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How beneficial are nurse plants? A meta-analysis of the effects of cushion plants on high-Andean plant communities

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Abstract: Facilitation by nurse plants is one of the most commonly reported interactions between plants and is regarded as an important factor in structuring plant communities. We used a meta-analysis to examine the generality of these effects, focusing on cushion plants, a common life-form occurring in high-Andean ecosystems. We targeted the following questions: (1) is there a generalized positive effect of cushions on other vascular plant species along the Andes? (2) do different species groups (i.e., annuals and perennials, natives and exotics) display different association responses to cushions? (3) does the nurse effect of cushions increase with environmental severity? Results indicated that the overall effect of cushions is positive, however these positive effects were more significant amongst exotic plants than in native plants; effects were only positive for perennial plants, and were notably negative for annuals. The positive effects of cushions also increased with physical stress, but only for perennial plants. These results allow us to suggest that as a whole cushions may be acting as keystone species that maintain the structure and diversity of high-Andean plant communities. Nevertheless, since cushions also positively affect the performance of exotic plants, we should be aware of their potential role in promoting biological invasions.

Introduction

Facilitation between plants is a non-consumptive interaction that benefits at least one of the participants (for review, see Callaway 1995). Facilitation is regarded as important in structuring plant communities, particularly in harsh environments such as deserts (Franco and Nobel 1988, Valiente-Banuet et al. 1991, Tirado and Pugnaire 2003), salt-marshes (Hacker and Bertness 1995, Callaway and Pennings 2000), rocky intertidal zones (Molina-Montenegro et al. 2005) and high-mountain ecosystems (Callaway et al. 2002). The most commonly reported facilitative interaction among plants is the "nurse effect," where a species (the nurse) interacts with the environment to create more favourable micro-habitats than its surroundings for germination, establishment and survival of other plants (Valiente-Banuet et al. 1991, Suzán et al. 1996, Haase et al. 1996, 1997, Tewksbury and Lloyd 2001, Molina-Montenegro et al. 2005a). However, most of these studies have only addressed positive effects of nurse plants on a few focal beneficiary species, paying less attention to the potential negative or neutral impacts that such putative nurses may have on other plant species composing the communities. For example, *Olneya tesota* trees have been recognized as important nurse plants for several species in the Sonoran Desert (McAuliffe 1984, Suzán et al. 1996), but more recent studies have indicated that the importance of facilitation varies across species, even with negative effects on a number of species (Tewksbury and Lloyd 2001). Therefore, considering that facilitation may vary across species or natural communities, it is interesting to ask whether the nurse effect is indeed a generalized phenomenon. In this study, we address this issue and focus on the effects of a well-recognized group of nurses in South American alpine habitats: the cushion-forming plants (*cushions* hereafter). This growth-form includes recumbent plants with short internodes, closed canopies and a subsurface accumulation of tightly-packed living non-photosynthetic and dead plant tissues, and is one of the best adapted growth-forms across alpine habitats (Körner 2003). These plants comprise about 338 species around the world, belonging to 78 genera and 34 plant families. Approximately half of these species grow in the South American Andes (Hauri and Schröter 1914); the most frequently reported cushions belong to the family Apiaceae followed by Asteraceae, Rubiaceae, Caryophyllaceae, Rhamnaceae and Fabaceae (Marticorena and Quezada 1985). Cushion plants can persist over decades or even centuries in natural communities (Kleier and Rundel 2004, Le Roux and McGeoch 2004). These discrete, conspicuous plants create a marked abiotic contrast relative to the surrounding rocky mi-

Table 1. Summary of articles included in meta-analyses (in chronological order) indicating the bibliographic reference, the cushion species whose effects were evaluated, the geographic location, elevation and aspect of the study, and the number of plant species on which the effects of the respective cushion were evaluated. For those studies that evaluated changes in the effects of cushions with variations in environmental stress, the stress level (low or high) assigned to each site by the respective authors is also indicated; SS indicates that the study was conducted considering a single site.

Reference	Cushion species	Geographic location	Elevation	Slope aspect	Number of species	Stress level
Cavieres et al. (1998)	*Laretia acaulis*	33°S 70°W	3200 m	N	26	Low
Cavieres et al. (1998)	*Laretia acaulis*	33°S 70°W	2700 m	N	33	High
Molina-Montenegro et al. (2000)	*Azorella trifurcata*	37°S 71°W	1400 m	SW	27	SS
Badano et al. (2002)	*Oreopolus glacialis*	37°S 71°W	1900 m	SE	18	SS
Cavieres et al. (2002)	*Bolax gummifera*	50°S 73°W	700 m	SE	25	Low
Cavieres et al. (2002)	*Bolax gummifera*	50°S 73°W	900 m	SE	34	High
Arroyo et al. (2003)	*Azorella monantha*	50°S 73°W	700 m	SW	29	Low
Arroyo et al. (2003)	*Azorella monantha*	50°S 73°W	900 m	SW	33	High
Badano and Cavieres (2006a)	*Pycnophyllum bryoides*	23°S 68°W	4400 m	NW	11	SS
Badano and Cavieres (2006a)	*Laretia acaulis*	33°S 70°W	3200 m	NW	36	SS
Badano and Cavieres (2006a)	*Mulinum leptacanthum*	41°S 71°W	1700 m	N	25	SS
Badano and Cavieres (2006a)	*Oreopolus glacialis*	41°S 71°W	1700 m	N	24	SS
Badano and Cavieres (2006a)	*Discaria nana*	41°S 71°W	1700 m	N	25	SS
Badano and Cavieres (2006b)	*Azorella monantha*	33°S 70°W	3200 m	SW	56	Low
Badano and Cavieres (2006b)	*Azorella monantha*	33°S 70°W	3600 m	SW	28	High
Badano and Cavieres (2006b)	*Azorella madreporica*	30°S 70°W	3700 m	N	23	Low
Badano and Cavieres (2006b)	*Azorella madreporica*	30°S 70°W	4000 m	N	16	High
Badano and Cavieres (2006b)	*Adesmia subterranea*	30°S 70°W	3700 m	N	22	Low
Badano and Cavieres (2006b)	*Adesmia subterranea*	30°S 70°W	4000 m	N	12	High
Cavieres et al. (2006)	*Laretia acaulis*	33°S 70°W	3200 m	NW	44	Low
Cavieres et al. (2006)	*Laretia acaulis*	33°S 70°W	2800 m	NW	46	High
Badano et al. (2006)	*Azorella monantha*	33°S 70°W	3600 m	NW	24	SS

crohabitats. Firstly, cushions have been reported to reduce wind speed by up to 98% relative to their surroundings which in turn decreases heat loss by convection (Hager and Faggi 1990), thus maintaining higher temperatures compared to the external environment (Arroyo et al. 2003, Badano et al. 2006, Cavieres et al. 2005, 2007). Secondly, soils below cushions can retain more water (Cavieres et al. 1998, 2006, 2007, Badano et al. 2006), and more nitrogen (Núñez et al. 1999, Cavieres et al. 2006, Badano et al. 2006), than the soil of the surrounding microhabitats. These microclimatic contrasts are presumably responsible for the significant concentration of vascular plants within cushions relative to the surrounding microhabitats, suggesting that cushion plants are pivotal in the maintenance of plant diversity in Andean plant communities (Núñez et al. 1999, Molina-Montenegro et al. 2000, Badano et al. 2002, Cavieres et al. 2002, Arroyo et al. 2003, Badano and Cavieres 2006a). Here, we use published studies which examined the association of other vascular plant species to cushions and surrounding micro-habitats. Via a meta-analysis we investigated the following questions: (1) is there a generalized positive effect of cushions on other plant species across the Andes? (2) do different groups of plant species (annuals and perennials, natives and exotics) display different association responses to cushions? Furthermore, since the importance of facilitative interactions between plants is thought to increase with environmental severity (see Bertness and Callaway 1994, Bertness and Leonard 1997, Brooker and Callaghan 1998, Bertness et al. 1999, Pugnaire and Luque 2001, Callaway et al. 2002), we also ask: (3) does the positive effect of cushions on other species increase with environmental severity?

Methods

Meta-analysis is a statistical tool that synthesizes the results of several independent studies to search for generalizations (Gurevitch and Hedges 1999). It has been applied in a wide variety of ecological topics including competition, facilitation and predation (Gurevitch et al. 1992, 2000, Goldberg et al. 1999). To conduct a meta-analysis, each study case has to be represented by a common estimator, the effect size, to allow comparisons between contrasting situations – i.e., experimental vs. control (Rosenberg et al. 2000). Given that we were interested in determining generalizations for the effects of cushions on plant communities, we compared the incidence (i.e., the frequency of occurrence) of other vascular plant species within vs. outside cushion plants. We conducted a search of published articles containing data on the incidence of plant species within and outside cushions. This search was conducted in two specialized web sites: ISI Web of Knowledge of the Thompson Corporation (www.isiknowledge.com) and the Scientific Electronic Library Online (www.scielo.org). We found a total of nine articles containing such information. These articles were published between 1998 and 2006, covering the effects of 10 cushion species and indicating the incidence of 204 species within and outside cushion plants (life span: 20 annuals, 181 perennials, 3 without classification; origin: 192 native, 12 exotics) at 22 localities in the southern Andes (Table 1). Given that many species were present in more than one locality, each species from each locality constituted a study case in the meta-analysis, resulting in a total of 617 study cases. The effect size of cushions on plant species was estimated using the odds ratio. This metric is very appropriate when the data available are counts or frequency of occurrence. Then, odds ratios were transformed to natural logarithm (see Rosenberg et al. 2000, for details) in such a way that values higher than 0 indicate positive effects of cushions, values lower than 0 indicate negative effects, and 0 indicates no effects. To determine whether the overall effect of cushions on plant communities is positive, negative or neutral, the odds ratios were averaged across all study cases (n = 617) and 95% confidence intervals were calculated. In this case, the overall effect of cushions on plant communities is positive if the average of odds ratios is significantly higher than 0, negative in the converse situation, and neutral if 95% confidence intervals include the 0 value. To determine whether different groups of species display different association responses to cushions, species from each site were classified according to their biogeographical origin (natives or exotics), and according to their life span (annuals or perennials). These classifications were made following Marticorena and Quezada (1985). Those species whose origin or life span was not clearly established were excluded from the analyses. A meta-analysis was then conducted separately for each group as described above; the odds ratios of each group were averaged and compared to the 0 value through 95% confidence intervals. To further assess whether the positive effect of cushions on other plants increases with environmental severity, we focused on data in the five articles that have addressed this issue. For this meta-analysis, species (427 study cases in total) were assigned to the level of physical stress of each of the study localities, as defined by the authors of the respective articles (Table 1). Physical stress was reported to increase with elevation in three of these articles (Cavieres et al. 2002, Arroyo et al. 2003, Badano and Cavieres 2006b), so that species from higher elevations were assigned to the category "high stress" while species from lower elevations were assigned to the category "low stress." In the remaining two articles (Cavieres et al. 1998, 2006), physical stress was indicated to increase with drought, so that species from drier sites were assigned to the category "high stress" while species from more mesic sites were assigned to the category "low stress." Initially, we included all species in the meta-analysis in order to assess whether the overall positive effect of cushions increases with physical stress. Later, two additional meta-analyses were conducted by grouping species according to their biogeographical origin and life span in order to perform factorial comparisons of (1) origin and stress level simultaneously and (2) life span and stress level simultaneously. Finally, differences between categories were evaluated via heterogeneity tests using the Q statistic. Q is basically a weighted sum of squares which follows the χ^2 distribution and describes the variation in effect size between groups. A significant value of Q indicates that the variance of the effect size among groups is greater than expected by random chance and thus deserves biological explanation (Rosenberg et al. 2000). We used a fixed-effect categorized model because we assumed that the observed variation within the range of study cases (these studies were conducted by only one research group) was due to sampling. All meta-analyses were conducted with METAWIN 2.0 (Rosenberg et al. 2000).

Results

The overall effect size of cushions on high-Andean plant communities was significantly positive when all plant species were included in the meta-analysis (Figure 1). Positive effects of cushions were also indicated for both native and exotic plant species, but the effect on exotics was significantly higher than the effect on natives (heterogeneity test, Q = 59.15, $P < 0.05$, Figure 1a).

A different pattern was observed when the meta-analysis included the life span of species as a grouping factor. Here, the effect of cushions on perennial species was positive, while in annuals it was negative (heterogeneity test, Q = 605.81, $P < 0.05$, Figure 1b). When species were categorized according to the level of physical stress experienced by their respective study site, the effect sizes indicated that the overall effects of cushions on plant communities were positive at both stress levels. Nevertheless, the positive effect of cushions was significantly higher at the high-stress level than at the low-stress level (heterogeneity test, Q = 85.03, $P < 0.05$, Figure 2). When combining the biogeographical origin of plants and stress levels, a significant variation among conditions was detected (heterogeneity test, Q = 193.86, $P < 0.05$). At high stress, the positive effect of cushions on exotic plants was significantly higher than on native plants (Figure 3a). On

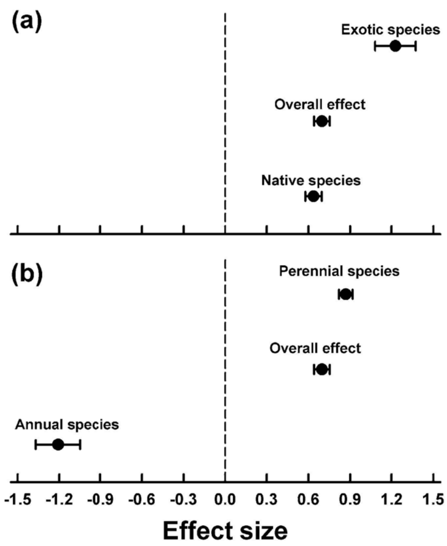

Figure 1. Effect size of cushions plants on high-Andean plant communities (n = 617). **a:** on natives (n = 561), overall effects and on exotics (n = 46); **b:** on annuals (n = 47) and perennial species (n = 568). The vertical dashed line indicates the 0 value. Effects are significantly positive or negative if the 95% confidence intervals of the effect size do not include 0.

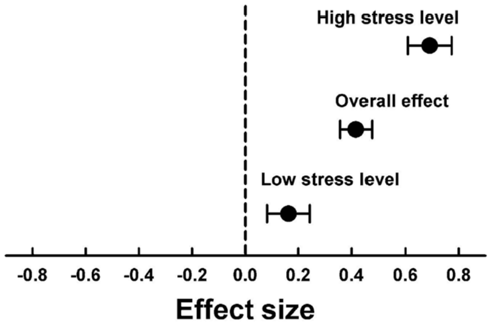

Figure 2. Effect size of cushions on high-Andean plant communities from sites with high (n = 202) and low (n = 225) levels of physical stress. Interpretation of graph is identical to Figure 1.

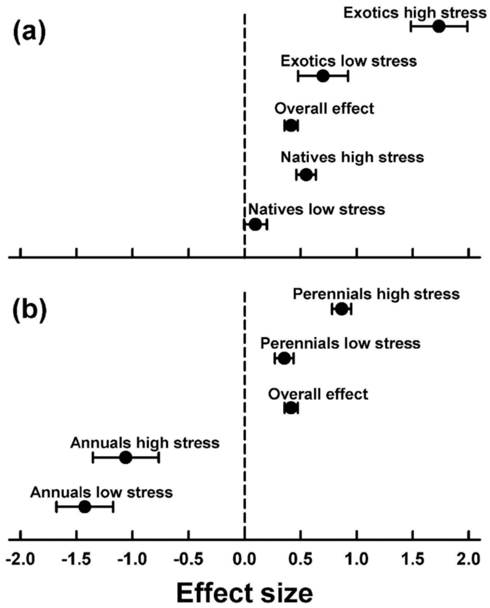

Figure 3. Effect size of cushions at high and low levels of physical stress on **a:** native (high stress n = 185; low stress n = 209) and exotic (high stress n = 17; low stress n = 16) plants; **b:** annual (high stress n = 15; low stress n = 18) and perennial (high stress n = 187; low stress n = 207) plants. Interpretation of graph is identical to Figure 1.

the other hand, at low stress these positive effects were only detected for exotic species, while neutral effects were detected for native plants (Figure 3a). Combining life span and stress levels also indicated significant variation among conditions (heterogeneity test, $Q = 193.86$, $P < 0.05$). In fact, cushions positively affected perennial species at both high and low stress levels, but the size of such effect was higher at the high stress level (Figure 3b). Conversely, the effect of cushions on annual species was negative at both stress levels (Figure 3b).

Discussion

Our results indicate that the overall effect of cushion plants on other high-Andean plant species is positive. Since our meta-analysis included several cushion species and covered their effects along almost the entire range of the southern Andes (see Table 1), this finding allows us to suggest that cushions are nurses for most vascular plants. These positive effects of cushions clearly agree with local studies of the abiotic modifications resulting from the presence of cushions in environments originally composed of bare soil and rocks (i.e., more nutrients, greater water supply and more homogeneous thermal conditions relative to their surroundings). However, irrespective of the underlying mechanisms, the nurse effect of Andean cushions on plant communities seems to be a generalized phenomenon across Andean environments. Interestingly, the meta-analysis revealed that the nurse effect of cushions seems to be stronger on exotic rather than native species (see Figure 1a). Such disproportionate positive effects of cushions on exotic species may be mediated by two mechanisms: cushions provide resource opportunities for exotics, thus increasing their tolerance to biotic/abiotic stress. Resource opportunities arise when the resources that an exotic species needs are readily available (Shea and Cheeson 2002). Then, given the ability of cushions to ameliorate extreme abiotic conditions and provide higher concentrations of resources compared to the surrounding habitat, they may provide invasion opportunities for exotic plants (Badano et al. 2007). Despite the overall positive effect of cushions on high-Andean plant species, drastically different association patterns were observed when the effects of cushions were analyzed separately for species with different life spans. While perennial species displayed a strong positive association response to cushions, annual species displayed a strong negative association (see Figure 1b). These differences in association responses may be linked with differences in the life history of these groups. Annual plants often avoid physically stressful conditions and strong competition by investing heavily in rapid development and early flowering, restricting their life span to seasons with favorable environmental conditions (Lamberts et al. 1998). They are therefore not reliant on the abiotic conditions provided by nurse plants. Furthermore, annual plants may be excluded from resident plants of cushion plants by competition. On the other hand, because of their longevity, perennials cannot avoid physically stressful periods, which therefore repeatedly affect their performance during their life span (Lamberts et al. 1998). Thus, the strong nurse effect of cushions on perennials may be a consequence of long-term responses, where the benefits of this association overcompensate for any possible competitive disadvantage, especially at early stages of the life cycle. Our meta-analysis also revealed that the facilitation of cushions increases with environmental severity (see Figure 2), for both native plants and particularly for exotic species (see Figure 3a). This strong positive effect on exotic plants suggests that cushions are promoting the spread of exotic plants towards more stressful habitats of the high Andes. In fact, recent experimental evidence suggests that the survival and growth of the exotic plant *Cerastium arvense* are significantly enhanced by cushion plants (Badano et al. 2007). Despite the nurse effects of cushions on perennial species increasing with environmental severity, strong negative effects were detected at both high and low stress levels for annual plants (see Figure 3b). Positive responses of perennials to nursing by cushions agree with theoretical models which predict an increase in positive plant-plant interactions with increasing physical stress (see, Bertness and Callaway 1994, Brooker and Callaghan 1998, Michalet et al. 2006). Conversely, the negative responses of annual plants to cushions depart from theoretical and empirical expectations, a finding that deserves further empirical research.

Given the conspicuousness of cushion plants across the southern Andes, and given their strong positive effects on other species, we confirm the fact that cushions may be acting as keystone species that maintain the structure and diversity of high-Andean native plant communities. Nevertheless, positive plant responses to cushion plants seem to be idiosyncratic, resulting in annuals being inhibited by cushions, while perennial and exotic plants are facilitated. Paradoxically, in the context of the conservation of the Andean flora, we should be aware of the potential role of cushion plants in increasing plant diversity via the promotion of biological invasions.

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References

Acuña-Rodríguez I., L.A Cavieres and E. Gianoli. 2006. Nurse effect in seedling establishment: facilitation and tolerance to damage in the Andes of central Chile. *Rev. Chil. Hist. Nat*. 79:329-336. **NOT CITED**

Agrawal A.A., S.Y. Strauss and M.J. Stout. 1999. Cost of induced responses and tolerance to herbivory in male and female components of wild radish. *Evolution* 53:1093-1104. **NOT CITED**

Arroyo M.T.K., L.A. Cavieres, A. Peñaloza and M.A. Arroyo-Kalin. 2003. Positive interactions between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecol.* 169:121-129.

Badano, E.I. and L.A. Cavieres. **2006a**. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *J. Biogeogr.* 33:304-313.

Badano, E.I. and L.A. Cavieres. **2006b**. Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Divers. Distrib.* 12:388-396.

Badano, E.I., C.G. Jones, L.A. Cavieres and J.P. Wright. 2006. Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* 115:369-385.

Badano E.I., M.A. Molina-Montenegro, C.L. Quiroz and L.A. Cavieres. 2002. Efectos de la planta en cojín *Oreopolus glacialis* (Rubiaceae) sobre la riqueza y diversidad de especies en una comunidad alto-andina de Chile central. *Rev. Chil. Hist. Nat*. 75:757-765.

Badano, E.I., E. Villarroel, R.O. Bustamante, P. Marquet and L.A. Cavieres. 2007. Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *J. Ecol.* 95:682-688.

Bertness, M.D. and E.M. Callaway. 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9:191-193.

Bertness, M.D. and G.H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976-1989.

Bertness, M.D, G.H. Leonard, J.M. Levine, P.R. Schmidt and A.O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711-2726.

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

Callaway, R.M. 1995. Positive interactions among plants. *Bot. Rev.* 61:306-349.

Callaway, R.M., S.C. Pennings. 2000. Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *Am. Nat.* 156:416-424.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B. Newingham, E.T. Aschehoug, C. Armas and B.J Cook. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844-847.

Cavieres, L.A., A. Peñaloza, C. Papic and M. Tambutti. 1998. Efecto nodriza del cojín *Laretia acaulis* (Umbelliferae) en la zona alto-andina de Chile central. *Rev. Chil. Hist. Nat.* 71:337-347.

Cavieres, L.A., M.T.K Arroyo, A. Peñaloza, M.A. Molina-Montenegro and C. Torres. 2002. Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *J. Veg. Sci.* 13:547-554.

Cavieres, L.A., C.L. Quiroz, M.A. Molina-Montenegro, A.A. Muñoz and A. Pauchard. 2005. Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspect. Plant Ecol.* 7:217-226.

Cavieres, L.A., E.I. Badano, A. Sierra-Almeida, S. Gómez-González and M.A. Molina-Montenegro. 2006. Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytol.* 169:59-69.

Cavieres, L.A., E.I. Badano, A. Sierra-Almeida and M.A. Molina-Montenegro. 2007. Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. *Arct. Antarct. Alp. Res.* 39:229-236.

Franco, A.C. and P.S. Nobel. 1988. Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida. Ecology* 69:1731-1740.

Goldberg, D.E., T. Rajaniemi, J. Gurevitch and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80:1118-1131.

Gurevitch, J., L.L. Morrow, A. Wallace and J. Walsh. 1992. A meta-analysis of competition field experiments. *Am. Nat.* 140:539-572.

Gurevitch, J. and L.V. Hedges. 1999. Statistical issues in conducting ecological meta-analyses. *Ecology* 80:1142-1149.

Gurevitch, J., J.A. Morrison and L.V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. *Am. Nat.* 155:435-453.

Haase, P., F.I. Pugnaire, S.C. Clark and L.D. Incoll. 1996. Spatial patterns in a two-tiered semiarid shrubland in southeastern Spain. *J. Veg. Sci.* 7:527-534.

Haase P., F.I. Pugnaire, S. C. Clark and L. D. Incoll. 1997. Spatial pattern in *Anthyllis cytisoides* shrubland on abandoned land in southeastern Spain. *J. Veg. Sci.* 8:627-634.

Hacker, S.D. and M.D. Bertness. 1995. Morphological and physiological consequences of a positive plant interaction. *Ecology* 76:2165-2175.

Hager, J. and A.M. Faggi. 1990. Observaciones sobre distribución y microclima de cojines enanos de la isla de Creta y del noroeste de la Patagonia. *Parodiana* 6:109-127.

Hauri, H. and C. Schröter. 1914. Versuch einer uebersicht der siphonogamen polsterpflanzen. *Engler's Botanische Jahrbucher* 50:618-656.

Kleier, C. and P.W. Rundel. 2004. Microsite requirements, population structure and growth of the cushion plant *Azorella compacta* in the tropical Chilean Andes. *Austral. Ecol.* 29:461-470.

Körner, C. 2003. *Alpine Plant Life*. Springer, Berlin, Gremany.

Lambers, H., F.S. Chapin III and T.L. Pons. 1998. *Plant Physiological Ecology.* Springer-Verlag, New York, USA.

Le Roux, P.C. and M.A. McGeoch. 2004. The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Arct. Antarct. Alp. Res.* 36:509-517.

Marticorena, C. and M. Quezada. 1985. Catálogo de la flora vascular de Chile. *Gayana Bot*. 42:1-157.

McAuliffe, J.R. 1984. Saguaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* 64:319-321.

Michalet, R., R.W. Brooker, L.A. Cavieres, Z. Kikvidze, C.J. Lortie, F.I. Pugnaire, A. Valiente-Banuet and R.M Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol. Lett.* 9:767-773.

Molina-Montenegro, M.A., C. Torres, M.J Parra and L.A. Cavieres. 2000. Asociación de especies al cojín *Azorella trifurcata* (Gaertn.) Hook. (Apiaceae) en la zona andina de Chile central (37ºS). *Gayana Bot.* 57:161-168.

Molina-Montenegro, M.A., E.I. Badano, P. Inostroza and L.A. Cavieres. **2005a**. Intercambio gaseoso en dos especies de plantas alto andinas de Chile central: efecto de la asociación a plantas en cojín. *Austral Ecol.* 15:49-58.

Molina-Montenegro, M.A., A.A. Muñoz, E.I. Badano, B.W. Morales, K.M. Fuentes and L.A. Cavieres. **2005b**. Positive associations between macroalgal species in a rocky intertidal zone and their effects on the physiological performance of *Ulva lactuca. Mar. Ecol-Prog. Ser.* 292:173-180.

Molina-Montenegro, M.A., E.I. Badano and L.A. Cavieres. 2006. Cushion plants as microclimatic shelters for two ladybird beetles species in alpine zone of central Chile. *Arct. Antarct. Alp. Res.* 38:224-227. **NOT CITED**

Núñez, C., M. Aizen and C. Ezcurra. 1999. Species associations and nurse plant effect in patches of high-Andean vegetation. *J. Veg. Sci.* 10:357-364.

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

Rosenberg, M.S., D.C. Adams and J. Gurevitch. 2000. *MetaWin: Statistical Software for Meta-analysis.* Sinauer, Sunderland, Massachusetts, USA.

Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17:170-176.

Suzán, H., G.P. Nabhan and D.T. Patten. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *J. Veg. Sci.* 7:635-644.

Tewksbury, J.J. and J.D. Lloyd. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127:425-434.

Tirado, R. and F.I. Pugnaire. 2003. Shrub spatial aggregation and consequences for reproductive success. *Oecologia* 136:296-201.

Tirado, R. and F.I. Pugnaire. 2005. Community structure and positive interactions in constraining environments. *Oikos* 111:437-444.

Valiente-Banuet, A., F. Vite and J.A. Zavala-Hurtado. 1991 Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. *J. Veg. Sci.* 2:11-14.

Wright, J.P., C.G Jones, B. Boeken and M. Shachak. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *J. Ecol.* 94:815-824. **NOT CITED**

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