Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile

E.I. Badano*, L.A. Cavieres, M.A. Molina-Montenegro, C.L. Quiroz

ECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales & Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile

Abstract

The most important processes shaping communities are likely to leave observable imprints on their spatial structure. The net outcome of positive and negative interactions among plants has been proposed to vary inversely with environmental harshness. In the Mediterranean-type matorral of central Chile, slope aspect strongly influences mesoclimatic conditions: equatorial-facing slope are xeric and are dominated by spiny shrubs and cacti, while evergreen sclerophyllous trees dominate polar-facing slopes due to their more mesic conditions. Here we use spatial pattern analyses to infer on the interactions that shape community structure in this matorral. We sampled the vegetation on two polar- and equatorial-facing slopes and assessed the dominant interaction at each slope through: (1) a species co-occurrence index (C-score) for the entire community; (2) the frequencies of negative and positive associations between species pairs; and (3) the species richness at each slope. Our results indicated that negative spatial associations dominated plant assemblages on all slopes, but the importance of negative associations decreased from mesic ($\sim$30%) to xeric slopes ($\sim$16%). Species richness was higher on xeric than on mesic slopes. Although competition seems to be the main biotic force structuring communities on both mesic and xeric slopes, we suggest that the decrease in

---

*Corresponding author. Tel.: $+$56 41 203846; fax: $+$56 41 246005.

E-mail address: ebadano@udec.cl (E.I. Badano).

importance of negative interactions from mesic to xeric habitats could produce an increase in diversity.

1. Introduction

The spatial structure of a plant community is the product of many processes acting in concert including both abiotic and biotic processes such as dispersal, herbivory, disturbance, competition, and distribution of available resources. The most important processes structuring the community are likely to leave strong imprints on the spatial distribution of species, and therefore, it should be possible to use spatial pattern analyses to infer on the processes shaping community structure (Schenk et al., 2003).

Competition has been proposed as one of the main forces determining the structure and diversity of plant communities in highly productive habitats (Grubb, 1977; Grime, 1979). These negative interactions are generally thought to decrease the abundance of competitors (Sammul et al., 2000) and generate negative patterns of spatial associations between species (Keddy, 1990; Pacala and Levin, 1997). However, the importance of competition on community structure decreases in stressful environments (Grime, 1974, 1979). On the other hand, it has also been proposed that this decrease in importance of negative interactions is accompanied by an increase in importance of positive interactions (i.e. facilitation) (Bertness and Callaway, 1994; Brooker and Callaghan, 1998).

More specifically, Bertness and Callaway (1994) proposed a conceptual model in which the relative importance of competition and facilitation vary inversely along stress gradients. The empirical support for this model has come from observations of spatial associations between species pairs (Valiente-Banuet and Ezcurra, 1991; Haase et al., 1996; Cavieres et al., 2002), as well as from results of the effects of experimental neighbor removal along stress gradients (Quinos et al., 1998; Pugnaire and Luque, 2001; Callaway et al., 2002). However, few studies have focused on the relative effects of competition and facilitation along stress gradients at the level of the entire community. This is mainly due to the unfeasibility of performing experiments with many species within a community. For this reason, it is common to rely on measures of spatial association between species to indirectly infer on the possible effects of interactions on community structure and diversity along environmental gradients (Pugnaire et al., 1996; Tewksbury and Lloyd, 2001). For example, Tewksbury and Lloyd (2001) reported greater species richness of annual plants beneath the canopies of *Olneya* spp. compared to open areas in xeric habitats of the Sonoran Desert. In contrast, *Olneya* tree canopies had little or no impacts on species diversity in mesic habitats. In this study, we use a similar approach to determine if spatial associations allow us to infer on the importance of positive and negative in plant communities of the Mediterranean Chilean matorral.

The Chilean matorral consist of sclerophyllous vegetation covering relatively undisturbed areas in the Mediterranean-type climate zone of central Chile. Plant species are distributed in shrub-clumps interspaced among large open spaces (Dallman, 1998). A marked contrast between vegetation occurring on equatorial- and polar-facing slopes has been observed in this area (Armesto and Martínez, 1978; Fuentes et al., 1984). While equatorial-facing slopes bear open scrub vegetation with spiny shrubs and cacti, shade-tolerant evergreen trees and shrubs dominate in polar-facing slopes (Armesto and Martínez, 1978; Dallman, 1998). Although changes in productivity and species composition between slopes have been attributed to an increase in water stress on equatorial-facing slopes (Armesto and Martínez, 1978; Armesto et al., 1979; Martínez and Armesto, 1983), experimental results for some species of this matorral suggest that variations in the intensity of competition and facilitation could influence the community structure on polar- and equatorial-facing slopes (Holmgren et al., 2000).

In this study, we measured the spatial patterns of association of woody species in the Chilean matorral to assess the sign of the dominant interaction (i.e. negative or positive) of entire plant assemblages on mesic polar- and xeric equatorial-facing slopes. We also compare the relative frequencies of positive and negative associations between all species pairs on mesic and xeric slopes to assess changes in the relative frequencies of both types of associations between both slope exposures. Based on the model of Bertness and Callaway (1994), we predict a decrease in the relative frequency of negative associations, and an increase in positive associations, from mesic to xeric slopes. Moreover, since species association frequencies are expected to change with slope aspect, we hypothesized that relative species richness within clumps would be lower on mesic polar-facing slopes and higher on xeric equatorial-facing slopes.

2. Methods

2.1. Study sites

This study was carried out at two sites on the Andean foothills of the Mediterranean-type climate zone of central Chile: Corral Quemado (33°25′S, 70°35′W, 1400 m elevation) and San Carlos de Apoquindo (33°23′S, 70°31′W, 900 m elevation). At each site, a polar- and an equatorial-facing slope was sampled in order to analyse the species association patterns within shrub-clumps.

Mean annual temperature in the study area is 18 °C, but exceeds 30 °C in summer and falls below 0 °C during winter (di Castri and Hajek, 1976). Annual rainfall ranges from 300 to 500 mm and the dry season occurs in summer (op. cit.). In the Andean foothills, patterns of temperature and moisture are primarily a function of topography. This way, equatorial-facing slopes are dryer than polar-facing ones because they receive more solar radiation and have greater evapo-transpiration rates (Rundel, 1981).

Most of the dominant species within shrub-clumps on xeric equatorial-facing slopes are drought-tolerant, such as *Baccharis* spp. (Asteraceae) and *Proustia* spp. (Asteraceae), and these clumps are inter-spaced by large open areas of bare ground. Clumps on mesic-polar-facing slopes are dominated by shade-tolerant tree species, such as *Quillaja saponaria* (Rosaceae), *Kageneckia* spp. (Rosaceae) and *Lithraea caustica* (Anacardiaceae). Open spaces on mesic slopes are smaller than on xeric slopes, and are covered by small annual grasses, mainly exotics, introduced from Eurasia (Rundel, 1981; Dallman, 1998).

2.2. Vegetation sampling

On each selected slope, five 50 m parallel transect lines, spaced 10 m apart, were used to sample the vegetation. All shrub-clumps that intercepted each transect line were recorded, considering a 'clump' as any group of woody species forming a discrete spatial unit (i.e. separated from similar units by open areas). All woody plants growing within these clumps were identified and counted, and species were classified according to their life-form (tree, shrub or succulent) and functional group (drought tolerant or shade tolerant) using the classifications proposed by Rundel (1981) and Rodríguez et al. (1983). At each transect, clump cover was measured using the percentage intercept method (i.e. the percentage of the line length covered by clumps). The area of clumps intercepted by lines was also estimated by measuring the longest diameter of each clump and its orthogonal axis. Thus, the area was calculated assuming an elliptical shape for clumps. Both cover and area of shrub-clumps were compared between slope aspects (polar- or equatorial-facing) and localities (San Carlos de Apoquindo–Corral Quemado) with a nested ANOVA (slope aspect nested within localities).

2.3. Species association analyses

To assess the sign of interactions dominating communities on different slopes we used the *C*-score index (Stone and Roberts, 1992). This index is the average of all possible 'checkerboard units' (CU) calculated for all the pairs of species that occur at least once in the clumps. A CU is any sub-matrix with the form:

	Sample 1	Sample 2			Sample 1	Sample 2
Species 1	0	1	or	Species 1	1	0
Species 2	1	0		Species 2	0	1

The number of *CU* for each species pair is calculated as $CU = (r_i - S)(r_j - S)$, where r_i and r_j are the numbers of samples (clumps) where species i and j were detected, and S is the number of samples containing both species. The observed *C*-score calculated for each slope was contrasted against an expected *C*-score value generated by randomizing species occurrences between samples (Gotelli and Entsminger, 2001). Matrix rows corresponded to species and columns to clumps, and the entries indicated the presence (1) or absence (0) of a given species within a particular clump

(Gotelli and Graves, 1996). Expected *C*-score values were obtained by averaging the *C*-scores of 1000 null communities simulated from the respective co-occurrence matrix. Null communities were constructed by placing the species randomly and independently of each other, but the probability of a particular clump being 'hit' by a given species was a function of its relative area (i.e. the area of the *j*th sample/the total area of the clumps on a that slope) (Gotelli and Entsminger, 2001). *C*-score values higher than expected by chance suggest competitively structured communities, while *C*-score values lower than expected by chance suggest that communities are dominated by positive interactions (Stone and Roberts, 1992).

To assess the relative frequencies of positive and negative associations between species pairs on each slope we performed a series of randomization tests. In these analyses, for each species pair, the observed occurrence frequency of each species was randomized 1000 times to generate an expected frequency of co-occurrence. The observed frequency of co-occurrence was compared with this randomly generated frequency distribution. We then calculated the probability of the observed co-occurrence frequency being generated by chance (cf. Fortin and Jacquez, 2000). When significant differences were detected, negative or positive associations were assumed if the observed frequency was lower or higher than that expected by chance, respectively (Kikvidze et al., 2001). Relative frequencies of positive and negative associations were computed as the ratio between the number of significant species associations and the total number of species pairs on the respective slope.

To compare species richness within clumps on mesic and xeric slopes we estimated species richness through rarefaction. Since at each study site the area and the number of individuals within clumps varied with slope aspect, individual-based rarefactions were used to standardize the number of species (Gotelli and Colwell, 2001). The slope aspect with fewer individuals defined the sub-sample size (number of individuals pooled) used to estimate the species richness through rarefaction on the opposite slope. Estimated species richness was defined as the average number of species calculated from 1000 random sub-samples of individuals. Thus, the observed species richness on the slope aspect with fewer individuals was compared with the estimated species richness on the opposite slope. To assess statistical differences between slopes we calculated the 95% confidence interval for the estimated value of species richness, and significant differences were assumed if the observed value did not fall within this interval (cf. Gotelli and Entsminger, 2001).

3. Results

3.1. Species, cover and clump areas

The number of sampled shrub-clumps varied among slopes, but it was always lower on equatorial-facing than on polar-facing slopes (Table 1). Fifteen species were detected on the polar-facing slope at Corral Quemado (hereafter CQP), being the assemblage with the highest species richness. Ten species were detected on the polar-facing slope at San Carlos de Apoquindo (hereafter SCP). Observed species richness

Table 1
Relative frequencies of occurrence of species (i.e. number of clumps where species i was detected / the total number of clumps on that slope) within clumps on polar- and equatorial-facing slopes at San Carlos de Apoquindo and Corral Quemado

Species	Life-form	Functional group	San Carlos de Apoquindo		Corral Quemado	
			Polar	Equatorial	Polar	Equatorial
Adesmia confusa	Deciduous shrub	Drought-tolerant	ND	ND	ND	0.21
Azara dentata	Evergreen shrub	Shade-tolerant	0.03	ND	ND	ND
Baccharis paniculata	Semi-deciduous shrub	Drought-tolerant	0.03	0.95	0.05	1.00
Colliguaja integerrima	Semi-deciduous shrub	Shade-tolerant	ND	ND	0.13	0.04
Colliguaja odorifera	Semi-deciduous shrub	Shade-tolerant	0.37	0.14	0.05	0.04
Echinopsis chiloensis	Stem succulent	Drought-tolerant	ND	0.09	ND	0.33
Gochnatia foliolosa	Semi-deciduous shrub	Shade-tolerant	0.03	ND	0.63	0.13
Guindilia trinervis	Evergreen shrub	Shade-tolerant	ND	ND	0.42	ND
Haplopappus sp.	Semi-deciduous shrub	Unknown	ND	0.50	ND	ND
Haplopappus chrisanthemifolius	Semi-deciduous shrub	Unknown	ND	ND	0.03	ND
Kageneckia angustifolia	Semi-deciduous tree	Shade-tolerant	ND	ND	0.05	ND
Kageneckia oblonga	Semi-deciduous tree	Shade-tolerant	0.73	ND	0.87	0.43
Lithraea caustica	Evergreen tree	Shade-tolerant	0.63	0.18	0.13	0.04
Maytenus boaria	Evergreen tree	Shade-tolerant	ND	ND	0.03	ND
Porlieria chilensis	Semi-deciduous tree	Shade-tolerant	ND	ND	0.05	ND
Proustia cuneifolia	Deciduous shrub	Drought-tolerant	ND	0.05	ND	0.04
Puya berteroniana	Stem succulent	Drought-tolerant	ND	0.05	ND	UN
Quillaja saponaria	Evergreen tree	Shade-tolerant	0.23	ND	0.11	ND
Schinus montanus	Evergreen tree	Shade-tolerant	0.03	ND	ND	ND
Solanum ligustrinum	Deciduous shrub	Shade-tolerant	ND	0.27	0.11	ND
Teucrium bicolor	Semi-deciduous shrub	Shade-tolerant	ND	ND	0.18	0.08
Trevoa quinquenervia	Deciduous tree	Shade-tolerant	0.13	ND	ND	ND
Trevoa trinervis	Deciduous tree	Shade-tolerant	0.16	0.07	ND	ND
Viviana marifolia	Deciduous shrub	Shade-tolerant	ND	ND	0.03	ND
Total species richness			10	9	15	10
Number of sampled clumps			30	22	38	24

Species were classified by life-form and functional group according to Rundel (1981) and Rodriguez et al. (1983). 'ND' indicates the species was not detected on that slope, and 'Unknown' indicates that no information is available on the functional classification of the species.

in both xeric slopes was lower than on mesic slopes; ten species were detected on the equatorial-facing slope at Corral Quemado (hereafter CQE) and nine species at San Carlos de Apoquindo (hereafter SCE).

The drought-tolerant shrub *Baccharis paniculata* and the shade-tolerant tree *Kageneckia oblonga* were the more frequent species on xeric and mesic slopes, respectively. At both sites, the relative frequencies of occurrence of these dominant species were lower on the opposite slopes. In addition to *B. paniculata*, five drought-tolerant species detected on xeric slopes were not registered within clumps on mesic slopes (Table 1). On the other hand, nine shade-tolerant species were detected exclusively on the mesic slopes, while another six shade-tolerant species were less frequent at xeric than at mesic slopes (Table 1).

Shrub-clump cover on mesic slopes was higher than on xeric ones ($F = 31.85$, $p < 0.01$), with no significant differences being detected between localities ($F = 2.34$, $p = 0.15$) (Fig. 1). Sizes (area) of clumps were significantly different between slopes ($F = 27.39$, $p < 0.01$) and localities ($F = 20.95$, $p < 0.01$). Overall, clumps on mesic slopes were larger than on xeric ones. However, differences between localities were due to clumps at SCP being significantly larger than at CQP, while no differences were observed between SCE and CQE (Fig. 1).

3.2. Species association patterns

Observed *C*-scores were higher than values expected by chance at all slopes (Fig. 2). These results indicated lower species co-occurrence within clumps than what is expected when species are distributed independently of each other, which suggest competitively structured communities on all slopes.
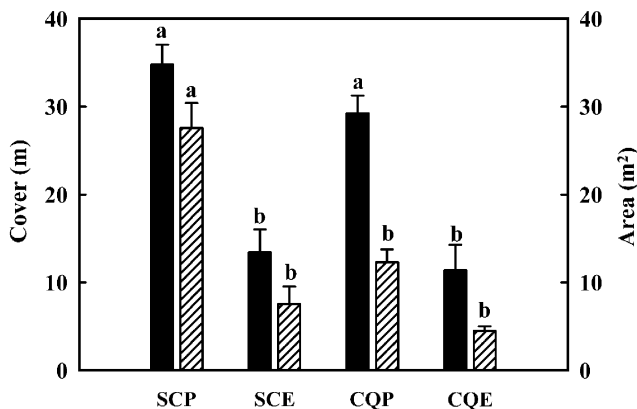

Fig. 1. Average (± 1 S.E.) cover (solid bars) and area (dashed bars) of shrub-clumps on polar- and equatorial-facing slopes at San Carlos de Apoquindo and Corral Quemado. Bars with different letters indicate differences between sampled slopes (a posteriori Tukey test $\alpha = 0.05$).
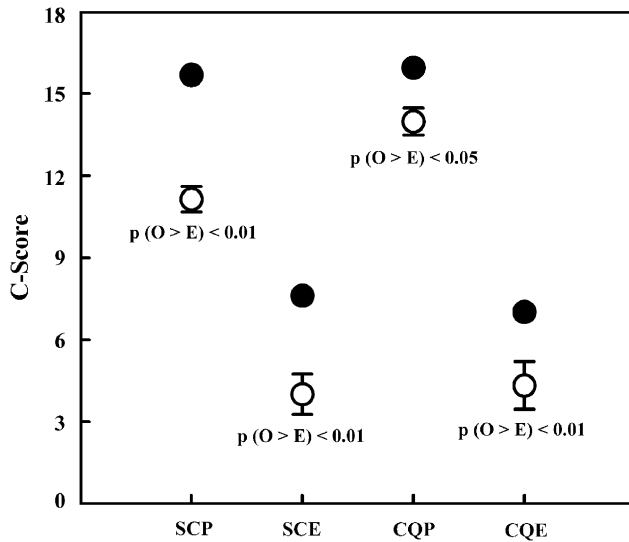
Fig. 2. Observed (solid circles) and expected (empty circles) *C*-scores (± 1 S.D.) for polar- and equatorial-facing slopes at San Carlos de Apoquindo and Corral Quemado. Probability values for statistical differences between observed (O) and expected (E) *C*-score values are shown below each plot ($\alpha = 0.05$).

Randomization tests between species pairs indicated one positive and six negative associations in SCE, one positive and 17 negative associations in SCP, one positive and eight negative associations in CQE, and two positive and 31 negative associations in CQP (see Appendix A). Negative associations proved to be almost twice as frequent on mesic slopes compared to xeric slopes (Fig. 3). On the other hand, relative frequencies of positive associations were similar among all slopes, and were lower than those of negative associations (Fig. 3).

3.3. Comparison of species richness

At San Carlos de Apoquindo, 119 individuals were detected on the equatorial-facing slope, and 301 on the polar-facing slope. At Corral Quemado, 168 individuals were recorded on the equatorial facing slope and 361 on the polar facing one. Therefore, at both sites, the equatorial-facing slopes defined the size of the sub-sample used to estimate the species richness on polar facing slopes through rarefactions. Considering these differences in the number of individuals, at both localities, observed species richness on the equatorial-facing slope was significantly higher than the corresponding estimated species richness on the polar-facing slope. At San Carlos de Apoquindo, observed species richness on the equatorial-facing slope was 9 and estimated species richness ($\pm 95\%$ confidence interval) on the opposite slope was 7.1 (± 0.2). At Corral Quemado observed species richness on the equatorial-facing slope was 10, while estimated species richness on the polar-facing slope was 8.8 (± 0.4).
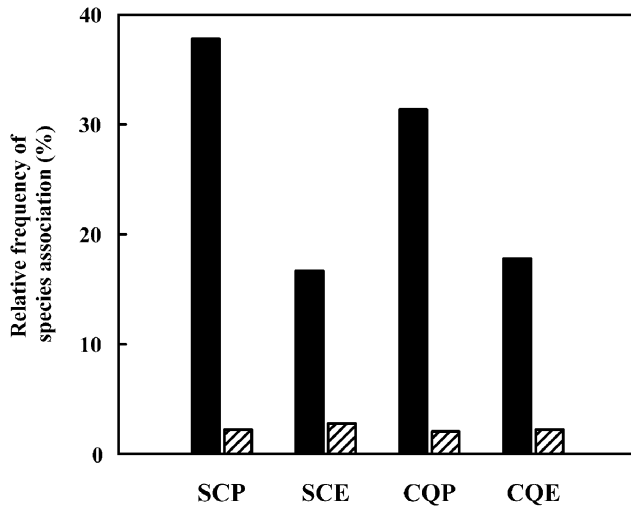
Fig. 3. Relative frequencies of significant negative (black bars) and positive associations (dashed bars) between species pairs on polar- and equatorial-facing slopes at San Carlos de Apoquindo and Corral Quemado.

4. Discussion

Our results concur with those of previous studies (Armesto and Martínez, 1978; Fuentes et al., 1984) in that plant cover and shrub-clump size are significantly affected by slope aspect in the matorral of central Chile. However, although we predicted species assemblages dominated by competitive interactions on mesic sites and by facilitation on xeric sites, spatial pattern analyses suggested competitively structured species assemblages on both slope aspects.

The negative patterns of species co-occurrence on mesic polar-facing slopes could be due to competition for light. In previous studies on polar-facing slopes of the Chilean matorral, Segura et al. (1998) and Holmgren et al. (2000) have shown that, despite seed germination of several species being greater beneath the canopy of shade-tolerant species than in open spaces, no seedling recruitment occurred. They suggested, following Armesto and Martínez (1978), that strong asymmetrical competition for light prevents recruitment within clumps on these habitats, especially for drought-tolerant species. In contrast, experiments performed on xeric equatorial-facing slopes have shown that seedling survival of several species was greater beneath shrub-clumps than on open areas, indicating a strong nurse effect of the clumps on most species from this matorral (Fuentes et al., 1984). However, these experiments only evaluated 'first year' seedling survival without further monitoring of species establishment. It is well known that the outcome of positive and negative effects changes with plant life-stage, with many examples of positive effects of nurse plants on seedlings of beneficiary species and strong competition as seedlings grow (see Callaway and Walker, 1997). Thus, while Fuentes et al. (1984) indicated that

protection from desiccation and herbivores are the main mechanisms behind the nurse effect of shrub-clumps on seedling recruitment in xeric sites, our results suggest that an increase in competition when facilitated species increase in size could explain the competitive patterns obtained on the xeric slopes. The desiccant conditions on equatorial-facing slopes suggest that competition could be related with water availability.

Water limitation could generate strong belowground competition (Tilman, 1994; Reynolds, 1999) thereby causing plants to invest more resources in root development rather than on above-ground biomass (Holmgren et al., 1997). As far as we are aware, there are no studies on belowground biomass distribution patterns in this type of environment. However, field experiments carried out in other arid ecosystems have reported increasing root competition between species from mesic to xeric habitats (Pugnaire and Luque, 2001). Thus, we suggest that drought-tolerant plants dominating the clumps on xeric slopes could exclude other species by belowground competition, generating the negative species association patterns observed at the whole community level.

In spite of the competitive patterns obtained for species assemblages on mesic and xeric slopes, randomization analyses indicated a decrease in the relative frequencies of negative associations from polar- to equatorial-facing slopes. These results agree with the prediction of Grime (1974, 1979) that the importance of competitive interactions on the structure of plant communities should decrease under harsher conditions. On the other hand, although positive associations had a low relative importance on all slopes, they could be an important factor for the recruitment of a few shade-tolerant species on xeric slopes in some years. For instance, seedling survival of some shade-tolerant species (e.g. *Lithraea caustica* and *Kageneckia oblonga*) beneath the nurse shrubs increases during high rainfall ENSO (El Niño) years (Fuentes et al., 1984; Jiménez and Armesto, 1992). Although both competition and facilitation could be acting on community structure in this ecosystem, species association patterns suggest that competition seems to be more important. Nevertheless, long-term experiments analysing the effects of competition and facilitation at different life-stages are urgently needed to assess how species interactions affect community structure.

The observed change in the intensity of negative associations could be related with the observed increase in species richness within shrub-clumps from mesic to xeric slopes. Some authors have suggested that the integrated effect of abiotic stress and biotic interactions is the main force driving community diversity (Callaway, 1995; Bruno et al., 2003). This theoretical framework states a dominance of competitive interactions (which reduce diversity) in benign habitats and a dominance of facilitation (that increases diversity) in stressful habitats (Grime, 1979; Bertness and Callaway, 1994). Our results indicate that increases in aridity from mesic to xeric slopes cannot eliminate the dominant effects of competition. However, regarding this apparent dominance of competition, species richness within clumps was higher in the stressful environments (i.e. xeric slopes). This suggests that the greater observed plant diversity within clumps in xeric habitats could have resulted from the decrease in the frequency of competitive interactions on these slopes.

Although we are aware that our approach is correlative and further experiments are needed, particularly long-term experiments related with the net outcome of positive and negative effects with life-stage under different slope exposures, our analyses suggest that negative interactions are more intense than positive ones in the Chilean matorral. Notwithstanding, species association patterns also suggested that slope aspect could regulate the intensity of negative interactions and, in consequence, the diversity within shrub-clumps in the sclerophyllous matorral of central Chile.

Appendix A

Results of randomization tests ($\alpha = 0.05$) performed between all species pairs detected within shrub-clumps on polar- and equatorial-facing slopes of San Carlos de Apoquindo and Corral Quemado. Probability values for positive (+) and negative (−) associations are showed

San Carlos de Apoquindo, equatorial-facing slope	Colliguaja odorifera	Haplopappaus sp.	Lithraea caustica	Proustia cuneifolia	Puya berteroniana	Solanum ligustrinum	Trevoa trinervis	Echinopsis chiloensis
Baccharis paniculata	0.11	0.02$^{(+)}$	0.18	0.01$^{(-)}$	0.02$^{(-)}$	0.16	0.08	0.02$^{(-)}$
Colliguaja odorifera		0.15	0.38	0.39	0.43	0.28	0.33	0.04
Haplopappaus sp.			0.02$^{(-)}$	0.14	0.04$^{(-)}$	0.06	0.03$^{(-)}$	0.17
Lithraea caustica				0.24	0.21	0.32	0.19	0.23
Proustia cuneifolia					0.58	0.12	0.40	0.55
Puya berteroniana						0.14	0.40	0.57
Solanum ligustrinum							0.10	0.13
Trevoa trinervis								0.42

San Carlos de Apoquindo, polar-facing slope	Baccharis paniculata	Colliguaja odorifera	Gochnatia foliolosa	Kageneckia oblonga	Lithraea caustica	Quillaja saponaria	Schinus montanus	Trevoa quinquenervia	Trevoa trinervis
Azara dentata	0.58	0.04$^{(-)}$	0.58	0.01$^{(-)}$	0.03$^{(-)}$	0.34	0.55	0.24	0.41
Baccharis paniculata		0.04$^{(-)}$	0.58	0.01$^{(-)}$	0.01$^{(-)}$	0.09	0.57	0.22	0.43

	Baccharis paniculata	Colliguaja integerrima	Colliguaja odorifera	Gochnatia foliolosa	Kageneckia oblonga	Lithraea caustica	Proustia cuneifolia	Teucrium bicolor	Echinopsis chiloensis
Colliguaja odorifera			0.15	0.11	0.10	0.23	$0.03^{(-)}$	$0.01^{(-)}$	$0.03^{(-)}$
Gochnatia foliolosa				$0.01^{(-)}$	$0.01^{(-)}$	0.09	0.58	0.24	0.42
Kageneckia oblonga					$0.01^{(+)}$	$0.01^{(-)}$	$0.014^{(-)}$	$0.04^{(-)}$	$0.01^{(-)}$
Lithraea caustica						0.10	$0.01^{(-)}$	$0.01^{(-)}$	0.07
Quillaja saponaria							0.09	0.18	0.09
Schinus montanus								0.23	0.41
Trevoa quinquenervia									0.18

Corral Quemado, equatorial-facing slope	Baccharis paniculata	Colliguaja integerrima	Colliguaja odorifera	Gochnatia foliolosa	Kageneckia oblonga	Lithraea caustica	Proustia cuneifolia	Teucrium bicolor	Echinopsis chiloensis
Adesmia confusa	0.19	0.17	0.15	0.09	0.09	0.13	0.20	0.14	0.12
Baccharis paniculata		$0.01^{(-)}$	$0.01^{(-)}$	0.08	$0.01^{(+)}$	$0.01^{(-)}$	$0.01^{(-)}$	$0.04^{(-)}$	0.16
Colliguaja integerrima			0.54	0.30	0.08	0.54	0.57	0.44	0.08
Colliguaja odorifera				0.23	$0.01^{(-)}$	0.55	0.57	0.41	0.08
Gochnatia foliolosa					$0.01^{(-)}$	0.43	0.42	0.34	0.22
Kageneckia oblonga						0.07	0.07	$0.04^{(-)}$	0.20
Lithraea caustica							0.57	0.39	0.26
Proustia cuneifolia								0.39	0.24

Corral Quemado, polar-facing slope	Colliguaja integerrima	Colliguaja odorifera	Gochnatia foliolosa	Guindilia trinervis	Haplopappus chrisanthemifolius	Kageneckia angustifolia	Kageneckia oblonga	Lithraea caustica	Maytenus boaria	Porlieria chilensis	Quillaja saponaria	Solanum ligustrinum	Teucrium bicolor	Viviania marifolia
Baccharis paniculata	0.23	0.30	0.18	0.20	0.34	0.28	0.04$^{(-)}$	0.19	0.13	0.10	0.33	0.23	0.13	0.13
Colliguaja integerrima		0.23	0.04$^{(-)}$	0.13	0.08	0.04$^{(-)}$	0.12	0.24	0.25	0.22	0.13	0.15	0.01$^{(-)}$	0.08
Colliguaja odorifera			0.01$^{(-)}$	0.03$^{(-)}$	0.13	0.09	0.03$^{(-)}$	0.21	0.14	0.09	0.04$^{(-)}$	0.04$^{(-)}$	0.04$^{(-)}$	0.11
Gochnatia foliolosa				0.06	0.01$^{(-)}$	0.02$^{(-)}$	0.01$^{(+)}$	0.04$^{(-)}$	0.01$^{(-)}$	0.03$^{(-)}$	0.14	0.13	0.04$^{(-)}$	0.01$^{(-)}$
Guindilla trinervis					0.01$^{(-)}$	0.03$^{(-)}$	0.01$^{(+)}$	0.15	0.01$^{(-)}$	0.01$^{(-)}$	0.17	0.02$^{(-)}$	0.04$^{(-)}$	0.03$^{(-)}$
Haplopappus chrisanthemifolius						0.40	0.01$^{(-)}$	0.13	0.41	0.44	0.24	0.20	0.09	0.58
Kageneckia angustifolia							0.04$^{(-)}$	0.12	0.41	0.31	0.18	0.17	0.26	0.43
Kageneckia oblonga								0.04$^{(-)}$	0.01$^{(-)}$	0.01$^{(-)}$	0.01$^{(-)}$	0.01$^{(-)}$	0.09	0.01$^{(-)}$
Lithraea caustica									0.39	0.27	0.25	0.33	0.21	0.20
Maytenus boaria										0.37	0.43	0.41	0.09	0.56
Porlieria chilensis											0.41	0.22	0.08	0.41
Quillaja saponaria												0.27	0.22	0.23
Solanum ligustrinum													0.04$^{(-)}$	0.23
Teucrium bicolor														0.10

References

Armesto, J.J., Martínez, J.A., 1978. Relationships between vegetation structure and slope aspect in the Mediterranean region of Chile. Journal of Ecology 66, 881–889.

Armesto, J.J., Gutiérrez, J.R., Martínez, J.A., 1979. Las comunidades vegetales de la región mediterránea de Chile: distribución de especies y formas de vida en un gradiente de aridez. Medio Ambiente 4, 62–70.

Bertness, D., Callaway, R.M., 1994. Positive interactions in communities. Trends in Ecology & Evolution 9, 191–193.

Brooker, R.W., Callaghan, T.V., 1998. The balance between positive and negative interactions and its relationship to environmental gradient: a model. Oikos 81, 196–207.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18, 119–125.

Callaway, R.M., 1995. Positive interactions among plants. Botanical Review 61, 306–349.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–848.

Cavieres, L., Arroyo, M.T.K., Peñaloza, A., Molina-Montenegro, M., Torres, C., 2002. Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. Journal of Vegetation Science 13, 547–554.

Dallman, P.R., 1998. Plant Life in the World's Mediterranean Climates. University of California, Los Angeles.

di Castri, F., Hajek, E., 1976. Bioclimatología de Chile. Ediciones Universidad Católica de Chile, Santiago.

Fortin, M., Jacquez, G., 2000. Randomization test and spatially autocorrelated data. Bulletin of Ecological Society of America 81, 201–205.

Fuentes, E.R., Otaiza, R.D., Alliende, M.C., Hoffmann, A.J., Poiani, A., 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia 62, 405–411.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.

Gotelli, N.J., Entsminger, G.L., 2001. EcoSim: Null Models Software for Ecology, Version 7.0. Acquired Intelligence Inc. and Kesey-Bear, Burlington.

Gotelli, N.J., Graves, G.R., 1996. Null Models in Ecology. Smithsonian Press, Washington.

Grime, J.P., 1974. Vegetation classification by reference to strategy. Nature 250, 26–30.

Grime, J.P., 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52, 107–145.

Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D., 1996. Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. Journal of Vegetation Science 7, 527–534.

Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. Ecology 78, 1966–1975.

Holmgren, M., Segura, A.M., Fuentes, E.R., 2000. Limiting mechanisms in the regeneration of the Chilean matorral. Plant Ecology 147, 49–57.

Jiménez, H., Armesto, J.J., 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. Journal of Vegetation Science 3, 579–586.

Keddy, P.A., 1990. Competitive hierarchies and centrifugal organization in plant communities. In: Grace, J.B., Tilman, D. (Eds.), Perspectives on Plant Competition. Academic Press, San Diego, pp. 265–290.

Kikvidze, Z., Khetsuriani, L., Kikodze, D., Callaway, R.M., 2001. Facilitation and interference in sub-alpine meadows of the central Caucasus, Europe. Journal of Vegetation Science 12, 833–838.

Martínez, J.A., Armesto, J.J., 1983. Ecophysiological plasticity and habitat distribution in three evergreen sclerophyllous shrubs of the Chilean matorral. Acta Oecologica 4, 211–219.

Pacala, S.W., Levin, S.A., 1997. Biologically generated spatial pattern and the coexistence of competing species. In: Tilman, D., Kareiva, P. (Eds.), Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University, Princeton, pp. 204–232.

Pugnaire, F.I., Luque, M.T., 2001. Changes in plant interactions along a gradient of environmental stress. Oikos 93, 42–49.

Pugnaire, F.I., Haase, P., Puigdefábregas, J., Cueto, M., Clark, S.C., Incoll, L.D., 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. Oikos 76, 455–464.

Quinos, P.M., Insausti, P., Soriano, A., 1998. Facilitative effects of *Lotus tenuis* on *Paspalum dilatatum* in a lowland grassland of Argentina. Oecologia 114, 427–431.

Reynolds, H.L., 1999. Plant interactions: competition. In: Pugnaire, F.I., Valladares, F. (Eds.), Handbook of Functional Plant Ecology. Marcel Dekker, New York, pp. 649–676.

Rodriguez, R., Matthei, O., Quezada, M., 1983. Flora Arbórea de Chile. Universidad de Concepción, Concepción.

Rundel, P.W., 1981. The matorral zone of Central Chile. In: di Castri, F., Goodall, D.W., Spetch, R.L. (Eds.), Mediterranean Type Shrublands. Elsevier, Amsterdam, pp. 175–201.

Sammul, M., Kull, K., Oksanen, L., Veromann, P., 2000. Competition intensity and its importance: results of field experiments with *Anthtoxanthum odoratum*. Oecologia 125, 18–25.

Schenk, H.J., Holzpfel, C., Hamilton, J.G., Mahall, B.E., 2003. Spatial ecology of a small desert shrub on adjacent geological substrates. Journal of Ecology 91, 383–395.

Segura, A.M., Holmgren, M., Anabalón, J.J., Fuentes, E.R., 1998. The significance of fire intensity in creating local patchiness in the Chilean matorral. Plant Ecology 139, 259–264.

Stone, L., Roberts, A., 1992. Competitive exclusion, or species aggregation? An aid in deciding. Oecologia 91, 419–424.

Tewksbury, J.J., Lloyd, J.D., 2001. Positive interactions under nurse plants: spatial scale, stress gradient and benefactor size. Oecologia, 425–434.

Tilman, D., 1994. Competition and diversity in spatially structured habitats. Ecology 78, 81–92.

Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetezo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. Journal of Ecology 79, 961–971.