



Facilitation by nurse plants regulates community invasibility in harsh environments

Ernesto I. Badano, Ramiro O. Bustamante, Elisa Villarroel, Pablo A. Marquet & Lohengrin A. Cavieres

Keywords

Alien species; Alpine environments; Biological invasions; Biotic acceptance; Biotic resistance; Cushion plants; Positive interactions

Nomenclature

Marticorena & Quezada (1985)

Received 4 October 2014

Accepted 1 January 2015

Co-ordinating Editor: Stephen Roxburgh

Badano, E.I. (corresponding author, ernesto.badano@ipicyt.edu.mx)¹,

Bustamante, R.O. (rbustama@uchile.cl)²,

Villarroel, E. (sli666@gmail.com)²,

Marquet, P.A. (pmarquet@bio.puc.cl)^{3,4},

Cavieres, L.A. (lcaviere@udec.cl)⁵

¹División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica, A.C. Camino a la Presa San José 2055, C.P. 78216, San Luis Potosí, México;

²Departamento de Ciencias Ecológicas, Instituto de Ecología y Biodiversidad (EIB), Universidad de Chile, Casilla 653, Las Palmeras 3425, Ñuñoa, Santiago, Chile;

³Departamento de Ecología, Laboratorio Internacional en Cambio Global (LINCGlobal), Instituto de Ecología y Biodiversidad (EIB), Pontificia Universidad Católica de Chile, Avda. Libertador Bernardo O'Higgins 340, Santiago, Chile;

⁴The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM, 87501, USA;

⁵Departamento de Botánica, Instituto de Ecología y Biodiversidad (EIB), Universidad de Concepción, Barrio Universitario, Casilla 160-C, Concepción, Chile

Introduction

The spread of alien species due to human activities is a worldwide threat to biodiversity (Kowarik & von der Lippe 2007) because they may colonize natural communities and displace native species (Richardson et al. 2011). However, the *invasibility* of natural communities – i.e. their

Abstract

Question: The biotic resistance hypothesis states that species diversity is a barrier for plant biological invasions because alien species are more likely to find strong competitors as diversity of native plants increases. In stressful environments, however, these negative relationships could be diluted because increased physical harshness might reduce the importance of competition as a structuring force in plant communities. Nevertheless, if nurse plants facilitate other species and create more diverse vegetation patches than those found in their surroundings, the performance of invaders should be negatively related to diversity within these patches. Conversely, diversity would not regulate invasibility in the surroundings of nurses because these habitats are subjected to higher levels of environmental harshness.

Location: A high-Andean landscape of central Chile, dominated by cushion plants that facilitate native species and field chickweed (*Cerastium arvense*), an invasive exotic species.

Methods: To test our hypotheses we used observational data taken in two consecutive growing seasons by sampling plant assemblages within and outside cushion-protected patches. Additionally, a field experiment with artificially assembled plant communities was conducted to assess why the abundance and performance of the invasive species was related to native plant diversity.

Results: Contrary to our expectations, observational data indicated that the abundance of the invader species was positively related to native plant diversity within cushion patches, while negative relationships were found in the surrounding habitat. Similarly, the field experiment indicated that the performance of *C. arvense* increased with plant diversity within cushion patches but, in this case, neutral relationships were found in the surrounding open areas.

Conclusions: Our findings indicate that nurse plants can modulate invasibility–diversity relationships in harsh environments. Overall, the results suggest that the biotic resistance hypothesis may fail to predict the direction of these relationships within nurse-protected patches. Instead, these results suggest that the alternative biotic acceptance hypothesis could operate at small spatial scales.

inherent susceptibility to be invaded – depends on the local diversity of native species (Alpert et al. 2000). On this issue, the *biotic resistance hypothesis* proposes that newly arrived species are more likely to find strong competitors that preclude their success as the number of native species increases and, thus, local diversity acts as a barrier for biological invasions (Rejmanek 1996; Levine & D'Antonio

1999; Byers & Noonburg 2003). This hypothesis has been tested through manipulating plant communities, where the physiological and/or reproductive performance of invader plants was shown to decrease as native species richness increases (Levine 2000; Naem et al. 2000; Kennedy et al. 2002; Maron & Marler 2007). Nevertheless, when spatial scales are expanded beyond the neighbourhoods of two or more interacting species, the cover and biomass of alien plants have been reported to increase with native species richness (Sax 2002). This has led to the *biotic acceptance hypothesis*, which states that increased resource availability and/or habitat heterogeneity associated with increased surface area is the main force regulating the performance and diversity of both, native and alien species (Shea & Chesson 2002; Stohlgren et al. 2006). The apparent disconnect between these two hypotheses is paradoxical (Sax & Brown 2000) and is the subject of an active debate among invasion biologists (Fridley et al. 2007).

Although these two hypotheses attempt to predict the direction of invasibility–diversity relationships, neither of them takes into account that local variations in environmental conditions may also affect interactions between native and invasive species. For instance, increased environmental harshness reduces the overall performance of plants and, consequently, has the potential to reduce the importance of competition as a structuring force in plant communities (Bertness & Callaway 1994; Grime 2001; Badano et al. 2005; Callaway 2007; Brooker & Kikvidze 2008). If so, the negative invasibility–diversity relationships predicted by the biotic resistance hypothesis may not hold in harsh ecosystems (Alpert et al. 2000; Von Holle 2013). In these ecosystems, however, some plants are able to mitigate extreme environmental conditions through their physical structures (i.e. canopies and/or root systems), hence facilitating the establishment of other species (Maestre et al. 2001; Cavieres et al. 2006). These nurse plants usually create vegetation patches with higher diversity than those found in the surrounding habitat (Tewksbury & Lloyd 2001; Cavieres & Badano 2009), but alien species can also spread within these patches (Badano et al. 2007; Von Holle 2013). Thus, if native and exotic species benefit from nurse plants, it could be predicted that increased species diversity within these patches will lead to negative invasibility–diversity relationships because of increased interspecific competition due to niche overlap. Further, negative invasibility–diversity relationships could also result from density-dependent competition processes, where increased density of native plants, instead of increased diversity, would reduce establishment rates and/or the performance of invaders within facilitated vegetation patches. On the contrary, vegetation patches surrounding nurse plants should exhibit no invasibility–diversity relationships because the high levels of physical

stress associated with this habitat type should decrease the importance of competitive effects among plants.

To test these hypotheses we focused on an alpine landscape from South America, where native and invasive plants grow within and outside nurse-protected patches. The target invader species was the field chickweed, *Cerastium arvense* L. (Caryophyllaceae), a perennial herb native to North America (Ugborogho 1977) that has largely invaded the southern Andes (Matthei 1995). In these landscapes, however, the invasive success of *C. arvense* depends on the presence of cushion plants that act as nurses (Badano et al. 2007; Cavieres et al. 2007). High-Andean cushion plants have closed and compact canopies, and subsurface accumulation of tightly packed living and dead plant material. This allows cushion plants (hereafter *cushions*) to decouple their surface temperature from that of the external environment (Badano et al. 2006; Cavieres et al. 2007), as well as increase soil moisture and the concentration of mineral nutrients beneath their canopies (Núñez et al. 1999; Badano et al. 2006; Cavieres et al. 2007). These abiotic modifications enhance the establishment and survival of several plant species (Cavieres et al. 2007; Badano & Marquet 2009), creating more diverse vegetation patches than those found in the surrounding habitat, or open areas, which are mainly composed of rocks and bare soil (Cavieres & Badano 2009). Thus, our overall expectation was to find strong negative relationships between the performance of *C. arvense* and the diversity or density of native plants within cushions, while no relationships were expected in their surrounding habitat. These hypotheses were tested using observational data taken in the field during two consecutive growing seasons, which should reflect the natural distribution patterns of native and invasive species across cushions and open areas. Additionally, a field experiment was conducted to determine the putative mechanisms behind these invasibility–diversity relationships.

Methods

Study site

This study was conducted on the southwest-facing slope of Mt. Tres Puntas (33°19′24.19″ S, 70°14′20.53″ W, 3420 m a.s.l.), within the ski centre Valle Nevado, high Andes of Central Chile. Climate is alpine, but it is strongly influenced by the mediterranean-type climate that predominates at lower elevations (Di Castri & Hajek 1976). Annual precipitation exceeds 900 mm and mainly occurs as snow during winter months (June–August; Santibáñez & Uribe 1990). The snow cover usually remains until October and the growing season for plant communities starts in November (Badano et al. 2007). Air temperature during the growing season varies between 4 and 6 °C (Cavieres &

Arroyo 1999), but can fall below 0 °C predawn (Badano et al. 2006). Soils in this region are mainly composed of clay, mixed with sedimentary and volcanic rocks. The cushion plant *Azorella madreporica* Clos (Apiaceae) is the most conspicuous element in plant communities above 3200 m a.s.l., but small perennial and annual herbs, including *C. arvensis*, can be found within and outside these cushions (Appendix S1). This cushion species creates semi-circular, spatially discrete habitat patches composed of a single individual that are isolated from similar units by large open areas (Appendix S1). Cushions of *A. madreporica* may reach up to 3 m in diameter and persist over several decades (Fajardo et al. 2008), covering between 14% and 20% of the total surface area in these landscapes (Badano et al. 2007).

Vegetation sampling and diversity measures

First, we focused on determining whether the abundance of naturally established individuals of *C. arvensis* was related to the diversity of plant assemblages growing within and outside *A. madreporica* cushions. For this, vegetation was sampled in the middle (February) of two consecutive growing seasons (2006 and 2007). At each growing season, a plot of 50 m × 50 m was laid out in the study area and all cushions and sites in the open areas where *C. arvensis* was detected were marked. On each mark, a 0.2-m² metallic ring was centred on the tallest *C. arvensis* individual and all plants within the ring, including the invader, were identified and counted. The cushions of *A. madreporica* were not included in this sampling (i.e. they were not recorded as another native species) because we were interested in assessing their effects on *C. arvensis* and the diversity of native plants. Although the fieldwork was conducted within a ski centre, plants from the study site are not affected by anthropic disturbances because these sport activities are only developed in winter, when vegetation is protected by a coarse snow cover (>3-m depth).

Diversity of native species at each sample was estimated through their three main components: species richness, proportional diversity and species dominance (Stirling & Wilsey 2001). Species richness was estimated as the number of different native species recorded in each sample. Proportional diversity was estimated with the Shannon–Wiener index, calculated as $\sum_{i=1}^S p_i \ln(p_i)$, where p_i is the proportion of individuals of the i th species in the sample (Magurran 2004). Species dominance was estimated as the fraction of individuals in the sample that belonged to the most common native species (Magurran 2004). We used these diversity metrics because the values of the Shannon–Wiener index are positively related to increases in species richness, while they are negatively related to increases in species dominance (Stirling & Wilsey 2001). Therefore,

computing these three metrics allows us to identify how each diversity component relates to invasion success of *C. arvensis*.

These data were used to assess whether the observed abundance of *C. arvensis* was related to diversity metrics of samples. For this, we used multiple linear regression analyses with categorical variables, where the number of *C. arvensis* individuals detected in the samples was the dependent variable. These values were transformed to natural logarithms to achieve normality of data. Diversity metrics (species richness, Shannon–Wiener index or species dominance) were separately included in the regression model as the continuous predictive variable, and the habitat type where samples were taken (cushions and open areas) constituted the two levels of the categorical predictive variable. Further, to assess whether the abundance of *C. arvensis* was affected by density-dependent effects, an additional analysis was performed by including the log-transformed abundances of native individuals, irrespective of the species they belong to, as continuous predictive variable. All regression models included the interaction term between predictive variables to account for differences in the slopes of regression functions obtained for each level of the categorical variable (Kutner et al. 2005).

Field experiment

A field experiment was conducted to assess whether the performance of *C. arvensis* changes with varying levels of diversity and density of native plants, and hence to elucidate the putative mechanisms behind the invasibility–diversity relationships. For this, seeds of *C. arvensis* and 29 native plant species that were found within and outside cushions were collected in March 2006 at the study site (details on species collected for this experiment are provided in Appendix S2). Soil from open areas was also collected at this time and sieved to remove stones and coarse material. This soil was sterilized in a ventilated oven at 200 °C to eliminate any biological activity and used as substrate to develop experimental plant assemblages with different diversity levels of native plants (see below). Only soil from open areas was used in this experiment because concentrations of organic matter and mineral nutrients differ between cushions and open areas (Cavieres et al. 2006) and, thus, we preferred to standardize these effects using a single soil type in our experiments.

In October 2006, 100 cylindrical plastic pots (10-cm diameter, 15-cm depth) were filled with sterilized soil and 20 seeds of *C. arvensis* sown in each pot. These pots were later pooled into five groups of 20 units each and seeds of native species were sown to generate five different levels of species diversity (0, 1, 2, 4 and 8 species). The first group of pots received no seeds of native species because it was

the control group (i.e. native species diversity = 0) on which we evaluated the performance of *C. arvensis* in the absence of native plants. All other pots received 48 seeds of native species. The propagule pressure of native species was evenly distributed across these experimental pots. To achieve this, pots with one native species received 48 seeds of a single species that was randomly selected from the seed pool; pots containing two native species received 24 seeds of two randomly selected species; pots with four native species received 12 seeds of four randomly selected species; and pots containing eight native species received six seeds of eight randomly selected species (species composition of the different experimental pots is provided in Appendix S2).

Because germination is hard to obtain in the field, seeds were germinated in growth chambers between November and December 2006 (25 °C, 70% RH, photoperiod 12 h light/dark). However, despite the high sowing density applied to each experimental pot (48 seeds of native species plus 20 seeds of *C. arvensis* per pot), some seeds did not germinate during the incubation period and the number of seedlings of both *C. arvensis* and native species varied across pots. To avoid confounding effects due to differences in germination ratios, seedlings were selectively removed to standardize plant assemblages. In all experimental pots we left ten seedlings of *C. arvensis* and, although the number of native species initially sown was maintained, the number of seedlings of native species was reduced to 24 individuals per pot. In this way, pots containing no native species only had ten seedlings of *C. arvensis*, while pots with one, two, four and eight native species had ten seedlings of *C. arvensis* plus 24 seedlings of the native species that were originally sown.

These experimental pots were taken to the field on 15 Jan 2007 and, after removing the plastic container, were transplanted into either cushions or into the surrounding open areas. All cushions selected for this experiment were between 80-cm and 100-cm diameter to avoid potential biases due to cushion size. Both cushions and sites in open areas were selected by following random walking procedures. For this, we initially selected a cushion that met the criteria indicated above and drilled a small hole (10-cm diameter, 15-cm depth) in the canopy to transplant the first experimental plant assemblage. After that, a random number generator was used to establish a cardinal direction, which was followed until the next cushion was intercepted. Transplants in open areas were conducted at the mid-point between these two cushions, taking care to maintain a minimum distance of 1 m to the nearest other cushion. This procedure was repeated until all pots were transplanted, which resulted in ten experimental replicates of each diversity level (0, 1, 2, 4 and 8 native species) at each habitat type (details on experimental pots

transplanted within cushions and open areas is provided in Appendix S2). The transplanted experimental pots were watered after planting to reduce the impact of seedling manipulation, but no water was supplied thereafter. All transplanted pots were marked with numbered metallic strips.

At the end of the growing season (16 Mar 2007) we counted the number of survivors of *C. arvensis* and native species within all transplanted pots. Survivors of native species at each location were used to estimate the three diversity metrics described in the previous section. After that, we carefully removed each of the *C. arvensis* individuals and stored them in separate labelled paper bags. To avoid metabolic degradation of tissues, these bags were placed in a ventilated oven (75 °C) within 2 h of collection until they were completely dried. Each *C. arvensis* individual was weighed to record total dry biomass and, after that, shoots and roots of each individual were weighed separately to determine above-ground and below-ground biomass. For transplants containing more than one surviving individual of *C. arvensis*, biomass values were averaged across individuals to avoid pseudoreplication in the analyses described below (Hurlbert 1984). The average shoot/root ratio of *C. arvensis* was also calculated for each pot to assess the mechanisms by which native plants may affect the performance of this exotic species. This ratio is commonly used to determine whether competition occurs in plant communities, where shoot/root ratios >1.0 suggest that above-ground competition is higher than below-ground competition, while values close to zero indicate the converse situation (Reynolds & Pacala 1993).

Multiple linear regression analyses with categorical variables were used to assess whether the abundance, dry biomass (total, shoot and root biomass) and shoot/root ratios of *C. arvensis* were related to the different diversity metrics calculated for each pot, as well as to the number of native individuals that survived until the end of the experiment. These analyses were conducted by following the same procedure described in the previous section. The abundance of *C. arvensis* in experimental pots was transformed to the natural logarithm to achieve normality.

Results

Naturally established plant assemblages

In both growing seasons, the abundance of *C. arvensis* was positively related to the richness of native plant assemblages growing within cushions, but negatively related in the open areas (Table 1, Fig. 1a,b). Positive relationships were also found between the abundance of *C. arvensis* and the proportional diversity of plant assemblages within cushions, while these relationships were negative in the open areas (Table 1, Fig. 1c,d). Conversely, while the

Table 1. Results of multiple regression analyses conducted to assess whether the abundance of *Cerastium arvense* was related to diversity metrics (species richness, Shannon–Weiner index, species dominance and abundance of native individuals) in samples taken within *Azorella madreporica* cushions ($n = 31$ in 2006; $n = 27$ in 2007) and the surrounding open areas ($n = 19$ in 2006; $n = 15$ in 2007). The table shows ANOVA results for each growing season and probability values for differences between intercepts (β_0) and slopes (β_1) of regression functions obtained for each habitat type (critical $\alpha = 0.05$). Differences in intercepts indicate different origin points for these regression functions, while differences in slopes indicate significant effects of the interaction term between predictive variables.

Diversity Measure	Growing Season	Overall Goodness of Fit ANOVA			Parameters of Regression Functions	
		F-Value (df)	P-Value	R ²	β_0 P-Value	β_1 P-Value
Species Richness	2006	69.7195 (3,46)	<0.0001	0.8197	<0.0001	<0.0001
	2007	83.9851 (3,38)	<0.0001	0.8689	<0.0001	<0.0001
Shannon–Weiner Index	2006	67.7199 (3,46)	<0.0001	0.8154	<0.0001	<0.0001
	2007	95.2031 (3,38)	<0.0001	0.8826	<0.0001	<0.0001
Species Dominance	2006	39.2807 (3,46)	<0.0001	0.7192	<0.0001	<0.0001
	2007	40.8283 (3,38)	<0.0001	0.7632	<0.0001	<0.0001
Abundance of Native Individuals	2006	39.6235 (3,46)	<0.0001	0.7210	<0.0001	<0.0001
	2007	40.2946 (3,38)	<0.0001	0.7608	<0.0001	<0.0001

abundance of *C. arvense* decreased with increasing native species dominance within cushions, positive relationships between these two variables were found in the open areas (Table 1, Fig. 1e,f). Finally, in both growing seasons, the abundance of *C. arvense* was positively related to the abundance of individuals of native plants inhabiting cushions, while these relationships were negative in the open areas (Table 1, Fig. 1g,h).

Experimental plant assemblages

Of the 50 experimental pots transplanted into each habitat type, only 15 pots from cushions and nine pots from the open areas contained at least one living individual of *C. arvense* when they were recovered in March 2007. Besides affecting the abundance of *C. arvense*, plant mortality also led to different diversity levels of native species than those originally implemented. For instance, no pot with eight native species was recovered, but some replicates of this treatment persisted until the end of the experiment with fewer species (see Appendix S2 for details on surviving species in each experimental pot). Therefore, the analyses conducted with experimental data only included pots where at least one individual of *C. arvense* survived until the end of the experiment. Pots containing no native species were excluded from regression analyses where the Shannon–Wiener index or species dominance were used as predictive variables because these diversity measures could not be computed.

The average number of surviving individuals of *C. arvense* was higher within cushions than in the open areas. No relationships were found in the open areas (Table 2). Within cushions, the number of *C. arvense* survivors was positively related to native species richness (Fig. 2a), the Shannon–Wiener index (Fig. 2b) and the abundance of

native species individuals (Fig. 2d), but negatively related to increases in species dominance (Fig. 2c). The average biomass of *C. arvense* individuals was higher within cushions than in the open areas (Table 1), but the values of this variable were not related to diversity metrics in either of these habitat types (Fig. 2e–h).

Shoot biomass of *C. arvense* was higher within cushions than in the open areas, and showed different relationships to diversity metrics (Table 2). Within cushions, shoot biomass was positively related to native species richness (Fig. 3a), the Shannon–Wiener index (Fig. 3b) and the abundance of native species individuals (Fig. 3d), but it was negatively related to species dominance (Fig. 3c). In the open areas, however, no relationships were found between the shoot biomass of *C. arvense* and any of these predictive variables (Fig. 3a–d). Root biomass of *C. arvense* was also higher within cushions than in the open areas (Table 1), but no relationships were found between this variable and diversity metrics estimated for experimental pots recovered from cushions or open areas (Fig. 3e–h). Shoot/root ratios of *C. arvense* were higher within cushions than in the open areas and were differentially related to diversity metrics (Table 1). Shoot/root ratios within cushions increased with species richness (Fig. 3i), the Shannon–Wiener index (Fig. 3j) and the abundance of native individuals (Fig. 3l), but decreased with increasing species dominance (Fig. 3k). In the open areas, no relationships were found between shoot/root ratios and diversity measures (Fig. 3i–l).

Discussion

It has been widely reported that amelioration of environmental harshness by cushion plants improves the survival and increases the biomass of other high-Andean plant

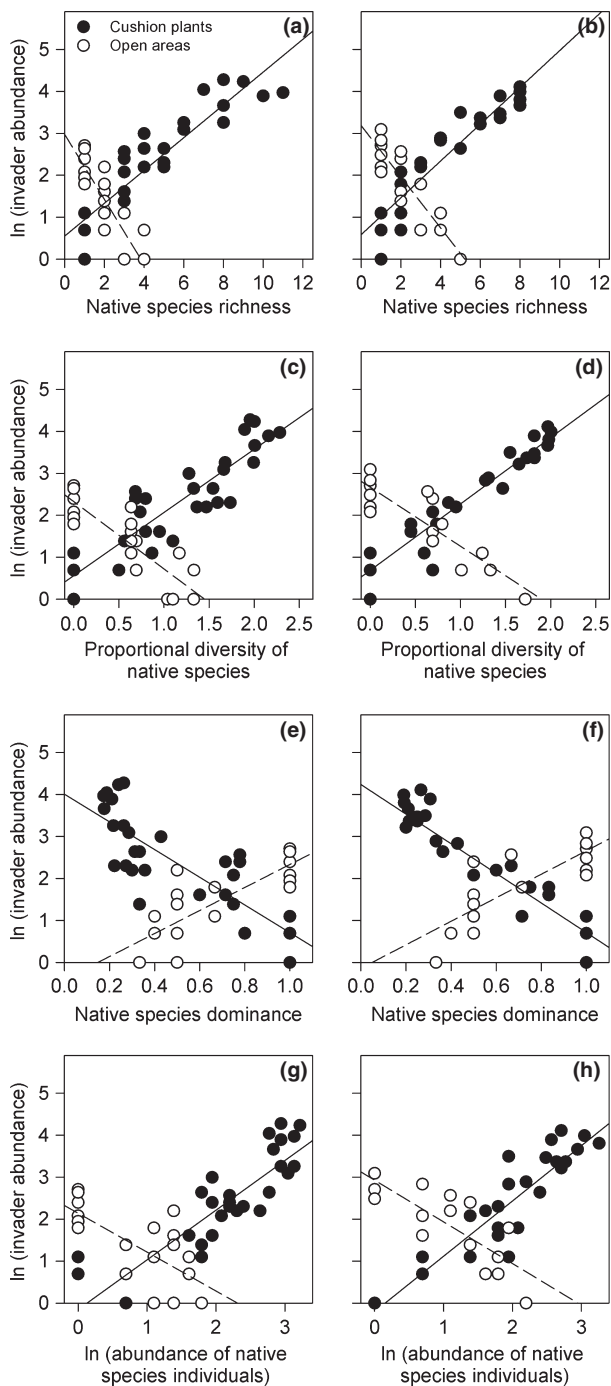


Fig. 1. Relationships between the abundance of *C. arvensis* and the different diversity metrics estimated for native plant assemblages sampled within *A. madreporica* cushions and in open areas in growing seasons 2006 (left column) and 2007 (right column). Diversity metrics include species richness (a,b), Shannon–Wiener index of proportional diversity (c,d), species dominance (e, f) and abundance of native species individuals (g, h).

species (e.g. Cavieres et al. 2006, 2007; Badano & Marquet 2009), leading to more diverse vegetation patches than those established in the surrounding open areas (Badano

et al. 2006; Cavieres & Badano 2009). According to our initial hypothesis, this increased diversity of species within cushions should decrease the success of exotic plants, as compared to that occurring in the less diverse plant assemblages inhabiting the surrounding open areas. In sharp contrast, both observational and experimental results of this study indicated that the performance of the invasive plant *C. arvensis* was positively affected by increasing diversity of native species within the habitat patches created by the cushion plant *A. madreporica*, while these relationships were negative or absent in the surrounding open areas. This suggests that other factors, besides interspecific competition due to niche overlap or density-dependent limited resource availability, might influence the strength and direction of invasibility–diversity relationships in these two habitat types.

In the open areas, observational data obtained from two consecutive growing seasons indicated negative relationships between the abundance of *C. arvensis* and native species richness. This suggests that, despite the elevated environmental harshness in this habitat type, negative interactions between native and exotic species occur to some extent, and this would partially support the biotic resistance hypothesis (Chesson & Huntly 1997; Levine & D’Antonio 1999; Byers & Noonburg 2003). Nevertheless, these data also indicated that the abundance of *C. arvensis* in open areas decreased with increased proportional diversity (i.e. the Shannon–Wiener index), while converse relationships were obtained with rising native species dominance. Thus, species richness is not the only component of diversity that affects the success of the invader in open areas, and other mechanisms, beside pair-wise interspecific interactions, may be involved in determining the performance of *C. arvensis* in this habitat type. Related to this issue, Mitchley (1987) proposed that competitive interactions within local plant assemblages might involve many neighbours and, therefore, the net impact of competition on a single target species should be stronger as the number and/or abundance of other species increases in their surroundings. This *diffuse competition* (Mitchley 1987) may be responsible, at least in part, for the negative relationships observed between the abundance of *C. arvensis* and the diversity metrics that involved the abundance of native species in open areas, as occurred with the Shannon–Wiener index. Further, because the Shannon–Wiener index involves both the number of different species and their respective relative abundances (Magurran 2004), this diversity metric is positively related to species richness and negatively related to species dominance (Stirling & Wilsey 2001). Thus, our results suggest that increases in proportional diversity due to decreased dominance and increased species richness may preclude the success of the invader via diffuse competition, leading to negative

Table 2. Results of multiple regression analyses conducted to assess whether performance of *Cerastium arvense* were related to diversity metrics (species richness, Shannon–Weiner index, species dominance and abundance of native individuals) in experimental plant assemblages located within *Azorella madreporica* cushions ($n = 15$) and the open areas ($n = 9$). Full data were only included in regressions where species richness was the predictive variable. In all other analyses, pots containing no native species were excluded because diversity measures could not be computed. The table shows the ANOVA results for each performance measure and the probability values for differences between intercepts (β_0) and slopes (β_1) of regression functions obtained for each habitat type (critical $\alpha = 0.05$). Differences in intercepts indicate different origin points for these regression functions, while differences in slopes indicate significant effects of the interaction term between predictive variables.

Diversity Measure	Performance Measure of <i>C. arvense</i>	Overall Goodness of Fit ANOVA			Parameters of Regression Functions	
		F-Value (df)	P-Value	R ²	β_0 P-Value	β_1 P-Value
Species Richness	Number of survivors	11.7459 (3,20)	0.0001	0.638	0.0119	0.0027
	Individual biomass	35.2091 (3,20)	<0.0001	0.841	0.0002	0.0683
	Shoot biomass	62.5315 (3,20)	<0.0001	0.903	0.0015	0.0011
	Root biomass	12.9086 (3,20)	<0.0001	0.659	<0.0001	0.1452
	Shoot/root ratio	62.3253 (3,20)	<0.0001	0.910	0.0899	<0.0001
Shannon–Weiner Index	Number of survivors	12.3836 (3,13)	0.0004	0.741	0.0053	0.0044
	Individual biomass	20.6095 (3,13)	<0.0001	0.826	0.0024	0.1302
	Shoot biomass	35.0655 (3,13)	<0.0001	0.890	0.0035	0.0161
	Root biomass	8.6762 (3,13)	0.0020	0.667	0.0008	0.4405
	Shoot/root ratio	42.6725 (3,13)	<0.0001	0.902	0.9676	0.0012
Species Dominance	Number of survivors	16.2701 (3,13)	0.0001	0.790	0.0196	0.0294
	Individual biomass	19.9697 (3,13)	<0.0001	0.821	0.0045	0.1354
	Shoot biomass	32.208 (3,13)	<0.0001	0.881	0.0004	0.0168
	Root biomass	10.0200 (3,13)	0.0011	0.698	0.0176	0.3363
	Shoot/root ratio	47.6639 (3,13)	<0.0001	0.917	<0.0001	0.0005
Abundance of Native Individuals	Number of survivors	6.3186 (3,13)	0.0034	0.487	0.0235	0.0085
	Individual biomass	31.0271 (3,13)	<0.0001	0.823	0.0013	0.0949
	Shoot biomass	39.1244 (3,13)	<0.0001	0.854	0.0482	0.0044
	Root biomass	10.5028 (3,13)	<0.0001	0.612	0.0002	0.0925
	Shoot/root ratio	18.6416 (3,13)	<0.0001	0.737	0.1495	0.0030

relationships between *C. arvense* invasibility and species diversity in the open areas. Alternatively, the positive relationships between invasibility and species dominance observed in the open areas may be due to greater niche space availability for the invader as native plant richness decreases, which would also lead to negative relationships between invasibility and proportional diversity (i.e. the Shannon–Wiener index).

The experimental results obtained in the open areas, however, indicated that neither the abundance nor the biomass of *C. arvense* is related to native species diversity or the abundance of individuals. Although this concurs with our overall expectation that severe environmental conditions predominating in the open areas relax the intensity of competition between native and alien plants, these results contradict those obtained from observational data taken in this habitat type. This lack of congruence between observational and experimental results suggests that negative invasibility–diversity relationships in the open areas result from long-term processes. On this issue, it is important to note that most species from these high-Andean environments are perennial plants that re-sprout every year after the snowmelt (Cavieres et al. 2000), but their

seedlings are subject to elevated mortality in the open areas (Cavieres et al. 2006, 2007; Badano et al. 2007). Therefore, the natural distribution patterns of *C. arvense* and native plants in this habitat type may be the output of establishment processes that have occurred across several growing seasons, and the negative invasibility–diversity relationships obtained from observational data would be a consequence of these long-term processes. The absence of these relationships in the experimental plant assemblages may thus be a consequence of the time scale used in our experiment (a single growing season), which would not be long enough to fully capture the competitive processes that structure these plant assemblages. Further, it is important to recognize that the number of experimental pots recovered at the end of the growing season was much lower than that originally transplanted, and this reduced number of replicates could make it more difficult to obtain significant invasibility–diversity relationships from experimental data. Thus, experiments including several years of monitoring and an elevated number of replicates would be required to assess the exact mechanisms by which native species affect the performance of *C. arvense* in the open areas of these high-Andean ecosystems.

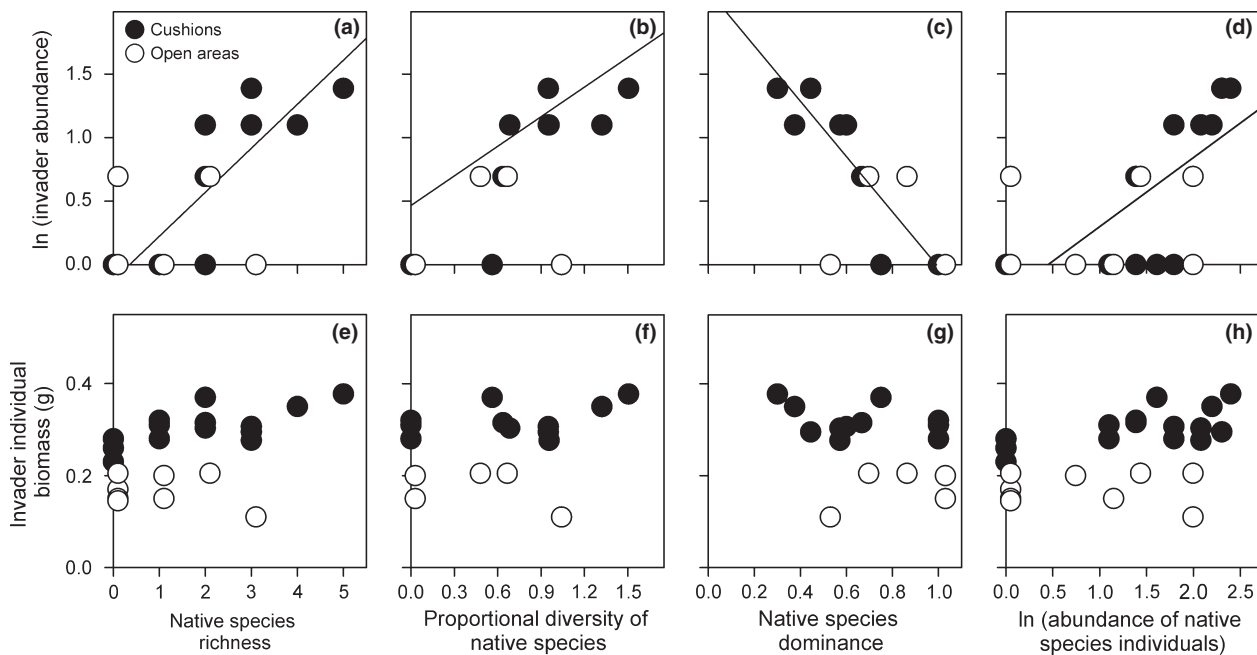


Fig. 2. Relationships between the abundance (a–d) and individual biomass (e–h) of *C. arvensis* and diversity metrics estimated for experimental native plant assemblages located within *A. madreporica* cushions and in open areas. Diversity metrics include species richness, Shannon–Wiener index of proportional diversity, species dominance and abundance of native species individuals.

Within *A. madreporica* cushions, both observational and experimental results contradicted our expectation that increased species diversity would reduce invasibility within these plant assemblages. On the contrary, the abundance and performance of the invader were positively related to native species diversity. These results suggest that the biotic acceptance hypothesis may be operating within cushion-facilitated vegetation patches (Stohlgren et al. 2006). However, this suggestion implies the existence of considerable variation in the magnitude with which different cushions modulate habitat conditions to other species. This may occur, for instance, if cushions differentially modulate resource availability for plant species that germinate and establish on their canopies. In this scenario, nurse-protected patches of different quality would exist across the landscape and, by following the biotic acceptance hypothesis, it could be predicted that those patches of higher habitat quality would harbour more species and would be more strongly invaded by *C. arvensis* than patches of lower environmental quality. Nevertheless, determining the viability of this proposal would require detailed studies focused on assessing the ability of different cushion individuals to modulate environmental conditions for other species.

The increased performance of *C. arvensis* with rising species diversity within cushions may also be due to positive interactions that occur among species that are already facilitated by these nurse plants. By following this line of

reasoning, two mechanisms might explain these positive relationships. On the one hand, these positive relationships could be merely due to sampling effects, where the likelihood of occurrence of a given event depends on the number of favourable conditions that promote the occurrence of that event in the system (Wardle 2001; Aarssen et al. 2003). If so, increased diversity of plant assemblages within nurse-protected patches would increase the likelihood of including an additional facilitator species that positively impacts on the performance of the invader. However, the relationships between the abundance of *C. arvensis* and diversity metrics are considerably sub-linear (i.e. the slopes of regression functions were much <1) for both observational and experimental data. This suggests that sampling effects would not be the only processes involved in these relationships (as they would lead to linear or proportional trends) but something else causes this nonlinearity, such that as native species richness increases the per capita positive effect of an additional native species upon the abundance of *C. arvensis* becomes smaller. The most likely explanation for these relationships is that *diffuse positive interactions* are occurring in plant assemblages inhabiting cushions. Concerning this issue, Callaway et al. (2002) have shown that several neighbouring species, rather than a single nurse, may be responsible for protecting a target plant in alpine environments. Thus, once plant assemblages are facilitated through *A. madreporica* cushions, an increased diversity of neighbours may facilitate

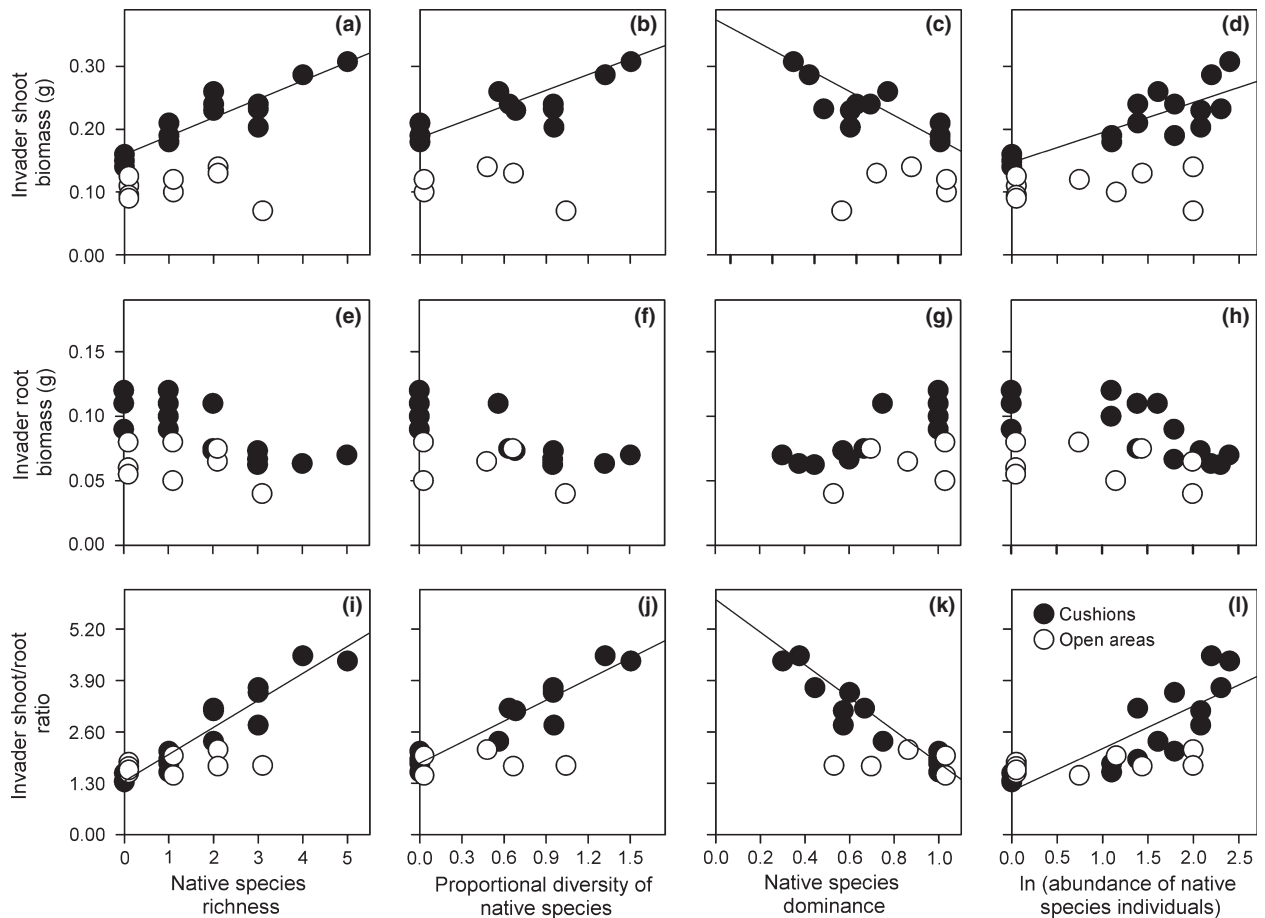


Fig. 3. Relationships between the shoot biomass (a–d), root biomass (e–h) and shoot/root ratio (i–l) of *C. arvense* and diversity metrics estimated for experimental native plant assemblages located within *A. madreporica* cushions and in open areas. Diversity metrics include species richness, Shannon–Wiener index of proportional diversity, species dominance and abundance of native species individuals.

the establishment of the invader and improve its performance. Nevertheless, it is also important to note that both the abundance and the performance of *C. arvense* decreased with increased species dominance within cushions. These results support the idea that a single, highly abundant native species could monopolize the resources within cushion patches and lead to more competitive environments for other plants. Therefore, the increased abundance of a single species within cushions could reduce the performance of both the invader and other native species. In consequence, reductions in the abundance of dominant species could dilute competitive pressure among species inhabiting cushions, and this might also lead to the observed positive relationships between invasibility and proportional diversity.

Regarding the interactions between *C. arvense* and native species within cushion patches, it is important to note that the shoot biomass of this invasive species increased with species diversity and the abundance of native plant individuals, which also supports the biotic

acceptance hypothesis and the existence of diffuse positive effects between native and invasive plants. Nevertheless, root biomass of *C. arvense* was inconsistently related to diversity metrics within cushion patches, suggesting that increased diversity of native plants would not necessarily affect below-ground interactions with the invader. In consequence, these relationships led to increased shoot/root ratios of *C. arvense* with increasing diversity of native plants within cushions. Increased shoot/root ratios have been proposed to occur in light-limited environments where plants shade each other and, therefore, individuals prioritize stem elongation in response to competition for light (Tilman 1988; Wilson 1988; Olff et al. 1990). However, despite the large number of plants growing on the cushions, their aerial structures cover small areas and they are separated enough to avoid shading each other. Indeed, most plant that grow on cushions are fully exposed to sunlight (see Appendix S1). Therefore, other mechanisms may be involved in determining the increased shoot/root ratios of *C. arvense* with increasing diversity and abundance of

native plants within cushion-protected patches. On this issue, it is likely that the elevated amount of hydric and mineral resources accumulated below cushion canopies (see Núñez et al. 1999; Badano et al. 2006; Cavieres et al. 2007) are preventing below-ground competition, which would allow for higher allocation of materials and energy to shoots of *C. arvensis*.

The positive relationships between the abundance and performance of *C. arvensis* and native species within cushion patches reinforce the idea that, in addition to the positive effects that cushions have *per se* on other plants, native plant assemblages inhabiting these patches may also facilitate the invader. Thus, although it is almost axiomatic to think that plant competition increases with plant density as a consequence of resource depletion (Harper 1977), this study suggests that these effects are not occurring within cushions. Instead, the results indicate that there is no resource limitation within cushion patches and that this overrides any potential negative interaction occurring among native plants and the invader because of niche overlap or density-dependent effects. To the best of our knowledge, this positive effect has not been reported in previous studies of plant invasion, but it could constitute a novel mechanism to sustain the biotic acceptance hypothesis.

As a concluding remark, it is important to highlight that the mechanisms proposed above to explain invasibility–diversity relationships within and outside nurse-protected patches will remain as hypotheses until additional experiments are carried out. Studies on this issue are scarce and, as far as we are aware, only Levine (2000) and Von Holle (2013) have assessed how interactions among plants may affect biological invasions at local spatial scales. These studies, however, indicated that the performance of invader species decreases with increased species richness. Our study, instead, indicates that the opposite pattern is occurring within cushion plants from high-mountain environments. Further, to the best of our knowledge, this is the first study to include other components of diversity, besides species richness, to assess the shape of these relationships (i.e. proportional diversity and species dominance). Although neither the sampling nor the experiment specifically addressed how these diversity metrics relate to niche overlap or density-dependent effects, our results might lay the groundwork for more detailed studies designed to disentangle these issues. Finally, it is important to highlight that invasibility–diversity relationships appear to result from a number of complex interspecific interactions whose strength and direction are locally controlled by physical stress, and where facilitation occurring at different hierarchical levels (i.e. facilitation by nurse plants on species assemblages plus diffuse positive

interactions occurring within these plant assemblages) might also modulate the shape of these relationships.

Acknowledgements

We thank the staff of La Parva and Valle Nevado ski centres for logistic support provided during the sampling season. We also thank the valuable comments from two anonymous reviewers and the editor for this article, which helped to improve the quality of its final version. This study was funded by FONDECYT 3060095 (EIB), FONDECYT 1130592 (LAC) and FICM P05-002 and PBF-023 supporting the Institute of Ecology and Biodiversity (IEB).

References

- Aarssen, L.W., Laird, R.A. & Pither, J. 2003. Is the productivity of vegetation plots higher or lower when there are more species? Variable predictions from interaction of the ‘sampling effect’ and ‘competitive dominance effect’ on the habitat tement. *Oikos* 102: 427–432.
- Alpert, P., Bone, E. & Holzapfel, C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3: 52–66.
- Badano, E.I. & Marquet, P.A. 2009. Biogenic habitat creation affects biomass–diversity relationships in plant. *Perspectives in Plant Ecology, Evolution and Systematics* 11: 191–201.
- Badano, E.I., Cavieres, L.A., Molina-Montenegro, M.A. & Quiroz, C.L. 2005. Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile. *Journal of Arid Environments* 62: 93–108.
- 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.
- Badano, E.I., Villarroel, E., Bustamante, R.O., Marquet, P.A. & Cavieres, L.A. 2007. Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *Journal of Ecology* 95: 682–688.
- Bertness, M.D. & Callaway, R. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9: 191–193.
- Brooker, R.W. & Kikvidze, Z. 2008. Importance: an overlooked concept in plant interaction research. *Journal of Ecology* 96: 703–708.
- Byers, J.E. & Noonburg, E.G. 2003. Scale-dependent effects of biotic resistance to biological invasion. *Ecology* 84: 1428–1433.
- Callaway, R.M. 2007. *Positive interactions and interdependence in plant communities*. Springer, Dordrecht, NL.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., (...) & Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.

- Cavieres, L.A. & Arroyo, M.T.K. 1999. Tasa de enfriamiento adiabático del aire en el Valle 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. 2009. Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology* 97: 1181–1191.
- Cavieres, L.A., Peñaloza, A. & Arroyo, M.T.K. 2000. Altitudinal vegetation belts in the high-Andes of central Chile (33° S). *Revista Chilena de Historia Natural* 73: 331–344.
- 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.A. 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.
- Chesson, P. & Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150: 519–553.
- Di Castri, F. & Hajek, E.R. 1976. *Bioclimatología de Chile*. Universidad Católica de Chile, Santiago, CL.
- Fajardo, A., Quiroz, C. & Cavieres, L.A. 2008. Distinguishing colonization modes from spatial structures in populations of the cushion plant *Azorella madreporica* in the high-Andes of central Chile. *Austral Ecology* 33: 703–712.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88: 3–17.
- Grime, J.P. 2001. *Plant strategies, vegetation processes and ecosystem properties*, 2nd edn. John Wiley & Sons, Chichester, UK.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417: 636–638.
- Kowarik, I. & von der Lippe, M. 2007. Pathways in plant invasions. In: Nentwig, W. (ed.) *Biological invasions*, pp. 29–47. Springer, Berlin, DE.
- Kutner, M.H., Nachtsheim, C.J., Neter, J. & Li, W. 2005. *Applied linear statistical models*, 5th edn. McGraw-Hill/Irwin, New York, NY, US.
- Levine, J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852–854.
- Levine, J.M. & D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15–26.
- Maestre, F.T., Bautista, S., Cortina, J. & Bellot, J. 2001. Potential for using facilitation by grasses to establish shrubs on a semi-arid degraded steppe. *Ecological Applications* 11: 1641–1655.
- Magurran, A.E. 2004. *Measuring biological diversity*. Blackwell, Oxford, UK.
- Maron, J. & Marler, M. 2007. Native plant diversity resists invasion at both low and high resource levels. *Ecology* 88: 2651–2661.
- Marticorena, C. & Quezada, M. 1985. Catálogo de la flora vascular de Chile. *Gayana Botánica* 42: 1–157.
- Matthei, O. 1995. *Manual de las malezas que crecen en Chile*. Alfabetta, Santiago, CL.
- Mitchley, J. 1987. Diffuse competition in plant communities. *Trends in Ecology & Evolution* 2: 104–106.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91: 97–108.
- Núñez, C.I., Aizen, M.A. & Ezcurra, C. 1999. Species associations and nurse plant effects in patches of high-Andean vegetation. *Journal of Vegetation Science* 10: 357–364.
- Olf, H., Van Andel, J. & Bakker, J.P. 1990. Biomass and shoot/root allocation of five species from a grassland succession series at different combinations of light and nutrient supply. *Functional Ecology* 4: 193–200.
- Rejmanek, M. 1996. Species richness and resistance to invasions. In: Orians, G.H., Dirzo, R. & Cushman, J.H. (eds.) *Biodiversity and ecosystem processes in tropical forests*, pp. 153–172. Springer, Berlin, DE.
- Reynolds, H.L. & Pacala, S.W. 1993. An analytical treatment of root-to-shoot ratio and plant competition for soil nutrient and light. *The American Naturalist* 141: 51–70.
- Richardson, D.M., Pyšek, P. & Carlton, J.T. 2011. A compendium of essential concepts and terminology in invasion ecology. In: Richardson, D.M. (ed.) *Fifty years of invasion ecology: The legacy of Charles Elton*, pp. 409–420. Wiley-Blackwell, Oxford, UK.
- Santibáñez, F. & Uribe, J.M. 1990. *Atlas agroclimático de la V Región y Región Metropolitana*. Universidad de Chile, Santiago, CL.
- Sax, D.F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* 8: 193–210.
- Sax, D.F. & Brown, J.H. 2000. The paradox of invasion. *Global Ecology and Biogeography* 9: 363–371.
- Shea, K. & Chesson, P. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170–176.
- Stirling, G. & Wilsey, B. 2001. Empirical relationships between species richness, evenness, and proportional diversity. *The American Naturalist* 158: 286–299.
- Stohlgren, T.J., Jarnevich, C., Chong, G.W. & Evangelista, P.H. 2006. Scale and plant invasions: a theory of biotic acceptance. *Preslia* 78: 405–426.

- Tewksbury, J.J. & Lloyd, J.D. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127: 425–434.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ, US.
- Ugborogho, R.E. 1977. North American *Cerastium arvense* Linnaeus: taxonomy, reproductive system and evolution. *Phyton* 35: 169–187.
- Von Holle, B. 2013. Environmental stress alters native–nonnative relationships at the community scale. *Biological Invasions* 15: 417–427.
- Wardle, D.A. 2001. Experimental demonstration that plant diversity reduces invasibility – evidence of a biological mechanism or a consequence of sampling effect? *Oikos* 95: 161–170.
- Wilson, J.B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* 25: 279–296.

Supporting Information

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

Appendix S1. Typical high-Andean landscape of central Chile with cushions of *Azorella madreporica* surrounded by open areas.

Appendix S2. Experimental design used to assess whether the performance of *Cerastium arvense* varied with changing levels of native species diversity within and outside *Azorella madreporica* cushions.