Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: are there differences between nurses?

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Summary

1. Positive interactions between species are known to play an important role in the dynamics of native plant communities, particularly in stressful habitats. However, their role in plant invasions is less known, although recent studies have started to highlight the importance of positive interactions as a driver of invasion. It has been suggested that facilitative interactions during invasions are not expected to be species-specific.

2. The perennial herb *Taraxacum officinale* (dandelion) is a conspicuous alien plant species invading the central Chilean Andes. In contrast to other alien species that are restricted to human-disturbed sites at high elevations, *T. officinale* is frequently observed growing within native plant communities dominated by cushion plants. We selected sites where two cushion species coexist (*Laretia acaulis* and *Azorella monantha*), and evaluated whether *T. officinale* is equally associated with the two cushion species or shows a preference for one of them. We assessed facilitative effects of the two cushion species on *T. officinale* via seedling survival experiments, measurements of photochemical efficiency of photosystem II (Fv/Fm and ΦPSII), reproductive output and recording the differences in soil temperature, humidity and nutrient contents between these cushion species and open areas.

3. *Taraxacum officinale* was significantly and positively associated with only one of the two cushion species (*A. monantha*). Seedling survival was higher in *A. monantha* than on *L. acaulis* or the bare ground. Photochemical efficiency and reproductive output were higher within the two cushion species than outside them. However, performance of *T. officinale* was significantly better within the cushions of *A. monantha* than those of *L. acaulis*. Soil temperature, humidity and contents of nitrogen and phosphorous were similar within the two cushion species; however, potassium was two times higher in the soil beneath *L. acaulis* than beneath *A. monantha*.

4. Results indicate that the native cushion species facilitates the establishment and performance of a non-native invasive species, and that this interaction is highly species-specific due to differences in soil nutrient content beneath different benefactor species. Our results indicate that native plants can have facilitative effects on invasive plants, particularly in stressful habitats such as alpine environments.

Key-words: positive interactions, invasions, species-specific, Alpine, cushion plants

Introduction

The presence and spread of non-native organisms into new areas where they have been deliberately or accidentally introduced by humans is occurring worldwide, with an increasing number of studies reporting the ecological and economic impacts of the presence of alien species (see Mooney & Hobbs 2000; Mooney 2005). Much research has been done with the purpose of unravelling the mechanisms responsible for successful invasion, with many of the suggested mechanisms relating to negative interactions among native and exotic species, such as competition (Vilà & Weiner 2004) and allelopathy (Hierro & Callaway 2003). In recent years, however, the potentially important role of positive species interactions for invasion processes has received attention (Simberloff &

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Von Holle 1999; Richardson *et al.* 2000; Bruno *et al.* 2005; Rodriguez 2006). The most commonly reported mechanisms whereby facilitative interactions determine invasion processes are non-native animals pollinating and dispersing invasive plants, and non-native animals and plants modifying the environment in ways that favour the spread of other non-native species (Simberloff & Von Holle 1999; Richardson *et al.* 2000; Crooks 2002). For instance, introduced animals disperse seeds of invasive non-native plant species, increasing the magnitude of the invasion process and generating 'invasional meltdown' (Simberloff & Von Holle 1999; Simberloff 2006). However, despite recognition of the role of positive interactions in invasions, examples of direct positive interactions among plants (i.e. facilitation) during invasions, either between invasive species or between native and invasive species, are scarce (Maron & Connors 1996; Carino & Daehler 2002; Lenz & Facelli 2003; Reinhart, Maestre & Callaway 2006; Tecco *et al.* 2006; Badano *et al.* 2007).

Positive interactions among species are expected to be important in stressful habitats (Bertness & Callaway 1994; Brooker & Callaghan 1998), and several studies have reported that facilitative interactions are common in alpine habitats (Kikvidze 1993; Kikvidze & Nakhutsrishvili 1998; Choler, Michalet & Callaway 2001; Callaway *et al.* 2002), particularly those whose key processes involve nurse plants (Cavieres *et al.* 2002, 2006; Arroyo *et al.* 2003). Alpine habitats are well known for their severe environmental conditions, where plants must withstand low temperatures, short growing seasons, excessive radiation and unstable substrates (Billings & Mooney 1968; Körner 2003). It is widely assumed that the climatic severity of alpine habitats precludes the successful establishment of invasive species. Recently, however, several studies have started to report the presence of non-native species in a number of alpine habitats (e.g. Johnston & Pickering 2001; Dullinger, Dirnböck & Grabherr 2003; Arévalo *et al.* 2005; Beccker *et al.* 2005; McDougall *et al.* 2005). Nevertheless, the mechanisms involved in these invasions have seldom been addressed, and only disturbances have been pointed out as important drivers of plant invasions in these harsh environments (Johnston & Pickering 2001; Dullinger *et al.* 2003; Johnston & Johnston 2004). However, Bruno, Stachowicz & Bertness (2003) suggested that in stressful habitats, such as alpine areas, facilitation between species could be an important mechanism for successful invasions.

A conspicuous component of the alien alpine flora of the central Chilean Andes is the perennial herb *Taraxacum officinale* or common dandelion. In contrast to other alien species, *T. officinale* is not restricted to human-disturbed sites, but rather is frequently observed growing within undisturbed native vegetation, particularly within canopies of *A. monantha* cushion plants in communities where *A. monantha* is dominant (Cavieres *et al.* 2005). However, in some areas, cushions of *A. monantha* coexist with cushions of *Laretia acaulis*, another native nurse that facilitates the survival of several native species (Cavieres *et al.* 2006). It is well known that many of the positive interactions among plants are species-specific (Callaway 1998); hence, it is worth asking whether *T. officinale*

is facilitated by *L. acaulis* as well as *A. monantha* cushions and if the mechanisms involved are similar. Recently, Bruno *et al.* (2005) have pointed out that a very small proportion of the facilitative interactions associated with invasions are species-specific. The species-specificity of facilitation of *T. officinale* in the Andes is relevant because *L. acaulis* cushions predominant at lower elevations, where the presence of *T. officinale* has been shown to reduce pollinator visitation rates, duration of pollinator visits and seed set on several co-occurring native Asteraceae species (A. A. Muñoz & L. A. Cavieres, unpublished data). In this study, we address whether *T. officinale* is equally positively associated with different cushion species or whether it shows a preference for one nurse species. Specifically, we asked: (i) Do different cushion species facilitate the survival of *T. officinale* seedlings with similar intensity? (ii) Do *T. officinale* individuals growing within different cushion species have a similar photosynthetic performance? and (iii) What is the reproductive output of *T. officinale* individuals growing within different cushion species?

Materials and methods

STUDY SITE

Our study site was at 3200 m elevation in the central Chilean Andes (33° S), where the two target cushion species co-exist. This site is located in the vicinity of the Valle Nevado ski complex (33°20′ S 70°16′ W), *c.* 50 km east of Santiago. Although there are domestic herbivores in the study area, particularly cattle and horses, they occur at abundances unlikely to affect plant distributions at this elevation.

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. Santibáñez & Uribe (1990) estimated mean total annual precipitation at 3200 m as 943 mm, falling predominantly as snow between May and September, with snow always occurring between June and August. Mean monthly air temperature during the growing season at 3150 m ranges from 3 °C in April to 7·6 °C in February (Cavieres & Arroyo 1999).

STUDY SPECIES

At the elevation studied, native vegetation is highly patchy and dominated by cushion plant species such as *A. monantha* and *L. acaulis* (Cavieres, Peñaloza & Arroyo 2000) that co-occur with rosette-forming perennial herbs such as *Nastanthus agglomeratus*, *Pozoa coriacea*, *Barneoudia major* and *Viola philippii* that usually grow in open areas away from cushions (Cavieres *et al.* 2000, 2006).

Azorella monantha Clos (Apiaceae) is a very flat and tightly knit dioecious cushion species, distributed from 33° to 55° South, and from 3200 to 3600 m elevation in the Andes of central Chile (33° S), although its range approaches elevations close to sea level at 55° S (Hoffmann *et al.* 1998). This species does not lose its foliage during the winter, and usually blooms in February.

Laretia acaulis (Cav.) Gillies & Hook (Apiaceae) is also a very flat and tightly knit dioecious cushion species, occurring widely throughout the alpine zone of central Chile (30–35° S, and between 2400–3200 m elevation, Hoffmann *et al.* 1998). Vegetative growth commences as soon as the ground thaws, and flowering occurs in mid-January, with its leaves dying (wilted) at the end of the growing season (Hoffmann *et al.* 1998). According to Armesto, Arroyo & Villagrán (1980), the

size of individual cushions of both *A. monantha* and *L. acaulis* at our study area ranges between 10 and > 100 cm diameter.

Taraxacum officinale Weber (Asteraceae) probably originated in Europe (Holm *et al.* 1997), but is now found in most countries of the world. It is a stemless, deeply rooted perennial herb having a thick taproot, and leaves in rosettes at soil level. Each plant has one or more 2- to 5-cm-diameter capitula or flower heads, terminally positioned on 5- to 45-cm long, hollow, cylindrical peduncles. Each capitulum has a composite of 50–250 small, bright yellow ligulate or ray florets (Holm *et al.* 1997). *Taraxacum officinale* is generally apomictic, although sexually reproducing biotypes have been described, and it is considered a noxious weed in several countries, including Chile (Holm *et al.* 1997).

MICROCLIMATIC MEASUREMENTS

To characterize the microclimatic changes induced by the presence of *A. monantha* and *L. acaulis*, we recorded substrate temperature, soil moisture and soil nutrient contents within cushions of each species as well as in open areas outside them.

Substrate temperature

For each cushion species, four individuals were randomly selected. The following random selection protocol was used throughout the study. 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. We used this cushion size because it is the most abundant size class at this elevation (Armesto *et al.* 1980). For each selected cushion, a point on the bare ground at least 1 m away (in a random direction) was also selected. At each selected cushion, one temperature sensor connected to a mini-logger (HOBO-H8, Onset Corp., MA, USA) was placed at the centre of the cushion, within its tight 'canopy' at 2 cm below the canopy surface. Sensors on the bare ground were placed at a depth of 2 cm below the soil surface. The mini-loggers were programmed to record temperature once every hour for the duration of the growing season, starting on 28 November 2003 and finishing on 30 March 2004. Differences in substrate temperature among each cushion species and bare ground, and between the two cushion species were assessed through paired *t*-tests.

Soil moisture

The matric potential of the soil was used to compare the soil moisture outside and beneath individuals of both cushion species. Soil moisture was recorded in 2004, once per month starting in December (after snow melt) to March. On each date, four individuals of each cushion species of similar size (*c.* 50 cm diameter) and four points on the bare ground were randomly selected. At each cushion and associated bare ground point, a soil tensiometer (2725 Series Jet Fill Tensiometer, Soilmoisture Equipment Corp., CO, USA) was dug into the soil to a depth of 10 cm. Tensiometers were placed at 10.00 h, and after a stabilization period of 4 h, the matric potential of the soil was recorded. Data were analysed with a repeated measurements ANOVA using the software R v. 2·3 (R Development Core Team 2005).

Nutrient content of the soil

On 24 February 2004 (midpoint of growing season), *c.* 100 g soil samples were collected from beneath five randomly selected individuals of the two cushion species and five randomly selected points on the bare ground. Beneath each selected cushion and point on the bare ground, soil was excavated with a trowel to a 20-cm depth, and samples were placed in sealed plastic bags. After that, soil samples were sent to the Laboratory for Soil Analyses, Agronomy Faculty, University of Concepción, where availability of nitrogen (NO_3^- and NH_4^+), phosphorous and potassium were estimated. Data were compared with one-way ANOVA with position as a factor (beneath the cushions vs. outside them) using the software R v. 2·3 (R Development Core Team 2005).

DETERMINATION OF SPATIAL ASSOCIATIONS TO *AZORELLA MONANTHA* AND *LARETIA ACAULIS* CUSHIONS

To detect spatial associations of *T. officinale* with *A. monantha* and *L. acaulis* cushions, we used our random selection protocol to identify fifty 50- to 60-cm-diameter cushions of each species. For each selected cushion, a 50-cm-diameter metallic hoop was centred over the cushion surface, and all *T. officinale* individuals found inside the hoop were recorded. A hoop of identical size was located at random outside the cushion, where again all *T. officinale* individuals included in the hoop were recorded. The random location of hoops outside cushions was determined in a similar way as for cushions, although the selected point outside had to be at least 50 cm away from the nearest cushion.

To detect either positive or negative spatial associations between *T. officinale* and each cushion species, we performed randomization tests (Slade & Hall 1999) with the software 'RESAMPLING STATS' (Resampling Stats, Inc. 1990–1995). First, from the total frequency of incidence of *T. officinale*, we randomly redistributed the total number of presence recordings between the three microhabitats evaluated (i.e. within *A. monantha*, within *L. acaulis* and outside cushions). We performed 1000 runs of random redistributions, and calculated the probability of the observed frequency within each cushion species being generated by chance (see also Cavieres *et al.* 2002, 2005).

SEEDLING SURVIVAL

Seeds of *T. officinale* collected during March 2003 were germinated in growth chambers under controlled temperature conditions (20/10 °C day/night) during October 2003. Emerging seedlings were planted in small plastic bags (100 cm^3) with commercial soil, and were maintained in a growth chamber at 10/5 °C (day/night) for 1 month. The 1-month-old seedlings were taken to the field and planted in groups of 10 individuals into each of six previously randomly selected individuals of each cushion species and in six randomly selected bare ground locations. Seedlings were planted on 28 December 2003, along two lines of five seedlings each. Care was taken to leave 5-cm space between seedlings to avoid interference among them. Seedling survival was monitored every 2 weeks from January to February 2004. Survival curves of seedlings at each position (within *A. monantha*, within *L. acaulis* and outside cushions) were estimated by means of the Kaplan–Meier method, and statistical differences were assessed with the Cox–Mantel test (Fox 1993).

PHOTOCHEMICAL EFFICIENCY OF PHOTOSYSTEM II (FV/FM AND ΦPSII)

We quantified the efficiency of photosystem II (Fv/Fm and ΦPSII) as an indicator of the stress experienced by established individuals of *T. officinale* growing in the different microhabitats under study. On 20 December 2004 (early growing season), we randomly chose nine mature individuals of *T. officinale* of similar size occurring within *L. acaulis*, nine within *A. monantha* and nine on the bare ground (27 in total). Individuals growing within cushions were located on separate cushion plants (in both species), while individuals on bare ground were distant at least 1 m from each other. On each selected individual, fully developed leaves were dark adapted (to obtain open PSII centres) for 30 min to ensure maximum photochemical efficiency. Fluorescence signals were generated by a pulse-amplitude modulated fluorometer (FMS 2, Hansatech Instruments Ltd, Norfolk, England). Minimum fluorescence (F0) with all PSII reaction centres in the open state was determined by applying a weak modulated light ($0.4 \, \mu mol \, m^{-2} \, s^{-1}$). Maximum fluorescence (Fm) with all PSII reaction centres in the closed state was induced by a 0·8-s saturating pulse of white light ($9000 \, \mu mol \, m^{-2} \, s^{-1}$). After 15 s, the actinic light ($180 \, \mu mol \, m^{-2} \, s^{-1}$) was turned on and the same saturating pulse described previously was applied every 60 s, until steady-state photosynthesis was reached in order to obtain Fs and Fm′. Finally, F0′ was measured after turning the actinic light off. On 5 April 2004 (end of the growing season), the same individuals previously measured were re-evaluated to assess how the chlorophyll fluorescence and the photochemical efficiency of PSII changed during the growing season. Results were analyzed with repeated measures ANOVA using the software R v. 2·3 (R Development Core Team 2005).

SEED PRODUCTION

For each microhabitat, 12 *T. officinale* individuals, each with a single open capitulum, were selected using the random procedure described previously. Individuals growing within cushions were located on separate cushion plants (in both species), while individuals on bare ground were distant at least 1 m from each other. The capitulum of each selected individual was bagged with a transparent nylon mesh to prevent any loss of seeds. After 4 weeks, bags were recovered and transported to the laboratory where seed production per capitulum was recorded. An index of viable seeds produced was calculated by dividing the number of filled seeds recorded by the number of florets. Data were analyzed with a one-way ANOVA using the software R v. 2·3 (R Development Core Team 2005).

Results

SUBSTRATE TEMPERATURE

Paired *t*-tests indicated that substrate temperatures within each cushion species were significantly different from the temperatures recorded on bare ground ($t = 41.8$ and $t = 52.1$, df = 1988, $P < 0.01$, for *L. acaulis* and *A. monantha*, respectively,
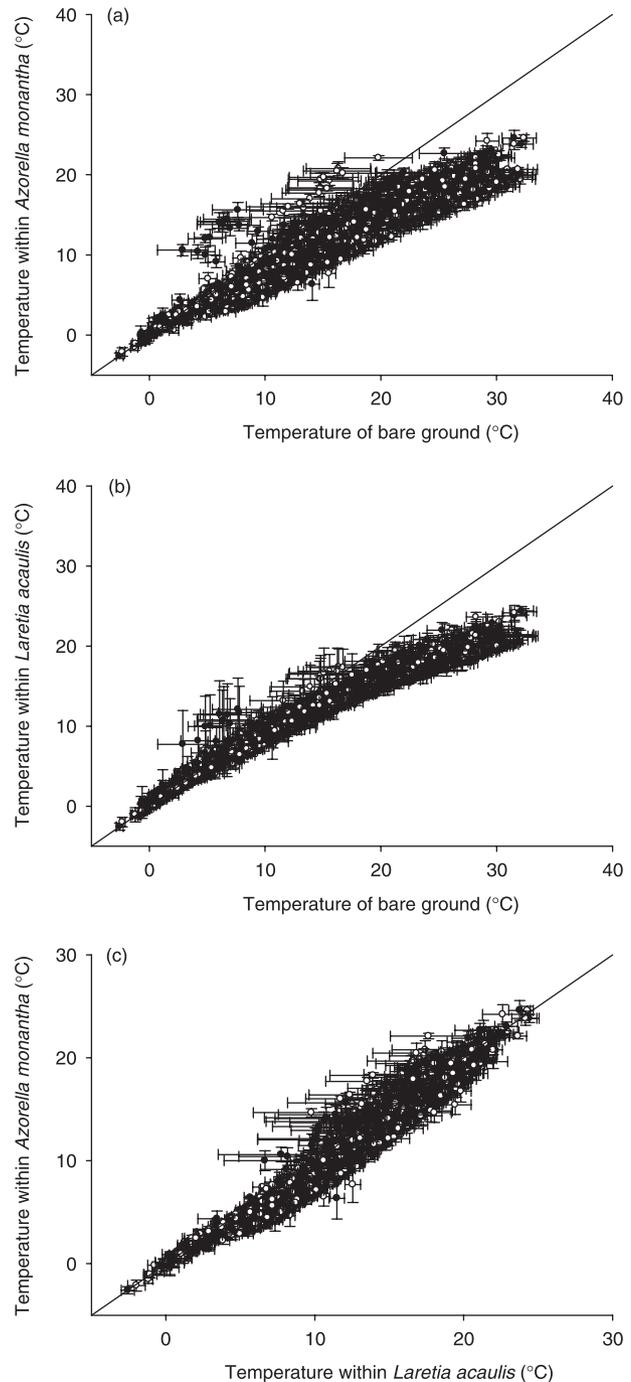
Fig. 1. Substrate temperatures simultaneously registered during the entire growing season within cushions of *Azorella monantha* and bare ground points (a), within cushions of *Laretia acaulis* and bare ground points (b), and within the two cushion species (c) at 3200 m elevation in the Andes of central Chile. Error bars indicate 2 SE.

Fig. 1). Overall, for those periods when temperature was above 20 °C for bare ground, temperatures within cushion plants were significantly lower, while for those periods when temperatures were below 20 °C for bare ground, there was no significant difference between temperatures below cushions and in the bare ground (Fig. 1). Temperatures within *L. acaulis* cushions did not differ from temperatures
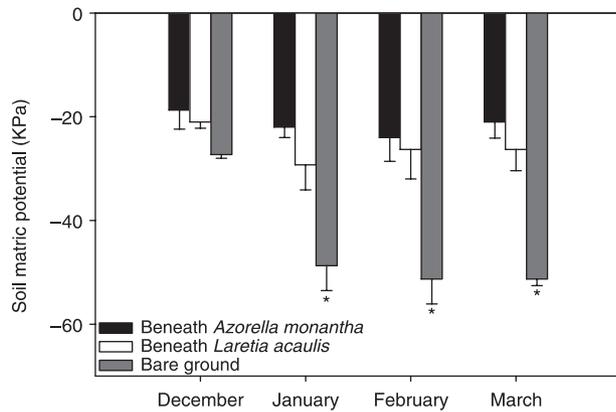
Fig. 2. Soil matric potential within cushions of *Azorella monantha*, *Laretia acaulis* and bare ground points during the growing season at 3200 m elevation in the Andes of central Chile. Error bars indicate 2 SE. Asterisks indicate significant differences (Tukey's HSD, $P < 0.05$).

Fig. 3. Abundance of *Taraxacum officinale* within cushions of *Azorella monantha*, *Laretia acaulis* and bare ground at 3200 m in the Andes of central Chile. Error bars indicate 2 SE. Different letters indicate significant differences (*t*-test, $P < 0.05$).

recorded within *A. monantha* cushions (paired *t*-test, $t = 1.5$, df = 1988, NS, Fig. 1).

SOIL MOISTURE

Soil moisture differed among microhabitats ($F_{2,9} = 456.9$; $P < 0.001$) and between different dates within the growing season ($F_{3,27} = 16.3$; $P < 0.001$), and there was a significant interactive effect of these factors on soil moisture ($F_{6,27} = 6.5$; $P < 0.01$). *Post-hoc* analyses (Tukey's HSD) showed that both cushion species maintained the same moisture levels in their underlying soil, and that these levels were higher than in bare ground during almost the entire growing season (Fig. 2). Only the measurements taken early in the growing season were similar among the different microhabitats (Fig. 2).
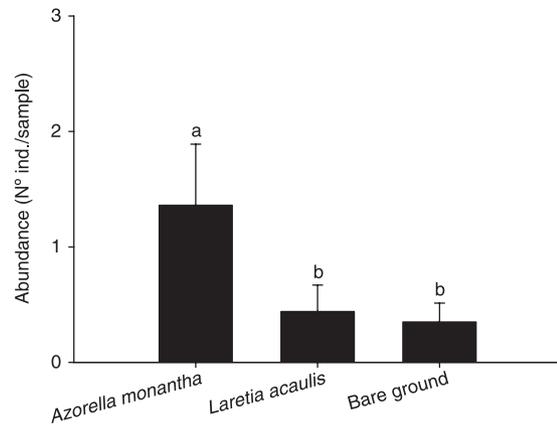
NUTRIENT CONTENT OF SOILS

Soil nitrogen content differed among microhabitats ($F_{2,12} = 12.94$; $P < 0.05$), being higher within cushions than in the bare ground (Table 1). However, no significant differences in soil nitrogen were found between the two cushion species (Table 1). Soil potassium was also higher beneath
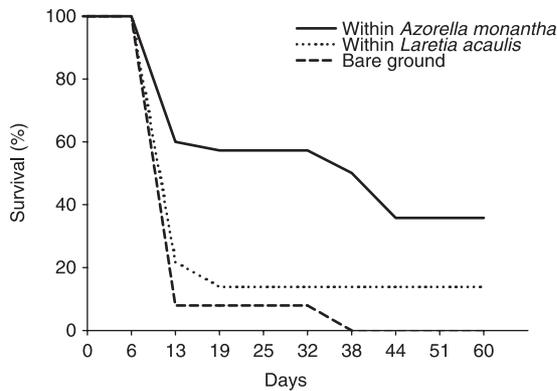
cushions than outside them ($F_{2,12} = 8.49$; $P < 0.005$), but soil samples under *L. acaulis* cushions showed significantly higher levels of this nutrient than soils under *A. monantha* cushions. Soil phosphorous content did not differ among microhabitats ($F_{2,12} = 1.40$; $P = 0.28$; Table 1).
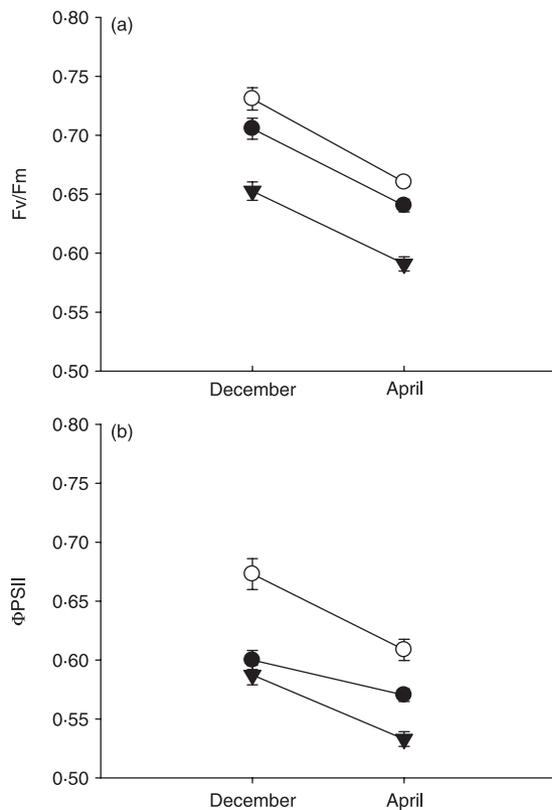
SPATIAL ASSOCIATIONS

While *T. officinale* was found within 28 out of the 50 sampled *A. monantha* cushions, it was found only in 11 out of 50 samples from outside the cushions, that is, *T. officinale* was positively associated with this cushion species ($P < 0.05$). In contrast, *T. officinale* was found within 15 out of the 50 sampled *L. acaulis* cushions, the number expected from an even distribution of *T. officinale* between the cushions of *L. acaulis* and open areas. Likewise, an average (± 2 SE) of 1.36 ± 0.53 *T. officinale* individuals per 50-cm-diameter hoop was found within *A. monantha* cushions, which was significantly higher than the abundance found within *L. acaulis* cushions (0.44 ± 0.23) and open areas away from cushions (0.35 ± 0.16; Kruskall–Wallis; $H = 11.867$, $P < 0.01$) (Fig. 3). According to multiple comparison *post-hoc* tests, the average number of individuals of *T. officinale* within *L. acaulis* cushions did not differ from that found outside cushions.

SEEDLING SURVIVAL

Planted seedlings of *T. officinale* only survived within cushions (Fig. 4). Among the studied cushion species, survival analyses showed that survival within *A. monantha* cushions was significantly higher than the survival within *L. acaulis* cushions (Cox–Mantel test = 3.35, $P < 0.05$; Fig. 4). Survival analyses also indicated that survival within *L. acaulis* cushions did not differ from that on bare ground (Cox–Mantel test = –1.7, NS), indicating that only *A. monantha* cushions facilitate the survival of *T. officinale* seedlings.

Table 1. Availability of nitrogen (N), phosphorous (P) and potassium (K) in soils below *Laretia acaulis* and *Azorella monantha* cushions, and open areas away from cushions (bare ground) at 3200 m elevation in the Andes of central Chile

Microhabitat	N (mg kg⁻¹ soil)	P (mg kg⁻¹ soil)	K (mg kg⁻¹ soil)
Laretia acaulis	5 (± 2·0)[a]	35 (± 4·0)[a]	1024 (± 108)[a]
Azorella monantha	8 (± 3·0)[a]	24 (± 3·9)[a]	486 (± 135)[b]
Bare ground	1 (± 0·1)[b]	27 (± 7·1)[a]	196 (± 35)[c]

Data are mean values (± 2 SE). Different letters indicate significant differences (test Tukey's HSD, $P < 0.05$).
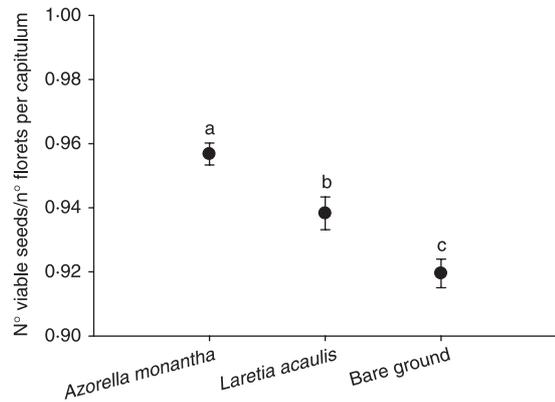
Fig. 4. Kaplan–Meyer estimation of survival of experimentally planted seedlings of *Taraxacum officinale* within cushions of *Azorella monantha*, *Laretia acaulis* and bare ground points at 3200 m elevation in the Andes of central Chile.

Fig. 6. Reproductive output of *Taraxacum officinale* individuals growing within cushions of *Azorella monantha*, *Laretia acaulis* and open areas outside cushions (bare ground) at 3200 m elevation in the Andes of central Chile. Error bars indicate 2 SE. Different letters indicate significant differences (*t*-test, $P < 0.05$).

Fig. 5. Chlorophyll fluorescence (Fv/Fm) (a) and photochemical efficiency of photosystem II (ΦPSII) (b) of *Taraxacum officinale* individuals growing within *Azorella monantha* cushions (○), within *Laretia acaulis* cushions (●), and outside cushions (▼) at 3200 m elevation in early (December) and late (April) periods of the growing season in the Andes of central Chile. Error bars indicate 2 SE.

PHOTOCHEMICAL EFFICIENCY OF PHOTOSYSTEM II (FV/FM AND ΦPSII)

Photochemical efficiency of photosystem II differed among the microhabitats ($F_{2,24} = 75.0$, $P < 0.001$; and $F_{2,24} = 56.9$, $P < 0.001$, for Fv/Fm and ΦPSII, respectively) and differed between the two recording dates ($F_{1,24} = 101.2$, $P < 0.001$; and $F_{1,24} = 40.2$, $P < 0.001$, for Fv/Fm and ΦPSII, respectively). Overall, on both recording dates, the lowest levels of photochemical efficiency were found for individuals growing outside cushions (Fig. 5). On both sampling dates, the highest levels of Fv/Fm and ΦPSII were found when individuals were growing within *A. monantha* cushions, followed by the individuals growing within *L. acaulis* (Fig. 5). Both Fv/Fm and ΦPSII values decreased with time (Fig. 5).

SEED PRODUCTION

Individuals of *T. officinale* growing within cushion plants showed a significantly greater seed production compared to those individuals growing on open areas away from cushions ($F_{2,33} = 18.0$; $P < 0.0001$). *A. posteriori* tests (Tukey's HSD) indicated that *T. officinale* individuals growing on *A. monantha* cushions showed a significantly greater viable seed production than individuals growing on *L. acaulis* cushions (Fig. 6).

Discussion

We found that in the high Andes of central Chile, the alien invasive species *T. officinale* spatially associates with only one (*A. monantha*) of the two cushion species studied. Further, although the two cushion species produced similar microclimatic modifications in terms of substrate temperature and soil moisture, experiments showed differences in the survival of seedlings planted within cushions, with higher survival of those planted within *A. monantha*. Similarly, photochemical efficiency and reproductive output of established individuals of *T. officinale* were highest within *A. monantha* cushions, although both of these response variables were higher within cushion species compared to bare ground. Thus, the species-specific spatial association observed in this system may result, at least in part, from species-specific facilitative effects on

seedlings survival and species-specific effects on the physiological performance of established individuals.

Although differences in seed rain and/or seed entrapment between cushions and bare areas could be involved in the observed spatial patterns, initial observations indicate that this is unlikely. First, preliminary seed trap experiments performed in the study area have indicated that a greater number of seeds fall into traps located in open areas away from cushions than into traps located within both cushion species, with no differences between both cushion species (P. Chacón & L. A. Cavieres, unpublished data). Second, and in contrast to other cushion species that have 'soft' canopies that trap seeds (e.g. *Silene acaulis*), *A. monantha* and *L. acaulis* form tightly knit cushions, with very few spaces for seed trapping within the canopy.

Cushion plants are one of the life-forms best adapted to the extreme alpine climate (Körner 2003), and because of their low stature and compact form, cushion plants promote the development of a particular microenvironment beneath and within their canopies (as reported here). However, unlike previous studies in alpine habitats where cushions were shown to provide warmer habitats compared to the surrounding environment (e.g. Arroyo *et al*. 2003; Körner 2003), the two cushions studied here maintained lower temperatures than the open spaces. In our study site, bare ground soil temperatures rarely went below 0 °C, and when they did, cushions maintained a similar temperature to that of the bare ground (Fig. 1), suggesting that mitigation of low temperatures could not be invoked as an important mechanism of facilitation. However, our results also showed that cushion temperatures were milder than those of the bare ground. For instance, while cushions maintained temperatures of *c*. 20 °C, soil temperatures reached *c*. 35 °C, which could be lethal for some alpine plants (Körner 2003). Such mitigation of high temperatures could not only be very important in terms of direct effects on survival but also in terms of regulating evaporative losses from the soil and the water status of facilitated plants. While differences in soil moisture between the cushions and the bare ground were not marked early in the growing season, cushions maintained higher soil moisture than the bare ground at the end of growing season. High temperatures and scarce rainfall during the summer characterize the Mediterranean zone of central Chile, and the combination of high temperature and the extended summer drought of 5–6 months could produce substantial water stress in plants inhabiting this alpine zone (Cavieres *et al*. 2006).

As has been previously reported (e.g. Núñez, Aizen & Ezcurra 1999; Cavieres *et al*. 2006), soils beneath cushions contained a higher concentration of nutrients than those of bare ground. Cushions can trap their own litter and intercept wind-blown litter from other sources. In combination with the higher availability of water and the milder temperatures, these mechanisms could enhance the activities of nitrogen-fixing organisms, resulting in locally increased concentrations of soil nutrients beneath cushions (as observed), making cushions another example of 'fertile islands' in alpine habitats (Escudero *et al*. 2004). Despite both cushions showing similar

amounts of soil nitrogen and phosphorous, soil samples from beneath *L. acaulis* cushions showed *c*. twofold higher content of potassium than soils collected from beneath *A. monantha* cushions. In general, due to their intrusive volcanic origin, soils in the high alpine zone of central Chile have high amounts of phosphorous and potassium compared to other mountain areas (C. L. Quiroz *et al*., unpublished data). Tilman *et al*. (1999) reported *T. officinale* as a species highly sensitive to low soil potassium content. However, in recent experiments conducted under greenhouse conditions, we grew *T. officinale* seedlings in soils with potassium contents similar to those found in the three microhabitats studied here and found evidence of toxic effects of high levels of potassium (similar to those found beneath *L. acaulis* cushions) for dandelions (C. L. Quiroz *et al*., unpublished data). Hence, considering that both cushion species did not differ in substrate temperature nor in water, nitrogen and phosphorous contents in soils, the species-specific nurse effect found in this study seems to be closely related to differences in the potassium levels found beneath the soils of the two cushion species.

Several not mutually exclusive mechanisms can account for the lower potassium contents observed under *A. monantha* cushions compared to those found under *L. acaulis* cushions. For example, the establishment of *A. monantha* could be limited by the amounts of potassium in the soil and thus recruits in patches of lower potassium levels. If this is true, we should expect a clumped distribution between young and adult individuals of *A. monantha*. However, a recent evaluation of the spatial distribution of this cushion species in different high-elevation sites indicated that young and adult individuals of *A. monantha* are randomly distributed with respect to each other (Fajardo, Quiroz & Cavieres 2007), suggesting that limitations on the recruitment of this cushion species by the amount of potassium in the soil are unlikely. Perhaps *A. monantha* has an associated soil biota that reduces soil potassium, or perhaps this cushion species has a high uptake of potassium. Further study is needed to investigate these hypotheses.

The climatic severity of alpine habitats has been hypothesized to limit the successful establishment of non-native invasive species (Williard & Marr 1971). However, several studies have reported the presence of non-native species in a number of alpine habitats (e.g. Arévalo *et al*. 2005; Beccker *et al*. 2005; McDougall *et al*. 2005), where disturbance and negative interactions among native and exotic species have been proposed as key factors determining invasion success. However, our results highlight the role of facilitation via habitat amelioration as another important driver for non-native plant invasions in the stressful alpine environments. Recently, Cavieres *et al*. (2007) demonstrated that the non-native species *Cerastium arvense* is facilitated by cushions of *L. acaulis* and *A. monantha* at 2800 and 3600 m elevation, respectively, in the Andes of central Chile, suggesting that facilitation may be a widespread and important driver of invasions in alpine habitats.

In conclusion, we have shown that facilitation of a non-native plant species by a native plant species may be an important mechanism for the invasion of stressful habitats

such as the high alpine zone of central Chile. In addition, we have shown that this facilitative process is highly species-specific, with differences in the amount of a particular nutrient in the soil (i.e. potassium) accounting for species-specific effects. Recognition of the importance of facilitation by native species in plant invasions is growing, forcing us to question current tenets concerning the role of species interactions and invasiveness (Bruno *et al.* 2005).

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