Spatial patterns in cushion-dominated plant communities of the high Andes of central Chile: How frequent are positive associations?

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Abstract

Question: In stressful abiotic environments positive plant interaction is expected to be a frequent and an important process driving community composition and structure. In the high Andes in central Chile, the cushion plant *Azorella madreporica* dominates plant communities and appears to benefit the assemblage of species that grows within it. However, there are also many other species that grow outside this nurse cushion plant, which may or may not interact with this species. What is the prevailing type of spatial associations among the plant species that are not growing inside the nurse plant? What is the type of interactions between cushion plants and those species growing outside them?

Location: Molina River basin (33°20' S, 70°16' W, 3600 m a.s.l.), in the Andes of central Chile, ca. 50 km east of Santiago.

Methods: Two accurate mapping plots of individual plants of different species were located at two summits (Franciscano and Tres Puntas sites). The spatial distributions and associations between species growing outside cushions and within cushions at each site were estimated by point-pattern analyses using the univariate and bivariate transformations of Ripley's *K*-functions.

Results: We found both positive and, especially, negative spatial associations (8 out of 12 species in Franciscano site) between *A. madreporica* cushions and plants growing outside them. However, most of the species showed positive spatial associations among them. The variation in spatial association was site-specific and also depended on the type of plants involved. *Adesmia* spp., the second most abundant non-cushion species, displayed negative associations with cushions and positive associations with other species growing outside cushions.

Conclusions: Our study suggests very complex interactions among species, which ranged from positive to negative, and are also affected by abiotic environmental conditions.

Keywords: *Adesmia* spp.; Alpine demography; *Azorella madreporica*; Negative association; Plant demography; Positive interaction; Ripley's *L*-function.

Introduction

In stressful abiotic environments positive plant interactions are expected to be a frequent and an important process driving community composition and structure (e.g. Bertness & Callaway 1994; Callaway et al. 2002; Tirado & Pugnaire 2005). Positive plant interactions imply that fitness of one plant species is benefited by the improved (micro) environmental conditions created directly or indirectly by other plants, which outweighs the costs of living close to other individuals, i.e., competition (Callaway 1995; Brooker & Callaghan 1998; Bruno et al. 2003). Positive plant interactions have been demonstrated in a broad range of stressful environments, where a gamut of mechanisms have been described (for a review see Callaway 1995). One of the approaches most widely used to assess the frequency of positive interactions in stressful habitat conditions has been the study of spatial associations between species (Callaway 1995), particularly with nurse species, which may be acting as facilitator (Pugnaire et al. 1996; Eccles et al. 1999). The presence of positive associations have been interpreted as evidence for nurse effects, where some species show extreme clumping within or beneath the influence of the nurse species (Pugnaire et al. 1996; Tewksbury & Lloyd 2001).

In high-elevation habitats, the presence of several plant species growing inside cushion plants has suggested that cushions act as nurse or facilitator plants (Núñez et al. 1999; Cavieres et al. 2002, 2006; Arroyo et al. 2003); e.g. leading to increased species diversity in alpine plant communities of the high Andes (Badano & Cavieres 2006). Cushion plants are known for their ability to transform the habitat where they establish, i.e., ecosystem engineers, *sensu* Jones et al. (1997), where their low stature and compact form attenuate the effect of extreme environmental conditions, enabling the persistence of other species (Cavieres et al. 2002, 2006, 2007).

However, there are many other species that grow

frequently outside the nurse species' scope. These species also constitute an important component of the local diversity which has not been covered properly in previous studies, and for which the type of prevailing interactions is unknown. We do know that the most important processes structuring a community are likely to leave strong imprints on the spatial distribution of species (Dale 1999; Jeltsch et al. 1999), hence an examination of the entire community spatial pattern would yield valuable information on other processes shaping such a community. It has been proved that in severe environments, such as high mountains and arid zones, spatial distributional patterns tightly correlate with species interactions, where positive interactions lead to positive spatial association between plants, whereas spatial segregation suggests interference (Kikvidze et al. 2005). Thus, for species growing outside cushions, non-positive association with cushions may be suggested. Nevertheless, given the importance of positive interactions for survival in high-alpine habitats (Callaway et al. 2002), a clumped spatial distribution would be mostly found among those species growing outside cushions, indicating a positive spatial association among them. Therefore, at the entire community level, a mix of positive and negative associations among plants may be expected, probably depending on the microsite size and the type of species involved (Tirado & Pugnaire 2005).

In this study, statistics summarizing univariate and bivariate spatial point patterns (Ripley's *L*-function) were used to infer the spatial distribution of species growing outside cushions, and the spatial association between these species and cushions with the general aim to generate appropriate *a posteriori* hypotheses about the possible processes behind the patterns found. Thus, our main objective was to examine how frequent positive spatial associations (i.e., interactions) are among species growing outside cushions. As we worked in two different sites that differ in productivity, we also examined whether differences in site quality will have an effect on the spatial distribution and association of these species. To accomplish these objectives, we worked in two cushion-dominated communities in the high Andes of central Chile.

Methods

Study sites, plant species and sampling

The study was conducted in the Molina River basin (33º20' S, 70º16' W), located in the Andes of central Chile, ca. 50 km east of Santiago. Climate is alpine with influence of the Mediterranean-type climate that prevails in lowlands (di Castri & Hajek 1976), which is

characterized by cool rainy winters and long dry summers. At 3200 m elevation, mean annual precipitation is ca. 943 mm, most of which falls as snow from May to late October. Mean monthly air temperature during the growing season ranges from 3 ºC in April to 7.6 ºC in February at 3150 m (Cavieres & Arroyo 1999). Above 3000 m, we selected two cushion-dominated communities, one at Mt. Franciscano (3580 m) and the other at Mt. Tres Puntas peaks (3660 m). Cushion's altitudinal distribution ranges from 3200 to 3700 m, hence these two sites are located within this range. *Azorella madreporica* (*Apiaceae*) cushions form flat, and tightly knit cushions with a diameter that can range from 10 cm to > 100 cm (Cavieres et al. 2000). *Azorella madreporica* cushions are accompanied by other species among which rosette-forming perennial herbs are the most common: e.g., *Adesmia capitellata*, *Adesmia glomerula*, *Nassauvia lagascae*, *Oxalis compacta*, *Barneoudia major* and *Viola atropurpurea*. Both sites differed in total plant cover, species richness and productivity, with all these variables being greater in Franciscano than in Tres Puntas (Badano et al. 2006). Further, nitrogen soil levels were similar between the two sites ($P > 0.05$, Franciscano, NO_3 = 11 mg kg^{-1}; Tres Puntas, NO_3 = 18 mg kg^{-1}), while phosphorous and potassium soil levels were very high in both sites, although lower for Franciscano (P = 7.5 and K = 200 mg kg^{-1}) than for Tres Puntas (P = 11.5 and K = 400 mg kg^{-1}) (unpubl. results). Both sites were quite homogeneous in appearance and rock outcrops were absent. Site homogeneity was also confirmed by a companion paper (Fajardo et al. in press), where another type of analysis was conducted to determine microsite heterogeneity.

At each site, a plot of 10 m × 30 m was established at random, with one axis perpendicular to the main direction of the slope. For simplicity, the plots were divided into mini-plots of 1 m × 1 m, and Cartesian coordinates (x,y) were recorded for every single individual located within each plot (inside and outside cushions), for which we used distance tapes. To determine the size of the cushions present in each plot, we measured two perpendicular diameters on each cushion and assumed an elliptical form. The centre of each cushion was located subjectively (roughly the geometrical centre), and the formula for the cushion's area we used was:

$$A = (\pi * L * W)/4 \qquad (1)$$

where L is the longest diameter and W is the shorter diameter perpendicular to the former one. Where more irregular shapes were found, we further divided the cushions to reach more accurate size estimation. The size of each cushion was expressed in square decimetres (dm^2). Plots were located on east-facing slopes at both sites. All sampling was conducted in January 2005.

Analysis of spatial distributions and associations

The coordinate data (x,y), corresponding to the centre of each plant, were used to determine the univariate spatial pattern (distribution) for each species, and the bivariate spatial pattern (association) between species using a modified version of Ripley's *K*-function (Lotwick & Silverman 1982). We examined the univariate and bivariate spatial patterns among those species that were registered at least 20 times within each plot as recommended by Haase (1995). Ripley's *K*-function is based on the variance (second-order analysis) of all point-to-point distances in a two-dimensional space, and gives a description of the spatial structure of points (e.g., plants) at different scales at the same time (Cressie 1993). In this function, the spatial relationship among individuals of the same species (univariate analysis) is defined as the expected number of conspecific individuals within a radius *t*, centred in an arbitrary individual, divided by the average density of such a class of individuals. On the other hand, the spatial relationship between two species (bivariate analysis) is defined as the expected number of individuals of species 2 within a radius *t*, centred in an arbitrary individual from species 1, divided by the average density of both species. We chose the *L*-function proposed by Bessag (1977), which is a linearized version of the Ripley's *K*-function (Ripley 1977), and it is preferred because it is easier to interpret. The *L*-function is estimated as:

$$\hat{L}(t) = \sqrt{(\hat{K}(t)/\pi)} - t \qquad (2)$$

which scales *K(t)*'s variance and then facilitates the testing against the null hypothesis of complete spatial randomness (CSR; i.e. all points are distributed independently). The linearized function has an expectation of zero for any value of *t* when the pattern is random. The spatial pattern can then be described as clumped, random, or regular at any distance *t* up to half the length of the shortest rectangular plot side if the calculated $\hat{L}$ (*t*) is greater, equal or lower than the 99% confidence envelopes (bounds), respectively (Haase 1995). The statistical significance of the departure from zero was tested using a Monte Carlo procedure that randomly repositions all points in the plot and generates *L(t)* functions. Thus, we computed the 99% confidence envelopes around the null hypothesis value (L(*t*) ≈ 0) by running 99 simulations at intervals of 0.1-m from 0.1 to 2 m. We used this small spatial scale interval, for both uni- and bivariate analyses, to better detect spatial distribution at neighbour scale. The Cramer-von Mises test was used to account for significance (Haase 2002). Since edge effects become a concern at greater distances, we used the weighting edge correction methods to account for this effect (Haase 1995).

To estimate the spatial association between *Azorella madreporica* cushions and species growing outside them, and between *A. madreporica* cushions of different size classes, we used the bivariate spatial function, $K_{1.2}(t)$ (a derivation from the univariate spatial function), which characterizes the relative location of one species with respect to another. We also used the modified $L_{1.2}(t)$-function (Lotwick & Silverman 1982), whose classical estimator is

$$\hat{L}_{1.2(t)} = \sqrt{(\hat{K}_{1.2}(t)/\pi)} - t \qquad (3)$$

which provides evidence of spatial association between species 1 and 2: if the value of $\hat{L}_{1.2}(t)$ is not significantly different from zero, the null hypothesis that the two species have independent spatial distribution cannot be rejected (Goreaud & Pélissier 2003). Monte Carlo simulations were used to evaluate the statistical evidence of a departure from zero; we built 99% confidence intervals from 99 shifts of one species with respect to the other. Values of $\hat{L}_{1.2}(t)$ greater, equal or lower than 99% confidence envelopes indicated significant positive spatial association (attraction), spatial independence and significant negative spatial association (repulsion) between the two species analysed, respectively (Dixon 2002; Goreaud & Pélissier 2003). *Azorella madreporica* size classes were defined based on the size histogram obtained: thus, size class 1 ranged from 0.1 to 10 dm^2, size class 2 from 10.1 to 50 dm^2, and size class 3 from 50.1 to 300 dm^2. As species of the genus *Adesmia* also form small but soft cushions and hence can be another potential key species in this system, we also evaluated their spatial association with the rest of the species growing outside cushions in both sites. The spatial statistics program SPPA (Haase 2002) was used for the computations of both univariate and bivariate analyses.

Results

Azorella madreporica was the dominant species at both sites: a total of 94 (3133/ha) and 84 (2800/ha) individual cushions were mapped in Franciscano and Tres Puntas (0.03 ha) sites, respectively. The cushions' size ranged from 1.33 to 199.66 dm^2 (median value of 18.85 dm^2) at the Franciscano site, covering an area of 2881.51 dm^2, and from 1.08 to 300 dm^2 (median value of 23.49 dm^2) at the Tres Puntas site, with a total area of 3211.02 dm^2. The two sites differed strongly in individual abundance, reflected in both the total number of individuals mapped (1680 for Franciscano vs. 520 for Tres Puntas), and the total number of species found. At the Franciscano site we found 25 species (9 of them inside cushions) vs. 16 at Tres Puntas (7 of them inside

cushions; Table 1). Apart from *A. madreporica*, three other species were abundant and present at both sites: *Adesmia capitellata*, *Hordeum comosum* and *Nassauvia lagascae* (Table 1).

Spatial pattern distribution

Azorella madreporica was, in general, significantly clumped at both sites and at most of the spatial scales (Fig. 1, Table 2). When analysed at different size classes, however, we found that size classes 1 and 2 (up to 50 dm^2) were significantly clumped, while large individuals (size class 3) were randomly distributed (Table 3). Furthermore, when cushions' size classes were compared, we found a significantly positive spatial association between Class 2 and 1 at both sites (Table 3) from ca. 0.5 up to 2 m at the Franciscano site, and up to 1.65 m at the Tres

Puntas site. Independent associations were found when compared Class 3 vs. Class 1 ($p > 0.05$; Table 3).

Likewise, most of the species growing outside *A. madreporica* cushions consistently displayed a clumped distribution across the range of distances examined (Table 2). The clumped pattern of each species began at short distances (0.05 m), except for *Azorella*, where the aggregation started at ca. 0.5 m, which might approximate average diameter extension (Fig. 1). The clumped pattern persisted up to higher scales (2 m) for most of the species with the exception of *Phacelia secunda* (Table 2), a pioneer stress-tolerant species that colonises disturbed sites (Cavieres & Arroyo 2001).

Table 1. Species and number of individuals sampled, and their capacity to growth either inside or outside of the cushion species *Azorella madreporica* at the Franciscano and Tres Puntas sites, Valle del Río Molina, Andes of central Chile (33° 20' S.).

Site	Franciscano (*n*)	Tres Puntas (*n*)	Condition
Species			
Azorella madreporica	94	84	
Adesmia capitellata	130	104	Outside
Adesmia glomerula	100		Outside
Barneoudia major	658		Outside
Cerastium arvense	41		Inside/Outside
Hordeum comosum	142	131	Inside/Outside
Nassauvia lagascae	56	70	Outside
Oxalis compacta	47	6	Outside
Phacelia secunda	28		
Trisetum preslei	13	87	Inside/Outside
Viola atropurpurea	277		Outside
Others	107	43	
Olsynium scirpoideum	16		Outside
Taraxacum officinale	13	7	Inside/Outside
Viola philippi	11		Outside
Thlaspi magellanicum	11	8	Inside/Outside
Pozoa coriacea	9		Outside
Erigeron andicola	9		Inside/Outside
Erigeron leptopelatus		1	Inside/Outside
Nastanthus agglomeratus	6		Inside/Outside
Cistanthe frigida	5		Inside/Outside
Senecio looseri	4		Outside
Chaetanthera flabellata	3		Inside/Outside
Chaetanthera lycopodiodes	1		Outside
Chaetanthera planiseta	2	4	Outside
Chaetanthera pusilla		2	Outside
Rytidosperma violaceum	3		Outside
Perezia carthamoides	1		Outside
Montopsis andicola		2	Inside/Outside
Luzula spec.		2	Outside
Festuca rubra		6	Inside/Outside
Calandrinia affinis		5	Outside
Total	1680	520	

Note: (*n*) stands for the total number of individuals.

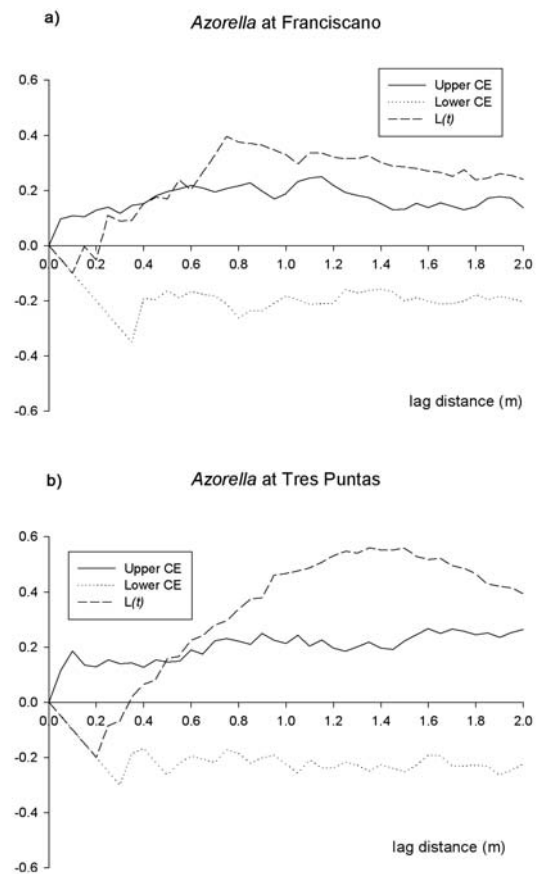**Fig. 1.** $L_{(t)}$ function and the confidence envelopes associated with it (giving an approximate 99% confidence envelope (CE) for the null hypothesis of Poisson random distribution) for the spatial distribution of *Azorella madreporica* at **(a)** Franciscano, and **(b)** Tres Puntas sites in an alpine cushion-dominated community at the Valle del Río Molina, Andes of central Chile (30°20' S).

Table 2. Patterns of spatial distribution based on the univariate L-function for alpine plant species at the Valle del Río Molina, Andes of central Chile (30°20'S). Cushions' size classes ranged from $0 - 10$ dm^2 (Size class 1), $10.1 - 50$ dm^2 (Size class 2), and $50.1 - 300$ dm^2 (Size class 3).

Species	n	Franciscano — Distance t (m) (0.1 / 0.5 / 1.0 / 1.5 / 2.0)	p†	n	Tres Puntas — Distance t (m) (0.1 / 0.5 / 1.0 / 1.5 / 2.0)	p
Azorella madreporica	94	c c c c c c c c c c c c c c c (from ~0.5)	0.01	84	c c c c c c c c c c c c c c c c c (from ~0.5)	0.01
Size class 1	33	c c c c c c c c c c (from ~0.3 to 1.0)	0.02	19	c c c c c c c c c c c c c (from ~0.3 to 1.0)	0.01
Size class 2	44	c c c c c c c c c c c c (from ~0.8)	0.01	42	c c c c c c c c c c c c (from ~0.8)	0.01
Size class 3	17		0.23	23		0.30
Adesmia capitellata	130	c c c c c c c c c c c c c c c c c c c c c (full)	0.01	104	c c c c c c c c c c c c c c c c c c c c c (full)	0.01
Adesmia glomerula	100	c c c c c c c c c c c c c c c c c c c c c (full)	0.01		===	
Barneoudia major	658	c c c c c c c c c c c c c c c c c c c c c (full)	0.01		===	
Cerastium arvense	41	c c c c c c c c c c c c c c c c c c c c c (full)	0.01		===	
Hordeum comosum	142	c c c c c c c c c c c c c c c c c c c c c (full)	0.01	131	c c c c c c c c c c c c c c c c c c c c c (full)	0.01
Nassauvia lagascae	56	c c c c c c c c c c c c c c c c c c c (from ~0.4)	0.01	70	c c c c c c c c c c c c c c c c c c c c c (full)	0.01
Oxalis compacta	47	c c c c c c c c c c c c c c c c c c c (from ~0.3)	0.01		===	
Phacelia secunda	28	c c c c c c (from ~0.3 to 0.6)	0.05		===	
Trisetum preslei		===		87	c c c c c c c c c c c c c c c c c c c c c (full)	0.01
Viola atropurpurea	277	c c c c c c c c c c c c c c c c c c c c c (full)	0.01		===	
Others	107	c c c c c c c c c c c c c c c c c c c c c (full)	0.02	43	c c c c c c c c c c c (from 0.1 to ~1.0)	0.02

*The symbol c indicates significant clumped distribution at distance t, based on $L(t)$-function values distribution. An empty cell indicates random distribution (= means not applicable). † Significance is using a 99% confidence envelope (99 simulations) with a 0.05-m step. Cramer-von-Mises test was used for overall significance of patterns over the complete range of t.

Table 3. Patterns of specific spatial association based on the bivariate $L_{1,2}$-function between *Azorella madreporica* (a cushion plant species) and the rest of the species growing outside the cushions at the Valle del Río Molina, Andes of central Chile (30°20'S). Cushions' size classes ranged from $0 - 10$ dm^2 (Size class 1), $10.1 - 50$ dm^2 (Size class 2), and $50.1 - 300$ dm^2 (Size class 3).

Species	n	Mt. Franciscano — Distance t (m) (0.1 / 0.5 / 1.0 / 1.5 / 2.0)	p†	n	Mt. Tres Puntas — Distance t (m) (0.1 / 0.5 / 1.0 / 1.5 / 2.0)	p
Azorella madreporica	94		0.70	84		0.39
Class 3 vs. Class 1			0.70			0.39
Class 3 vs. Class 2		+ + + + + + + + + (from ~0.2 to 0.8)	0.09			0.78
Class 2 vs. Class 1		+ + + + + + + + + + + + + + + + + (from ~0.5)	0.01		+ + + + + + + + + + + + (from ~0.5)	0.01
Adesmia capitellata	130	- (from ~0.5)	0.01	104		0.1
Adesmia glomerula	100	- (full)	0.01		===	
Barneoudia major	658	- (full)	0.01		===	
Cerastium arvense	41	+ + + + + + + + + + + + + + + + + + (from ~0.5)	0.01		===	
Hordeum comosum	142	- - - - - - - - - - - - - - - - (from ~0.7)	0.01	131	+ + + + + + (from ~0.5 to 0.8)	0.07
Nassauvia lagascae	56	- (full)	0.01	70		0.76
Oxalis compacta	47	- - - - - - - - - - - - - - - (from 0.1)	0.01		===	
Phacelia secunda	28	- - - (0.1 to ~0.4)	0.05		===	
Trisetum preslei		===		87	+ (full)	0.01
Viola atropurpurea	277	- (full)	0.01		===	
Others	107	+ (full)	0.02	43	+ (full)	0.01

* The symbol + means significant positive association; - means significant negative association at distance t, based on $L_{1,2}(t)$-function. An empty cell indicates independent association (= means not applicable). Significance is using a 99% confidence envelope (99 simulations) with a 0.05-m step. Cramer-von-Mises test was used for overall significance of patterns over the complete range of t.

Interspecific spatial associations

At the Franciscano site, *A. madreporica* mainly established negative associations with the rest of the assemblage across most of the spatial scales studied (from ca. 0.3 up to 2 m), that is: *Adesmia capitellata*, *A. glomerula*, *Barneoudia major*, *Hordeum comosum*, *Nassauvia lagascae*, and *Viola atropurpurea*, *Oxalis compacta* and *Phacelia secunda*, i.e., 8 out of 9 well-represented species ($p < 0.01$, Table 3). The only species that exhibited positive and significant spatial associations with *A. madreporica* cushions was *Cerastium arvense* (Table 3). At the Tres Puntas site, 2 out of 4 species, *Hordeum comosum* (between 0.4 and 0.9 m) and *Trisetum preslei* (from 0.3 up to 2 m), exhibited significant positive spatial associations with *A. madreporica* (Table 3). Two other species, *Adesmia capitellata* and *Nassauvia lagascae*, were found to be distributed independently from *A. madreporica* across most of the spatial scales. Thus, a higher frequency of positive associations to cushions occurs in the less productive site. All the species that grow at both sites (i.e., *Adesmia capitellata*, *Hordeum comosum* and *Nassauvia lagascae*) showed different association patterns with *A. madreporica* depending on the site. *Adesmia capitellata* and *N. lagascae* were negatively associated with *A. madreporica* at Franciscano, but independently distributed from each other at Tres Puntas. *Hordeum comosum* changed from negatively associated at Franciscano to positively associated at Tres Puntas.

When *Adesmia* was spatially analysed with respect to the other species, we mostly found that these species were either positively associated or distributed independently from the other species, particularly at the Franciscano site (Table 4). Species such as *Barneoudia major*, *Hordeum comosum*, and *Viola atropurpurea* were positively associated with *Adesmia capitellata* as well as with *A. glomerula*. There were also more species-specific relations like the positive association between *A. capitellata* and *Nassauvia lagascae*, between *A. glomerula* and *Oxalis compacta*, and between *A. glomerula* and *Phacelia secunda* (Table 4). For the Tres Puntas site, only *N. lagascae* showed positive associations with *A. capitellata* (*Trisetum preslei* also had positive association though at a very narrow spatial scale: 1.8 to 2 m). Interestingly, as with *A. madreporica*, *H. comosum* showed a different spatial association with *A. capitellata* depending on the site, i.e., positive in Franciscano and negative in Tres Puntas (Table 4). When the rest of the species were compared, a prevalence of positive spatial associations was found (see App. 1).

Discussion

Using high-precision mapping plots and spatial point pattern analyses (Ripley's *L*-functions), we found a complex spatial structure for all the species forming these important plant communities. Negative spatial associations among species were not rare. That is, in the stressful environments of the high Andes of central

Table 4. Patterns of specific spatial association based on the bivariate $L_{1,2}$-function between *Adesmia* spp. and the rest of the species growing outside of the cushions with at least 20 individuals at the Valle del Río Molina, Andes of central Chile (33° 20'S).

Mt. Franciscano Species	n	*Adesmia capitellata* 130) Distance t (m)					p†	*Adesmia glomerula* (100) Distance t (m)					p
		0.1	0.5	1.0	1.5	2.0		0.1	0.5	1.0	1.5	2.0	
Adesmia glomerula	100		+ + +	+ + + + + +	+ + + + + +	+ + + +	0.01	= = =	= = = = =	= = = = = =	= = = = = =	= = = = =	0.01
Barneoudia major	658			+ + + +	+ + + +	+ + + +	0.01			+ + + +	+ + + + +	+ + + + +	0.01
Cerastium arvense	41						0.06			- - -			0.01
Hordeum comosum	142			+ + + +	+ + + +	+ + + +	0.01		+ + + + +	+ + + + +	+ + + + +	+ + + + +	0.01
Nassauvia lagascae	56	+ + + +	+ + + +	+ + + + +	+ + + + +	+ + + + +	0.01						0.58
Oxalis compacta	47						0.25				+ + + + +	+ + + +	0.01
Phacelia secunda	28						0.83		+ + + + +				0.02
Viola atropurpurea	277	+ + + +	+ + + +	+ + + + +	+ + + + +	+ + + + +	0.01		+ + + +	+ + + + +	+ + + + +	+ + + + +	0.01
Others	107		+ +	+ + + + +	+ + + + +	+ + + +	0.01		+ + + +	+ + + + +	+ + + + +	+ + + + +	0.01
Mt. Tres Puntas		*Adesmia capitellata* (104)											
Hordeum comosum	131		- - -	- - - -	- - - -	- - -	0.01	= = = =	= = = = =	= = = = = =	= = = = = =	= = = = =	
Nassauvia lagascae	70	+ + + +	+ + + +	+ + + + +	+ + + + +	+ + + + +	0.01	= = = =	= = = = =	= = = = = =	= = = = = =	= = = = =	
Trisetum preslei	87					+ + +	0.06	= = = =	= = = = =	= = = = = =	= = = = = =	= = = = =	
Others	43						0.33	= = = =	= = = = =	= = = = = =	= = = = = =	= = = = =	

* The symbol + means significant positive association; - means significant negative association at distance *t*, based on $L_{1,2}(t)$-function. An empty cell indicates independent association (= means not applicable). Significance is using a 99% confidence envelope (99 simulations) with a 0.05-m step. Cramer-von-Mises test was used for overall significance of patterns over the complete range of *t*.

Chile, a mix of both positive and negative associations are found equally, which concur with other studies performed in stressful habitats (e.g., Tirado & Pugnaire 2005). This scenario opens a broader path for generating more specific hypotheses about the processes that finally shape the spatial patterns of these cushion-dominated communities in an extreme environment, where both positive and negative biotic interactions may be acting together with abiotic factors at similar or different scales (Callaway & Pugnaire 1999).

Spatial patterns and site specificity

Both sites differed in individual abundance, number of species, and spatial patterns, particularly for interspecific spatial associations. At the Franciscano site, with higher plant cover and species richness than Tres Puntas, 8 out of 12 species growing outside *A. madreporica* showed a certain degree (at some scale) of negative association with them, e.g., a consistent negative association occurred between *Adesmia* spp. and *A. madreporica*. In contrast, at Tres Puntas, negative associations were almost absent. Hence, a higher frequency of negative associations was found in the more productive site, which is in line with predictions derived from the stress gradient hypothesis (Bertness & Callaway 1994; Brooker & Callaghan 1998). Further, some species common in both sites shifted the sign of association from site to site. For example, while some species shifted from negative to independent spatial associations, others, e.g., *Hordeum comosum*, shifted from negatively associated to *A. madreporica* at Franciscano (more productive site) to positive spatial associations at the Tres Puntas site (less productive site). However, *H. comosum* shifted from positively associated to *Adesmia capitellata* in Franciscano to negatively associated in Tres Puntas. Thus, from these results we may suggest that spatial associations are site specific, which may obey to abiotic differences at a lower scale, e.g., microsite (Jackson & Caldwell 1993; Schlesinger et al. 1996; Escudero et al. 2004), or to the spatial structure of cushions, or both (Fajardo et al. in press).

The spatial distribution of cushions differed by size classes at both sites, e.g., larger size classes were randomly distributed whilst smaller size classes were clearly clumped. This may suggest that a process of self-thinning has occurred, similarly to what happens in old-growth forest stands (Veblen 1992). In a companion study, Fajardo et al. (in press) also found that the distribution of size classes was best-fit by a negative exponential curve, which resembles a reverse J-shaped curve, typical of populations with a regular success in the establishment of recruitment, i.e., all size classes of cushions were represented in the population.

Facilitative interactions have been suggested as the main process promoting co-existence in these extreme environments (Cavieres et al. 2002). However, the strong spatial segregation (i.e., negative spatial associations) showed by some species (e.g., *A. madreporica* and *Adesmia* spp.) at both sites suggests that negative interactions may also contribute to the co-existence of species in the system, e.g., niche differentiation. This pattern of spatial segregation among species may well be related to either the processes of colonization and establishment of cushion plants studied (a subject explored in a companion paper, Fajardo et al. in press), or to microsite level differences (e.g., nutrients). It is known that nutrients, especially nitrogen, are scarce here (Bowman et al. 1993; Nilsson et al. 2002), and that the availability of these resources can determine the success of recruitment in several alpine plant species (Chambers et al. 1990; Forbis 2003). Thus, a variation in the level of nutrients may result in changes in the spatial patterns of these plant communities. Future studies should focus on determining the complex relationships among rates of establishment and nutrient levels, and the dynamics of *Azorella madreporica* mortality as a way to better explain this specific spatial pattern differentiation among sites.

Spatial patterns and species specificity

The importance of *A. madreporica* as a nurse species that facilitates the establishment and growth of other species has been documented and experimentally demonstrated in this particular alpine system (Cavieres et al. 2005, 2007). Some studies, however, have shown that nurse species not always have beneficial effects on the other species, but also negative or neutral effects on some species of the community (Muller 1953; Callaway et al. 1996), i.e., they are 'selective' in their benefits. Among the species growing outside cushions, *Adesmia* spp. showed a consistent negative association when compared to *A. madreporica*. Additionally, *Adesmia* spp. displayed positive associations with many other outside-of-cushion species (e.g. *B. major*, *H. comosum*, *N. lagascae*, *V. atropurpurea*). *Adesmia* spp. are rosette-like alpine species that share some architectural characteristics with *A. madreporica*, i.e., low stature and compact form, which allow them to cover some ground area and hence be more effective when coping with extreme environmental conditions (Körner 2003). We may speculate that (1) *Adesmia* spp. might have some similar facilitation effects on other species of the community, and (2) that the spatial negative association between *Adesmia* spp. and *A. madreporica* may be due to pre-empted competition for suitable microsites between these similar species, as it has been shown in other alpine ecosystems (Kikvidze 1993; Gavilán et al. 2002).

In addition, negative associations with *A. madreporica* were also found in other species (e.g. *B. major*, *O.*

compacta and *V. atropurpurea*). *Azorella madreporica* forms tight cushions, which could limit the growth of some species, especially those that require conditions for rapid growth (e.g., annual species), or those that require substantial free space (e.g., suffruticose or woody species). This could be the case of species such as *Barneoudia major* and *Viola atropurpurea*, which are rhizomatous and therefore might need free space to grow. Nevertheless, an experimental approach is necessary here for getting insights that can clarify the mechanisms of these potential negative interactions.

Limitations

Spatial point pattern analysis assumes that observations are points. Cushions are clearly not points. We found that the median area values were 18.85 dm² at Franciscano and 23.49 dm² at the Tres Puntas site, showing both a reverse J-shaped curve for the distribution of cushion's size classes (area) (Fajardo et al. unpubl.), meaning that most of the cushions were of rather small size, which can smooth partially the misuse of applying point pattern analysis to individuals that are not points. As we consider the centre of each individual as its coordinates, the spatial association between larger cushions and other species may represent an oversimplification of the global spatial pattern of the community; i.e., neighbours that are very close to the cushion's border may appear to be far away from the cushion's centre. We are aware that this may imply an overrepresentation of negative associations between species growing outside cushions and larger cushions. However, we note that large cushions in the plots were scarce, which may off-set the negative effects.

Ecological implications

Intra- and interspecific spatial relationships influence the strength of plant interactions (Law & Dieckmann 2000); similarly, interactions may modify the spatial relationships between plants (Llambí et al. 2004). Here, the fact that the frequency of positive associations (i.e., positive interactions) in abiotically severe environments is not absolute (dampened for other more frequent negative associations) clearly emphasize that positive and negative interactions may be co-occurring forces (Callaway & Pugnaire 1999), where the net resulting interaction not only depends on the general stress level of the sites, but also on the ecological traits of the species (Michalet et al. 2006). Even though, the former explanation is conceptually accepted, we still continue to consider positive associations to be more frequent and important in stressful environments. Most of the studies documenting positive interactions in these environments have been focused on the key species within the community; i.e., the 'facilitator' or the 'ecosystem engineers'. Although, important in their findings and in noticing the key community role these 'facilitator' species have, previous studies have biased the attention towards a part of the community, hence partially explaining community properties like stability, invasiveness, and diversity. Here, we have found a rich spatial structure, which stresses the existence of both positive and negative biotic interactions that may also be acting together with abiotic interactions in determining the final spatial structure of plant communities in highly stressful habitats.

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App. 1. Patterns of specific spatial association based on the bivariate $L_{1,2}$-function among the rest of species (not including *Azorella madreporica* and *Adesmia* spp.) growing outside of the cushions with at least 20 individuals at the Valle del Río Molina, Andes of central Chile (30º20'S).

Mt. Franciscano

Barneoudia major (658) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	n	Pattern (0.1 – 2.0)	p†
Barneoudia major	658	================================	
Cerastium arvense	41	+ + (≈0.5)	0.08
Hordeum comosum	142	+ (0.1–2.0)	0.01
Nassauvia lagascae	56	+ + + + + + + + + + + + + + + + + + + (0.5–2.0)	0.02
Oxalis compacta	47		0.12
Phacelia secunda	28		0.45
Viola atropurpurea	277	+ (0.1–2.0)	0.01
Others	107		0.08

Cerastium arvense (41) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	Pattern (0.1 – 2.0)	p
Cerastium arvense	================================	
Hordeum comosum		0.68
Nassauvia lagascae		0.10
Oxalis compacta		0.99
Phacelia secunda		0.63
Viola atropurpurea	+ + + + + + + + (≈1.0–1.5)	0.02
Others		0.54

Hordeum comosum (142) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	n	Pattern (0.1 – 2.0)	p†
Hordeum comosum	142	================================	
Nassauvia lagascae	56	+ (0.1–2.0)	0.01
Oxalis compacta	47	+ + + + + + + + + + + + + + + (0.5–1.5)	0.01
Phacelia secunda	28		0.65
Viola atropurpurea	277	+ + + + + + + + + + + + + + + + + + + (0.5–2.0)	0.01
Others	107	+ (0.1–2.0)	0.01

Nassauvia lagascae (56) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	Pattern (0.1 – 2.0)	p
Nassauvia lagascae	================================	
Oxalis compacta	+ + + (≈0.5) + + + + + + (1.5–2.0)	0.02
Phacelia secunda		0.40
Viola atropurpurea	+ + + + + + + + + + + + + + + + + + + (0.5–2.0)	0.01
Others		0.39

Oxalis compacta (47) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	n	Pattern (0.1 – 2.0)	p†
Oxalis compacta	47	================================	
Phacelia secunda	28		0.19
Viola atropurpurea	277	+ + + + + + + + + + + + + + + + + + + (0.5–2.0)	0.01
Others	107		0.21

Phacelia secunda (8) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	Pattern (0.1 – 2.0)	p
Phacelia secunda	================================	
Viola atropurpurea	+ (0.1–2.0)	0.01
Others	- - - - - - (≈0.1–0.5)	0.05

Mt. Tres Puntas

Hordeum comosum (142) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	n	Pattern (0.1 – 2.0)	p†
Hordeum comosum	131	================================	
Nassauvia lagascae	70	+ + + (≈2.0)	0.12
Trisetum preslei	87	+ + + + + (≈0.1–0.5)	0.21
Others	43		0.37

Nassauvia lagascae (56) — Distance t (m): 0.1, 0.5, 1.0, 1.5, 2.0

Species	Pattern (0.1 – 2.0)	p
Hordeum comosum	================================	
Nassauvia lagascae	================================	
Trisetum preslei	+ + + + + + + + + (0.5–1.0) + + + + + + + + (1.5–2.0)	0.01
Others	+ + + + + + + + + + + + + + + + + + + (0.1–2.0)	0.01

* The symbol + means significant positive association; - means significant negative association at distance t, based on $L_{1,2}(t)$-function. An empty cell indicates independent association (= means not applicable). Significance is using a 99% confidence envelope (99 simulations) with a 0.05-m step. Cramer-von-Mises test was used for overall significance of patterns over the complete range of t.