

RESEARCH ARTICLE

Floristic changes in alpine plant communities induced by the cushion plant *Azorella madreporica* (Apiaceae) in the Andes of central Chile

Cambios florísticos en comunidades de plantas alpinas inducidos por la planta en cojín *Azorella madreporica* (Apiaceae) en los Andes de Chile central

CONSTANZA L. QUIROZ^{1,2,*}, ERNESTO I. BADANO^{2,3} & LOHENGRIN A. CAVIERES^{1,2}

¹ ECOBIOSIS, Departamento de Botánica, Universidad de Concepción, Casilla 160C, Concepción, Chile

² Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

³ Departamento de Ciencias Químico Biológicas, Escuela de Ingeniería y Ciencias, Universidad de las Américas-Puebla, ex Hda. de Sta. Catarina Martir, Cholula 72820, Puebla, México

* Corresponding author: cquiroz@udec.cl

ABSTRACT

It is well known that the number of plant species associated with nurse plants increases with elevation. However, studies conducted so far have largely ignored the effect of nurse plants on other community attributes, such as the species abundances, diversity and evenness. Moreover, changes in these community attributes along environmental gradients have also been seldom examined. The present study evaluates the effect of the cushion plant *Azorella madreporica* (Apiaceae) on species richness, species abundance, diversity and evenness of vascular plants at two elevations in the Andes of central Chile. Theoretically, the impact of this nurse cushion plant on these community attributes should be greater at a higher elevation. Results showed that the proportion of plant species associated with cushion plants increases with elevation, and the abundance of some species is also greater within cushions than on bare ground. Although the proportion of species growing within cushions increased with elevation, diversity and evenness were higher on bare ground. This is due to some few species that attained very high densities within cushions, generating assemblages highly dominated by some few species. Ordination analyses indicated differences in species assemblages within and outside *A. madreporica* at the higher elevation. Therefore, the influence of cushion plants on community structure changes with elevation. Accordingly, we suggest that attributes other than species richness must be included in future studies in order to analyze the impact of nurse species on community structure along environmental gradients.

Key words: positive associations, community structure, elevation, environmental gradients, nurse effect.

RESUMEN

Se sabe que el número de especies asociado a plantas nodrizas aumenta con la altitud. Sin embargo, el efecto de plantas nodrizas sobre otros atributos de las comunidades, como la abundancia de especies, diversidad y equidad, ha sido largamente ignorado. Más aún, cambios en estos atributos en gradientes ambientales han sido pocas veces examinados. Este trabajo evalúa el efecto de una planta en cojín, *Azorella madreporica* (Apiaceae), sobre la riqueza de especies, abundancia de especies, diversidad y equitatividad de la comunidad de plantas vasculares en dos altitudes en los Andes de Chile central. Teóricamente, el impacto de esta especie nodriza sobre la estructura comunitaria debería ser mayor a mayor altitud. Los resultados mostraron que la proporción de especies de plantas asociadas con plantas en cojín aumenta con la altitud, y que la abundancia de algunas especies también es mayor al interior de cojines que en el suelo desnudo. Aunque la riqueza relativa de especies al interior de los cojines aumenta con la altitud, la diversidad y la equidad fueron mayores en el suelo desnudo. Los resultados sugieren que la importancia de las plantas en cojín sobre la estructura comunitaria cambia con la altitud, produciendo mayores diferencias en los ensambles de especies presentes dentro y fuera de *A. madreporica* en la mayor altitud. Basándonos en esto, sugerimos que otros atributos además de la riqueza de especies deben ser incluidos en futuros estudios para analizar el impacto de las especies nodrizas en la estructura de las comunidades a lo largo de gradientes ambientales.

Palabras clave: asociaciones positivas, estructura comunitaria, altitud, gradientes ambientales, efecto nodriza.

INTRODUCTION

Determining the relative importance of processes that structure plant communities and maintain biological diversity is a primary focus in community ecology (Janzen 1970, Connell 1978, Tilman 1982). Early research focused on competition and disturbance regimes as the main factors structuring communities and regulating biological diversity (e.g., Connell 1978, Grime 1979). However, more recent studies have started to examine the importance of positive interactions on community structure and biological diversity (Bruno et al. 2003, Michalet et al. 2006). Positive interactions can increase species diversity either via habitat creation due to the physical presence of a species (Jones et al. 1997), or when the presence of a facilitator or nurse species modifies the environment in ways that reduce the frequency of some physical disturbance or ameliorate physical stress, allowing less tolerant species to perform better (Hacker & Gaines 1997, Michalet et al. 2006). Focused on the latter mechanism, a number of authors have suggested that positive interactions may have strong impacts in harsh environments, where the mitigation of extreme conditions by a facilitator species can benefit other species (Bertness & Callaway 1994, Callaway & Walker 1997, Brooker & Callaghan 1998). Indeed, Hacker & Gaines (1997) proposed a graphical model in which a facilitator species increases species diversity under conditions of high mortality such as disturbance (physical, stress or predation), by ameliorating physical stress or by providing protection from disturbance or predation. Moreover, these positive effects increased where harsh conditions became more intense (Hacker & Gaines 1997, see also Michalet et al. 2006).

Although ecological communities can be defined and described in very different ways (Morin 1999), there are some community attributes that have been extensively used in the literature to compare among communities or within a given community at different stages. Some of the most used community attributes are species richness, diversity, species abundance relations, and species composition (Morin 1999). While many studies on nurse species have focused on species richness as an indicator of species diversity, the impact of nurse species on

other community attributes, such as species abundance and evenness, remains unclear. Not all the species are represented with the same intensity within an assemblage, as they may occur repeatedly in a sample, or represented by a single individual (Magurran 1988). Hence, diversity indices (H') can be used to assess changes on this attribute as they weight the contribution of species according to their abundance (Schutler & Ricklefs 1993). Moreover, it has been shown that the study of diversity and evenness indices can reveal patterns of dominance that otherwise are ignored if only the species richness is considered (e.g., Wang et al. 2004, Li et al. 2006). The inclusion of these attributes on facilitation studies can provide information about differences in the response of certain species, to the interaction with the nurse species.

As nurse species provide microhabitats more suitable for survival, it is expected that nurse species enhance species richness, diversity (H') and evenness (J'), compared to the situation where the nurse species is absent. In addition, the positive effect of nurse species on those community attributes is expected to be higher at sites with increased environmental harshness (sensu Hacker & Gaines 1997, Michalet et al. 2006).

Alpine environments have stressful conditions and high disturbance frequencies, which affect the establishment and growth of vascular plants (Körner 2003). In these ecosystems, plants must face low temperatures, short growing seasons, excessive radiation, strong winds and unstable substrates as a result of local avalanching, cryoperturbation, and runoff associated with snow melt (Bliss 1985, Körner 2003). Therefore, mitigation of these unfavorable conditions is likely to increase the establishment of other species and species diversity (e.g., Chapin et al. 1994, Dona & Galen 2007).

Cushion plants (hereafter "cushions") are one of the life forms best adapted to these extreme environments (Armesto et al. 1980, Körner 1995). Their low stature and compact growth-form allow cushions to attenuate the negative effects of extreme environmental conditions (Körner 2003). For example, cushions are known to be efficient heat-traps, decoupling their temperature from that of the surrounding environment and generating

thermal differences as high as 15 °C regarding to the air temperature (Körner 2003). In windy habitats, such as lowland areas of the Patagonia, cushions reduce wind velocity up to 98 % thereby decreasing convective heat loss (Hager & Faggi 1990). Additionally, it has been shown that the soil beneath cushions contains higher nutrient content and higher moisture than the surrounding bare soil (Cavieres et al. 1998, 2006, 2007).

A number of studies have suggested that alpine cushions act as nurse or facilitator plants for other vascular plants. For instance, in the southern Andes, Núñez et al. (1999) showed that patches dominated by cushions supported higher species richness than patches lacking cushion. Some studies have indicated that the number of species associated to cushions increased with elevation, suggesting that the importance of the nurse effect increases with elevation (see Cavieres et al. 2002, Arroyo et al. 2003). Badano & Cavieres (2006a) have recently shown that the presence of cushion plants in high-Andean landscapes increase both species richness and diversity at the landscape scale. Further, these large scale effects of cushions on species diversity were more important at higher than at lower elevation sites (Badano & Cavieres 2006b). However, patch-scale effects of cushions on the structure of plant assemblages growing within them compared to those found on open areas away from cushions remain unexplored (but see Badano et al. 2002).

In order to elucidate the effects of cushions in other components of communities (such as H' and J'), we assessed the effects of the cushion plant *Azorella madreporica* Clos (Apiaceae) on the structure (species richness, composition, H' , J') of plant assemblages at two elevations in the central Chilean Andes. We specifically addressed the following questions (i) are species richness, diversity and evenness within cushions higher than outside them?; (ii) do cushions equally enhance the frequency of occurrence and abundances of all other species?; (iii) how similar are species assemblages growing within and outside cushions?; (iv) do these community attributes change when we compare habitats with different environmental harshness? We expected positive effects of *A. madreporica* cushions on species richness, diversity (H') and evenness (J'). In addition, these positive effects

of cushions are expected to be greater at higher elevations. As a consequence we anticipated that cushions of *A. madreporica* will harbor qualitatively different species assemblages than those found on bare ground, with this difference being greater at higher elevations.

METHODS

Study site

This study was carried out in the Molina River basin (33°20' S, 70°16' W), in the central Chilean Andes. In central Chile, the alpine zone extends from just above the treeline of *Kageneckia angustifolia* D. Don (Rosaceae) at 2,200 m (Piper et al. 2006), to the upper distribution limit of plants at 3,800 m elevation (Cavieres et al. 2000). Climate in the study area is alpine with a strong influence of the Mediterranean-type climate predominating at lower elevations (Cavieres & Arroyo 1999). Precipitation mainly occurs as snow during the southern hemisphere winter months, with annual estimations of 400 mm just above the treeline, and increasing with elevation. At 3,150 m elevation, mean air temperatures are 1.7 °C in winter and 6.8 °C in summer, decreasing with elevation (Cavieres & Arroyo 1999).

Azorella madreporica is a flat, tightly-knit cushion species that can reach sizes of up to one meter in diameter (C. Quiroz, unpublished results). In Chile, the distribution of this cushion plant ranges from 33° to 50° S, being detected from 3,800 m elevation in its northern limit to sea level in its southern limit (Hoffmann et al. 1998). Two plant communities dominated by the cushion plant *A. madreporica* located at different elevations, were selected. The first community corresponded to the lower altitudinal limit of distribution of *A. madreporica* (3,200 m), while the second was located in its upper limit (3,580 m). These sites differ in daily temperature of air and soil during the growing season (Fig. 1). During the entire growing season, the site at 3,200 m reached higher temperatures of both air and soil than the site at 3,580 m elevation (Fig. 1). At both elevations, the average cover of *A. madreporica* is ca. 10 %, while areas without vegetation (bare ground) cover ca. 70 and 90 % at the lower and upper site, respectively.

Besides *A. madreporica*, both plant communities are mainly comprised of small perennial herbs such as *Pozoa coriacea* Lag., *Barneoudia major* Phil., *Viola* spp., *Nassauvia* spp. and *Cerastium arvense* L. (Cavieres et al. 2000). *A. madreporica* is the only cushion species that is present at both elevations.

Vegetation sampling

Fifty *A. madreporica* individuals were randomly selected at each elevation. This sample size ensures a good knowledge of the species richness within and outside cushions on this alpine area (Badano & Cavieres 2006a, 2006b, Badano et al. 2006). By using a random number table, we selected four pairs of two consecutive numbers between 0 and 1. For each pair of numbers, the first number was multiplied by 100 and indicated a distance in meters to walk from the centre of our sampling area. The second number was converted to hexadecimal degrees, and indicated the direction in degrees from magnetic north to walk, where the first cushion found was selected. Since the size of cushions ranged from 20 to 80 cm in diameter, total species richness and the abundance of each species growing on *A. madreporica* were recorded by using metallic-hoops of known diameter (20, 30, 40, 50, 60 and 80 cm diameter). A metallic hoop of similar diameter to that of the selected cushion was placed on its surface, and all

individuals of each species within the hoop were recorded and identified. To assess species richness and species abundances in the contrasting environment without cushions (i.e., bare ground), the metallic hoop used on each cushion was placed 50 cm away from the cushion in a random direction.

Species distribution patterns

Randomization tests were performed to determine which species showed positive associations with *A. madreporica* (Kikvidze et al. 2001). At each elevation, and for each species, we generated 1000 random frequencies of occurrence within cushions. Then, we calculated the probability of the observed frequency of occurrence of each species within cushions being generated by chance, using Resampling Stats (Simon et al. 1990). According to the abiotic stress hypothesis (Bertness & Callaway 1994, Brooker & Callaghan 1998) the proportion of species positively associated with *A. madreporica* was expected to be greater at the higher elevation site. Additionally, the abundances of those species detected both within and outside cushions were compared. Species abundances were expressed as the density of individuals of each species in the sampled area (individuals dm⁻²), and compared between cushions and bare ground with Student t-tests using the software R v. 2.3 (R Development Core Team 2005).

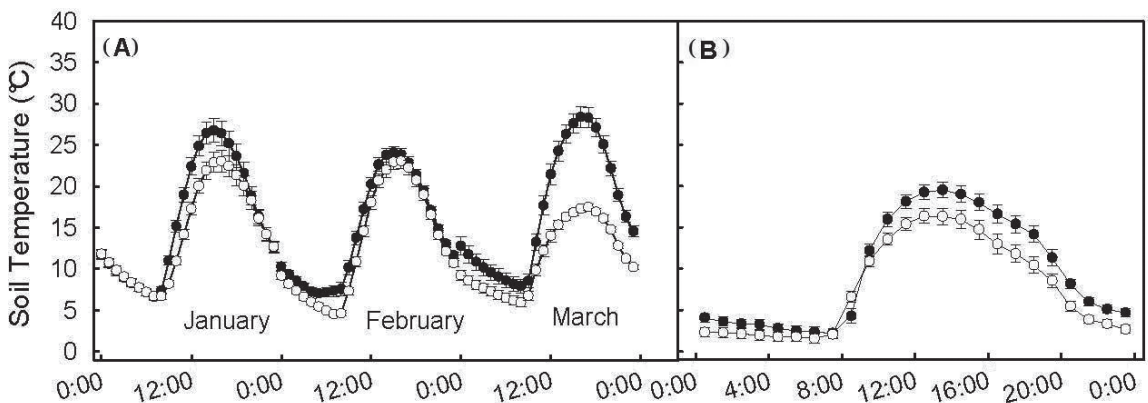


Fig. 1: Daily cycles of average temperatures (\pm SE) of bare ground during three months of the growing season (A), and daily cycle of average air temperatures (\pm SE) (B), at 3,200 (solid symbols) and 3,580 m of altitude (empty symbols).

Ciclos diarios de temperatura (\pm EE) en el suelo desnudo durante tres meses de la estación de crecimiento (A), y ciclos diarios de temperatura del aire (\pm EE) (B), a 3,200 (símbolos negros) y 3,580 m de altitud (símbolos blancos).

Community attributes

To assess differences in species richness between species assemblages within and outside cushions at each elevation, we constructed sample-based rarefaction curves using the software EstimateS v. 6 (Colwell 2005). These curves were performed by rarefying the species richness from 1 to 50 samples with Monte Carlo resampling techniques (Gotelli & Colwell 2001). The Coleman's algorithm (Coleman et al. 1982) was used to estimate species richness at each rarefaction run and these values were averaged for each sampling size (Colwell 2005). Rarefaction curves were estimated independently for species assemblages within and outside cushions at each elevation. 95 % confidence intervals were estimated for each curve to assess differences in species richness between species assemblages. In order to assess differences in the effect of cushions between elevations, maximum estimated species richness values were used to compute the ratio between species richness within and outside cushions at each elevation.

Shannon-Wiener diversity indices (H') and their associated evenness indicator (J') (Magurran 1988) were calculated for species assemblages within and outside cushions. These indices were calculated by including all individuals of all species detected in the samples taken within and outside cushions at each elevation. Variance of each H' index was also calculated, and H' values were compared within and outside cushions and between elevations with t-tests by following the procedure proposed by Magurran (1988). Bonferroni corrections were applied on the significance level of t-tests (critical $\alpha = 0.05$) to allow multiple contrasts (Neter et al. 1996).

Principal components analyses (PCA) were used to assess differences in floristic composition between within and outside cushions at both elevations. These analyses were performed with the software PC-ORD v. 4 (McCune & Mefford 1999). We used relative abundances to perform PCA in order to include the effect of cushions on species abundance. Relative abundances per sample were calculated as the ratio between the number of individuals of a given species and the number of individuals including all species in each sample, including the area (dm^2) of each hoop in the denominator

to standardize for differences in the sampled area. To assess differences between species assemblages, the eigenvalues obtained from the PCA for each sample on the first and the second axis were compared between within and outside cushions with Student t-tests (Tewksbury & Lloyd 2001). Differences were expected to be greater at the higher elevation site. T-tests were performed with R v. 2.3 (R Development Core Team 2005).

Finally, to analyze whether the presence of cushions change species abundance distributions, and whether these patterns change between the two elevations studied, species within and outside cushions at each elevation were ranked according to their relative abundances. Relative abundances were calculated as the ratio between the total number of individuals of each species and the total number of individuals within or outside cushions at a given elevation (3,200 - 3,580 m). Then, rank-abundance curves for within and outside cushions at each elevation were plotted with logarithm (log) of the species relative abundances in y-axis and species rank in the x axis (Magurran 1988). Subsequently, we assessed the goodness of fit of these curves to three traditional models: 'broken-stick', 'logarithmic series' and 'geometric series'. Non-linear regression analyses were used to assess goodness of fit, and values of the determination coefficient (r^2) were used to define what model showed the best model for within and outside cushion at each elevation. These analyses were performed with the R v. 2.3 (R Development Core Team 2005).

RESULTS

Species distribution patterns

A total of 32 species were detected at 3,200 m, 12 of which were recorded growing exclusively on *Azorella madreporica* and five exclusively on bare ground. Total species richness was lower (17 species) at 3,580 m, where five species were detected exclusively on cushions, and only three exclusively on bare ground (Table 1). Four species from the upper elevation site were not detected in the community at the lower elevation, while 19 species growing at 3,200 m were not recorded at the upper elevation site (Table 1).

TABLE 1

Frequencies of occurrence of species within and outside cushions of *Azorella madreporica* at 3,200 and 3,580 m of altitude in the Andes of central Chile. Signs indicate positive (+) or negative (-) association with cushions according to randomization tests; (*) indicate exotic species.

Frecuencias de ocurrencia de especies dentro y fuera de cojines de *Azorella madreporica* a 3.200 y 3.580 m de altitud en los Andes de Chile central. Los signos indican asociación positiva (+) o negativa (-) con los cojines de acuerdo a pruebas de aleatorización; (*) indica especies exóticas.

Species	Family	3,200 m				3,580 m			
		Within	Outside	P-value	Sign	Within	Outside	P-value	Sign
<i>Acaena pinnatifida</i>	Rosaceae	1	1	0.75					
<i>Adesmia</i> sp.	Fabaceae					0	6	< 0.05	-
<i>Calandrinia affinis</i>	Portulacaceae					6	0	< 0.05	+
<i>Calandrinia compacta</i>	Portulacaceae	0	4	0.06					
<i>Carex andina</i>	Cyperaceae	3	3	0.63					
<i>Carex gayana</i>	Cyperaceae	1	0	0.52					
<i>Cerastium arvense</i> *	Caryophyllaceae	28	6	< 0.01	+	15	0	< 0.01	+
<i>Chaetanthera flabellata</i>	Asteraceae	0	6	< 0.01	-				
<i>Erigeron andicola</i>	Asteraceae	4	0	0.06		3	1	0.32	
<i>Festuca magellanica</i>	Poaceae	15	9	0.15		7	0	< 0.01	+
<i>Galium gilliesii</i>	Rubiaceae	2	0	0.27					
<i>Gayophytum humile</i>	Onagraceae	0	3	0.11					
<i>Geranium sessiliflorum</i>	Geraniaceae	1	0	0.51					
<i>Hordeum comosum</i>	Poaceae	22	20	0.43		14	3	< 0.01	+
<i>Lactuca serriola</i> *	Asteraceae	1	0	0.52					
<i>Loasa sigmoidea</i>	Loasaceae	7	2	0.10					
<i>Luzula chilensis</i>	Juncaceae	1	0	0.52					
<i>Microsteris gracilis</i>	Polemoniaceae	5	6	0.48					
<i>Montiopsis potentilloides</i>	Asteraceae	3	13	< 0.01	-	0	1	0.51	
<i>Nassauvia cumingii</i>	Asteraceae	0	1	0.51					
<i>Nassauvia lagascae</i>	Asteraceae	1	1	0.74		1	2	0.49	
<i>Nastanthus agglomeratus</i>	Calyceraceae	4	0	0.06		6	0	< 0.05	+
<i>Oxalis compacta</i>	Oxalidaceae	2	0	0.24		1	1	0.76	
<i>Perezia carthamoides</i>	Asteraceae					0	1	0.49	
<i>Perezia pilifera</i>	Asteraceae	5	0	< 0.05	+				
<i>Phacelia secunda</i>	Hydrophyllaceae	10	10	0.60		1	1	0.68	
<i>Plantago barbata</i>	Plantagonaceae	1	0	0.52					
<i>Poa</i> sp.	Poaceae	1	0	0.51					
<i>Pozoa coriacea</i>	Apiaceae	0	5	< 0.05	-				
<i>Senecio looseri</i>	Asteraceae	4	0	0.06		1	1	0.75	
<i>Sisyrinchium philippii</i>	Iridaceae	4	5	0.47					
<i>Taraxacum officinale</i> *	Asteraceae	34	14	< 0.01	+	4	0	0.06	
<i>Thlaspi magellanicum</i>	Brassicaceae	12	3	< 0.05	+	2	1	0.46	
<i>Trisetum preslei</i>	Poaceae	12	2	< 0.01	+	21	2	< 0.01	+
<i>Viola philippii</i>	Violaceae	1	2	0.47					
<i>Viola atropurpurea</i>	Violaceae					1	7	< 0.05	-
Total number of species		27	19			14	12		
Evenness		0.51	0.75			0.42	0.70		

At 3,200 m, five species (15.6 % of the community) showed a significant positive association with *A. madreporica*, while three species (9.4 % of the community) were negatively associated with cushions (Table 1). At 3,580 m, six species (35.3 % of the community) were positively associated with *A. madreporica*, while two species (11.8 % of the community) were negatively associated with cushions (Table 1). Three species changed their association patterns with *A. madreporica* from neutral to positive with increasing elevation.

Fifteen species were found both within and

outside cushions at 3,200 m. At this elevation, four of these species (27 % of the shared species) were four to nine times more abundant within *A. madreporica* cushions and only one (7 % of the shared species) was nine times more abundant on bare ground (Table 2). At 3,580 m, nine species were detected growing both within and outside cushions, but only two of them (22 % of the shared species) were at least six times more abundant within cushions whereas one species (11 % of the shared species) was seventy times more abundant on bare ground (Table 2).

TABLE 2

Abundances (individuals $m^{-2} \pm SE$) of species detected both within and outside cushions of *Azorella madreporica* at 3,200 and 3,580 m of altitude in the Andes of central Chile. Results of t-tests ($\alpha = 0.05$) for differences in abundances between within and outside cushions are shown.

Abundancias (individuos $m^{-2} \pm EE$) de especies detectadas tanto dentro como fuera de cojines de *Azorella madreporica* a 3.200 y 3.580 m de altitud en los Andes de Chile central. Se muestran los resultados estadísticos para diferencias de abundancias entre tipos de hábitat, de acuerdo a pruebas t de Student ($\alpha = 0,05$).

Species	3,200 m		$t_{1,98}$	P-value
	Within	Outside		
<i>Acaena pinnatifida</i>	0.03 (± 0.03)	0.01 (± 0.01)	0.86	0.39
<i>Carex andina</i>	0.21 (± 0.16)	0.07 (± 0.04)	0.88	0.38
<i>Cerastium arvense</i>	7.15 (± 1.55)	0.78 (± 0.38)	4.00	< 0.01
<i>Festuca magellanica</i>	1.45 (± 0.44)	0.31 (± 0.14)	2.47	< 0.05
<i>Hordeum comosum</i>	1.56 (± 0.36)	0.82 (± 0.22)	1.76	0.08
<i>Loasa sigmoidea</i>	0.20 (± 0.08)	0.21 (± 0.15)	0.04	0.97
<i>Microsteris gracilis</i>	0.21 (± 0.13)	0.10 (± 0.04)	0.75	0.45
<i>Montiopsis potentilloides</i>	0.06 (± 0.03)	0.50 (± 0.21)	2.06	< 0.05
<i>Nassauvia lagascae</i>	0.11 (± 0.11)	0.14 (± 0.14)	0.16	0.88
<i>Phacelia secunda</i>	0.36 (± 0.15)	0.46 (± 0.17)	0.44	0.66
<i>Sisyrinchium philippii</i>	0.06 (± 0.03)	0.04 (± 0.02)	0.57	0.57
<i>Taraxacum officinale</i>	2.16 (± 0.42)	0.47 (± 0.13)	3.82	<0.01
<i>Thlaspi magellanicum</i>	0.41 (± 0.15)	0.07 (± 0.06)	2.11	<0.05
<i>Trisetum preslei</i>	3.43 (± 1.23)	1.10 (± 0.96)	1.49	0.14
<i>Viola philippii</i>	0.02 (± 0.02)	0.18 (± 0.16)	0.99	0.32
		3,580 m		
Species	Within	Outside	$t_{1,98}$	P-value
<i>Erigeron andicola</i>	0.06 (± 0.04)	0.01 (± 0.01)	1.37	0.17
<i>Hordeum comosum</i>	1.65 (± 0.53)	0.26 (± 0.17)	2.50	< 0.01
<i>Nassauvia lagascae</i>	0.01 (± 0.01)	0.06 (± 0.04)	1.21	0.23
<i>Oxalis compacta</i>	0.01 (± 0.01)	0.03 (± 0.03)	0.72	0.47
<i>Phacelia secunda</i>	0.03 (± 0.03)	0.03 (± 0.03)	0.08	0.93
<i>Senecio looseri</i>	0.08 (± 0.08)	0.01 (± 0.01)	0.90	0.37
<i>Thlaspi magellanicum</i>	0.01 (± 0.01)	0.01 (± 0.01)	0.07	0.94
<i>Trisetum preslei</i>	8.14 (± 1.29)	0.02 (± 0.02)	6.29	< 0.01
<i>Viola atropurpurea</i>	0.01 (± 0.01)	0.73 (± 0.29)	2.50	< 0.01

Community attributes

At both elevations, plant species richness within *A. madreporica* cushions was significantly higher than on bare ground, as indicated through the Coleman rarefaction curves (Fig. 2). Ratios between the estimated species richness within and outside cushions were 1.4 and 2 at 3,200 and 3,580 m, respectively, indicating that the effect of

cushions on species richness was greater at the higher elevation.

Plant diversity, as expressed through H' index, decreased with elevation both within and outside cushions (Fig. 3). Indeed, H' within *A. madreporica* was significantly lower than on bare ground at both elevations (Fig. 3). Additionally, at both elevations evenness was greater outside cushions than within them (Table 1).

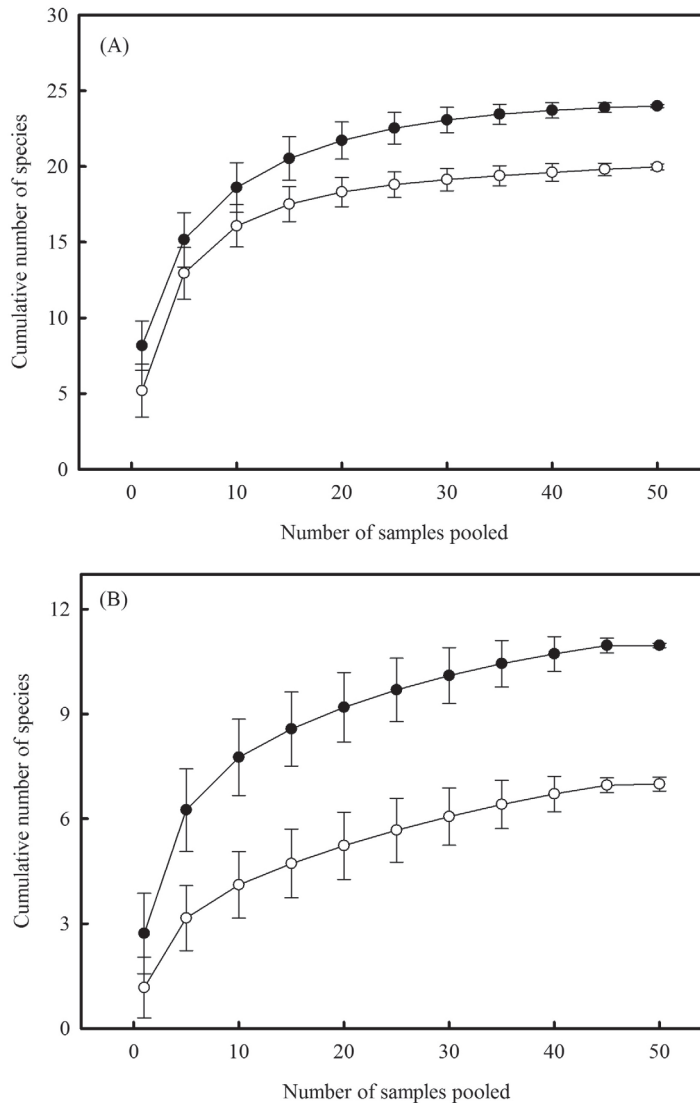


Fig. 2: Species accumulation curves of rarified values of the Coleman's estimator within (solid symbols) and outside (open symbols) cushions of *A. madreporica* at 3,200 (A) and 3,580 m (B) of altitude. Error bars represent the 95 % confidence intervals.

Curvas de acumulación de especies de valores del estimador de Coleman rarificados dentro (símbolos negros) y fuera de cojines de *A. madreporica* (símbolos blancos) a 3.200 (A) y 3.580 m (B) de altitud. Las barras de error representan los intervalos de 95 % de confianza.

The first two axes of the PCA ordination at 3,200 m accounted for 42 % of the variance of species abundances within *A. madreporica* cushions and on bare ground. The first ordination axis accounted for 31 % of the variation, while the second axis accounted for 11 % (Fig. 5A). Comparisons of eigenvalues indicated that there were no significant differences between the species assemblages growing within and outside *A. madreporica* cushions, neither on the first ($t_{1,93} = 1.70$, $P = 0.10$) nor on the second ordination axis ($t_{1,93} = 0.77$, $P = 0.44$). At 3,580 m, the first two axes of PCA accounted for 49 % of variance in the abundance of species within and outside cushions; the first axis accounted for 32 % of the ordination variance, while the second axis accounted for 17 % (Fig. 5B). Significant differences between within and outside cushions were detected on the first ordination axis at 3,580 m ($t_{1,53} = 4.83$, $P < 0.01$). In contrast, no significant differences were detected on the second axis ($t_{1,53} = 1.58$, $P = 0.12$).

Rank-abundance distribution curves of species inhabiting cushions and open areas

away from them at the two elevations are shown in Fig. 4. The geometric series model showed the best goodness of fit in the majority of cases; only the species assemblage on bare ground at 3,200 m showed a better fit to the broken-stick model (Table 3).

DISCUSSION

Azorella madreporica cushions alter the presence and abundance of other plants, thereby affecting the composition and structure of the vascular plant assemblage growing within cushions in comparison with that growing on bare ground.

We found that plant species richness within *A. madreporica* cushions was always higher than outside them, suggesting that cushions harbor species that otherwise would be absent from the community. For example, *Thlaspi magellanicum* Comm. ExPoir, *Nasthanthus agglomeratus* Miers and *Calandrinia affinis* Gill. Ex Arn were always detected growing within cushions. These results are concordant with other studies examining the effect of cushion plants on

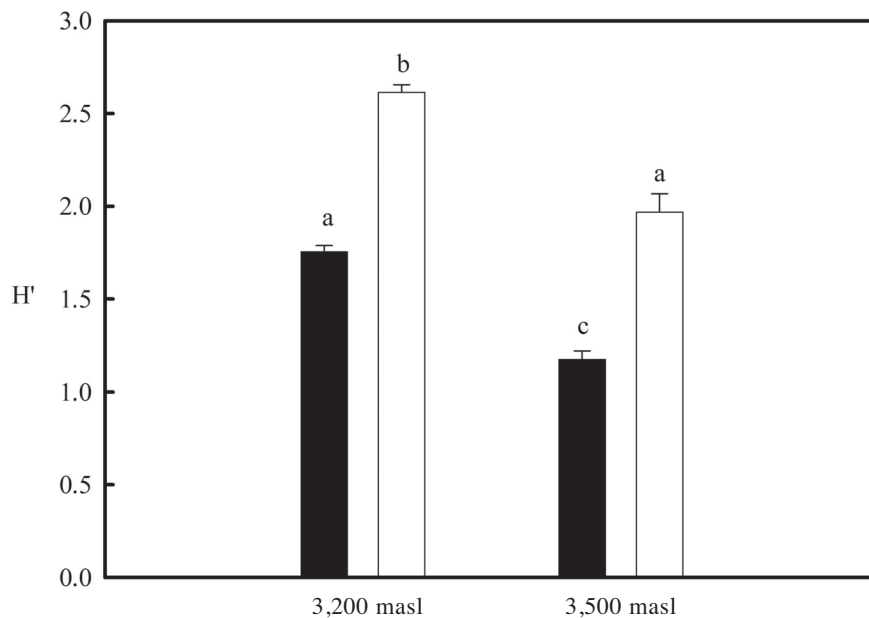


Fig. 3: Values of diversity indices of Shannon-Wiener ($H' \pm SD$) within (solid bars) and outside (open bars) *A. madreporica* cushions at 3,200 and 3,580 m of altitude. Different letters indicate statistically significant differences between bars (Bonferroni's critical value $\alpha = 0.01$).

Valores de índice de diversidad de Shannon-Wiener ($H' \pm DE$) dentro (barras negras) y fuera de cojines de *A. madreporica* (barras blancas) a (A) 3.200 y (B) 3.580 m de altitud. Letras diferentes indican diferencias estadísticamente significativas entre barras (valor crítico de Bonferroni $\alpha = 0,01$).

species richness (Núñez et al. 1999, Molina-Montenegro et al. 2000, Badano et al. 2002, Cavieres et al. 2002, Arroyo et al. 2003, Badano & Cavieres 2006b). For example, Cavieres et al. (2002) showed that plant species richness within cushions was twofold, and fourfold higher than on bare ground in two different sites. In our study, the ratio between the estimated species richness within and outside *A. madreporica* in both elevations indicated that plant assemblages within cushions were 1.4 and 2.0 times more

species-rich than those found on bare ground. Therefore, although there is a positive effect of *A. madreporica* on species richness, this effect seems to be weaker than the richness enhancement effect of other cushion species on species richness. The ratio of species richness within and outside *A. madreporica* was greater at the higher elevation, indicating that the effect of this cushion on species richness also increases with environmental harshness. Similar effects of nurse plants on species richness in sites with

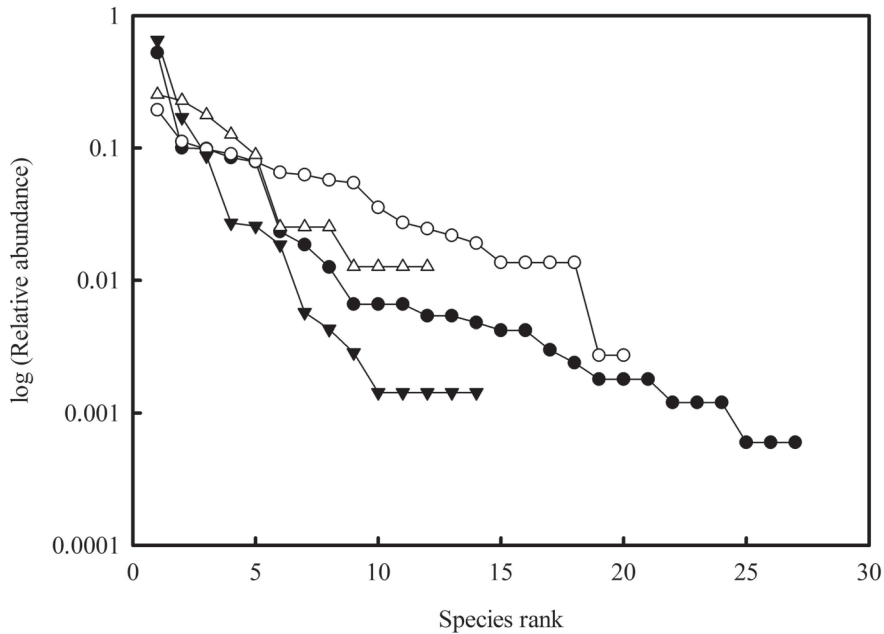


Fig. 4: Ranking of relative abundances of species growing within (solid symbols) and outside (open symbols) *A. madreporica* cushions at 3,200 m (circles) and 3,580 m (triangles) of altitude.

Ranking de abundancias relativas de especies creciendo dentro (símbolos negros) y fuera (símbolos blancos) de cojines de *A. madreporica* a 3.200 (círculos) y 3.580 m (triángulos) de altitud.

TABLE 3

Values of r^2 obtained with a goodness of fit to different models of relative abundance distribution (broken-stick, geometric series and logarithmic series) to the species assemblages found within and outside cushions of *Azorella madreporica* at both elevations in the Andes of central Chile.

Valores de r^2 obtenidos con una bondad de ajuste a diferentes modelos de distribución de abundancias relativas (broken-stick, geometric series and logarithmic series) a los ensambles de especies encontrados dentro y fuera de cojines de *Azorella madreporica* en ambas altitudes en los Andes de Chile central.

Elevation	Position	Model Broken-stick	Geometric series	Logarithmic series
3,200 m	Within	0.37	0.91	0.50
	Outside	0.95	0.90	0.87
3,580 m	Within	0.42	0.99	0.55
	Outside	0.86	0.95	0.54

different environmental stress were reported by Tewksbury & Lloyd (2001) in the Sonoran desert. These authors reported that the number of plant species beneath *Olneya tesota* A. Gray trees in highly xeric sites was almost twice that of open areas, with this difference in species richness disappearing at mesic sites. At the same

time, these authors reported that 45 % of the species were found exclusively beneath the canopy of *O. tesota* in xeric areas, while this number decreased to 25 % in mesic sites. In contrast, other studies found no effects of nurse species on plant species richness beneath their canopies (e.g., Holzapfel & Mahall 1999).

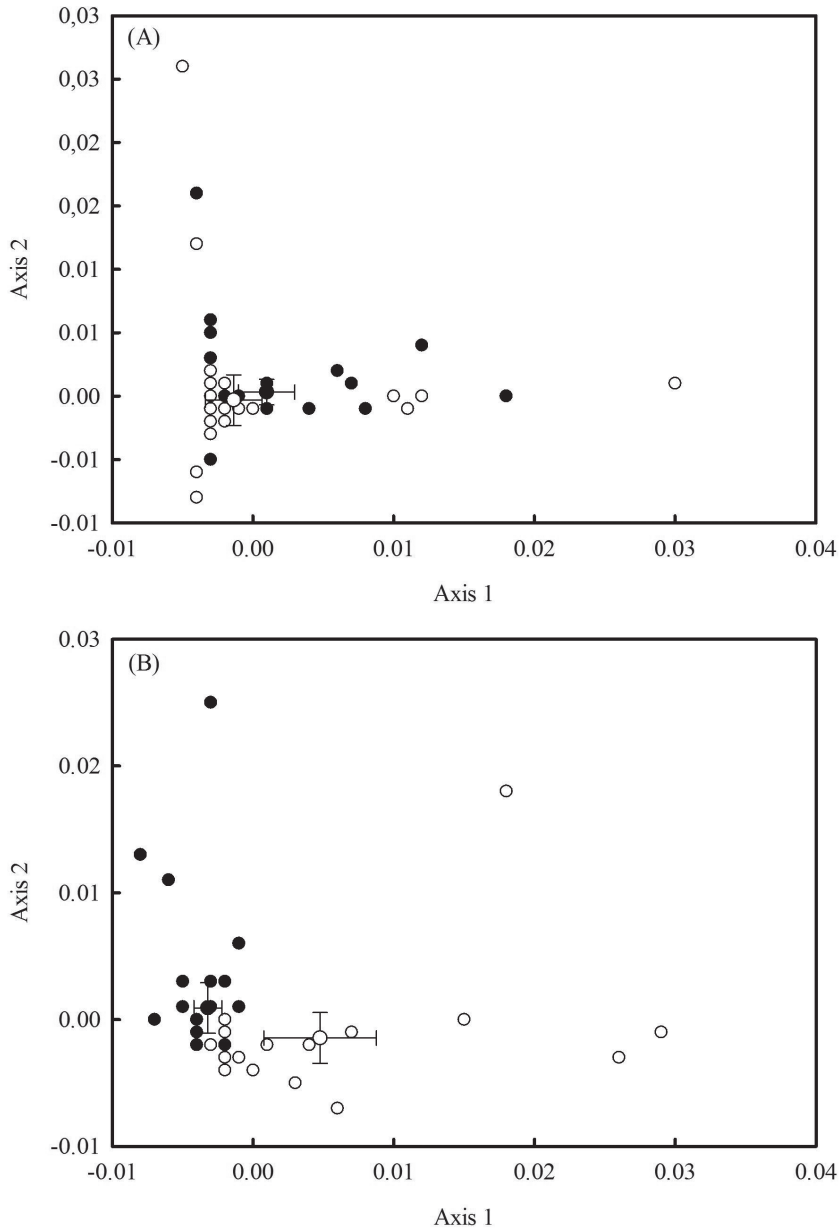


Fig. 5: PCA ordinations for species assemblages growing within (solid symbols) and outside (open symbols) *A. madreporica* cushions at 3,200 m (A) and 3,580 m (B) of altitude. Larger symbols are the centroids (\pm SE) for each situation.

Ordenamientos de PCA para los ensambles de especies creciendo dentro (símbolos negros) y fuera (símbolos blancos) de cojines de *A. madreporica* a 3.200 (A) y 3.580 m (B) de altitud. Los símbolos más grandes son los centroides (\pm EE) para cada situación.

H' and J' were expected to increase within cushions. Nevertheless, the positive effects of cushions on species richness did not translate into a higher H' or J'. At both elevations, values of H' and J' within *A. madreporica* cushions were lower than those estimated for the surrounding open areas. These results may be attributed to the higher abundance of some few species that grow within cushions, generating highly-dominated plant species assemblages within *A. madreporica*. For example, abundance and frequency of *Cerastium arvense* at both elevations were at least 10 times higher within cushions than outside them, indicating a stronger positive effect of *A. madreporica* on this particular species when compared with other species inhabiting cushions such as *Festuca magellanica* Lam. or *Montiopsis potentilloides* (Barneoud) D.I. Ford. Badano et al. (2002) reported similar effects on diversity for plant assemblages associated with cushions of *Oreopolus glacialis* (P. et E.) Ricardi, and also attributed the decrease in H' values within cushions to unequal responses of the local species to the presence of the cushion.

In contrast, the distribution of species abundance present outside cushions was much more even, especially at the lower elevation site. Indeed, species abundances on bare ground at 3,200 m followed a broken-stick distribution (Magurran 1988). These results contrast with those reported by Callaway et al. (2000), who studied the plant species assemblages associated with two nurse species in a sub-alpine community in the Caucasus mountains, and found that the species assemblages associated with the nurses were more even than the species assemblage growing outside nurses.

The differences in species richness, diversity and abundance (observed with the rank abundance distribution curves) found between within and outside cushions generated structurally different species assemblages. This is corroborated by the ordination analyses. As we expected, these differences in floristic composition between plant assemblages growing within and outside cushions increased with elevation. These differences could be attributed to the greater number of species that positively responded (in terms of incidence or abundance) to the presence of cushions at the higher elevation site when compared with the

lower elevation. Similar results have been reported in other studies carried out in arid systems (e.g., Tewksbury & Lloyd 2001, Rebollo et al. 2002).

Proportionally more species grew positively associated with cushions as elevation increases. Similar findings were reported by Olofsson (2004), who found that positive interactions and positive spatial associations between dwarf shrubs and *Carex bigelowii* Torr. ex Schwein in a Norwegian arctic-alpine tundra were higher in the site with higher elevation. Positive spatial associations are highly correlated with positive interactions (Callaway 1995), particularly in stressful habitats (Tirado & Paganire 2005, Kikvidze et al. 2006). Thus, as our higher elevation site has lower temperatures of both air and soil during the growing season than the lower elevation site, we suggest that our results support the predictions of the models proposed by Bertness & Callaway (1994) and Brooker & Callaghan (1998) on the increase in the frequency of positive interactions with increasing environmental harshness.

The low ambient temperature of high-mountain ecosystems is well known to limit plant performance, but the low stature and compact architecture of *A. madreporica* cushions allow them to ameliorate these harsh environmental conditions. For example, in a study focused on an other species of the genus *Azorella* realized in the Chilean Patagonian Andes (ca. 1,500 km further south from our study site), cushions of *A. monantha* Clos have been reported to maintain substrate temperatures 5-15 °C higher than the surrounding soil (Arroyo et al. 2003). Furthermore, although air temperature decreases with elevation (Cavieres & Arroyo 1999), the altitudinal decrease in temperature within *A. monantha* cushions was reported to be lower than in the surrounding environment (Arroyo et al. 2003), suggesting that cushions may have a stronger "buffer effect" on this limiting condition with increasing elevation (see also Cavieres et al. 2007).

In summary, even when total species richness present in the community decreased with elevation, the positive effects of *A. madreporica* on species richness were more intense in the higher elevation site. However, *A. madreporica* enhanced the incidence and

abundance of some species, which caused dominance effects that reduced species diversity and evenness within cushions and led to species assemblages with a different structure from those outside cushions. Our results provide support for the contention that the impact of a nurse or facilitator species on community structure increases with environmental harshness (*sensu* Hacker & Gaines 1997, Michalet et al. 2006), and highlight the importance of the cushion growth-form in maintaining the structure of high-Andean plant communities (Badano & Cavieres 2006a). As diversity is much more than the list of species present in a community, studies related with the impact of nurse species on diversity should include other community attributes than species richness to gather information of the magnitude and extent of the changes induced by these species, especially across environmental gradients.

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