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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