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Temporal changes in local spatial structure of late-successional species: establishment of an Andean caulescent rosette plant

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Summary

1 We analyse successional changes in local spatial structure of populations of a dominant late-successional species (*Espeletia schultzii*) in the high tropical Andes.
2 Spatial maps of plants of *E. schultzii* and important features of their environment were recorded at early (year 3) and middle (year 8) stages of succession after agricultural disturbance, and in non-cultivated páramo.
3 Spatial covariance functions were calculated from the maps to provide information on the changing 'plant-eye's view' of seedlings and adults during succession, and on the coupling of spatial structure to dynamics of successional communities.
4 Seedlings of *E. schultzii* appeared at high densities shortly after agricultural disturbance ceased. Spatial aggregation, which among seedlings was strongest in later stages of succession, was absent among adults, suggesting greater mortality within aggregations of conspecifics plays a part in regulating population dynamics.
5 Early in succession, seedlings of *E. schultzii* were slightly segregated from the dominant early successional species, *Rumex acetosella*. By year 8 of succession, *R. acetosella* was strongly segregated from adults of *E. schultzii*, but not from seedlings. This suggests that competitive exclusion caused by asymmetric competition may contribute to decline in early successional species.
6 Spatial sorting in relation to abiotic factors was most evident in the mature páramo, with *E. schultzii* adults occurring on steeper slopes and on less stony ground. *E. schultzii* adults here were also segregated from *Hypericum laricifolium*, the other dominant species.
7 The coupling of local spatial structure to community dynamics may have profound effects on succession. In particular, the development of interspecific segregation could contribute to the continued coexistence of early and late successional species throughout succession.

Key-words: competition, *Espeletia*, local density dependence, páramo, spatial pattern

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Introduction

Plant species that occur late in succession establish populations in communities already dominated by other species. How do the populations of such species develop over time and space? Under what conditions do they become established? Where are individuals most likely to survive; that is, how do the spatial relations of older surviving individuals differ from those of their younger counterparts? What does this suggest about the factors influencing succession?

To answer these questions, the environment of late-successional species has to be analysed at a spatial scale small enough to detect the local neighbourhoods in which the individual plants live and interact, the so-called plant's-eye view (Hubbell 1979; Turkington & Harper 1979). Both theoretical (e.g. Bolker & Pacala 1997; Law & Dieckmann 2000; Law *et al*. 2003) and empirical (e.g. Pacala & Silander 1990; Stoll & Prati 2001) studies have shown that the spatial relationships of conspecifics and heterospecifics strongly modulate the strength of plant interactions (e.g. competition and facilitation), while these interactions in turn modify the spatial relationships between plants. Hence, the local interplay between spatial structure and plant–plant interactions would

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be expected to have profound effects on community dynamics.

However, the local spatial relations of successional species remain largely unexplored, with limited empirical research from a plant-centred perspective (*sensu* Purves & Law 2002). Most previous analyses of spatial pattern of successional species have been more concerned with describing changes in the intensity and scale of aggregations as a result of patch growth and coalescence (Kershaw 1957; Greig-Smith 1964; Brereton 1971; Yarranton & Morrison 1974; Dale & Blundon 1990; Schaeffer 1993). Accordingly, the techniques used for spatial pattern analysis (e.g. block-quadrat variance) are not usually plant-centred, emphasizing multiple-scale patterns across whole fields. These studies also emphasize the relationships between vegetation patterns and environmental heterogeneity at different scales (e.g. Sterling *et al*. 1984).

Plant-based studies of local neighbourhoods have avoided the complications of succession by focusing on mature, non-successional systems (Hubbell 1979; Turkington & Harper 1979; Mahdi & Law 1987; Purves & Law 2002). Although local replacements of species are often found at small spatial scales, e.g. the ‘mosaic cycles’ of Watt (1947) and the ‘carousel model’ of van der Maarel & Sykes (1993) (see Herben *et al*. (2000)), such changes are not synchronized over space, and do not result in the large-scale changes in community structure characteristic of primary and secondary succession. Even so, there is increasing recognition that the analysis of changes in local spatial structure can provide important information on intra- and interspecific interactions during succession (Frelich *et al*. 1993; Frelich & Reich 1995; Rejmanek & Leps 1996; Haase *et al*. 1997; Eshel *et al*. 2000). Analyses of spatial structure in successional chronosequences (where space is substituted for time) can help in this regard; although measurements are taken at a single time, differences in spatial structure at locations in different seral stages should reflect changes over time. For instance, Rejmánek & Leps (1996) and Haase *et al*. (1997) have used this strategy to suggest hypotheses about the competitive relations between early- and late-successional species based on their local spatial relations.

Here we analyse changes in the fine-scale spatial structure of a late-successional species, *Espeletia schultzii* Wedd., as it becomes established in old fields in the high Venezuelan Andes. *E. schultzii* is a giant rosette species, so abundant that it is the emblem of the Venezuelan ‘páramo’, the open vegetation of the northern Andes above montane forests and below the permanent snow line. Traditional potato agriculture in small fields in the páramo is one of the most common forms of intervention in the Northern Andes (Luteyn 1999). Yields in these fields decline rapidly and, after 2 or 3 years of cultivation, they are left fallow for a maximum of about 12 years (Sarmiento *et al*. 1993). At any point in time, such agriculture leads to a patchwork comprising many fallow plots at different seral stages, scattered within areas of natural páramo dominated by *E. schultzii* and the sclerophyllous shrub *Hypericum laricifolium* Juss. This offers an unusually well documented and replicated field system for studying changes in plant communities during succession.

We used the patchwork of fallow plots as a replicated chronosequence to gain insight into the changing local spatial structure of *E. schultzii* during its build-up in biomass over succession. This entailed characterizing the neighbourhoods of *E. schultzii* in terms of: (a) the density of conspecific seedlings and adults; (b) the abundance of other dominant species in early and late seral stages; and (c) microtopographic conditions. Based on this information, we analysed the influence of local spatial interactions on successional dynamics.

Materials and methods

ESPELETIA SCHULTZII

The genus *Espeletia* (Asteraceae) is endemic to the northern tropical Andes (Monasterio & Sarmiento 1991). *E. schultzii* is one of the most widespread and abundant species throughout the elevational range of the páramo in Venezuela (*c*. 2800–4200 m a.s.l.) (Baruch 1979; Fariñas & Monasterio 1980). It is polycarpic, with a semiwoody, unbranched stem up to 1.2 m tall, supporting a single evergreen rosette that can live from 50 to 100 years. It is slow growing, having an annual height growth of about 1.2 cm at 3600 m in the mature ecosystem (Smith 1981).

There have been very few studies on the ecology of *Espeletia* spp. at a plant-neighbourhood scale. Notable exceptions are Perez (1992, 1995), who showed that soil organic matter and other associated soil properties were significantly higher in the neighbourhood of rosette plants, and Smith (1980, 1981, 1984), who showed that neighbouring adults and seedlings can affect one another’s growth and survival.

STUDY AREA

The study was carried out in Las Piñuelas Valley in the Páramo de Gavidia, situated between 3300 and 3900 m a.s.l., in the Venezuelan Andes (8°35′45″ N, 70°52′58″ W). Gavidia is in an area of glacial origin with stony inceptisols of a sandy-loam texture, low pH (4.3–5.5) and high organic matter levels (up to 20%) but low mineral nutrient contents (Llambí & Sarmiento 1998). Precipitation is unimodal, with a dry season between December and April, and a mean annual rainfall of *c*. 1300 mm. These high tropical environments show wide daily rather than yearly fluctuations in temperature (with annual means falling from *c*. 10 °C at 3200 to 6 °C at 3800 m a.s.l.). Extensive cattle grazing is common within both cultivated and uncultivated areas.

Changes in vegetation structure in Las Piñuelas during fallow periods have been studied in detail by Sarmiento *et al*. (2003). Early succession is dominated by the introduced forb *Rumex acetosella* L., which accounts for about 50% of the total above-ground biomass in the first 2 years. Even so, most páramo species are able to colonize soon after field abandonment, with *E. schultzii* and *H. laricifolium* gradually increasing in biomass, and displacing *R. acetosella* as the dominant species after about 6 years. These two species show their peak abundance in mature páramo areas, where they account for about 20% of total above-ground biomass. Because most late-successional species are present from early seral stages, and ruderal species are not completely excluded in advanced seral stages, changes in relative abundance characterize the dynamics more than complete species replacements (i.e. autosuccession, Sarmiento *et al*. 2003).

DATA COLLECTION

Plots were chosen high on the slopes of Las Piñuelas Valley, where the mature páramo vegetation was co-dominated by *E. schultzii* and *H. laricifolium.* Plots were located in the non-cultivated páramo, in the third year of fallow (early succession), there being too few seedlings of *E. schultzii* in plots younger than this to allow spatial analysis, and in the eighth year of fallow (mid-succession). Adult individuals of *E. schultzii* were common by year 8 (their relative abundance then close to that found in non-cultivated areas, Sarmiento *et al.* 2003), and were likely to be the survivors of seedlings that appeared in the third year (maturation takes a minimum of 4 to 5 years). Although the inclusion of plots with longer fallow times would have been desirable, these were scarce in the valley, as farmers rarely abandon plots for more than 10 years.

Non-cultivated páramo areas served as a reference point against which to compare the spatial structure of early and mid-successional communities. Although it is possible that succession after agricultural disturbance does not lead in the long term to the same vegetation structure as in uncultivated páramo, Sarmiento *et al*. (2003) showed that, after 8 to 9 years, the relative abundance of the dominant life-forms becomes similar to that found in the páramo.

Five replicates of each age of plot were picked at random from high areas in the valley using a spatial data base on the fallow periods of 1200 old fields from 1991 onwards (Smith 1995; updated to the year 2001). Areas high on the slopes were used because these have a relatively similar vegetation physiognomy (rosette-shrubland paramo dominated by *E. schultzii* and *H. laricifolium*), topography (the valley bottom can be boggy) and land use (extensive cattle grazing and few cultivation-fallow cycles). Natural areas were located close to the fallow plots, to minimize environmental differences between them. This land was probably uncultivated due to the long distance from farmer houses rather than because of inherent differences such as a higher cover of stones or the presence of rock outcrops, as might be the case in the extensively cultivated valley bottom.

One 10 × 10 m grid, comprising 20 × 20 square cells (cell dimensions 0.5 × 0.5 m), was placed at random in each of the five plots selected for each seral stage, with one axis perpendicular to the main direction of the slope. Within each cell, we recorded the abundance of *E. schultzii*, *H. laricifolium* and *R. acetosella*, as well as slope and stoniness. All sampling was carried out at the end of the wet season during November 2001.

In the case of *E. schultzii*, an individual was considered to lie within a cell if the cell contained the central point of the rosette. We counted the number of individuals belonging to two distinct size classes: seedlings (< 5 cm in rosette diameter) and adults (> 25 cm diameter, i.e. above the approximate size at which individuals start reproduction, Smith 1981). Intermediate-sized individuals might have been either seedlings or older individuals experiencing repressed growth and, although counted, were for the most part excluded from analyses to ensure that growth repression did not interfere with a size-based distinction between young and old individuals.

In the case of *H. laricifolium*, we counted small (< 10 cm in height) and large (> 10 cm in height) individuals in each cell. The abundance of *R. acetosella* was determined visually by classifying each cell into 10 categories, from 0 (absent) to 9 (dense cover in all nine 17 × 17 cm subsections of the cell).

Slopes were classified as: low (< 30°), intermediate (30°–60°) and steep (> 60°), the values assigned being, respectively, 0, 1 and 2. Stones were considered to be present in a cell if they showed more than an estimated 50% cover in the cell; otherwise they were recorded as absent.

QUANTIFICATION OF SPATIAL STRUCTURE

Small-scale spatial structure in each grid was measured using a non-centralized radial covariance function (Condit *et al*. 2000; Purves & Law 2002), which measures the covariation of pairs of observations at a given radial distance. This function is closely related to other plant-centred measures used in the ecological literature, such as spatial autocorrelation and the semivariogram (see Burrough 1995; Dale 1999), but is mathematically simpler.

The covariance function was defined as follows. Consider the *k*th replicate grid, comprising a set of cells in which measurements of two variables, labelled i and j, have been taken in each cell; the variables might be number of individuals of one or more species, but could equally well be properties of the abiotic environment. In the kth replicate grid, denote $p_{ik}(x)$ as the value i takes in cell x with Cartesian coordinates (x_1, x_2), and $p_{jk}(x + \xi)$ as the value j takes in cell $x + \xi$ with Cartesian coordinates $(x_1 + \xi_1, x_2 + \xi_2)$. The covariance of i and j with radial displacement r is defined as

$$C_{ijk}(r) = \frac{1}{|S_r|} \sum_{x \in S_r} p_{ik}(x) \cdot p_{jk}(x + \xi) \qquad \text{eqn 1}$$

Here $S_r = \{(x, x+\xi): r \le |\xi| < r+\delta r\}$ and $|\xi| = \sqrt{\xi_1^2 + \xi_2^2}$. S_r is therefore the set of all cell pairs separated by radial distances between r and $r + \delta r$, where δr is taken as 0.5 m, the linear dimension of a single cell in this study; the subscript k is not used here because all replicate grids have the same size and shape. $|S_r|$ is the number of cell pairs within S_r. If $i = j$, equation 1 defines an auto-covariance for variable i; if $i \neq j$, equation 1 defines a cross-covariance between variables i and j.

The spatial averaging in equation 1 assumes *stationarity* and *isotropy* of the spatial pattern (see Burrough 1995). There was little visual indication of non-stationarity in our data, and a correction for gradients, based on the non-ergodic measure of Rossi *et al*. (1992), gave results similar to uncorrected ones (Llambi 2002); below we therefore use the simplest measure of spatial structure without correction for gradients.

A dimensionless measure of spatial structure can be obtained by dividing the covariance function by its expected value $E[C_{ijk}(r)]$ under complete spatial randomness. The expected value is approximately the product of the spatial average values of i and j in grid k (see Purves & Law 2002). To obtain an average of this over all replicate grids, we used the statistic

$$\bar{C}_{ij}(r) = \sum_k C_{ijk}(r) \Big/ \sum_k E[C_{ijk}(r)] \qquad \text{eqn 2}$$

which is unbiased by differences in density between grids (Purves & Law 2002). A value of this statistic close to unity implies that values of i and j are distributed close to their spatial average values at distance r; a value greater than one implies that i and j both tend to take large values at distance r (i.e. that there is spatial aggregation); a value less than one implies that large values of i are associated with small values of j at distance r (i.e. that there is spatial segregation).

In addition, to test for *anisotropy* (i.e. directionality), we calculated the *angular* auto-covariance function, $C_{iik}(\phi)$, for *E. schultzii* seedlings and adults (based on Purves & Law 2002; see Llambi 2002 for details), where ϕ represents the angular component of the displacement vector ξ. Angular displacements were grouped in eight categories, each of 45°. For the angular covariance functions, we did not take an average over replicate grids, as there was no *a priori* reason to expect consistency of spatial structure in different directions in different grids; this is in contrast with the radial covariance functions, where spatial structure would be expected to be strongest at short distances.

STATISTICAL TESTS FOR DEPARTURES FROM RANDOMNESS

To test the statistic $\bar{C}_{ij}(r)$ for significance of departure from randomness (i.e. from the value 1), we followed a Monte-Carlo procedure, independently randomising the values of each grid 1000 times, on each occasion computing $\bar{C}_{ij}(r)$, to obtain 99% confidence intervals of $\bar{C}_{ij}(r)$ under the assumption of randomness. The null model for a single spatial pattern ($i = j$) was that cell values were located independently at random within each grid. The null model for a joint spatial pattern of two variables ($i \neq j$) was taken to be independence of the spatial patterns of i and j. In this case the whole spatial pattern of j was displaced by a random amount relative to i, using a so-called 'toroidal shift' to keep spatial structure intact within i and j as far as possible (Upton & Fingleton 1985; Purves & Law 2002); see Roxburgh & Matsuki (1999) for alternative null models. (In the angular auto-covariance case the confidence intervals were calculated separately for each grid after randomization of cell values in each grid.)

Results

As expected, there was a major change in the size structure of *E. schultzii* populations during succession, from a high density of seedlings and a complete absence of adults in year 3, to a more even size distribution in year 8 and mature páramo plots (Table 1). Seedling density was an order of magnitude lower in the mature páramo than in the year 3 plots.

SUCCESSIONAL CHANGES IN SPATIAL STRUCTURE OF *E. SCHULTZII*

Figure 1 shows spatial maps of seedlings and adults for representative plots of each stage of succession. The tendency for seedling density to decrease during succession is clear from Fig. 1a–c. In addition, while seedlings were present in relatively distinct patches, aggregation is visually less obvious in the case of the adults (Fig. 1d–e). The analysis of the average auto-covariance functions supports this conclusion.

Averaging over the replicates within seral stages, the covariance functions for the seedlings showed statistically significant aggregation at short radial distances (0.5 m), irrespective of seral stage (Fig. 2a–c). Although

Table 1 Average density (m^{-2}) of seedlings (< 5 cm diameter), adults (> 25 cm diameter) and total density of *E. schultzii* (including intermediate-sized plants of diameter > 5 cm and < 25 cm) at different stages of succession. Numbers in brackets are standard errors. Differences between successional stages in average density within size classes and in total density were compared using a non-parametric Kruskal–Wallis (K–W) test. Values with different letters denote significant differences (Dunnet's C multiple comparisons test)

Seral stage	Seedlings (m^{-2})	Adults (m^{-2})	Total (m^{-2})
Year 3	9.5 (1.2)^{a}	0	10.1 (1.1)^{a}
Year 8	4.5 (1.5)^{b}	0.5 (0.1)	6.9 (2.1)^{a}
Páramo	0.9 (0.4)^{c}	0.5 (0.1)	1.9 (0.4)^{b}
K–W	$P = 0.004$	$P = 0.530$	$P = 0.007$

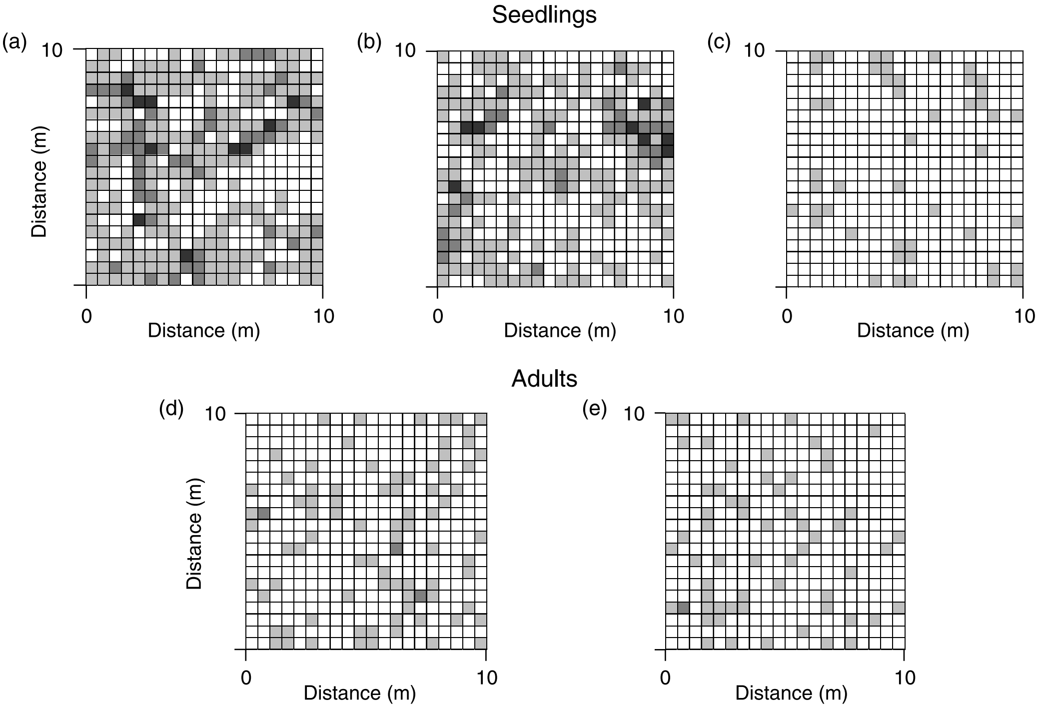

Fig. 1 Representative examples of the spatial maps of *E. schultzii*. Seedlings: (a) year 3, (b) year 8, (c) mature páramo. Seedlings per cell: 0 (white), 1–5 (light grey), 6–10 (dark grey), > 10 (black). Adults: (d) year 8, (e) mature páramo. Adults per cell: 0 (white), 1 (light grey), 2–3 (dark grey). Cells in each grid are 0.5 × 0.5 m.

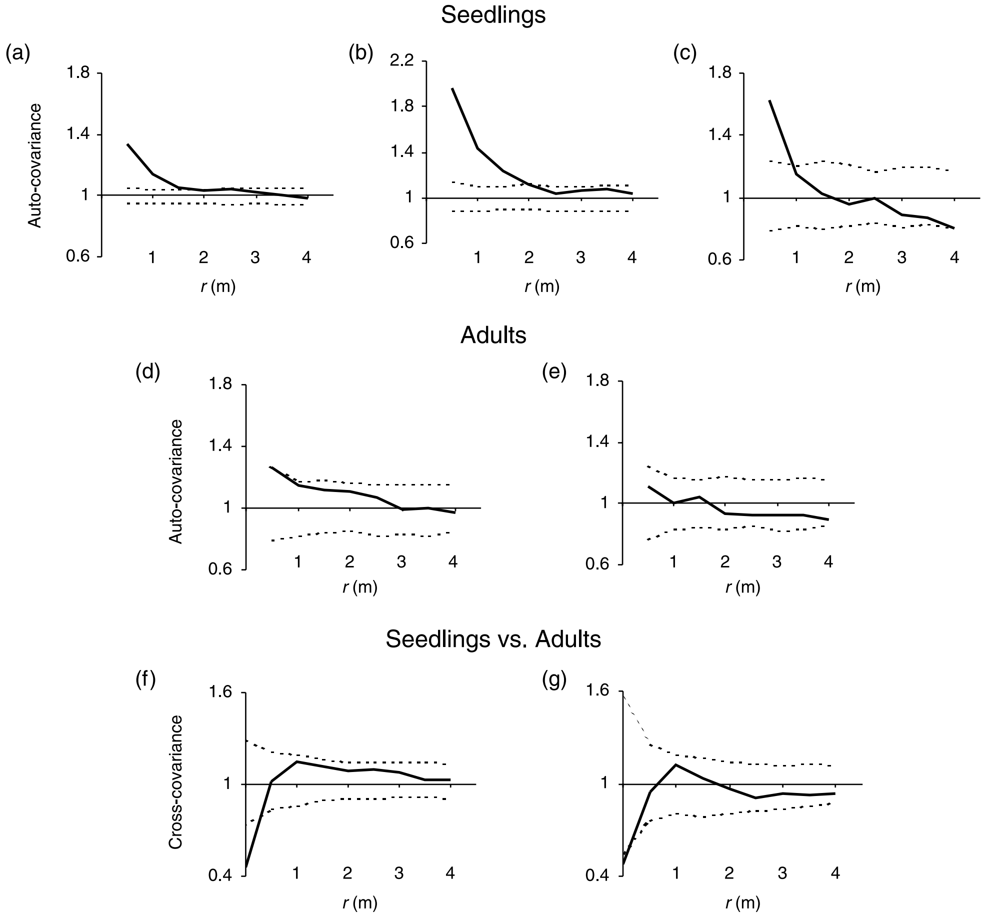

Fig. 2 Average covariance functions (continuous line) for *E. schultzii* as a function of radial distance r, with 99% confidence limits (dashed lines). Seedlings: (a) year 3, (b) year 8, (c) mature páramo. Adults: (d) year 8, (e) mature páramo. Cross-covariance between seedlings and adults: (f) year 8, (g) mature páramo.

the maximum average seedling density was observed in year 3 plots, the height of the peak of the covariance function indicates a higher intensity of aggregation in year 8 and mature páramo (Fig. 2a–c), with the density at a distance of 0.5 m being nearly twice the spatial average over the whole grid. The scale of aggregation (the range of distances over which the covariance function stays above the upper 99% confidence limit) was greatest in year 8, extending up to 2 m.

In contrast, no departure from randomness could be detected for adults in either year 8 or mature páramo plots (Fig. 2d,e). Although the smaller number of adults necessarily means that the confidence intervals were wider, the adult covariance functions were quite different in shape from those of the seedlings. In the case of mature páramo, this suggests a strong decline in aggregation during the period of growth from the seedling to adult stage (the same does not seem to apply for year 8 plots, as adults were likely to be the survivors of seedlings in year 3 plots and the covariance functions in Fig. 2a,d are similar in shape). Some reduction in aggregation during development would be expected because the number of seedlings in some cells was much greater than the maximum number of large adults (approximately three individuals per cell) that could be packed into the same space. However, even after transforming seedling numbers into presence and absence within cells, seedling aggregation was still significant at all seral stages (results not shown).

There was also a clear indication of segregation of seedlings from adults (Fig. 2f,g). Average cross-covariance values at distance zero (within the same cell) of seedlings with adults were significantly less than 1 in both year 8 and mature páramo plots (this segregation was also significant if seedling densities were transformed into presence-absence data). The degree of segregation was very similar in both cases, the density of seedlings close to adults being about half of the spatial average density. In no case did segregation extend as far as 0.5 m; in fact, there were signs of slight aggregation at intermediate distances, although this was not statistically significant.

DIRECTIONALITY OF *E. SCHULTZII* SPATIAL PATTERNS

There was some evidence of directionality, especially for *E. schultzii* seedlings, for which eight of the 15 plots showed significant anisotropy (i.e. angular auto-covariance functions $C_{iiq}(\phi)$, outside the 99% confidence limit in some directions). An example of a year 3 plot with significant directionality for *E. schultzii* seedlings is shown in Fig. 3(a) (with a maximum $C_{ii}(\phi)$ on the 135°–315° axis). In contrast, for the adults, seven of the 10 year 8 and páramo plots showed no significant directionality (e.g. Fig. 3b). Interestingly, in all significant cases, both for seedlings and adults, there were more individuals than expected by chance in the directions diagonal to the main slope within each plot (i.e. on the 45°–225° or 135°–315° axis).

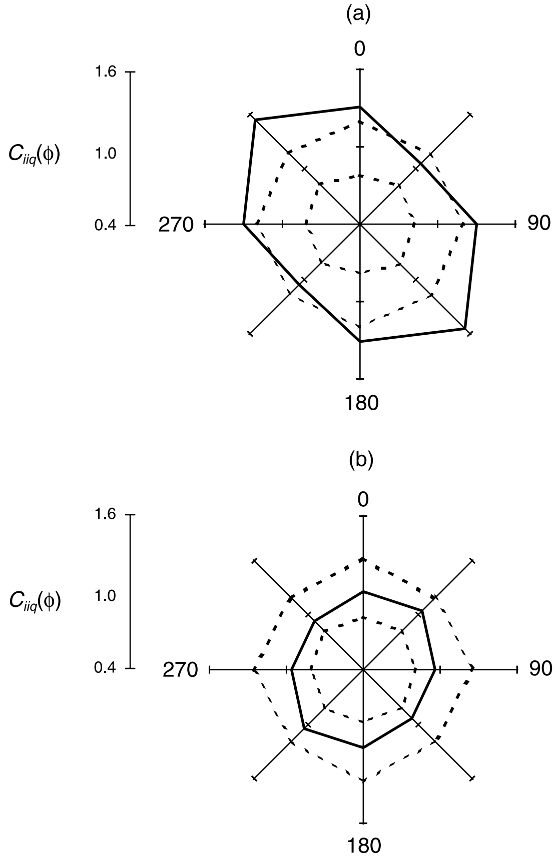

Fig. 3 Two examples of angular auto-covariance functions for *E. schultzii*: (a) seedlings in a year 3 plot showing significant anisotropy, (b) adults in a year 8 plot, with no evidence of directionality. Angular auto-covariance, $C_{ii}(\phi)$ (continuous line) given as a function of angular displacement ϕ, with 99% confidence limits (dashed lines). The 0–180° axis is aligned parallel to the main direction of the slope within the plot. The bar next to each figure is the scale for the $C_{ii}(\phi)$ values.

SPATIAL SEGREGATION OF *E. SCHULTZII* FROM OTHER DOMINANT SPECIES

In year 3, seedlings of *E. schultzii* were slightly segregated at distance zero from *R. acetosella* (the dominant species of early succession), the cross-covariance function at distance zero being just below the lower confidence limit (Fig. 4a). These seedlings were also weakly positively associated with small individuals of *H. laricifolium* in year 3 plots at intermediate radial distances (1–3 m, Fig. 4c).

Adults of *E. schultzii* showed stronger evidence of spatial segregation from other species than did seedlings. They were spatially segregated from *R. acetosella* up to 0.5 m in year 8 plots (Fig. 4b) and the intensity of segregation was larger than that found for seedlings in year 3 plots (see Table 2). Insufficient *R. acetosella* individuals remained in the mature páramo to allow spatial analysis. The average cross-covariance functions at distance zero of adult *E. schultzii* with small and large *H. laricifolium* was again significantly below one in the mature páramo, segregation intensity being stronger with small *H. laricifolium* individuals (Fig. 4d–e, Table 2).

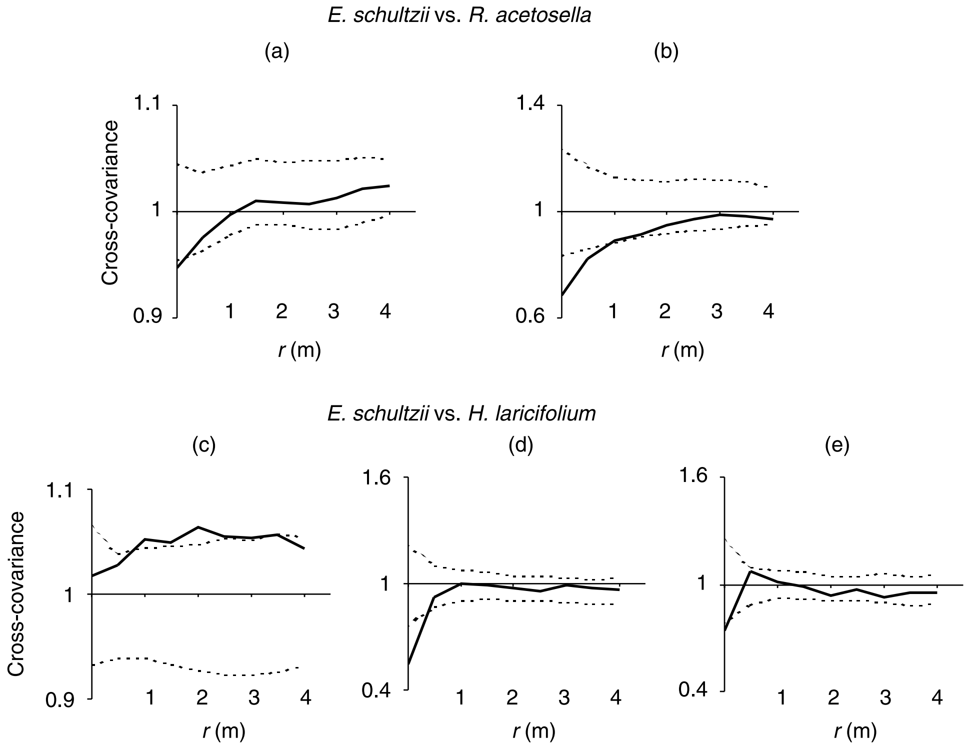

Fig. 4 Average cross-covariance functions (continuous line) for the spatial association between *E. schultzii* and two other dominant species as a function of radial distance *r*, with 99% confidence limits (dashed lines). *E. schultzii* and *R. acetosella*: (a) seedlings in year 3, (b) adults in year 8. *E. schultzii* and *H. laricifolium*: (c) seedlings of *E. schultzii* and small *H. laricifolium* (year 3), (d) *E. schultzii* adults and small *H. laricifolium* (mature páramo), (e) *E. schultzii* adults and large *H. laricifolium* (mature páramo).

Table 2 Spatial associations of *E. schultzii* (seedlings and adults) with *R. acetosella* (*Ra*) and small (s) or large (l) *H. laricifolium* (*Hl*). Values are given for the average radial cross-covariance at distance zero (within cells). Values outside the 99% confidence intervals are indicated (*)

	Seedlings			Adults		
Seral stage	*Ra*	*Hl* (s)	*Hl* (l)	*Ra*	*Hl* (s)	*Hl* (l)
Year 3	0.95*	1.01	–	–	–	–
Year 8	0.98	1.02	0.91	0.68*	0.75	0.91
Páramo	–	0.77	0.77	–	0.54*	0.74*

Table 3 Spatial associations between *E. schultzii* and two microtopographic variables: slopes and stones. For each class of individuals (seedling and adults), values are given for the average radial cross-covariance at distance zero (within cells). Values outside the 99% confidence intervals are indicated (*)

	Seedlings		Adults	
Seral stage	Slopes	Stones	Slopes	Stones
Year 3	0.87*	0.84*		
Year 8	0.84	0.88	1.41*	0.86
Páramo	1.09	1.26	1.42*	0.78*

No other significant spatial interactions between *E. schultzii* and the other species were detected (see Summary in Table 2).

SPATIAL ASSOCIATIONS BETWEEN *E. SCHULTZII* AND MICROTOPOGRAPHIC FEATURES

Seedlings of *E. schultzii* only showed significant spatial relationships with microtopography in early successional plots (Fig. 5a,b, Table 3). Seedlings had average cross-covariance values below 1 with local slopes, indicating an association with slopes of low angle. In addition, they were spatially segregated from stones, although the cross-covariance was only slightly beyond the 99% confidence limit. In neither case did segregation extend beyond the within-cell scale.

Adults, on the other hand, showed a strong tendency to be associated at the within-cell scale with steep slopes both in the year 8 and mature páramo (Table 3, Fig. 5c,d). There was also some tendency for *E. schultzii* adults to be segregated from stones, although this interaction was only significant (with the cross-covariance function just extending beyond the confidence limit) in the mature páramo (Table 3, Fig. 5e).

Discussion

This study points to a gradual increase in spatial structure of plant communities during succession, modulated by the local environments in which individual plants find themselves (see also Seabloom *et al.*, personal communication). The local environment affects the

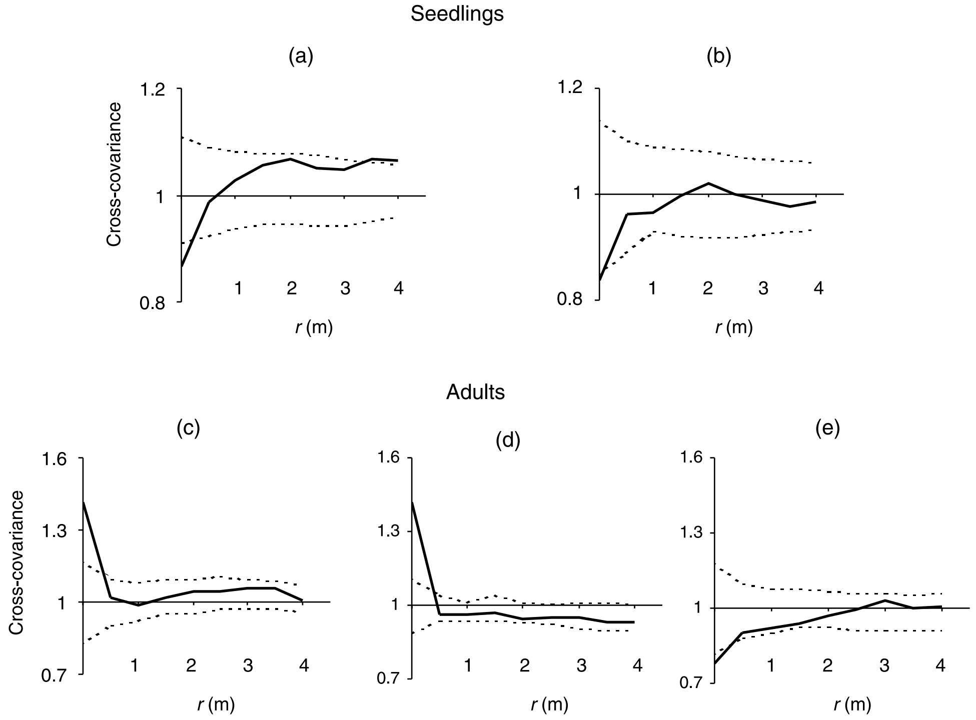

Fig. 5 Average cross-covariance functions (continuous line) for the spatial association between *E. schultzii* and two topographic variables as a function of radial distance *r*, with 99% confidence limits (dashed lines). Seedlings: (a) slope (year 3), (b) stones (year 3). Adults: (c) slope (year 8), (d) slope (mature páramo), (e) stones (mature páramo).

rates of reproduction and mortality of plants, and it does so both through its physical and its biotic properties. Plants are sorted according to their capacity to live under local physical conditions, so that they become increasingly associated with particular environmental states. Adult *E. schultzii* thus become associated with steeper slopes and less stony soils. Such progressive sorting into niches is well documented (e.g. Werner & Platt 1976).

The local biotic environment has more intricate effects, because, as well as affecting reproduction and mortality, it is changed as a result of these two processes. The local biotic environment thus needs to be envisaged as a state variable of successional dynamics. In fact, the biotic spatial covariance functions measure the local biotic environment and can be used as the state variables of community dynamics (e.g. Law & Dieckmann 2000). Hence, we consider below the coupling of these covariance functions to two of the main biological determinants of spatial structure (seed dispersal and neighbourhood-dependent mortality), and discuss the possible effects of this coupling for succession.

Seed dispersal generates spatial aggregation within species because seeds are typically dispersed only short distances from their parents; in the case of *E. schultzii*, 90% of fruits are estimated to fall within 2 m of the parent plant (Smith 1984). As *E. schultzii* was starting to flower in year 8 plots, the simplest explanation for the change from weak to strong aggregation of its seedlings during succession is local seed dispersal. The limited aggregation of seedlings prior to reproduction in year 3 plots is less easy to account for. The normal length of cultivation coincides with the reported maximum dormancy time for *E. schultzii* (Smith 1981), so most seeds during early seral stages probably come from outside the plot and are unlikely to show local aggregations. Some parts of the environment may, however, provide better microsites for germination and early establishment than others (see also Seabloom *et al.*, personal communication), as suggested by the tendency for seedlings to be weakly segregated from high slopes and stones. In addition, the common occurrence of anisotropy diagonal to the main slope suggests that directional factors such as drainage patterns or cattle tracks could influence the distribution of *E. schultzii* seedlings.

Mortality due to competition with conspecific neighbours moves spatial structure away from aggregation. Such a decline in aggregation has been documented within cohorts of trees as they grow and undergo self-thinning in successional forests (e.g. Christensen 1977; Sterner *et al.* 1986; Rejmánek & Leps 1996; Gavin & Peart 1997). The reduction in aggregation from seedling to adult *E. schultzii* in native páramo is also consistent with local competition causing greater mortality of close neighbours. The lack of a clear change in aggregation between seedlings in year 3 and the adults in year 8 is also consistent, because this early cohort started life with relatively weak aggregation.

It has been understood since the work of Janzen (1970) and Connell (1971) that local dispersal and neighbourhood-dependent mortality may, in conjunction, have important effects on spatial structure.

There is evidence of this in the cross-covariance of seedlings and adult individuals of *E. schultzii.* The short distances over which seeds are dispersed from adults (Smith 1984) should lead seedlings to be aggregated with adults and there was a weak, albeit not significant, association at intermediate distances (Fig. 2f,g). However, the most striking feature is the segregation at the shortest distances: seedlings tended not to occur close to adults, suggesting deleterious effects on their offspring. This is consistent with Smith's (1984) finding that removal of adults in xeric páramo areas led to greater survival of seedlings. An obvious mechanism leading to mortality after dispersal and early in growth would be asymmetric competition (Weiner 1990), but the presence of host-specific enemies (Janzen 1970; Connell 1971) and autotoxicity (e.g. McNaughton 1968) are also possible.

Mortality due to competition with neighbours of other species is likely to have the strongest effect on succession. Such mortality leads to species becoming segregated in space, and this may reduce the capacity of one species to replace another during succession. *E. schultzii*, for instance, although late successional, was present at the earliest stages of succession when the community was dominated by *R. acetosella*, and weakly segregated from it at short distances. This could mean that tolerance (*sensu* Connell & Slatyer 1977) of *E. schultzii* to the strong dominance of this ruderal species was at least partially achieved through spatial segregation, but the cause, competition or differences in the preferred physical environment of the species, remains to be determined.

A clearer case of segregation between species driven by competition comes from the much increased segregation of *R. acetosella* once the first cohort of *E. schultzii* was reaching adulthood in year 8 plots. It seems likely that asymmetric competition was involved here because *R. acetosella* was strongly segregated only from large individuals of *E. schultzii* in these plots (see Rejmánek & Leps 1996 for a similar example of size-mediated interaction between early and late successional species). Such spatial segregation could contribute to the long-term persistence of early successional species, and may explain why succession in the páramo and other extreme environments is characterized more by changes in relative abundance than by complete species replacement (MacMahon 1981; Svoboda & Henry 1987; Sarmiento *et al*. 2003). Spatial segregation may also contribute to the codominance of late successional species such as *E. schultzii* and *H. laricifolium* (Murrell & Law 2003).

The spatial structures that develop during succession therefore appear to have a strong potential effect on succession. Accurate predictions may need to make use of information on the changing local spatial relations between plants (e.g. individual-based models of forest succession, Botkin 1992; Pacala *et al*. 1996). However, studies of the kind described here are 'snapshots' of spatial structure, that need ultimately to be complemented by demographic and experimental analysis of neighbourhood-dependent birth and death rates to confirm generalizations about the role of space in succession.

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