

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

ALEX FAJARDO,^{1,4*} CONSTANZA L. QUIROZ² AND LOHENGRIN A. CAVIERES^{2,3}

¹*Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Bilbao 449, Coyhaique, Chile (Email: alex.fajardo@ciep.cl, fajardo.alex@gmail.com),* ²*ECOBIOSIS, Departamento de Botánica, Universidad de Concepción, Concepción,* ³*Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile;* and ⁴*College of Forestry and Conservation, The University of Montana, Missoula, Montana, USA*

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 & Gadgil 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 fluctua-

tions, 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 & Fröberg 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

*Corresponding author.

Accepted for publication February 2008.

1994). At the population level, however, it has been very difficult to directly measure the age of cushion individuals and, consequently, to study the long-term and spatial cushion dynamics in these habitats, namely, the ways that biotic and abiotic factors interact to alter plant numbers through time and space (Watkinson 1997). Because of these age-measurement difficulties, we still have a poor understanding of the dynamics and structure of cushion plant populations (Halloy 2002; Kleier & Rundel 2004; Zoller & Lenzen 2004; Mark & Wilson 2005). Given that cushion plants facilitate the establishment of several other species (i.e. having positive interactions), and thus influence diversity at local scales in alpine habitats (Cavieres *et al.* 2002; Badano & Cavieres 2006; Cavieres *et al.* 2006), an understanding of the successional processes operating in these harsh environments is critical (Mark & Wilson 2005). We propose that the difficulties mentioned above can be partially overcome if the spatial pattern of plants is studied (Dale 1999). Considering that spatial patterns in nature necessarily obey and, to some extent, create underlying mechanisms or processes (Watt 1947; Legendre & Fortin 1989; Turner *et al.* 2001), one may infer or interpret the link between pattern and process (MacArthur 1972; Dale 1999). The fundamental point of this conceptualisation is that direct relationships can be identified between observed or predicted spatial patterns of vegetation and the processes occurring in the population, such as colonisation (Watt 1947; Dale 1999; Jeltsch *et al.* 1999; Fajardo & McIntire 2007).

Using this approach in alpine habitats dominated by cushion species, we can evaluate colonisation modes by studying spatial autocorrelation, adopting cushion size as a surrogate of its age. Here we adopt the simplest definition of plant colonisation that has to deal with the addition of new individuals to the population in some specific area. There are several studies that have demonstrated strong and positive correlations between size and age in different alpine cushion species (e.g. Benedict 1989; Morris & Doak 1998; Kleier & Rundel 2004; le Roux & McGeoch 2004). Thus, spatial patterns of cushion plants can then be analysed using spatial analytical tools such as semivariograms or wavelets (Fortin & Dale 2005; Fajardo & McIntire 2007) to infer colonisation modes. We hypothesize that if the colonisation of cushions has occurred gradually in time, the cushion population would display similarities in neighbours' size (e.g. positive spatial autocorrelation). Conversely, if colonisation of cushions has occurred in a rather episodic mode, whatever might be the primary cause (e.g. climatic fluctuation, masting years), cushions would display strong dissimilarities in neighbours' size (e.g. negative spatial autocorrelation). Ultimately, if colonisation is not spatially associated to any recognizable biotic or abiotic process, cushions will be randomly

distributed in space (e.g. no significant spatial autocorrelation could be detected), suggesting stochastic variation (null model). Because microsite distribution can play a key role in habitat niche occupation in alpine ecosystems (Germino & Smith 2001; Kleier & Rundel 2004), and might account for the observed patterns attributed to colonisation processes, we need to consider this factor in our spatial expectations scenario. Thus, gradual and episodic modes of colonisation may occur in a specific site with either heterogeneous or homogeneous microsite (resource) distribution. We define here the heterogeneity and homogeneity based on the scale of patchiness (Kleb & Wilson 1999). For example, a heterogeneous microsite distribution will be the result of an increase in the frequency of both resource-rich and resource-poor patches in the site; the contrary works for a homogeneous microsite distribution; the result of an increase in the frequency of either resource-rich patches or resource-poor patches in the site.

In this study we explored the probable colonisation modes of two populations of a cushion species, *Azorella madreporica* (Apiaceae), based on the spatial pattern of their size structure in the high-Andes of Central Chile. In doing so, we used a standard spatial analytical tool (semivariograms) to test specific biological *a priori* hypotheses relative to the mode of colonisation: continuous or episodic. By using semivariograms and assuming a positive correlation between size and age, a constant mortality rate at all ages, and no vegetative reproduction (not observed in *A. madreporica*), our aim was to explore which colonisation mode prevailed based on the spatial characteristic and variation (e.g. size) in these particular cushion populations.

METHODS

Study system

The study was conducted in the Molina River basin (33°20' S, 70°16' W), located in the Andes of central Chile, approximately 50 km east of Santiago. The climate is alpine with influences 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 943 mm, most of which falls as snow from May to late October. Mean air temperature during January and April reached 6.8°C at 3600 m of altitude (Cavieres *et al.* 2007). We selected two cushion-dominated communities above 3000 m of altitude, one at Mt. Franciscano (3580 m elevation) and the other at Mt. Tres Puntas peaks (3660 m elevation) (Fajardo *et al.* 2008). Cushion ranges in altitudinal distribution from 3200 to 3700 m; hence these two sites are located within this range.

Studied species

Azorella madreporica (Apiaceae) cushions are non-clonal, low-growing dwarf, tightly knit, and flat-forming dioecious plants, which form rounded mounds of foliage, with a diameter that can range from 0.1 to >1 m, with mean size increasing with elevation (Armesto *et al.* 1980; Cavieres *et al.* 2005). The low stature and compact form of these cushions may attenuate the effect of extreme environmental conditions (Körner 2003; Cavieres *et al.* 2007), enabling the persistence of a high proportion of other species that have been found growing within them, suggesting that these cushions act as nurse or facilitator plants (Arroyo *et al.* 2003; Cavieres *et al.* 2005).

Data collection

At each site, a plot of 10 × 30 m was established at random, with one axis perpendicular to the main direction of the slope. At these locations, slope was less than 5%. To facilitate the mapping task, the plots were further divided into mini-plots of 1 × 1 m, and Cartesian coordinates (x,y) were recorded for every individual cushion located within each plot, for which we used distance tapes. To determine the area 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 cushion's area we used was: $A = (\pi * L * W) / 4$, 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 metres (m²) and was used as a surrogate for age in two analyses: a population distribution analysis (based on histograms), and a semivariogram analysis (see below). Plots were located on east-facing slopes at both sites. All sampling was conducted in January 2005.

Fitting area-class distributions

To determine whether or not the distribution of the cushion area classes follows a negative exponential form (assumed to represent a continuously regenerating population) we used the distribution of both populations. We fitted our empirical distributions with two functions, exponential and normal (Ricci 2005), and compared relative fit using Akaike's Information Criterion (AIC) (Burnham & Anderson 2002). The lowest AIC value indicates the model with stronger performance, and therefore was adopted as a straightforward criterion to decide the form of the cushion's area-classes curve (see below).

Semivariograms fitting

To characterize the spatial autocorrelation of cushions, we computed empirical semivariograms and modelled the spatial autocorrelation found for cushions' size. Spatially autocorrelated data represent any variables that are distributed continuously in space (Goovaerts 1997). This type of analysis requires response values that need to be labelled with the spatial coordinates at which measurements were collected (e.g. the cushion size and its location in our study). The basic principle is that correlation between values of a regionalized variable Z will decrease as the distance between the sample points increases. The semivariogram is the variance of the difference between random variables at two units (locations), given by: $\text{Var}(Z_i - Z_j)$ for two sites *i* and *j*. The empirical semivariogram is half the estimated variogram, and is defined as:

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_i [z(x_i) - z(x_i + h)]^2,$$

where: *h* is the distance lag between sampled cushions, *N*(*h*) is the number of paired comparisons at lag *h*, *z*(*x_i*) and *z*(*x_i* + *h*) are the observed cushion's size values at location *x_i* and *x_i* + *h*, respectively (Webster & Oliver 2001). Under a typical spatial dependence model, two units that are close together will tend to have a smaller variance of the difference (Fortin & Dale 2005). As units get further apart, their differences become larger and usually the variance of the difference becomes larger too.

In a semivariogram, the semivariance ($\gamma(h)$) is plotted on the y-axis against lag distance (*h*) on the x-axis (Fig. 1). The lag distance is the step-size used, and the active lag denotes the largest distance considered between points in the semivariance dataset, though the whole dataset is included in the analysis (Isaaks & Srivastava 1989). A semivariogram has three parameters known as the nugget, sill, and range. The nugget is a measure of the microscale variation in the response. The sill, or total sample variance, is the ordinate value at which the semivariogram becomes flat. The range represents the distance beyond which samples are spatially independent (Isaaks & Srivastava 1989; Webster & Oliver 2001).

In our study, we selected five different theoretical semivariogram models to analytically depict the spatial autocorrelation of a cushion's size shown in the empirical semivariograms (Fig. 1; in addition, see semivariogram formulae in Table 1). We did not just directly represent the processes of interest in our models; in this approach we tried to link semivariance to biological processes logically and by limiting parameter values to be mechanistically meaningful (see below) in the semivariance fitting. To describe lack of spatial autocorrelation in cushion size (i.e. our null hypothesis) we considered the 'nugget' model (pure

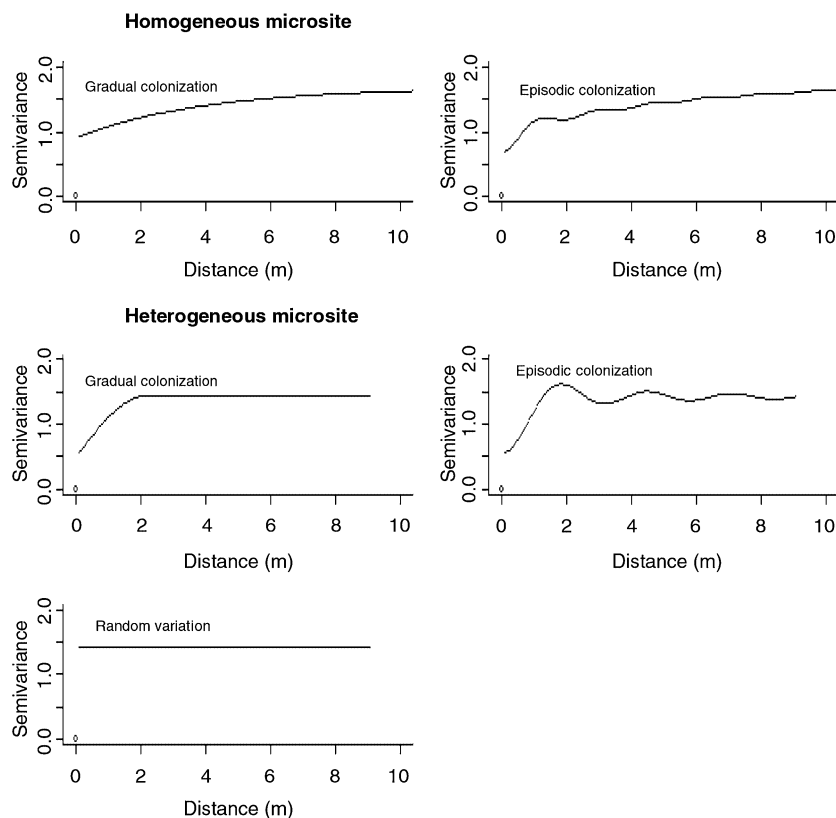


Fig. 1. Theoretical semivariogram models representing both microsite distribution and colonisation mode processes: for homogeneity in microsite distribution gradual colonisation was represented by an exponential theoretical model (upper left), episodic colonisation mode by a nested semivariogram (upper right); for heterogeneity in microsite distribution gradual colonisation was represented by a spherical theoretical model (lower left), episodic colonisation mode by a wave semivariogram (lower right). We considered the inclusion of a null model (nugget semivariogram), which represents the absence of any spatial autocorrelation.

Table 1. Theoretical semivariogram formulae used in this study

Nugget:

$$\gamma(h) = c_0$$

Exponential:

$$\gamma(h) = c_0 + c_1 \left[1 - \exp\left(-\frac{h}{a}\right) \right] \quad 0 < h < a$$

Spherical:

$$\gamma(h) = c_0 + c_1 \left[\frac{3h}{2a} - \frac{1}{2} \left(\frac{h}{a} \right)^3 \right],$$

$$\gamma(h) = c_0 + c_1, \quad h \geq a$$

Wave:

$$\gamma(h) = c_0 + c_1 \left[1 - \frac{a \sin\left(\frac{\pi h}{a}\right)}{\pi h} \right]$$

Nested Exponential and Wave:

$$\gamma(h) = c_0 + c_{1e} \left[1 - \exp\left(-\frac{h}{a_e}\right) \right] + c_{1w} \left[1 - \frac{a_w \sin\left(\frac{\pi h}{a_w}\right)}{\pi h} \right]$$

Where, $\gamma(h)$ is the spatial variance at distance lag h (the distance between successive points in the semivariogram), c_0 is the nugget parameter, c_1 is the sill parameter, a is the range. In the nested variogram that we used, subscripts e and w represent parameters fitted to the exponential and wave portions of the functions, respectively. All of these are for $h > 0$.

nugget effect–stochastic variation). The nugget model represents no spatial pattern at the scales we measured, suggesting a discontinuity in spatial autocorrelation at a short scale (size of neighbouring cushions differs randomly). To describe gradual colonisation, we used an exponential theoretical model for homogeneous microsite distribution and a spherical theoretical model for heterogeneous microsite distribution. An exponential semivariogram better describes positive spatial autocorrelation continuity on a larger scale (e.g. smaller sill-nugget difference and larger range), and a spherical semivariogram better describes positive spatial autocorrelation continuity on a shorter scale (e.g. higher sill-nugget difference and shorter range; Fig. 1). To describe episodic colonisation, we chose a nested semivariogram model for homogeneous microsite conditions and a wave model for heterogeneous microsite conditions. A nested model (a mixture between exponential and wave theoretical models) accounts for both a larger scale effect of microsite homogeneity (positive spatial autocorrelation continuity on a larger scale) and shorter scale of colonisation (negative spatial autocorrelation in the size of cushions on a shorter scale); the wave model captures a strong spatial discontinuity in the size of cushions on a shorter scale (e.g. larger sill-nugget difference and shorter range; Fig. 1). When fitting the spherical and wave semivariograms, we only accepted local optima for the range parameters that fell within less than 1.5 m, reflecting the short scale inter-cushion distance according to a heterogeneous microsite distribution. Thus, we computed semivariances and then fitted curves to the semivariograms using the different models described above (Cressie 1985). To set minimum lag distance, average lag distances or active lag, we followed the criteria described by Isaaks and Srivastava (1989). We also removed any larger scale site-level trend whenever it emerged (stationary assumption) prior to fitting the semivariogram model. The range, nugget and sill for each site were determined from each model.

Non-linear regression (weighted least squares) with weights proportional to $N(h)$ (the number averaged for each lag h in the semivariogram equation) was used to fit the different theoretical semivariogram models to the empirical semivariogram (Cressie 1985). Since we used non-linear regression, least squared solutions can be sensitive to initial parameter values. Because of this, we iterated through many initial parameter values for each semivariogram, keeping the best model that had biologically meaningful parameter values for the nugget, sill and range (i.e. we rejected negative or extremely large parameter values). In cases where no least squared minimum existed within biologically meaningful parameter values (e.g. a positive nugget), we interpreted this as there being no good fit of the data to that model.

Model selection

Each empirical cushion size semivariogram was fit to the five theoretical semivariograms and relative fit was assessed using AIC for small samples (AIC_c) (Webster & Oliver 2001; Burnham & Anderson 2002). Because results depended on the entire set of candidate models, models should be identified before data analysis (*a priori* approach). Relative fitting using information-theoretic statistics minimizes some of the pitfalls of traditional analyses that lead to weak inference in non-experimental studies (Anderson & Burnham 2002). A small sample version of AIC, AIC_c , was calculated for each model with the algorithm:

$$AIC_c = -2\log(\hat{L}(\theta)) + 2K + (2K(K+1))/(n-K-1)$$

where $\log(\hat{L}(\theta))$ is the maximized log-likelihood value, K is the number of parameters, and n is the sample size (Burnham & Anderson 2002). Nominally, the information criterion estimates the amount of information lost when using a particular model to approximate reality, relative to other candidate models (i.e. a low AIC value indicates strong performance of a model) (Burnham & Anderson 2002). Since better models lose less information (Welch & MacMahon 2005), it is always convenient to re-scale the AIC_c values such that the model with the minimum AIC_c has a value of 0. Thus, information-criterion values can be re-scaled as simple differences,

$$\Delta_i = AIC_{ci} - AIC_{cmin}$$

Then we have an estimate of the size of the increments of information loss for the various models compared with the estimated best model (the model with the minimum AIC_c). Where $\Delta_i < 2$, there is equal statistical support for the models (Burnham & Anderson 2002). We also computed normalized Akaike weights (w_i), where each w_i provides the weight of evidence that model i is the best model (Burnham & Anderson 2002). Empirical semivariograms were estimated using the 'geoR' package (Ribeiro & Diggle 2001) of the statistical software 'R' (R-Foundation 2004), as well as other model fitting in R (for variogram and distributions fitting).

RESULTS

General demography

Azorella madreporica was the dominant species at both sites: a total of 94 (3133 individuals*ha⁻¹) and 84 (2800 individuals*ha⁻¹) individual cushions were mapped in Franciscano and Tres Puntas (0.03 ha) sites, respectively. The size of cushions ranged from 0.01 to 1.99 m² (median value of 0.18 m²) at

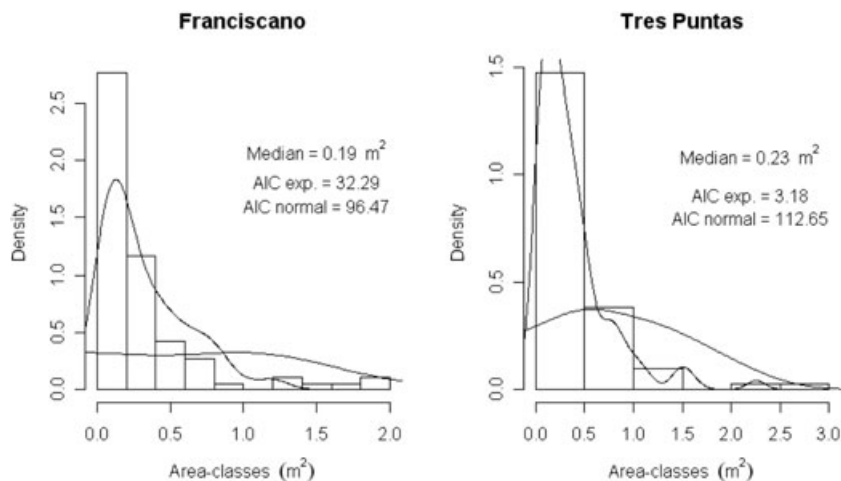


Fig. 2. Cushion size distribution for the Franciscano and Tres Puntas sites for an alpine cushion-dominated community at the Valle del Río Molina, Andes of central Chile (30°20'S.).

Table 2. Model coefficients and Akaike's Information Criterion for small sample (AIC_c) values for describing cushion size (*Azorella madreporica*) spatial interactions in an alpine community at the Valle del Río Molina, Andes of central Chile (30°20'S.).

Site	Models	Model coefficients					AIC_c
		Nugget	Sill [†]	Range [†]	Sill [‡]	Range [‡]	
Franciscano	Exponential	1.1260	0.6032	7.4304			57.6738
	Nested	0.3608	0.8357	0.9116	0.9769	20.0524	55.1698
	Spherical	0.2605	1.2119	1.4932			58.1003
	Wave	0.3614	1.1037	0.9423			59.5205
	Nugget	1.4619					60.4044
Tres Puntas	Exponential	0.9983	0.7888	5.3951			59.9708
	Nested	0.8109	0.2538	1.0406	0.7994	7.1203	63.7002
	Spherical						
	Wave	0.6314	0.9095	1.3993			62.8362
	Nugget	1.5343					64.1289

For Nested model parameters only: [†]corresponds to the wave part of the nested model; [‡]corresponds to the exponential part of the nested model. Remember that the Nested model is a combination between wave and exponential models.

Franciscano site, covering an area of 28.82 m², and from 0.01 to 3 m² (median value of 0.23 m²) at Tres Puntas, with a total area of 32.11 m². We compared the frequency distributions of cushion area-classes to models often assumed to represent a continuously regenerating population, and at both sites, the size distribution of *A. madreporica* proved to be best fitted by a negative exponential or inverse-J pattern; most of the cushions belonged to relatively smaller area classes (Fig. 2).

Semivariograms

Spatial autocorrelation of individual cushion size was strong across both sites; the computed semivariograms

were significantly different from the nugget spatial model, suggesting that stochastic processes are not the main determinants of the spatial structure of *A. madreporica* populations (Tables 2,3; Fig. 3). At Franciscano, the nested (i.e. wave and exponential) semivariogram model was the best fit model describing the spatial autocorrelation of cushion size (lowest AIC_c , $w_i = 0.5239$; Table 3). At Tres Puntas, the exponential semivariogram model was the best fit model describing the spatial autocorrelation of cushion size (lowest AIC_c , $w_i = 0.6605$, Table 3); cushions of similar sizes were neighbours. The models of gradual and episodic colonisation in heterogeneous microsite distributions (named spherical and wave models) did not fit well to the data (higher AIC_c and lower w_i values, Table 3).

DISCUSSION

Population structure of *Azorella madreporica*

Our results suggest that both cushion populations contained a large number of small size individuals and a declining number of larger individuals at both study sites. This may be indicative of regular success in the establishment of cushion seedlings, where all size classes of cushions were represented in the population with a reverse J-shaped curve of population distribution. Assuming a positive correlation between cushion size and age, these distributions could be adduced as representative of a steady-state or stable population condition (Platt *et al.* 1988; Veblen 1992). Similar results were found by Kleier and Rundel (2004) for *Azorella compacta* in the altiplano of northern Chile, and le Roux and McGeoch (2004) for

Azorella selago in the sub-antarctic Indian Ocean. Likewise, Zoller and Lenzin (2004) reported a reverse J-shaped curve of population distribution for several plots with cushions of *Eritrichium nanum* in the Austrian Alps. These authors also reported that such size-age structure is maintained by episodic but frequent seedling recruitment, followed by high seedling mortality during the first year but decreasing mortality rates as seedlings grow (see also Diemer (1992), for an example with *Ranunculus glacialis*). However, for other long-lived alpine species, Monasterio (1979) and Pérez (1992) found the lowest frequency of individuals in the smallest size class for *Espeletia timotensis*, a giant rosette of the Venezuelan Andes. Likewise, Young and Peacock (1992) found equally represented frequencies of individuals for all size classes for the giant Afro-alpine rosette *Lobelia telekii* in Kenya. Both examples demonstrated irregular and infrequent establishment of individuals in alpine habitats. It is important to note

Table 3. Summary of Akaike's Information Criterion for small sample (AIC_c) selection models, Akaike differences (Δ_i), and Akaike weights (w_i) for describing cushion size (*Azorella madreporica*) spatial interactions in an alpine community at the Valle del Río Molina, Andes of central Chile (30°20'S.)

Site	Model support									
	Exponential (3)		Nested (5)		Spherical (3)		Wave (3)		Nugget (1)	
	Δ_i	w_i	Δ_i	w_i	Δ_i	w_i	Δ_i	w_i	Δ_i	w_i
Franciscano	2.0888	0.1875	0	0.5329	2.5153	0.1515	3.9355	0.0745	4.5962	0.0535
Tres Puntas	0	0.6605	4.1986	0.0809	9.0292	0.0072	2.8654	0.1576	3.9069	0.0937

Figures within parentheses represent the number of parameters of the theoretical model used to fit the empirical semivariogram.

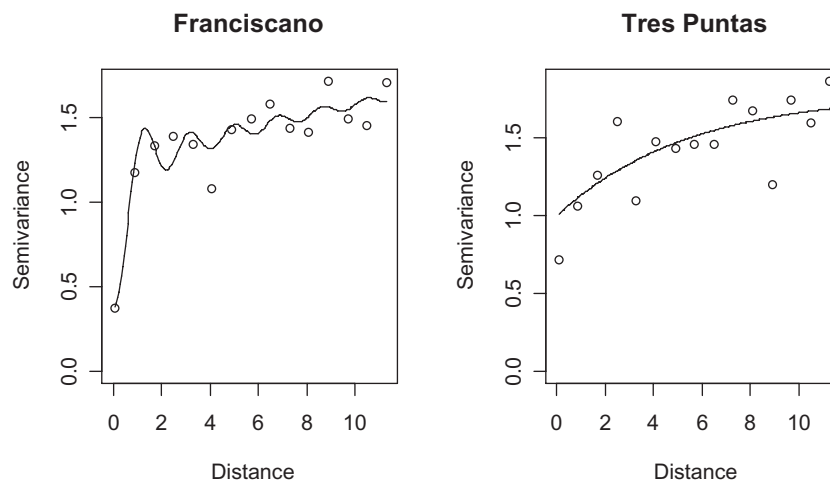


Fig. 3. Empirical semivariograms (○) and the best theoretical semivariogram fitted to cushion size (*Azorella madreporica*) spatial autocorrelation data in an alpine community at the Valle del Río Molina, Andes of central Chile (30°20'S.).

that the last two examples, namely, the irregular and infrequent establishment, were reported from species inhabiting tropical mountains where the growing season spans the whole year. This contrasts with mountains located in temperate latitudes where the growing season is restricted to a short, snow-free period, the duration of which is highly unpredictable from 1 year to another (Körner 2003). Therefore, more studies focused on the size-age population distribution of alpine species covering a variety of mountains and climates are needed to draw more definitive conclusions about the frequency and magnitude of the reproductive pulses in these harsh environments.

Colonisation processes

Depending on the site, our results supported two different semivariogram models (i.e. best fit); the nested for Franciscano site and the exponential semivariogram model for Tres Puntas. From these best fit semivariogram models, we can suggest that, first, colonisation processes derived from a rather homogeneous distribution of microsites in the field for both sites, indicating that resources might be over-dispersed in these harsh and relatively young environments. Second, the prevalent mode of colonisation differed between sites; cushions followed a gradual colonisation at Tres Puntas (positive spatial autocorrelation of cushions' size), but an episodic colonisation at Franciscano (negative spatial autocorrelation of cushions' size). From the latter, we can speculate that an episodic mode of colonisation may imply short distances over which seeds have been dispersed from adults (e.g. Dirnböck & Dullinger 2004), leading seedlings to be aggregated with adults but with different time lags (Zoller & Lenzin 2004, 2006). The Franciscano site was found to be more productive and have many more species (and total number of individuals) than the Tres Puntas site (Badano *et al.* 2006). In addition, most of the species growing outside the shelter of *A. madreporica* cushions in the Franciscano site had negative spatial associations with them (Fajardo *et al.* 2008), suggesting negative interactions (i.e. competition) between cushions and those specific species. More species in the community and negative associations with the cushions may work against a continuous recruitment of cushions in time and space because suitable microsites may be pre-empted by other species. In contrast, the lower species richness and fewer negative associations established with cushions in the Tres Puntas site may suggest a more gradual recruitment of new cushion individuals. Furthermore, in these environments nutrients, especially nitrogen, are scarce (Bowman *et al.* 1993; Nilsson *et al.* 2002), and the availability of these resources can determine the

success of recruitment in several alpine plant species (e.g. Chambers *et al.* 1990; Forbis 2003). Thus, it is expected that variation in the level of nutrients can result in changes in the spatial patterns of these cushion populations. Future studies should focus on determining the complex relationships among rates of establishment and nutrient levels, and the dynamics of *Azorella madreporica* mortality and its role on the population structure of this species. In addition, a more integral and functional perspective between the cushion's population dynamics and the whole alpine community assemblage will provide a more consistent understanding of colonization dynamics in these communities (cf. Dirnböck & Dullinger 2004).

Possible limitations

Our study relies on some assumptions for which we have limited information regarding *Azorella madreporica*, for example, the age of cushions correlates well with size, and each cushion sampled represents a single individual. The relationship between size and age is very well known in some other cushion species (see Körner 2003). We are aware, though, that this may not be true for our cushion populations, and size may be an inadequate correlate of age for several reasons (see Veblen 1992; Lusk 2003). With this acknowledgement in mind, the upshot of analysing size as a surrogate of cushion age may appear to be weakened. This limitation also has implications for our conclusions about population structure, since we have not recorded past mortality rates. Nevertheless, there are studies that have found good correlation between size and age in other closely related cushion species. For instance, on Marion Island, sub-Antarctic Indian ocean, le Roux and McGeoch (2004) successfully related cushion age and size using a phytometric model for the cushion species *Azorella selago*. In addition, age and growth rates in *Azorella compacta* have been examined in Peru (Ralph 1978) and Argentina (Halloy 2002), showing a linear relationship between both variables is acceptable. Future studies must investigate the strength of the relationship between age and size of cushions for these particular populations.

Second, we relied on the assumption that each cushion sampled represented a single individual. We know that *A. madreporica* has no vegetative reproduction and only grows horizontally (Lohengrin A. Cavieres, *pers. obs.*, 1992–2008), however, we cannot discard merging. Another limitation with the current study has to do with proper representativeness (two sample sites). The fact that both sites presented different modes of colonisation raises the fundamental issue of variation and the call for more replicates.

General implications

Using high-precision mapping plots and *a priori* multiple hypotheses along with semivariogram models fitting, we were able to: (i) distinguish different colonisation modes, which proved to be site-specific; and (ii) detect that microsites are rather homogeneously distributed (e.g. resource continuity). The study presented here could not have been done using more traditional approaches because they require manipulations that are not always possible. With this snapshot approach on the spatial pattern found, we have provided a novel insight into the understanding of alpine population dynamics, for example, the role and interaction between a prevalent colonisation mode and microsite distribution. As most ecological data are spatially dependent (Legendre 1993; Dale 1999), researchers can model the spatial variability that characterizes each set of data and attach them to specific processes (Fajardo & McIntire 2007). The challenge here is to always accurately translate deductive predictions of processes into spatial patterns in order that they reflect the underlying process of interest. Further field studies are required to quantify cushion seed dispersal and interactions with other species, and also to elucidate how climatic fluctuation may affect colonisation patterns.

ACKNOWLEDGEMENTS

This research was funded by FONDECYT 1030821 and P05-002-F ICM supporting the Instituto de Ecología and Biodiversidad (IEB). Further funding for this project was partially provided to A. Fajardo by the USDA McIntire-Stennis program, which is a contribution of the University of Montana College of Forestry and Conservation. The BBVA Prize for Conservation of Biodiversity in Latin America 2005 is also acknowledged.

REFERENCES

- Anderson D. R. & Burnham K. P. (2002) Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manage.* **66**, 910–16.
- Armesto J. J., Arroyo M. T. K. & Villagrán C. (1980) Altitudinal distribution, cover and size structure of umbelliferous cushion plants in the high Andes of central Chile. *Acta Oecol.* **1**, 327–32.
- Arroyo M. T. K., Cavieres L. A., Peñaloza A. & Arroyo-Kalin M. A. (2003) Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecol.* **169**, 121–9.
- Badano E. I. & Cavieres L. A. (2006) Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *J. Biogeogr.* **33**, 304–13.
- Badano E. I., Jones C. A., Cavieres L. A. & Wright J. P. (2006) Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* **115**, 369–85.
- Bartha S., Meiners S. J., Pickett S. T. A. & Cadenasso M. L. (2003) Plant colonization windows in a mesic old field succession. *Appl. Veg. Sci.* **6**, 205–12.
- Begon M. (1984) Density and individual fitness: asymmetric competition. In: *Evolutionary Ecology* (ed. B. Shorrocks) pp. 175–94. Blackwell Scientific, Oxford.
- Benedict J. B. (1989) Use of *Silene acaulis* for dating: the relationship of cushion diameter to age. *Arct. Alp. Res.* **21**, 91–6.
- Bertness M. D. & Callaway R. M. (1994) Positive interactions in communities. *Trends Ecol. Evol.* **9**, 187–91.
- Billings W. D. & Mooney H. A. (1968) The ecology of arctic and alpine plants. *Biol. Rev.* **43**, 481–529.
- Bowman W. D., Theodose T. A., Schardt J. C. & Conant R. T. (1993) Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* **74**, 2084–97.
- Burnham K. P. & Anderson D. R. (2002) *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- di Castri F. & Hajek E. (1976) *Bioclimatología de Chile*. Pontificia Universidad Católica de Chile, Santiago.
- Cavieres L. A., Arroyo M. T. K., Peñaloza A. & Molina-Montenegro M. A. (2002) Nurse effect of *Bolax gummifera* (Apiaceae) cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *J. Veg. Sci.* **13**, 547–54.
- Cavieres L. A., Badano E. I., Sierra-Almeida A., Gómez-González S. & Molina-Montenegro M. A. (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**, 59–70.
- Cavieres L. A., Badano E. I., Sierra-Almeida A. & Molina-Montenegro M. A. (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**, 229–36.
- Cavieres L. A., Quiroz C. L., Molina-Montenegro M. A., Muñoz A. A. & Pauchard A. (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. Evol. Syst.* **7**, 217–26.
- Chambers J. C., MacMahon J. A. & Brown R. W. (1990) Alpine seedling establishment: the influence of disturbance type. *Ecology* **71**, 1323–41.
- Cressie N. A. C. (1985) Fitting variogram models by weighted least squares. *J. Int. Assoc. Math. Geol.* **17**, 563–86.
- Dale M. R. T. (1999) *Spatial Pattern Analysis in Plant Ecology*. Cambridge University Press, New York.
- DeAngelis D. L. & Gross L. J. (1992) *Individual-Based Models and Approaches in Ecology: Populations, Communities, and Ecosystems*. Chapman & Hall, London.
- Diemer M. (1992) Population dynamics and spatial arrangement of *Ranunculus glacialis* L., an alpine herb, in permanent plots. *Plant Ecol.* **103**, 159–66.
- Dirnböck T. & Dullinger S. (2004) Habitat distribution models, spatial autocorrelation, functional traits and dispersal capacity of alpine plant species. *J. Veg. Sci.* **15**, 77–84.
- Dovciak M., Frelich L. E. & Reich P. B. (2005) Pathways in old-field succession to white pine: seed rain, shade, and climate effects. *Ecol. Monogr.* **75**, 363–78.

- Eriksson O. & Fröberg H. (1996) 'Windows of opportunity' for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Can. J. Bot.* **74**, 1369–74.
- Fajardo A. & McIntire E. J. B. (2007) Distinguishing microsite and competition processes in tree growth dynamics: an *a priori* spatial modeling approach. *Am. Nat.* **169**, 647–61.
- Fajardo A., Quiroz C. L. & Cavieres L. A. (2008) Spatial patterns in cushion-dominated plant communities of the high-Andes of central Chile: how frequent are positive associations? *J. Veg. Sci.* **19**, 87–96.
- Forbis T. A. (2003) Seedling demography in an alpine ecosystem. *Am. J. Bot.* **90**, 1197–206.
- Fortin M.-J. & Dale M. R. T. (2005) *Spatial Analysis: A Guide for Ecologists*. Cambridge University Press, Cambridge.
- Germino M. J. & Smith W. K. (2001) Relative importance of microhabitat, plant form and photosynthetic physiology to carbon gain in two alpine herbs. *Funct. Ecol.* **15**, 243–51.
- Goovaerts P. (1997) *Geostatistics for Natural Resource Evaluation*. Oxford University Press, New York.
- Gurevitch J., Scheiner S. M. & Fox G. A. (2002) *The Ecology of Plants*. Sinauer Associates, Inc., Sunderland.
- Halloy S. R. P. (2002) Variations in community structure and growth rates of high-Andean plants with climatic fluctuations. In: *Mountain Biodiversity. A Global Assessment* (eds C. Körner & E. M. Spehn) pp. 225–38. Parthenon Publishing Group, New York.
- Isaaks E. H. & Srivastava R. M. (1989) *An Introduction to Applied Geostatistics*. Oxford University Press, Inc., New York.
- Jeltsch F., Moloney K. A. & Milton S. (1999) Detecting process from snap-shot pattern: lessons from tree spacing in the southern Kalahari. *Oikos* **85**, 451–67.
- Kleb H. R. & Wilson S. D. (1999) Scales of heterogeneity in prairie and forest. *Can. J. Bot.* **77**, 370–6.
- Kleier C. & Rundel P. W. (2004) Microsite requirements, population structure and growth of the cushion plant *Azorella compacta* in the tropical Chilean Andes. *Austral Ecol.* **29**, 461–70.
- Körner C. (2003) *Alpine Plant Life*, 2nd edn. Springer, Berlin.
- Legendre P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**, 1659–73.
- Legendre P. & Fortin M.-J. (1989) Spatial pattern and ecological analysis. *Végétatio* **80**, 107–38.
- Lusk C. (2003) Tree-species competition and coexistence. *Nature* **422**, 580–1.
- MacArthur R. H. (1972) *Geographic Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton.
- Mark A. F. & Wilson J. B. (2005) Tempo and mode of vegetation dynamics over 50 years in a New Zealand alpine cushion/tussock community. *J. Veg. Sci.* **16**, 227–36.
- McIntire E. J. B. & Fajardo A. (2008) Beyond description: The active and effective way to infer processes from spatial patterns. *Ecology* (in press).
- Monasterio M. (1979) El Páramo desértico en el altiandino de Venezuela. In: *El medio ambiente Páramo* (ed. M. L. Saldago-Labouriau) pp. 117–76. Instituto Venezolano de Investigaciones Científicas, Caracas.
- Morris W. F. & Doak D. F. (1998) Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *Am. J. Bot.* **85**, 784–93.
- Nilsson M. C., Wardle D. A., Zackrisson O. & Jäderlund A. (2002) Effects of alleviation of ecological stresses on an alpine tundra community over an eight-year period. *Oikos* **97**, 3–17.
- Platt W. J., Evans G. W. & Rathbun S. L. (1988) The population dynamics of a long-lived conifer (*Pinus palustris*). *Am. Nat.* **131**, 491–525.
- Pérez F. L. (1992) Ecological impact of cattle on caulescent Andean rosettes in a high Venezuelan páramo. *Mt. Res. Dev.* **12**, 29–46.
- R-Foundation (2004) *R: A Language For Statistical Computing*, Vienna, Austria. [Cited December 2006.] Available from URL: <http://www.R-project.org>
- Ralph C. P. (1978) Observations on *Azorella compacta* (Umbelliferae), a tropical Andean cushion plant. *Biotropica* **10**, 62–7.
- Ribeiro P. J. & Diggle P. J. (2001) geoR: a package for geostatistical analysis. *R-NEWS* **1**, 15–18.
- Ricci V. (2005) *Fitting Distributions with R*. [Cited December 2006.] Available from URL: <http://cran.r-project.org/doc/contrib/Ricci-distributions-en.pdf>
- le Roux P. & McGeoch M. A. (2004) The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Arct. Antarct. Alp. Res.* **36**, 509–17.
- Sarukhán J. & Gadgil M. (1974) Studies on plant demography: *Ranunculus repens* L., *R. balbosus* L. and *R. acris* L.: III. A mathematical model incorporating multiple modes of reproduction. *J. Ecol.* **62**, 921–36.
- Silvertown J. W. & Charlesworth D. (2001) *Introduction to Plant Population Biology*, 4th edn. Blackwell Publishing Limited, Oxford.
- Turner M. G., Gardner R. H. & O'Neill R. V. (2001) *Landscape Ecology in Theory and Practice. Pattern and Process*. Springer, New York.
- Veblen T. T. (1992) Regeneration dynamics. In: *Plant Succession: Theory and Prediction*, Vol. 11 (eds D. C. Glen-Lewin, R. K. Peet & T. T. Veblen) pp. 152–87. Chapman & Hall, London, New York.
- Watkinson A. R. (1997) Plant population dynamics. In: *Plant Ecology* (ed. M. J. Crawley) pp. 359–400. Blackwell Publishing Limited, Oxford.
- Watt A. S. (1947) Pattern and process in the plant community. *J. Ecol.* **35**, 1–22.
- Webster R. & Oliver M. A. (2001) *Geostatistics for Environmental Scientists*. John Wiley & Sons, New York.
- Welch N. E. & MacMahon J. A. (2005) Identifying habitat variables important to the rare Columbia spotted frog in Utah (U.S.A.): an information-theoretic approach. *Cons. Biol.* **19**, 473–81.
- Young T. P. & Peacock M. M. (1992) Giant senecios and alpine vegetation of Mount Kenya. *J. Ecol.* **80**, 141–8.
- Zoller H. & Lenzin H. (2004) Survival and recruitment favored by safe site-strategy – the case of the high alpine, non-clonal cushions of *Eritrichium nanum* (Boraginaceae). *Flora* **199**, 398–408.
- Zoller H. & Lenzin H. (2006) Composed cushions and coexistence with neighbouring species promoting the persistence of *Eritrichium nanum* in high alpine vegetation. *Botanica Helvetica* **116**, 31–40.