum comosum* planted within (closed symbols) and outside (open symbols) *Laretia acaulis* cushions at 2800 m (circles) and 3200 m (triangles) elevation in the Andes of central Chile.

1956; Alliende & Hoffmann, 1985; Pysek & Lyska, 1991; Nuñez *et al.*, 1999; Molina-Montenegro *et al.*, 2000; Badano *et al.*, 2002; Cavieres *et al.*, 2002; Arroyo *et al.*, 2003), with one of the most consistent findings being that positive associations increase with elevation (Cavieres *et al.*, 2002; Arroyo *et al.*, 2003).

By contrast, our results demonstrated stronger facilitation by cushion plants at lower elevations. First, considering both slope aspects, *c.* 40% of the whole community was significantly associated with cushions at lower elevations, whereas at higher elevations only *c.* 7% of the species grew more frequently within them. Second, while at higher elevations no species were restricted to cushions, at the lower sites four species were restricted to them, and another seven species changed the nature of their association with *L. acaulis* in comparison with 3200 m, either from negative to neutral or from neutral to positive. Third, in experimentally planted seedlings of species that changed their spatial association with cushions with elevation, a greater survival during the growing season was observed within cushions than on the bare ground, with these differences in survival being greater at the lower elevation. In their study, Callaway *et al.* (2002) showed that in the Sierra Nevada of Spain, the only site (out of 11) located in an arid

zone, facilitation occurred at both high and low elevations, while in the remaining sites facilitation was only observed at high elevations. This pattern supports our finding that shifts in positive and negative interactions with elevation are different in arid mountains.

Microsites with appropriate temperature and soil moisture conditions are crucial for survival of plants in the harsh alpine climate (Forbis, 2003; Körner, 2003). Unlike previous studies in alpine habitats where neighbours provide warmer habitats compared with the surrounding environment, *L. acaulis* cushions maintained lower temperatures than the open spaces at both elevations. Temperatures registered on the bare ground at both elevations are higher than those reported for other alpine sites. For example, Arroyo *et al.* (2003) reported bare ground temperature at midday of *c.* 6°C in sunny days at the upper limit of cushion plants in the Patagonian Andes of Chile (50°S). In our study, surface bare ground temperatures at midday at the upper site were *c.* 25°C on sunny days, suggesting that mitigation of low temperatures could not be invoked as an important mechanism in the facilitation of *L. acaulis* cushions, particularly at the higher elevations. Conversely, our results showed that cushion temperatures were milder than that of the bare ground, particularly at the lower

elevation. For example, while cushions maintained temperatures of *c.* 25°C at 2800 m elevation, soil temperatures reached *c.* 45°C, which could be lethal for some alpine plants (Körner, 2003). This mitigation of high temperatures could not only be very important in terms of direct effects on survival, but also in terms of the evaporative demand of the soil and in their consequences for the hydraulic economy of the facilitated plant.

While at the high elevation differences in soil moisture between the cushions and the bare ground were not marked, at lower elevations cushions maintained higher soil moisture than the bare ground. Hence, the higher survival of seedlings and the increased association of plant species with cushions of *L. acaulis* at lower elevations in the Mediterranean zone Andes of central Chile is likely to result from several factors acting in concert, although the provision of moisture seems to be the most important.

High temperatures and scarce rainfall during the summer characterize the Mediterranean zone of central Chile (di Castri & Hajek, 1976). The combination of high temperature and the extended summer drought of 5–6 months could produce substantial water stress in alpine plants at lower elevations, as occurs in plants in the montane and lowland matorral of central Chile (Mooney & Dunn, 1970). Water limitations in the performance of alpine plant species have been demonstrated by Ehleringer & Miller (1975), who showed that water stress can be high in the alpine tundra of Colorado, with water stress limiting the distribution of some species (e.g. *Caltha leptosepala* and *Deschampsia caespitosa*). Enquist & Ebersole (1994) also support the importance of water shortage periods in alpine areas by reporting that photosynthetic rates in *Bistorta vivipara* were limited by lack of water during growing seasons with average or below-average precipitation in Pikes Peak, Colorado. Rada *et al.* (1999) for example, showed that in the alpine of north-central Chile, individuals of *Adesmia subterranea* growing at 3750 m maintained lower leaf water potentials and lower stomatal conductances compared with individuals growing at 4200 m, indicating that water stress is higher at lower elevations. Chabot and Billings (1972) and Mooney *et al.* (1965), have reported that in the Sierra Nevada of California, USA, while soil moisture increases with elevation, evaporative demand decreases, suggesting that environmental conditions leading to water stress are higher at lower elevations. Hence, the fact that cushions maintained higher soil moisture than bare ground, suggests that species growing within cushions could mitigate water shortage conditions that develop at the end of the growing season, particularly at lower elevations. We have found that some species growing within cushions attained higher photosynthetic rates and higher stomatal conductance than their conspecifics growing in open areas away from cushions only at the end of growing season (Cavieres *et al.*, 2005).

In addition to enhancing the physiological function for already established individuals, the availability of water in the

soil below cushions may have important implications for seed germination and seedling survival. Chambers *et al.* (1990), for example, showed that in the alpine zone of the Rocky Mountains, microsites with good availability of water showed higher seedling recruitment in many species compared with microsites less favourable in terms of water (see also Bell & Bliss, 1980; Gold & Bliss, 1995). Similar results have been recently reported by Forbis (2003), who showed that seedling survival in several alpine species at Niwot Ridge, CO, USA, was higher in meadows with good availability of water. Therefore, the fact that cushions at the lower elevations can maintain higher soil moisture during the summer could benefit both the recruitment and survival of some species. This suggests that, for those species sensitive to water shortage, cushions could represent a 'hydric refuge'.

In addition, in a high arctic-alpine zone, Gold & Bliss (1995) showed that the humidity of the soil below cushion plants remains relatively constant among years, even when there were strong interannual variations in the amount of precipitation. This last result is highly relevant for areas with high interannual fluctuations in rainfalls, as occur in central Chile as a result of the El Niño (ENSO) events, suggesting that cushions are important not only because water availability is greater beneath them but also because they provide environments that fluctuate less. This has important consequences for understanding the response of alpine plant communities to global climate changes scenarios. Lower elevation alpine plant communities located in arid mountains, may be more sensitive to changes in the precipitation regime than changes in temperature (Körner, 2003). Hence, increases in precipitation, either during the growing season or during winter (affecting snow accumulation), could have important consequences on the intensity of the cushions nurse effect and ultimately on the structure of plant communities (cf. Welker *et al.*, 2001).

Despite our focus on the generality of the cushion effect, we observed a wide variety of different responses among species. For example, at 2800 m, considering both aspects, 11 species showed preference for cushions whereas four did not, suggesting that the nurse effect of alpine cushions is a species-specific phenomenon (cf. Callaway, 1998). This implies that only some species will be sensitive to the microclimatic changes generated by cushions (e.g. water availability); other species will be more sensitive to other factors (e.g. nutrients availability, low temperatures, etc.) supporting the individualistic response of species to different limiting resources (Chapin & Shaver, 1985). Further, at each elevation more than two species were found either significantly more frequently outside cushions or found only on the open ground, suggesting that *L. acaulis* cushion established negative associations with these species as well (e.g. *Chaetanthera euphrasoides*, *Chaetanthera pusilla*, *Phacelia secunda* and *Nassauvia uniflora*). Thus, despite the fact that cushions establish positive interactions with some species, for others interactions are

negative. Hence, if environmental stress regulates the balance between competition and facilitation, amelioration of this stress may alter this balance and drive more rapid changes in composition and diversity than predicted by models based on climate envelopes (Callaway *et al.*, 2002).

An alternative hypothesis for our findings is that the facilitative effects of cushions at lower elevations result from the presence of cushions at local environmental conditions that also facilitate the establishment of the other species. However, although this alternative hypothesis can not be completely ruled out, the fact that cushions are spatially randomly distributed at both elevations suggests that this alternative is less likely.

In conclusion, our results demonstrate that positive interactions are frequent and important in the arid alpine habitat of the Chilean Andes. However, unlike previous studies, we have found that facilitation is stronger at lower elevations, which could be related to higher aridity. Thus, the altitudinal stress gradients in the alpine are not always lower at the bottom and higher at the top. While the common denominator of the alpine habitat is low temperature, alpine communities vary enormously with respect to precipitation and wind conditions, as reflected in the wide physiognomic and cover variations. Thus, only as studies encompassing such variation become available, will it be possible to evaluate the global importance of positive and negative interactions in alpine habitats and how they change with elevation. Understanding of these patterns is critical to produce more realistic models of plant responses to global climate changes.

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