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Distinguishing colonisation modes from spatial structures in populations of the cushion plant *Azorella madreporica* in the high-Andes of central Chile

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Abstract We developed multiple *a priori* hypotheses to link the observed spatial patterns with colonisation processes in the high alpine cushion plant, *Azorella madreporica*. We conducted this study in the Molina River basin (33°20′ S, 70°16′W, 3600 m a.s.l.), in the Andes of central Chile, approximately 50 km east of Santiago. We mapped and measured size (as a surrogate for age) of individual cushions in two populations and used a standard spatial analytical tool (semivariograms) to test our alternative *a priori* hypotheses related to colonisation mode of the cushion species. In both populations, the size distribution of *A. madreporica* reflected a negative exponential or inverse-J pattern, typical of uneven-aged populations, where most of the cushions belonged to relatively smaller size classes, in effect, a regular success in the establishment of seedlings, where all size classes of cushions were represented in the population. The results were site-specific, where best-fit semivariograms for spatial cushion's size distribution suggested a gradual colonisation in one population and an episodic colonisation in the other population. Microsite distribution proved to be homogeneous at both sites. Thus, the study of the spatial explicit size-age population distribution of an alpine species provides valuable information about the frequency, magnitude and site variation of the reproductive pulses in these harsh environments.

Key words: Akaike's Information Criterion, alpine demography, Farellones, multiple hypotheses, semivariograms, spatial patterns.

INTRODUCTION

Plant population dynamics have been studied through either experimental, comparative (Sarukhán & Gagdil 1974; Begon 1984; Gurevitch *et al.* 2002) or modelling approaches (DeAngelis & Gross 1992). Although widely used in different environments (Silvertown & Charlesworth 2001), these conventional approaches face constraints when long-lived species populations in low-productivity systems are under scrutiny because processes may be very slow, and direct measurements of processes are not feasible. Alternatively, it is possible to model the spatial variability that characterises the plant population comparatively and relate the spatial patterns to specific processes (Fajardo & McIntire 2007), for example, colonisation. Incorporating these processes into *a priori* hypotheses and testing their support with data can thus provide us new ways for understanding ecological systems (McIntire & Fajardo 2008). In stressful environments seasonal climate fluctuations, masting years, or the abundance of suitable microsites, can alter plant colonisation in a manner that occurs in pulses, a phenomenon that has been called 'opportunity windows'. Thus, in contrast to more benign habitats, colonisation is expected to operate on restricted temporal and spatial scales (Eriksson & Fröborg 1996; Bartha *et al.* 2003; Dovciak *et al.* 2005), being episodic in time frequency. Therefore, the study of colonisation mode and extant spatial patterns in long-lived plant species is key to fully understand and assess the processes involved in vegetational changes in these stressful environments (Dirnböck & Dullinger 2004).

Alpine habitats are characterized by harsh, unpredictable environmental conditions, and the presence of long-lived plant species, like cushion plants (Billings & Mooney 1968; Armesto *et al.* 1980; Morris & Doak 1998; Körner 2003). Cushion plants constitute one of the growth forms best adapted to these harsh environmental conditions. In these stressful abiotic environments, positive plant interactions are expected to be a frequent and important process driving community composition and structure (Bertness & Callaway

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