

Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems

ERNESTO I. BADANO*§, ELISA VILLARROEL†, RAMIRO O. BUSTAMANTE†§, PABLO A. MARQUET*§¶ and LOHENGRIN A. CAVIERES‡§

*Center for Advanced Studies in Ecology and Biodiversity (CASEB), Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago 6513677, Chile,

†Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile,

‡Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile, §Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias Universidad de Chile, Casilla 653, Santiago, Chile, and ¶National Center for Ecological Analysis and Synthesis (NCEAS) 735 State Street, Suite 300 Santa Barbara, CA 93101-5504, USA

Summary

1 Ecosystem engineers are organisms that change abiotic conditions in ways that affect the performance and distribution of other species, including exotics. Several mechanisms have been proposed for the successful establishment of exotic plants in natural communities, but the positive effects that native engineer species may have on the distribution and performance of exotic plants remain unknown.

2 In this study, we propose that amelioration of extreme abiotic conditions by ecosystem engineers can make stressful habitats invadable by exotic plant species, with larger positive effects on the performance of exotic plants as environmental harshness increases. We tested this hypothesis by assessing the effects of a high-Andean ecosystem engineer, the cushion plant *Azorella monantha*, which is known to create habitat patches where environmental conditions are less extreme than in the surrounding habitats, on the distribution and the performance of two exotic plant species, field chickweed (*Cerastium arvense*) and common dandelion (*Taraxacum officinale*), along an elevation gradient in the Andes of central Chile.

3 We measured and compared the abundance, biomass and survival of both exotic species within and outside cushion habitat patches at three elevations (3200 m, 3400 m and 3600 m), and evaluated whether the effects of *A. monantha* varied across elevations.

4 The results indicated that cushion plants positively impact the performance of both exotics, and have greater facilitative effects at higher elevations. Indeed, at the higher elevation site, *C. arvense* was only detected within *A. monantha* patches, suggesting that cushions may expand the distribution range of exotics. These results suggest that ecosystem engineering by native species could promote biological invasions in harsh environments, leading to higher abundances of invaders than those expected in the absence of engineers.

5 Given the conspicuousness of ecosystem engineering in nature, we suggest that exotic species eradication programmes might be less successful by not taking into account the facilitative effects of native engineer species on invaders. Further, we suggest that the recent proposals to use engineer species in ecosystem restoration should be aware of their potential role in promoting invasions.

Key-words: alpine ecology, *Azorella monantha*, biological invasions, *Cerastium arvense*, cushion plants, ecosystem engineering, environmental gradient, facilitation, plant ecology, *Taraxacum officinale*

Journal of Ecology (2007) **95**, 682–688
doi: 10.1111/j.1365-2745.2007.01262.x

Introduction

Biological invasions are thought by some to be the largest biotic change around the world (Barnard & Waage 2004). Diverse mechanisms have been proposed to explain why exotic plants successfully invade natural communities, including the release of natural enemies of exotics (Keane & Crawley 2002), allelopathic effects of exotics on native plants (Hierro & Callaway 2003; Callaway & Ridenour 2004) and resource opportunities for exotics upon arrival in new ecosystems (Shea & Chesson 2002). Indeed, it has been proposed that mutualisms between exotic plants and native animals that act as pollinators and seed dispersers may also lead to successful invasions (Richardson *et al.* 2000; Rodriguez 2006). However, one mechanism that has received less attention is the facilitative impact that native ecosystem engineer species may have on the distribution and performance of exotic plants.

Ecosystem engineers are organisms that non-trophically change the distribution of materials and energy in the abiotic environment (Jones *et al.* 1994, 1997). The process of ecosystem engineering can result in the creation of habitat patches with different environmental conditions than surrounding unmodified habitat, and the presence of such habitat patches in natural landscapes has been shown to affect the distribution and performance of both native (Wright *et al.* 2002; Badano & Cavieres 2006a,b; Badano *et al.* 2006) and exotic (Crooks 2002; Cavieres *et al.* 2005; Reinhart *et al.* 2006; Tecco *et al.* 2006) plant species. Indeed, when environmental modifications performed by ecosystem engineers result in amelioration of physical stress, it has been observed that their positive effects on other species increase as the surrounding unmodified habitat becomes harsher (Wright & Jones 2004; Badano & Cavieres 2006a; Wright *et al.* 2006). Thus, if exotic plants are sensitive to the stress amelioration performed by ecosystem engineers, we may hypothesize that such engineering effects would have greater positive effects on the performance of exotic species in sites where environmental conditions in the surrounding unmodified habitat are harsher. In this manner, the presence of ecosystem engineers may make stressful landscapes more susceptible to biological invasions than would be expected in the absence of engineer species.

We have tested the above hypothesis by documenting the extent to which a high-Andean ecosystem engineer, the native cushion plant (*Azorella monantha* Clos.; Apiaceae; Fig. 1), affects the performance and survival of two common exotic forbs, field chickweed (*Cerastium arvense* L.; Caryophyllaceae) and common dandelion (*Taraxacum officinale* (L.) Weber; Asteraceae), along an elevation gradient in the high-Andes of central Chile. High-mountain ecosystems represent an ideal system to test our hypothesis because current global change simulation models predict these ecosystems are particularly resistant to biological invasions due to their extreme environmental conditions when



Fig. 1 An *Azorella monantha* cushion invaded by flowering individuals (white flowers) of *Cerastium arvense*.

compared with lower elevation ecosystems (Sala *et al.* 2000). However, in the high-Andes, *A. monantha* cushions modify a wide variety of environmental conditions when compared with the adjacent matrix habitat, or open areas, dominated by rocks and bare soil. For instance, these cushions may modulate substrate temperatures, maintaining lower extreme maximum temperatures and higher extreme minimum temperatures than surrounding habitats, and also increase soil moisture and nutrient availability (Arroyo *et al.* 2003; Badano *et al.* 2006; Cavieres *et al.* 2007). Hence, if exotic species respond to environmental modifications caused by *A. monantha* cushions, and if the importance of such cushion-driven environmental modifications increases with elevation, we predict that the performance of *T. officinale* and *C. arvense* would increase within *A. monantha* habitat patches, but decrease in surrounding unmodified habitat, as site elevation increases. Specifically, we predict that at upper elevations the abundance, biomass and survival of both exotics will increase within cushion patches, but decrease in open areas.

Methods

STUDY SITE

This study was conducted on the slopes of Mt Franciscano, at the Río Molina basin (33° S, 70° W) in the high-Andes of central Chile (50 km east of the city of Santiago). In this area, estimated mean annual air temperature at 3150 m is 3 °C, and the estimated annual lapse rate for this site is 6.1 °C km⁻¹ (Cavieres & Arroyo 1999). Precipitation exceeds 900 mm (Santibáñez & Uribe 1990), mainly occurring as snow during winter months. Summer months are dry and thus water shortage conditions are likely to occur during the growing season (Cavieres *et al.* 1998, 2006). The length of the snow-free period is 4–5 months, usually starting in November. Soil is mainly a clay-type mixed with sedimentary and volcanic rocks (Cavieres *et al.* 2000). In this study site, the effects of *A. monantha* cushions on both exotic forbs were measured at three elevations: 3200 m, 3400 m and 3600 m, almost covering the whole

altitudinal distribution range of the studied cushion species. Although *A. monantha* cushions can be found in both polar- and equatorial-facing slopes, all sampling sites were located on polar-facing slopes to avoid confounding effects due to differences in slope aspect. At all elevations, *T. officinale* and *C. arvensis* were the only exotic species detected in the plant communities.

ENVIRONMENTAL GRADIENT

Given that environmental stress probably results from the interaction of several factors, and given the difficulty in measuring all the environmental modifications that *A. monantha* cushion plants can perform, our assessment relied on the generally accepted negative relationship between plant biomass and environmental harshness proposed by Grime (1979). Hence, if environmental harshness increases with elevation, above-ground plant biomass should decrease in that direction. To assess such an effect, in January 2006, 40 cushions (diameter between 50 and 70 cm) and 40 points in open areas were selected at each elevation by using points at random directions and distances from the centre of a previously delimited 1-ha plot. If these random points did not coincide with a cushion, we considered the closest cushion to each point. On each selected cushion and at each point in open areas, a 0.2 m² circular plot was delimited and all native and exotic species within these plots were identified and counted. *Azorella monantha* itself was not included in this sampling because we were interested in measuring the effects of this species. All samples collected within *A. monantha* cushions recorded at least one species. Samples in open areas often contained zero species, but for our calculations we only included sample plots from open areas when they contained a minimum of one species. Aerial parts of species in plots were collected and stored in individual paper bags (one bag per species per sample). Bags with collected material were placed in a ventilated stove at 75 °C within 3–4 h of collection to avoid metabolic tissue degradation. Samples were dried for 72 h and weighed to determine the above-ground dry biomass of each species within each sample. Above-ground plant biomass per sample was then estimated in g m⁻² and compared across elevations separately for open areas and cushions with one-way ANOVAS.

We also compared biomass between cushions and open areas at each elevation with *t*-tests. Further, to assess the magnitude with which cushions modify above-ground plant biomass at each elevation, we used the relative interaction index (RII) proposed by Armas *et al.* (2004). RII is calculated as $(B_w - B_o)/(B_w + B_o)$, where B_o is the performance of a target species without neighbours and B_w is its performance with neighbours. This index was originally developed to measure individual or population effects of plant interactions but, given that it is based on arithmetical operators, Armas

et al. (2004) suggested that RII can be used to measure the community level effects of plant interactions. Here, we used RII to measure the relative effects of cushions on community biomass by replacing B_w with the average above-ground plant biomass within cushion patches, and replacing B_o with its equivalent value in open areas. Values of this index can vary between 1 and -1, with positive values indicating higher plant biomass within cushions and negative values indicating the converse situation. These RII values were multiplied by 100 to present the results as a percentage. Given that the amelioration of harsh climatic conditions (such as extremely low temperatures) by *A. monantha* increases with elevation (Arroyo *et al.* 2003), we expected higher RII values with increasing elevation, indicating greater positive effects of cushions on other plants.

PERFORMANCE OF INVADERS

To assess whether cushions affected the performance of both *T. officinale* and *C. arvensis*, we calculated the abundance (individuals m⁻²) and the above-ground biomass (g m⁻²) of both exotics in the 40 samples taken within and outside cushions at each elevation. These variables were compared across elevations separately for open areas and cushions with one-way ANOVAS, and compared between cushions and open areas at each elevation with *t*-tests. Further, to assess whether the magnitude with which cushions modify the performance of exotic species changes with elevation, we calculated RII (Armas *et al.* 2004) for each exotic species at each elevation. Here, B_w was replaced by the average abundance or biomass of exotics within cushions and B_o by their equivalent values in open areas.

SURVIVAL OF INVADERS

To assess whether cushions improve survival of exotic species, seedling transplant experiments were performed at 3600 m and 3200 m. Seeds of *T. officinale* and *C. arvensis* were collected in the field and germinated in growth chambers under controlled temperature conditions (20/10 °C day/night) for 1 month. Emerged seedlings were planted in small plastic bags (100 cm³) filled with commercial soil, and maintained in growth-chambers at 10/5 °C (day/night) for 1 month. The 1-month-old seedlings were taken to the field at the beginning of the growing season (December) and planted in groups of 10 individuals within six randomly selected cushions and six randomly selected points on open areas at each elevation. Seedlings were planted 5 cm from each other. Seedling survival was monitored every 2 weeks for 60 days. Survival curves of transplanted seedlings were estimated using Kaplan-Meier's method (Kaplan & Meier 1958) and compared between habitats at each elevation with the two-sample Cox-Mantel test (Lee *et al.* 1975).

Table 1 Average plant biomass including all species ($\text{g m}^{-2} \pm 2 \text{ SE}$) and average abundance (individuals $\text{m}^{-2} \pm 2 \text{ SE}$) and biomass ($\text{g m}^{-2} \pm 2 \text{ SE}$) of *Taraxacum officinale* and *Cerastium arvense* within *Azorella monantha* cushions and in open areas at the three elevations considered in this study. The last two columns are the *F*-values and the probability values (*P*) obtained from the one-way ANOVAs used to compare each variable across elevations. Differences between elevations were assessed *a posteriori* with Tukey tests; significant differences are indicated for each variable with different letters. Because *Cerastium arvense* was not detected in open areas at 3600 m, ANOVAs comparing abundance and biomass of this species in open areas did not include the highest elevation site (ND = not detected)

Variable	Habitat type	3200 m	3400 m	3600 m	<i>F</i>	<i>P</i>
Plant biomass	Open areas	80.05 (± 11.64) ^a	15.10 (± 2.85) ^b	25.50 (± 6.70) ^b	77.44	< 0.01
	Cushions	49.48 (± 6.78) ^a	50.95 (± 11.61) ^a	86.41 (± 23.17) ^b	7.47	< 0.01
<i>T. officinale</i> abundance	Open areas	7.38 (± 1.54) ^a	2.38 (± 1.62) ^b	1.75 (± 1.37) ^b	16.94	< 0.01
	Cushions	11.25 (± 2.55) ^a	7.75 (± 2.99) ^{ab}	5.00 (± 2.02) ^b	6.18	< 0.01
<i>C. arvense</i> abundance	Open areas	10.50 (± 8.22) ^a	1.13 (± 1.12) ^b	ND	5.92	< 0.01
	Cushions	85.38 (± 20.43)	68.88 (± 34.11)	66.89 (± 29.39)	0.52	0.60
<i>T. officinale</i> biomass	Open areas	8.76 (± 2.14) ^a	2.42 (± 1.48) ^b	1.31 (± 1.18) ^b	24.28	< 0.01
	Cushions	8.29 (± 1.74)	4.97 (± 1.54)	4.96 (± 3.19)	2.88	0.06
<i>C. arvense</i> biomass	Open areas	1.60 (± 0.92) ^a	0.15 (± 0.13) ^b	ND	10.98	< 0.01
	Cushions	11.94 (± 3.21)	8.46 (± 3.56)	8.66 (± 3.85)	1.24	0.29

Results

ENVIRONMENTAL GRADIENT

Total plant biomass in open areas decreased at upper elevation sites (Table 1). In contrast, biomass within cushions increased with elevation (Table 1). Interestingly, biomass found in cushions was higher than that found in open areas at the two upper sites only (*t*-test $P_{3600 \text{ m}} < 0.01$; *t*-test $P_{3400 \text{ m}} < 0.01$). Conversely, at the lowest elevation, open areas showed higher biomass than cushions (*t*-test $P_{3200 \text{ m}} < 0.01$). The relative difference in biomass between cushions and open areas indicated that cushion patches increased biomass up to 52% and 54% at 3600 and 3400 m, respectively, while they decreased biomass by 24% at 3200 m. These results indicate that *A. monantha* cushions have positive effects on plant biomass at upper elevations and negative effects at the lowest elevation site.

PERFORMANCE OF INVADERS

The number of samples containing at least one exotic species varied across elevations and between habitat types (i.e. cushions and open areas). Of the 40 samples taken in open areas at each elevation, *T. officinale* was detected in 34 samples at 3200 m, 11 samples at 3400 m and eight samples at 3600 m. In open areas, *C. arvense* was detected in 11 samples at 3200 m and six samples at 3400 m, and was not detected in open areas at 3600 m. The number of samples within cushions containing exotics also decreased with elevation. In this habitat type, *T. officinale* was detected in 35 samples at 3200 m, 28 samples at 3400 m and 23 samples at 3600 m. Within cushions, *C. arvense* was detected in 31 samples at 3200 m, 25 samples at 3400 m and 17 samples at 3600 m. All statistical analyses comparing the abundance and biomass of exotics across elevations and

between habitat types were conducted with these numbers of samples.

In open areas, the abundance of both exotic forbs decreased with elevation (Table 1). Within cushions, the abundance of *T. officinale* also decreased with elevation but the abundance of *C. arvense* did not (Table 1). At all elevations, abundances of both exotics were substantially higher within cushions than in open areas (*t*-test $P < 0.01$ at all elevations). At the highest elevation, *C. arvense* was only found within cushions (Table 1).

The biomass of both exotics decreased with elevation in open areas, but no differences were observed across elevations within cushions (Table 1). The biomass of *T. officinale* was higher within cushions than in open areas at 3400 m and 3600 m (*t*-test $P < 0.05$ at both elevations), but no differences between habitats were detected at 3200 m (*t*-test $P = 0.73$). On the other hand, the biomass of *C. arvense* was higher within cushions than in open areas at all elevations (*t*-test $P < 0.01$ in all cases).

For both exotic species, the relative differences in abundance (Fig. 2a) and biomass (Fig. 2b) indicated that the positive effects of cushions on the performance of both *T. officinale* and *C. arvense* increased towards upper sites. These results strongly suggest that *A. monantha* cushions improve the performance of exotic species, in terms of abundance and biomass, with greater effects at higher elevations.

SURVIVAL OF INVADERS

T. officinale seedlings showed higher survival within cushions than in open areas at both 3200 m (Cox-Mantel test $P < 0.05$) and 3600 m (Cox-Mantel test $P < 0.01$), but the difference in seedling survival between habitats was greater at the highest elevation site (Fig. 3a). In contrast, *C. arvense* seedlings showed

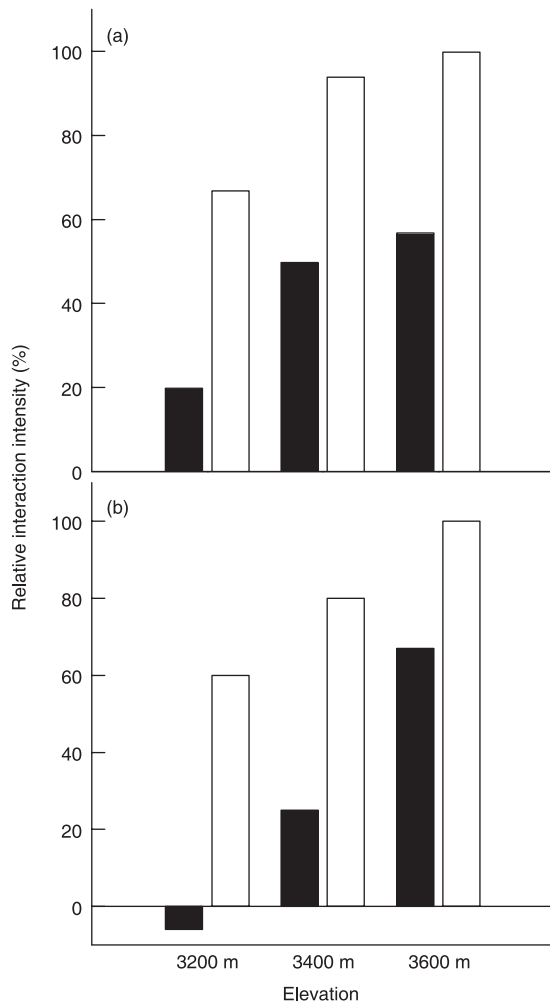


Fig. 2 Relative interaction intensity computed with the average abundance (a) and biomass (b) of *Taraxacum officinale* (black bars) and *Cerastium arvense* (white bars) within cushions and in surrounding open areas at the tree elevations considered in this study.

higher survival within cushions at the highest elevation site (Cox-Mantel test $P < 0.01$), but no differences were detected at the lowest elevation (Cox-Mantel test $P = 0.22$) (Fig. 3b). These results indicate that the effects of *A. monantha* cushions on the survival of both exotic forbs are higher at upper than lower elevation sites.

Discussion

There has been little research dealing with plant invasions in high-mountain ecosystems (e.g. Kitayama & Mueller-Dombois 1995; Johnston & Pickering 2001; Dullinger *et al.* 2003; Cavieres *et al.* 2005, 2007), and even fewer studies have evaluated how environmental gradients can affect biological invasions in these ecosystems (e.g. Western & Juvik 1983; Johnston & Pickering 2004; Becker *et al.* 2005). Our study clearly indicates that the harsher environmental conditions of open areas at high elevation sites decrease the performance of both *T. officinale* and *C. arvense*, concurring

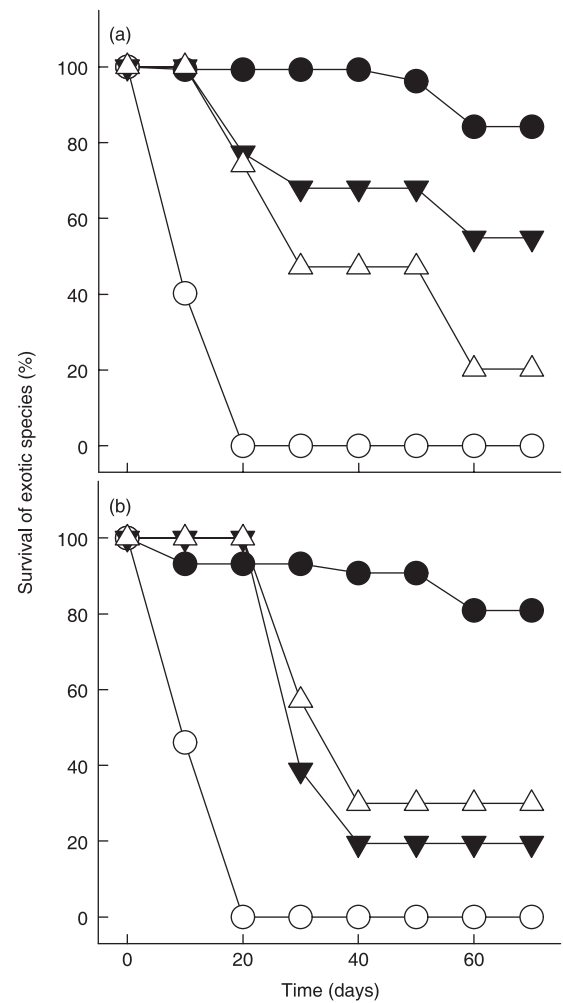


Fig. 3 Kaplan-Meier estimated survival of transplanted seedlings of *Taraxacum officinale* (a) and *Cerastium arvense* (b) within *Azorella monantha* cushions (black symbols) and in open areas (white symbols) at the highest (circles) and the lowest (triangles) elevation.

with the results of other studies that showed decreases in the success of plants with increasing environmental stress (Johnston & Pickering 2004; Becker *et al.* 2005; MacDougall *et al.* 2006). However, *A. monantha* had strong facilitative effects on both exotic species we studied, and these effects were stronger at higher elevations where abiotic conditions are harsher. *Azorella monantha* appears to act as an ecosystem engineer, ameliorating extreme high and low temperatures (Badano *et al.* 2006; Cavieres *et al.* 2007) and providing microsites with higher availability of soil nutrients (L. A. Cavieres, unpublished data).

Our results support the idea that amelioration of environmental harshness by cushions increases with elevation, agreeing with the general suggestion that organisms able to reduce environmental stress have more important impacts on other species as environmental stress increases (Bertness & Callaway 1994; Callaway 1998; Pugnaire & Luque 2001; Callaway *et al.* 2002; Cavieres *et al.* 2006; Crain & Bertness 2006). Moreover, our results concur with those reported in

previous studies showing positive effects of different cushion plant species on both exotic species in the high-Andes of Chile (Cavieres *et al.* 2007). For instance, at the lowest distribution limit of *A. monantha* cushions (3100–3200 m), it has been shown that *T. officinale* individuals have higher survival rates and higher net photosynthetic performances within than outside cushion-patches (Cavieres *et al.* 2005). Indeed, at lower elevations (2700–3100 m) where *A. monantha* cushions are not present, both *T. officinale* and *C. arvense* are commonly detected within habitat patches created by another cushion species belonging to the Apiaceae, *Laretia acaulis*, and it has been shown that *T. officinale* has higher photosynthetic performances, and *C. arvense* higher survival rates, within cushions of *L. acaulis* (Cavieres *et al.* 2006). In the present study we establish the potential of cushions to promote biological invasions along environmental gradients, making stressful landscapes more susceptible to biological invasions than expected in the absence of engineer species. Our results support the hypothesis that ecosystem engineering by *A. monantha* cushions would promote biological invasions towards higher stressful elevations through positive effects on both the recruitment and the performance of exotic species. While field observations indicate that both *T. officinale* and *C. arvense* produce viable seeds within and outside cushions, determining whether the reproductive success of exotics is higher within or outside cushions is an area for further research. Indeed, although results of the seedling transplant experiments suggest that improved seedling survival could be responsible for the higher abundance of exotics within cushion patches, other mechanisms such as seed delivery and germination may also influence the patterns observed.

Effects of invasive engineer species on native communities have been reported and discussed in recent years (Crooks & Khim 1999; Crooks 2002; Castilla *et al.* 2004; Cuddington & Hastings 2005). Indeed, Anderson *et al.* (2006) have reported that dam-building activities of introduced beavers (*Castor canadensis*) in Cape Horn, Chile, negatively affect the recruitment of native tree species while increasing the number of exotic herbaceous species. However, despite this large interest in evaluating the impacts of exotic ecosystem engineers, positive effects of native engineer species on exotic species, as in the present study, have not been previously recognized as a mechanism that may promote biological invasions. Our results support the hypothesis that engineer species that ameliorate environmental harshness positively affect the performance of invaders. Indeed, the fact that *C. arvense* was only detected within cushion-engineered habitat patches at the highest elevation strongly suggests that ecosystem engineering may increase the distributional range of exotic species along environmental gradients. Thus, given the conspicuousness of engineering processes in nature (Wright & Jones 2006), our results suggest that exotic species eradication

programmes might be less successful if they do not take into account the facilitative effects of native engineer species on invaders. Further, we suggest that the recent proposals to use engineer species in ecosystem restoration (Byers *et al.* 2006) should be aware of their potential role in promoting invasions. As our results suggest, the introduction of ecosystem engineers to restore degraded ecosystems may also result in an increased susceptibility of these ecosystems to invasion by exotic species.

Acknowledgements

This work was funded by FONDECYT 3060095 (E.I.B.), FONDAP-FONDECYT 1501–0001 (E.I.B., P.A.M.) and FONDECYT 1030821 (L.A.C.). Support from BBVA Foundation Prize in Conservation Biology Research 2004 and ICM P05-002 (R.O.B., P.A.M., L.A.C.) is also acknowledged. Part of this work was conducted while P.A.M. was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant DEB-0072909), the University of California, and the Santa Barbara campus.

References

- Anderson, C.B., Griffith, C.R., Rosemond, A.D., Rozzi, R. & Dollenz, O. (2006) The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile: do exotic beavers engineer differently in sub-Antarctic ecosystems? *Biological Conservation*, **128**, 467–474.
- Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: a new comparative index. *Ecology*, **85**, 2682–2686.
- Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A. & Arroyo-Kalin, M.A. (2003) Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, **169**, 121–129.
- Badano, E.I. & Cavieres, L.A. (2006a) Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Diversity and Distributions*, **12**, 388–396.
- Badano, E.I. & Cavieres, L.A. (2006b) Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography*, **33**, 304–313.
- Badano, E.I., Jones, C.G., Cavieres, L.A. & Wright, J.P. (2006) Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos*, **115**, 369–385.
- Barnard, P. & Waage, J.K. (2004) *Tackling Species Invasions Around the World: Regional Responses to the Invasive Alien Species Threat*. Global Invasive Species Programme, Cape Town.
- Becker, T., Dietz, H., Billeter, R., Buschmann, H. & Edwards, P.J. (2005) Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 173–183.
- Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks, J.A. & Wilson, W.G. (2006) Using ecosystem engineers to restore ecological systems. *Trends in Ecology and Evolution*, **21**, 493–500.

- Callaway, R.M. (1998) Competition and facilitation on elevation gradients in subalpine forest of the northern Rocky Mountains. *Oikos*, **82**, 561–573.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–847.
- Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436–443.
- Castilla, J.C., Lagos, N.A. & Cerda, M. (2004) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology Progress Series*, **268**, 119–130.
- Cavieres, L.A. & Arroyo, M.T.K. (1999) Tasa de enfriamiento adiabático del aire en la cuenca del Río Molina, Provincia de Santiago, Chile central (33° S). *Revista Geográfica de Chile Terra Australis*, **44**, 79–86.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Gómez-González, S. & Molina-Montenegro, M.A. (2006) Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist*, **169**, 59–69.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A. & Molina-Montenegro, M. (2007) Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native plants in the high-Andes of central Chile. *Arctic, Antarctic and Alpine Research*, **39**, 229–236.
- Cavieres, L.A., Peñaloza, A. & Arroyo, M.T.K. (2000) Altitudinal vegetation belts in the high-Andes of central Chile. *Revista Chilena de Historia Natural*, **73**, 331–344.
- Cavieres, L.A., Peñaloza, A., Papic, C. & Tambutti, M. (1998) Efecto nodriza del cojín *Laretia acaulis* (Umbelliferae) en la zona alto-andina de Chile Central. *Revista Chilena de Historia Natural*, **71**, 337–347.
- Cavieres, L.A., Quiroz, C.L., Molina-Montenegro, M.A., Muñoz, A.A. & Pauchard, A. (2005) Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 217–226.
- Crain, C.M. & Bertness, M.D. (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience*, **56**, 211–218.
- Crooks, J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, **97**, 153–166.
- Crooks, J.A. & Khim, H.S. (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology*, **240**, 53–75.
- Cuddington, K. & Hastings, A. (2005) Invasive engineers. *Ecological Modelling*, **178**, 335–347.
- Dullinger, S., Dirnböck, T. & Grabherr, G. (2003) Patterns of shrub invasion into high mountain grasslands of the northern calcareous Alps, Austria. *Arctic, Antarctic and Alpine Research*, **35**, 434–441.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, London.
- Hierro, J.L. & Callaway, R.M. (2003) Allelopathy and exotic plant invasion. *Plant and Soil*, **256**, 29–39.
- Johnston, F.M. & Pickering, C.M. (2001) Alien plants in the Australian Alps. *Mountain Research and Development*, **21**, 284–291.
- Johnston, F.M. & Pickering, C.M. (2004) Effect of altitude on resource allocation in the weed *Achillea millefolium* (yarrow, Asteraceae) in the Australian Alps. *Australian Journal of Botany*, **52**, 639–646.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.
- Kaplan, E.L. & Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association*, **53**, 457–481.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Kitayama, K. & Mueller-Dombois, D. (1995) Biological invasion on an oceanic island mountain: do alien plant species have wider ecological ranges than native species? *Journal of Vegetation Science*, **6**, 667–674.
- Lee, E.T., Desu, M.M. & Gehan, E.A. (1975) A Monte Carlo study of the power of some two-sample tests. *Biometrika*, **62**, 425–432.
- MacDougall, A.S., Boucher, J., Turkington, R. & Bradfield, G.E. (2006) Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science*, **17**, 47–56.
- Pugnaire, F.I. & Luque, M.T. (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.
- Reinhart, K.O., Maestre, F.T. & Callaway, R.M. (2006) Facilitation and inhibition of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a mountain ecosystem. *Biological Invasions*, **8**, 231–240.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000) Plant invasions: the role of mutualisms. *Biological Reviews*, **75**, 65–93.
- Rodríguez, L. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impact occur. *Biological Invasions*, **8**, 927–939.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Santibáñez, F. & Uribe, J.M. (1990) *Atlas Agroclimático de la V Región Y Región Metropolitana*. Universidad de Chile, Santiago.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.
- Tecco, P.A., Gurvich, D.E., Diaz, S., Pérez-Harguindeguy, N. & Cabido, M. (2006) Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. *Austral Ecology*, **31**, 293–300.
- Western, L. & Juvik, J.O. (1983) Roadside plant communities on Mauna Loa, Hawaii. *Journal of Biogeography*, **10**, 307–316.
- Wright, J.P. & Jones, C.G. (2004) Predicting the effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology*, **85**, 2071–2081.
- Wright, J.P. & Jones, C.G. (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Bioscience*, **56**, 203–209.
- Wright, J.P., Jones, C.G., Boeken, B. & Shachak, M. (2006) Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology*, **94**, 815–824.
- Wright, J.P., Jones, C.G. & Flecker, A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.

Received 18 November 2006; revision accepted 13 April 2007
Handling Editor: Ray Callaway