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ORIGINAL ARTICLE

Spatial patterns of tree recruitment in a relict population of *Pinus uncinata*: forest expansion through stratified diffusion

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ABSTRACT

Aim To infer future changes in the distribution of isolated relict tree populations at the limit of a species' geographical range, a deep understanding of the regeneration niche and the spatial pattern of tree recruitment is needed.

Location A relict *Pinus uncinata* population located at the south-western limit of distribution of the species in the Iberian System of north-eastern Spain.

Methods *Pinus uncinata* individuals were mapped within a 50 × 40-m plot, and their size, age and reproductive status were estimated. Data on seed dispersal were obtained from a seed-release experiment. The regeneration niche of the species was assessed based on the associations of seedling density with substrate and understorey cover. The spatial pattern of seedlings was described using point-pattern (Ripley's *K*) and surface-pattern (correlograms, Moran's *I*) analyses. Statistical and inverse modelling were used to characterize seedling clustering.

Results Pine seedlings appeared aggregated in 6-m patches. Inverse modelling estimated a longer mean dispersal distance (27 m), which corresponded to the size of a large cluster along the north to north-eastward direction paralleled by an eastward trend of increasing seedling age. The two spatial scales of recruitment were related to two dispersal processes. The small-scale clustering of seedlings was due to local seed dispersal in open areas near the edge of *Calluna vulgaris* mats: the regeneration niche. The long-range expansion might be caused by less frequent medium-distance dispersal events due to the dominant north-westerly winds.

Main conclusions To understand future range shifts of marginal tree populations, data on seed dispersal, regeneration niche and spatial pattern of recruitment at local scales should be obtained. The monitoring of understorey communities should be a priority in order to predict correctly shifts in tree species range in response to global warming.

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Keywords

***Calluna vulgaris*, correlogram, Iberian System, regeneration niche, Ripley's *K*, seed dispersal, spatial pattern.**

INTRODUCTION

The dynamics of tree populations depend on spatial patterns of seed production and recruitment. These patterns result from the succession of different processes, including seed arrival, seedling emergence, establishment and growth (Schupp & Fuentes, 1995). While spatial patterns of seed arrival are determined by the mechanisms of seed dispersal (Nathan & Muller-Landau, 2000), those related to recruitment depend on the interaction of multiple abiotic and biotic factors (Clark *et al.*, 1998, 1999). For instance, spatial patterns of seed rain may depend on the location of parents, but seedling distribution will be affected more by the presence of suitable microsites that control germination and seedling survival.

The seminal work of Grubb (1977) emphasized the relevance of the regeneration niche for understanding how

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plant communities are structured and evolve through time. The regeneration niche summarizes the requirements for the successful recruitment of individuals in the population. This involves many environmental features (climate, radiation, understorey and overstorey cover, soil, etc.) and biotic processes including seed production, dispersal, germination and establishment. Despite the importance of the regeneration niche, few studies have regarded this concept in relation to the invasibility of the understorey, which is critical for understanding how tree populations will shift in response to climate warming. This is the case for tree populations from European mountains, where a significant temperature rise has been recorded since the 1940s (Diaz & Bradley, 1997). In the case of these isolated and marginal tree populations from high-elevation areas, their dynamics will depend, among other factors, on the availability of suitable safe sites for regeneration in the understorey community.

The study of the spatial pattern and recruitment dynamics of tree species located at their distribution limits have provided insights on the processes influencing the expansion or retraction of these populations (Payette & Filion, 1985; Brubaker, 1986; Kullman, 1990; Chhin & Wang, 2002). To help infer the processes that generated a species' spatial pattern, a description of the size structure, age distribution and spatial pattern of tree populations can be used (Brodie *et al.*, 1995). Spatial analyses of tree features may summarize the dynamics of tree populations (Duncan & Stewart, 1991).

Species at the limit of their geographical range may be responding to climate change more drastically than those at the core of the range (Gaston, 2003). Climate is one of the main factors governing the geographical distribution of marginal tree populations (Woodward, 1987; Daniels & Veblen, 2004). In addition to climate, local human disturbances (e.g. grazing) greatly affect the dynamics of marginal tree populations in European mountains (Camarero & Gutiérrez, 1999a). Historical data and spatial analysis of relict populations could be informative about their potential response to future scenarios, and provide insights about their spatial dynamics under current climatic change. The study of relict populations is also justified by the need to manage populations across a species' range for conservation purposes, as species now face unprecedented changes that affect habitat availability. Given that geographical ranges are dynamic, determining the 'correct' spatial resolution for study is important as historic geographical ranges presumably reflect past processes (e.g. dispersal, persistence). To make inferences about future changes in the distribution of marginal tree populations in response to current global change, a deep knowledge of the regeneration niche and the recruitment spatial pattern of these populations at local scales is required. The description of the regeneration niche is complicated by the spatial heterogeneity of the understorey, which is essential for seedling establishment and growth (Kuuluvainen *et al.*, 1993).

In this paper, our aim is to study the regeneration niche and the spatial patterns of recruitment in a relict *Pinus uncinata* Ram. population, located at its southernmost distribution limit in north-eastern Spain. Our specific objectives are to: (1) describe the stand spatial structure of an expanding relict population, (2) characterize and model the spatial pattern of recruitment, and (3) define how the spatial patterns of substrate, understorey and overstorey determine the regeneration niche. The achievement of these objectives will provide a solid basis from which to make inferences about future changes in the distribution of marginal tree populations in response to current global change.

METHODS

Tree species

Relict populations of several tree species (e.g. *P. uncinata*, *Pinus sylvestris* L.) are located in Iberian ranges such as the Iberian System (Ceballos & Ruiz de la Torre, 1979). Current global change might negatively affect the regeneration ability of these remnant stands. Global mean surface temperatures have increased 0.3–0.6 °C during the past 40 years (Houghton *et al.*, 1996). Instrumental records from mountain areas of Western Europe showed an intense warming since the 1940s, the latter decades being the warmest of the instrumental period (Diaz & Bradley, 1997). These climatic trends were also recorded in mountain ranges of north-eastern Spain such as the Iberian System (Camarero & Gutiérrez, 1999b).

Pinus species have been present in north-eastern Spain since at least the beginning of the Holocene (Peñalba, 1994). Palynological studies in the Northwest Iberian System have shown an increase in pine cover during the twentieth century due to a decrease in grazing pressure and to climate warming (Gil García *et al.*, 1996). However, the relevance of these factors in the recent expansion of pines in this area has not been yet quantified.

Pinus uncinata Ram. is a shade-intolerant species that colonizes all kind of soils (Cantegrel, 1983). Its reproduction is mainly sexual and its small, winged seeds are primarily dispersed by wind. Seedlings are quite frost-resistant, even under a shallow snow layer (Frey, 1983). Two features make *P. uncinata* a potentially good invader (Richardson & Bond, 1991): a short pre-reproductive period (15–20 years); and frequent large crop sizes. The distribution area of *P. uncinata* is restricted to the south-east European mountains (south-eastern to eastern Alps, Pyrenees). In the Iberian Peninsula, its main distribution area comprises subalpine forests in the Central and Eastern Pyrenees. In addition, two isolated populations are situated in the Iberian System. One of these two populations, located in the Castillo de Vinuesa (*c.* 115 ha), forms the western limit of distribution of the species, where the study plot was placed (Fig. 1). The first report on this relict stand (Ceballos, 1968) noted a natural expansion of the population toward the north-eastern area, starting in the 1930s (Fernández Aldana *et al.*, 1989). Examination of aerial photographs of the study area (scale 1 : 5000; 1946, 1957, 1984, 1989, 1990) showed a trend of increasing tree density and

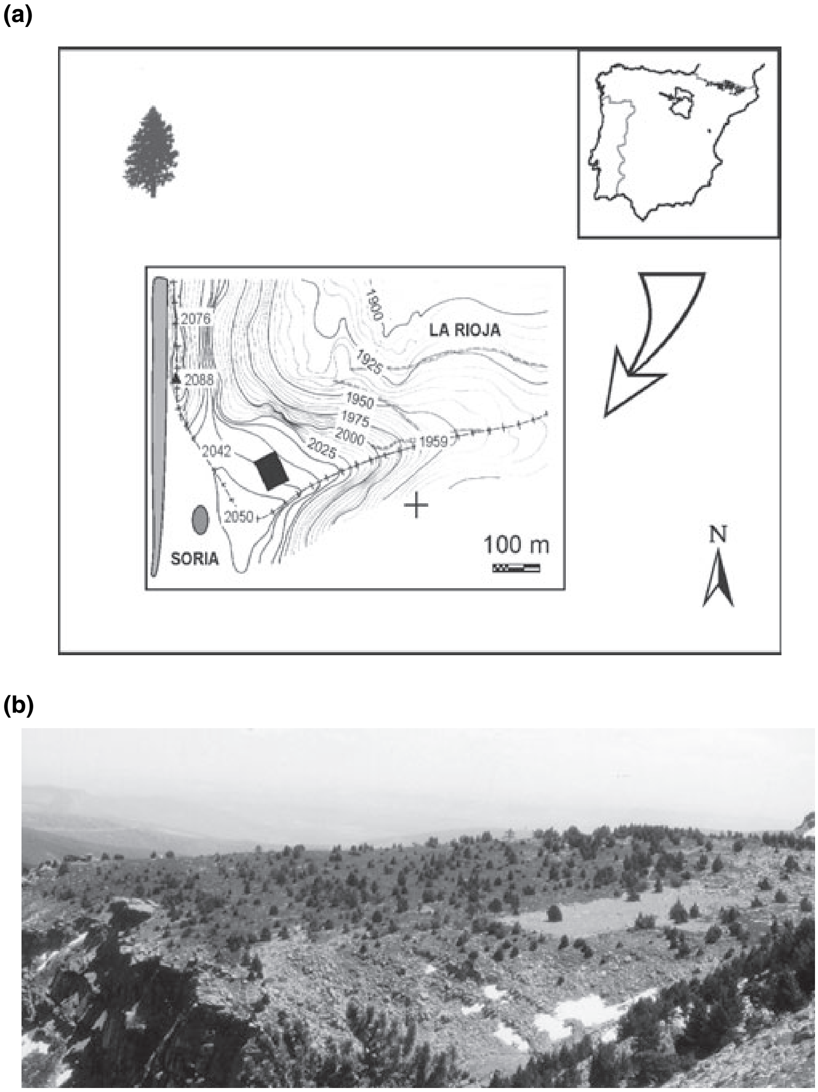

Figure 1 Geographical location and view of the study site. (a) Upper map, distribution of *Pinus uncinata* in the Iberian Peninsula (black areas) and the isolated study population (arrow); lower map, study site (black rectangle) and a nearby forest (grey shading). The elevation (in m a.s.l.) of the Castillo de Vinuesa peak is shown (black triangle). Cross shows area co-ordinates 42°01′ N, 02°44′ W. Line (−+−) separates Soria (west) and La Rioja (east). (b) View of the study site.

cover. According to dendroecological studies, the age of the oldest individuals is *c.* 700 years in the Pyrenees and *c.* 500 years in the study area (Gutiérrez *et al.*, 1998).

Study area

The stand studied is located in a relatively flat area (mean slope *c.* 5°) on moraine sediments (Fig. 1). The main bedrocks are limestones and quartzite conglomerates. The soils are acid and shallow (IGM, 1982). The climate is continental. In the Northwest Iberian System, the monthly thermal oscillation is greater in south to south-eastward slopes (occupied by pine forests) than in north to north-westward slopes (dominated by deciduous species) because of the greater oceanic influence on the latter (Ortega Villazán, 1992). Estimated annual precipitation is *c.* 1400 mm with July–August minima (Vinuesa station, 41°55′ N, 02°46′ W, 1107 m; 1961–86 data). Mean annual temperature is 2.0 °C. Maximum and minimum mean monthly temperatures correspond to July–August (12 °C) and December–January (0 °C), respectively. There are at least 8 months (October–May) with mean monthly temperatures < 10 °C. Dominant winds are from the west, north and north-west (Archilla Aldeanueva & Múñoz Múñoz, 1987). Most forests of the area are formed by *P. sylvestris* with an understorey composed mainly of *Erica* species and *Calluna vulgaris* (L.) Hull (Segura Zubizarreta *et al.*, 1998). In some cases the abundance of *C. vulgaris* can indicate the conversion of pine woodlands to heathlands.

Field sampling

We measured the location (two co-ordinates) and structural variables: basal diameter (d.b.); diameter at 1.3 m (=diameter at breast height, d.b.h.); height (*h*); four crown radii along the directions of axes; maximum number of needle-age classes (estimated by counting needle-age classes in four mid-canopy branches); and estimated age for each living individual located within a rectangular plot. Age was estimated by counting the number of internodes in stems for individuals lower than 2 m, and taking and cross-dating basal cores for the rest of the individuals. The plot axes followed approximately the south-eastern (50 m) and north-eastern (40 m) directions. Dead individuals were mapped and described according to their decomposition stage (e.g. with or without bark). There were no stumps, snags or recently fallen trees within the plot. Any browsing signal was observed and recorded because young pines can be grazed during winter by wild ungulates (García González & Cuartas, 1996). There was a pasture area at *c.* 100 m from the south-east axis of the plot. *Pinus uncinata* living individuals were classified according to size and growth form: d.b.h. > 17.5 cm, adults; $7.5 <$ d.b.h. < 17.5 cm, poles; d.b.h. < 7.5 cm and $h > 0.5$ m, saplings; $h < 0.5$ m, seedlings; dead trees; krummholz (shrubby individuals). We also noted whether each living individual was bearing or had produced cones.

To estimate the presence and cover of substrate types and understorey species, we used a systematic point-sampling method with transects perpendicular to the shortest axis and with a 2.5-m resolution along the longest axis (Barbour *et al.*, 1987). Every 2.5 m, we dropped a thin metal rod and recorded contacts for three vertical strata: substrate (height < 5 cm); understorey (height $= 5$–25 cm); and overstorey (only *P. uncinata*, considering the vertical projection of the pin for height > 25 cm). This gave a total of 357 sampling points and 1071 possible contacts. Substrate was classified into four types: organic matter, basal parts of herbs, rock and soil. We observed three dominant understorey species: *C. vulgaris*, *Juniperus communis* L. and *Vaccinium myrtillus* L. We carefully described the microenvironment (substrate and type of plant cover) around each *P. uncinata* seedling. Chi-square goodness-of-fit tests were used to test for significant differences between observed and expected distributions of seedlings associated with a given substrate or cover (understorey and overstorey) type. The Yates correction was applied because some expected frequencies were lower than 5% (Sokal & Rohlf, 1995).

To compare tree, cover and substrate data and to analyse the surface pattern of tree variables, we converted raw data into gridded data using 80 quadrats of 5×5 m. Tree variables were averaged for every quadrat, considering seedlings and bigger living trees separately. Density was computed as the number of individuals per 25 m^2 quadrat. Cover data were obtained considering four points per quadrat.

Soil observations (four equidistant samples) were made up to a depth of 15 cm along a diagonal transect crossing the plot from point (0, 0) to point (50, 40). No charcoal evidence was found. Mean thicknesses (±SD) of the organic horizons were 0.5 ± 0.0 cm (O) and 5.6 ± 4.2 cm (A). In December 1998, we measured the maximum snow depth at the northern corner of each 5×5-m quadrat to estimate snow thickness in winter within the plot. We acknowledge the fact that more sampling periods are needed to fully account for the year-to-year variability in snow depth, but these measures provide an estimate of the spatial variability of snow depth in the stand.

Spatial analyses

To describe the spatial distribution patterns of *P. uncinata* tree classes, we used Ripley's $K(t)$ function which is based on the variance (second-order analysis) of all tree-to-tree distances in a two-dimensional space (Ripley, 1977). The function $\lambda K(t)$, where λ is the intensity (mean number of trees per unit area), is the expected number of trees within a distance t of a randomly chosen tree. In a random distribution, $K(t) = \pi t^2$. The function $K(t)$ uses all tree-to-tree distances to calculate a measure of spatial pattern at any distance t up to half the length of the shortest side of the plot. To check for significance, we used Monte Carlo methods which simulate randomly generated plots of the same dimensions as the empirical plot. To obtain 95% confidence intervals, we computed 10,000 simulations (Besag & Diggle, 1977). The spatial pattern can then be described as significantly clumped or regular if the calculated $K(t)$ function is greater or lower than the 95% CIs, respectively. Mathematical details for the calculation of an unbiased estimator of $K(t)$, modifications of this function, and edge effects can be found elsewhere (Moeur, 1993; Haase, 1995).

To obtain information on the spatial relationships between tree classes, we examined bivariate spatial interactions using the $K_{12}(t)$ function, which is a generalization of $K(t)$ for a bivariate point process (Diggle, 1983). The results were represented graphically as $L(t) - (t)[L_{12}(t) - (t)$ in the bivariate case] against distance (t), where $L(t) = [K(t)/\pi]^{0.5}$ (Besag, 1977). The function $L(t)$ has a more stable variance than $K(t)$, and is easier to interpret as $L(t) = 0$ under complete spatial randomness (CSR). In the bivariate case, positive and negative values of $L_{12}(t)$ indicate positive (attraction) and negative association (repulsion), respectively, between the two tree classes analysed. To test the significance of departures from zero, we calculated the 95% CIs from 10,000 toroidal shifts of one class of trees with respect to the other. To represent the spatial heterogeneity of the $L(t)$ function within the study area, Getis & Franklin (1987) proposed to estimate a local $L_i(t)$ function around each point i, and to map the individual values of the function $L_i(t)$ at a given t (Pélissier & Goreaud, 2001). Point-pattern analyses were carried out using ADE-4 (Thioulouse *et al.*, 1997).

To quantify the spatial pattern of quantitative variables such as seedling height or age (objective 1), we calculated spatial correlograms based on Moran's I (Legendre & Fortin, 1989). To conserve mean and variance stationarity, we used gridded data (height, age) of *P. uncinata* seedlings that showed a reduced range of values compared with all trees (e.g. mean estimated age for the 5×5-m quadrats ranged 0–13 years). Moran's I spatial autocorrelation coefficient ranges from -1 to $+1$, with zero being the expected value for no spatial autocorrelation (Cliff & Ord, 1981). A graph showing how autocorrelation changes as a function of distance is an all-directional spatial correlogram. The distance at which the correlogram crosses the axis of null spatial autocorrelation ($I = 0$) corresponds to the mean size of influence for the studied variable (patch). We used equal distance classes (5 m).

Each individual autocorrelation coefficient of the correlogram was tested to check if it was significantly different from zero. In addition, the global correlogram was tested for global significance ($\alpha = 0.05$) using a Bonferroni correction (Legendre & Fortin, 1989). For globally significant correlograms, we interpreted the shape of the curve only for the distance classes with at least 20 pairs. All-directional correlograms were computed using programs developed by R.P. Duncan (He & Duncan, 2000).

Correlation corrected for spatial autocorrelation

To define the regeneration niche of *P. uncinata*, we calculated spatially corrected correlations between environmental and recruitment variables (objective 3). To determine the relationships between the spatial pattern of *P. uncinata* recruitment (density, age) and independent variables (substrate, understorey and pine cover), we used Pearson's correlation analysis. The related variables were previously gridded, as explained above. Because of the spatial autocorrelation present for several variables, a correction must be made when the significance of the correlation coefficient (r) is tested (Clifford *et al.*, 1989). This adjustment is based on the estimation of the effective sample size according to the amount of spatial autocorrelation (Dutilleul, 1993). For example, in the presence of positive spatial autocorrelation, the effective sample size (m) will be less than the actual sample size ($n = 80$ quadrats), being a function of the degree of spatial autocorrelation.

Modelling the spatial pattern of recruitment

Statistical modelling of point patterns

To infer the processes generating the spatial patterns of seedling recruitment (objective 2), we used a statistical modelling approach based on the seedlings' point pattern (Diggle, 1983). We applied such spatially explicit modelling to the univariate point patterns of *P. uncinata* seedlings. A clustering process, such as that usually observed in the recruitment of pine species, may be modelled using a Poisson cluster process; in this case, parent trees from a CSR process. Each parent produces a random number of offspring which are spatially distributed around each parent and form the final pattern. If we assume that the number of offspring follows a Poisson distribution and their locations have a bivariate Gaussian relative to parent trees, then the offspring can be simulated through a Neyman & Scott (1958) process given by:

$$K(t) = \pi \cdot t^2 + \frac{1 - e^{(-t^2/4\sigma^2)}}{\rho} \tag{1}$$

where ρ is the intensity of the parent CSR process (density of clumps); and $2\sigma^2$ the mean squared distance of an offspring from its parent (clump size). The unknown parameters (ρ,σ) must be fitted by comparing the empirical with the theoretical $K(t)$ functions (Diggle, 1983). Given that σ is the standard deviation of the distance between each offspring and its parents, the cluster size is *c.* 2σ. We estimated both parameters using the software PROGRAMITA (Wiegand & Moloney, 2004). After previous analyses, we restricted the interval of distances t for fitting the cluster model up to 12 m. As the $K(t)$ function is more sensible at larger scales, we simultaneously fit the $K(t)$ and the related $g(t)$ function to take into account of both smaller and larger scales. The final fit setting had the following intervals: $t = (1, 12)$; $\sigma = (1.47, 8.59)$; $100 \times \rho = (0.29, 2.17)$. Only fits with an error < 0.025 were accepted for the estimation of CIs of both parameters.

Inverse modelling of recruitment

In order to evaluate the assumed processes which generated recruitment patterns, we compared the spatial pattern of seedlings and seed-release data through inverse modelling (objective 2). We estimated the mean dispersal distance of seedlings based on the spatial distribution of adults and conspecific seedlings using RECRUITS, software to calibrate the spatial pattern of tree recruitment by comparing data of observed recruit distributions with data of adult distributions via a maximum-likelihood analysis (Ribbens *et al.*, 1994). RECRUITS finds those parameters that give the closest fit between the predicted and the observed number of recruits through inverse modelling. In addition, it fits 95% CIs to the parameter, and calculates the product–moment correlation between observed and expected values. We converted the original co-ordinates of 362 seedlings into counts using a 1 × 1-m grid ($n = 2000$ quadrats). The chosen quadrat size is smaller than the mean (±SE) canopy size of reproductive pines in the study plot (6.32 ± 0.62 m^2). However, this fine-grained scale allows a detailed description of the regeneration niche, which is determined not only by the position of parents, but also by the microenvironmental conditions of recruitment sites. We also used as input the location of 13 reproductive trees with an average d.b.h. of 20.4 cm. RECRUITS predicts the number of seedlings per unit area following a Poisson distribution, where the mean of the Poisson distribution is a function of parental size (d.b.h.) and distance from the parent, for all parents within a radius of 20 m. The number of recruits (R) in a 1-m^2 quadrat produced by a tree of size d.b.h. located M metres away can be described as:

$$R = \left[\mathrm{STR} \cdot \left(\frac{\mathrm{d.b.h.}}{\mathrm{d.b.h.}_s}\right)^{\beta}\right] \cdot \frac{1}{N} \cdot \left(e^{-D \cdot M^{\theta}}\right) \tag{2}$$

where D is the dispersion parameter; STR (standard total recruitment) is the number of recruits produced by a tree of standard size, d.b.h.$_s$; β is a parameter that converts biomass of trees (d.b.h.) into reproductive output; N is a normalizer that ensures the area under the distribution equals 1; and θ determines the shape of the distribution. RECRUITS estimates parameters STR, β, D and θ. STR is the reproductive success of a tree incorporating the production of seeds and their survivorship. STR was scaled to d.b.h.$_s$ = 30 cm, which is close to mean d.b.h. and facilitates comparison with other studies (Ribbens *et al.*, 1994). The first half of equation 2 represents the total number of offspring produced by a tree, while the second half describes the mean density of recruits located in a quadrat at a distance M from the parent tree. It must be emphasized that the estimated mean dispersal distance (MDD) from parent to offspring, which is correlated with D, is not adequate for estimating rare long-distance dispersal events.

Seed dispersal

To evaluate the importance of dispersal in generating the spatial patterns of recruitment (objective 2), we performed a seed-release experiment. We collected data on the dispersal of *P. uncinata* seeds following Greene & Johnson (1989). Seeds were extracted from cones collected in 2001 at a *P. uncinata* treeline population located in the East Pyrenees (Meranges, 42°23′ N, 02°08′ E, 2345 m). During a winter morning, seeds were released ($n = 96$) from a height of 4.5 m on an open field in the experimental station of CITA (Zaragoza, north-eastern Spain) under moderate wind conditions. This height was selected because it was close to 0.75 times the maximum observed tree height, which is closely related to the mean seed-dispersal distance (Greene & Johnson, 1996). The mean height (±SE) of reproductive individuals (poles, adults) was 4.3 ± 0.1 m. During the release experiment, wind blew from north to north-west, while mean air temperature and relative humidity ranged from 6 to 10 °C and 70% to 80%, respectively. Horizontal wind speed was measured at 4.5 m every 15 min during the release study, and ranged from 0.5 to 3 m s^{-1}. However, episodic wind turbulences (6–10 m s^{-1}) were also recorded. In order to obtain a frequency distribution of dispersal distances travelled by seeds, we noted the distance travelled by each seed released. Mean seed weight (±SE) was 12.47 ± 1.86 mg. Mean seed area was estimated by scanning all seeds and using an image-analysis system (NIH IMAGE VER. 1.63). Mean seed area (±SE) was 0.60 ± 0.01 cm^2.

RESULTS

Stand spatial structure

The stand consisted mainly of *P. uncinata* seedlings (Fig. 2), which constituted 83% of all living individuals ($n = 436$). The estimated seedling density was 2180 seedlings ha^{-1}. Seedling density, as calculated using 80 quadrats of 5 × 5 m, increased significantly along the north-eastern axis of the plot ($r_s = 0.49$, $n = 80$, $P \leq 0.05$). A larger seedling cluster was evident along the north-west to south-east direction in the middle of the plot, which was dominated by individuals recruited in the late 1980s. We also found within the plot: 34 saplings, 14 krummholz individuals, 13 adults, 13 poles, and three dead individuals. Adult individuals were abundant at the north-west and south-east sides of the plot. Only 10 saplings and seven seedlings showed grazing signals by ungulates. Browsing was mostly restricted to 0.5–1-m-tall pines (Fig. 3a), which were 16–25 years old. Most individuals (> 90%) older than 26 years or taller than 3 m did produce cones.

A bimodal d.b.h. distribution was observed (Fig. 3a). Similar results were obtained for the height distribution, with a maximum value for height < 1 m, and secondary peaks for 1–2 and 4–5 m. The distributions of d.b.h. and height suggested the existence of two cohorts, which were evident when relating basal diameter (d.b.) and estimated age (Fig. 3b). Power functions adequately described the relationships between variables (height = 1.31·d.b.h.$^{0.42}$, $n = 45$, $r^2 = 0.91$, $P < 0.001$; age = 11.81·d.b.$^{0.25}$, $n = 434$, $r^2 = 0.73$, $P < 0.001$). However, a more asymptotic relationship between

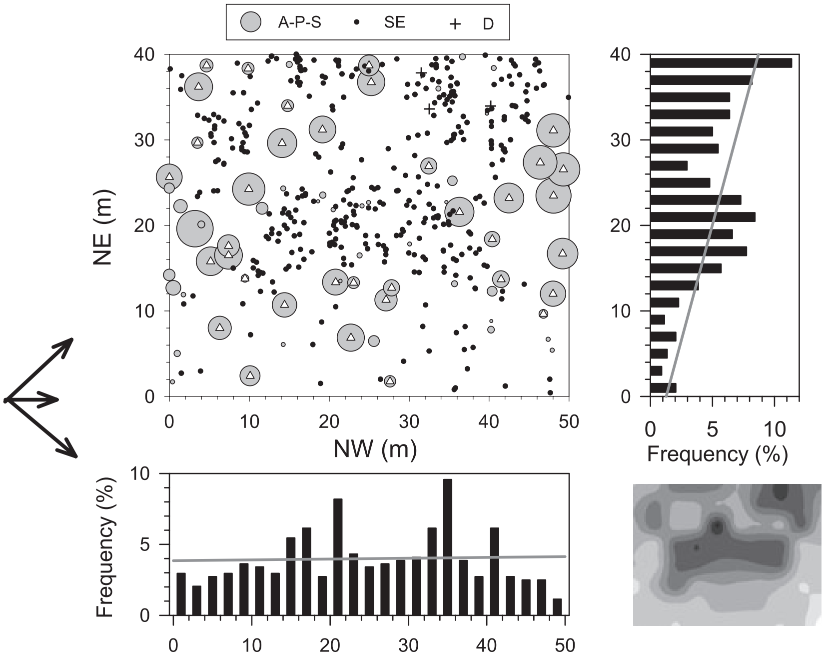

Figure 2 Spatial location and frequency of *Pinus uncinata* individuals across both plot axes. Grey circles and crosses represent living (A, adults; P, poles; S, saplings) and dead (D) individuals, respectively (circle size is proportional to tree height). Black circles are seedlings (SE). Reproductive individuals are circles with inner triangles. The bar diagrams show the relative frequency (%) of *P. uncinata* individuals along the plot axes (trend lines indicate the increasing density along the north-east axis). Black arrows (length proportional to frequency) indicate the direction of the annual dominant winds. The lower contour plot shows seedling density (increasing grey intensity corresponds to higher density).

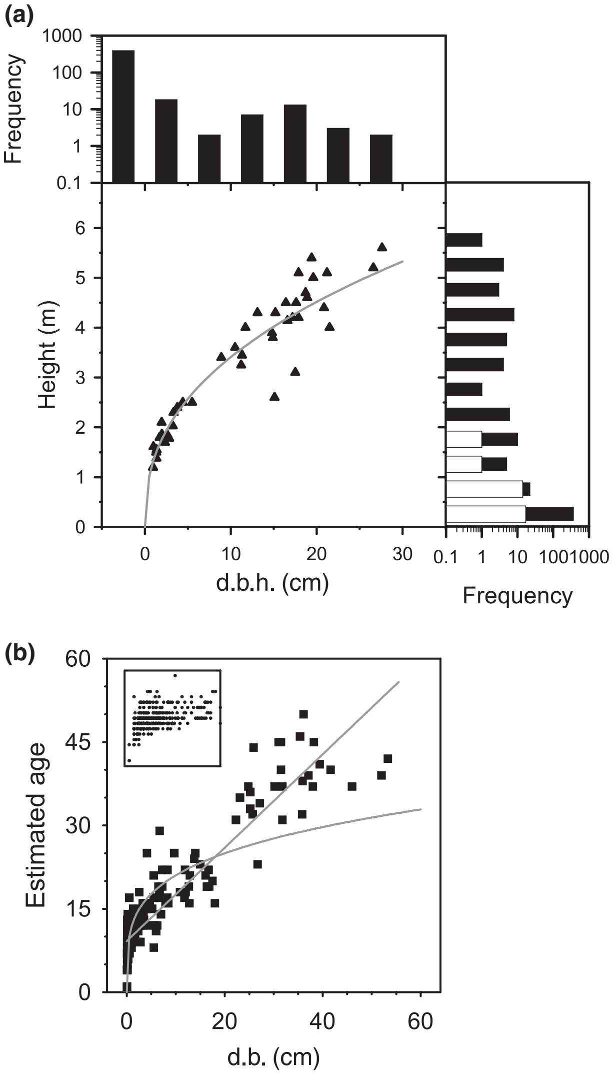

Figure 3 Relationships between structural variables suggest the existence of two cohorts. (a) Relationship between diameter at breast height (d.b.h.) and tree height (line corresponds to a power function). Bar charts show frequency of individuals according to their d.b.h. (5-cm classes) and height (0.5-m classes). Most living individuals were lower than 1.3 m (mostly seedlings) and did not reach d.b.h. Height distribution shows all individuals (black bars) and browsed individuals (white bars). Note logarithmic scales. (b) Relationship between basal diameter of living individuals (d.b.) and estimated age. Inset shows this relationship only for seedlings. Lines correspond to linear and power functions.

d.b. and age appeared when considering only seedlings, because they showed a minimum variation of age (1–12 years) but a greater range of d.b. (0.3–1.0 cm; Fig. 3b).

To describe crown asymmetry, we studied the relationship between the ratio of crown radii following opposite directions (north/south, east/west) and tree height for those individuals at least 1 m tall ($n = 33$). The ratio north/south of crown radii did not change as a function of tree height (north/south $= 1.05 + 0.01$ height; $r^2 = 0.003$, $P = 0.75$), while the ratio of east/west radii was positively and significantly related to tree height (east/west $= 0.82 + 0.08$ height; $r^2 = 0.19$, $P = 0.01$). In summary, eastward crown asymmetry increased as tree height increased, indicating the prevailing wind direction.

Most of the substrate was formed by organic matter (63.9%) and basal parts of herbaceous plants (32.5%), followed by rock–gravel (12.9%), soil (7.6%), excrement (7.6%), moss (1.1%) and lichens (0.3%). The dominant understorey species was *C. vulgaris* (64.7%), while *V. myrtillus* (0.3%) and *J. communis* (0.3%) were less abundant. The overstorey cover (*P. uncinata*) was low (16.0%). Snow-accumulation patterns in the winter of 1998 formed elongated areas of increasing snow depth going south to south-west in the leeward side of prostrate saplings and krummholz. The spatially corrected correlation between snow depth and seedling density was not significant ($r = 0.09$, $P = 0.43$).

Most *P. uncinata* seedlings (52.1%) were found in open areas near the border of *C. vulgaris* mats, on organic matter or mineral soil (Fig. 4). Some grew within clear *C. vulgaris* mats (32.1%). Few pine seedlings appeared in clearings within dead *C. vulgaris* mats (12.5%), near the crowns of *P. uncinata* adults (2.0%), or within herbaceous clumps (1.3%).

Spatial analyses

The spatial pattern of *P. uncinata* seedlings corresponded to aggregates in open areas (Figs 2 & 5). The observed frequency distribution of seedlings did not follow a Poisson function (Kolmogorov–Smirnov test, $Z = 1.66$, $n = 23$ density classes, $P < 0.01$), leading us to reject CSR. Point-pattern analyses revealed significant aggregation ($P < 0.01$) for seedlings at all distances analysed (Fig. 5a,b), especially at small (1.5–2 m) and medium-range (5.5–6 m) distances. The $L_i(t)$ plots indicated large-scale aggregation of seedlings. Moran correlograms of seedling density detected a mean patch size of 25–30 m (not presented), which matches the size of the central large cluster (Fig. 2). The rest of the individuals, including reproductive pines, did not show any significant spatial pattern (Fig. 5c). Saplings and seedlings showed significant ($P < 0.01$) repulsion at short (1–2 m) and long (14–20 m) spatial scales (Fig. 6a), while reproductive individuals and seedlings also showed negative spatial interaction at 1–10 m, especially at 4 m (Fig. 6b).

Surface-pattern analysis of seedling height based on Moran's *I* did not reveal any significant spatial structure (Fig. 7a). In the case of seedling age, the correlogram was globally significant ($P \leq 0.05$) and corresponded to a gradient of decreasing age from east to west (Fig. 7b). The mean patch size of seedling age was 20 m.

Spatially corrected correlation

The correlations among seedling variables were positive and highly significant ($P < 0.001$) even when corrected for spatial autocorrelation (Table 1). The density of seedlings was positively related with *C. vulgaris* cover, but negatively correlated with the presence of basal parts of herbaceous plants (Table 2).

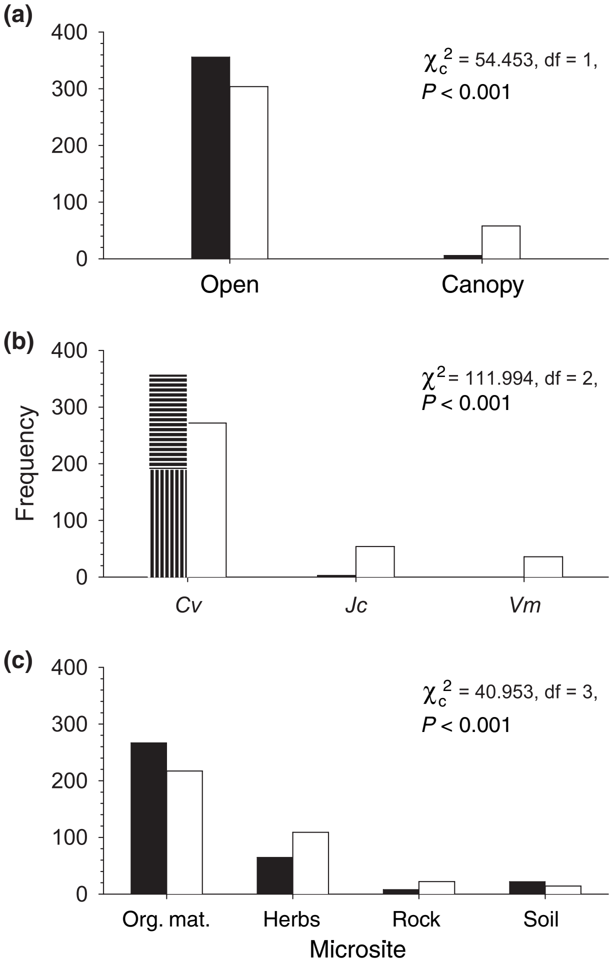

Figure 4 Microsite availability (cover of substrates and plants) vs. microsite preference (regeneration niche) for *Pinus uncinata* seedlings at the study site. Frequency of observed (black bars) vs. expected (white bars) number of seedlings per microsite is displayed for three vertical strata: (a) overstorey; (b) understorey; (c) substrate. Understorey species: *Cv*, *Calluna vulgaris* (vertical stripes, open areas near the border of *C. vulgaris* mats; horizontal stripes, within clear *C. vulgaris* mats); *Jc*, *Juniperus communis*; and *Vm*, *Vaccinium myrtillus*. The results of chi-square goodness-of-fit tests are shown for each analysis with (χ_c^2) or without Yates correction (χ^2).

The mean age of seedlings showed similar results, but it was also negatively related with *P. uncinata* cover and positively related with organic matter substrates. The relationship between mean age of seedlings and organic matter substrates became non-significant after correcting for spatial autocorrelation. The cover of *C. vulgaris* increased in open sites, but grasses dominated in sites with high *P. uncinata* cover and lack of organic matter (Table 2).

Spatial models of recruitment and seed dispersal

The estimate of the $K(t)$ function of *P. uncinata* seedlings based on a Neyman–Scott process produced the following parameters (95% CIs in parentheses): $\sigma = 3.34$ (1.68, 8.01); $100 \times \rho = 0.80$ (0.29, 1.83). Using these values, the expected cluster size (2σ) is 6.68 m in the study area (Fig. 8a), and the estimated ρ corresponds to a density of 16 parents. The measured cluster size based on point pattern was similar to the most frequently observed dispersal distance (4–6 m) of released *P. uncinata* seeds (Fig. 8b).

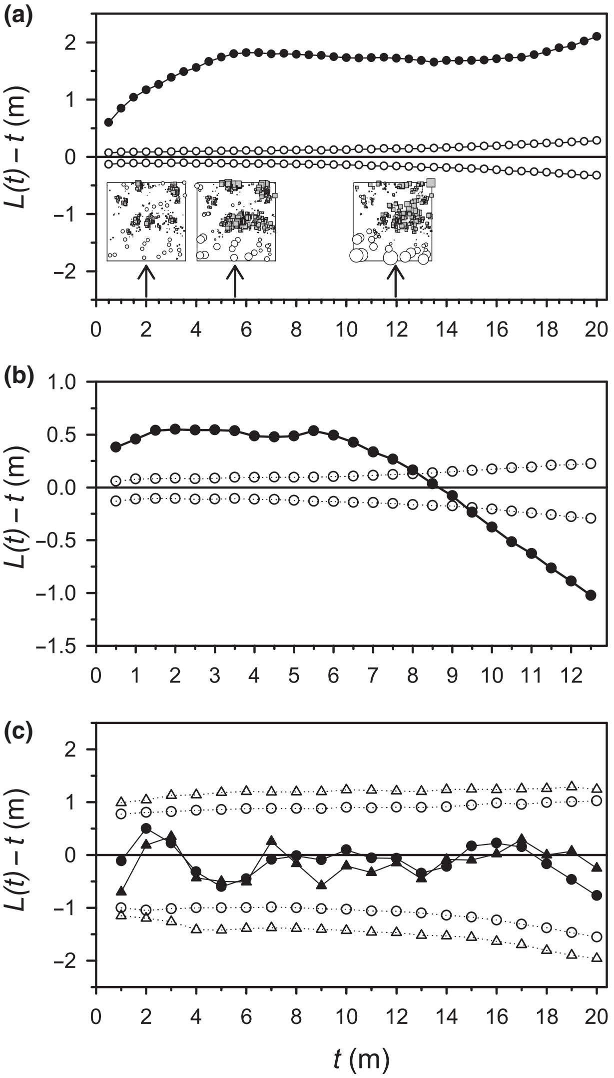

Figure 5 Point pattern analyses for univariate cases using $L(t)$. (a) All seedlings ($n = 313$); (b) seedlings located in the homogeneous subregion ($n = 213$) delimited by the points (x, y) (15, 15) and (40, 40); (c) adults, poles and saplings (circles, $n = 36$) or only reproductive individuals (triangles, $n = 26$). Values of calculated $L(t) - t$ (black symbols) above or below confidence intervals ($P < 0.01$, white symbols) indicate spatial aggregation or dispersion, respectively. In the case of all seedlings (a), smaller graphs show positive (grey squares) and negative (white symbols) local values of $L_i(t)$ within the study plot for selected distances (t = 2, 5.5 and 12 m) indicating aggregation and repulsion, respectively.

The inverse modelling of *P. uncinata* recruitment estimated a mean dispersal distance of 27.2 m (Table 3), which was

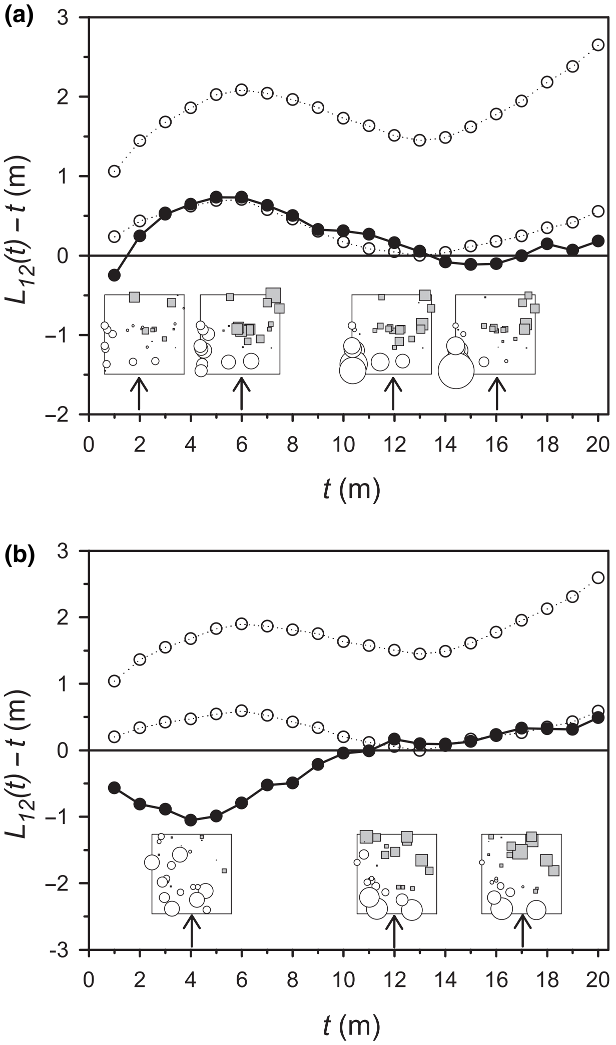

Figure 6 Point-pattern analyses for bivariate cases using $L_{12}(t)$. (a) Saplings ($n = 27$) vs. seedlings ($n = 313$). (b) Reproductive individuals ($n = 26$) vs. seedlings. Values of the calculated $L_{12}(t) - t$ (black symbols) above or below the confidence intervals ($P < 0.01$, white symbols) indicate positive or negative spatial interaction. Other symbols as Fig. 5.

similar to long dispersal distances (28–30 m). Other parameter estimates were: $\beta = 0.16$ (0.08, 0.40), $D = 283.14 \times 10^{-5}$ (236.81×10^{-5}, 329.73×10^{-5}), and $\theta = 1.71$ (1.67, 1.76). The low value of β indicated little variation in reproductive output as a function of tree diameter. The correlation between the observed values and expected number of recruits was low ($r = 0.11$) but significant ($P \leq 0.05$) due to the abundance of quadrats without seedlings.

DISCUSSION

Regeneration niche and understorey invasibility in relict tree populations

We have illustrated how description of the regeneration niche in relict tree populations is a valuable tool for evaluating the response of marginal populations to global change. The availability of suitable habitats for tree regeneration may be as important as climate warming in allowing forest encroachment in mountain areas. Thus biotic interactions may affect the shifts in species range in response to global warming (Davis *et al.*, 1998). Climate warming might also modify the understorey community and its spatial pattern, and reduce the area of suitable microsites for regeneration, thus preventing forest expansion in marginal populations despite the occurrence of reproductive adults and favourable climatic conditions. Therefore monitoring of understorey communities should be a priority if we want to predict accurately the impacts of global warming on marginal tree population at a species' distribution limit.

Seedlings that appeared spatially aggregated dominated the *P. uncinata* population studied. The presence of abundant and spatially aggregated recruits is typical of stand-initiation stages (Oliver & Larson, 1990). Given that *Calluna* heaths dominate in nutrient-poor sites of low productivity, such as the study site, the accumulation of litter was low. Seed beds formed by a thick layer of organic matter hamper the seed germination of many pines (Facelli & Pickett, 1991). However, we did not detect any negative physical effect of the litter layer on seedling recruitment. Most *P. uncinata* seedlings were found on a thin layer of organic matter, which agrees with previous studies where regeneration was better in non-compacted soils under low plant cover (Camarero & Gutiérrez, 2002).

We have described the regeneration niche of *P. uncinata* in relationship to the invasibility of the understorey community, which is crucial for understanding how forest ecotones will respond to climate warming (Hättenschwiler & Smith, 1999). The expansion of marginal tree populations will depend on the invasibility of understorey plant communities and the availability of suitable safe sites for regeneration. For instance, the short-term negative effects of herb competition on the survival of pine seedlings have been well documented (Berkowitz *et al.*, 1995; Kolb & Robberecht, 1996; Peltzer & Köchy, 2001). Ericaceous shrubs greatly reduce understorey light levels, thus preventing tree recruitment (Doche, 1984; Nieppola, 1992; Beckage *et al.*, 2000).

In our study site, the understorey community was dominated by *C. vulgaris*, which showed low resistance to *P. uncinata* invasion. *Pinus uncinata* recruited well within dead mats of *C. vulgaris*, indicating positive interactions (facilitation). Similar positive effects on recruitment have been observed in other harsh environments (Kitzberger *et al.*, 2000; Chambers, 2001). Facilitative effects may be direct through the improvement of microclimatic conditions, or they may be indirect. For instance, Scots pine seedlings suffered fewer snow blight attacks and showed greater survival inside *C. vulgaris* patches than on lichens (Burdon *et al.*, 1994). Germino *et al.* (2002) found the highest survival of *Picea engelmannii* seedlings in alpine treelines within herbaceous cover where seedlings experienced higher night temperatures. We suggest that the *P. uncinata* seedlings located within open *C. vulgaris* mats experienced a similar facilitative effect. However, contrasting life traits

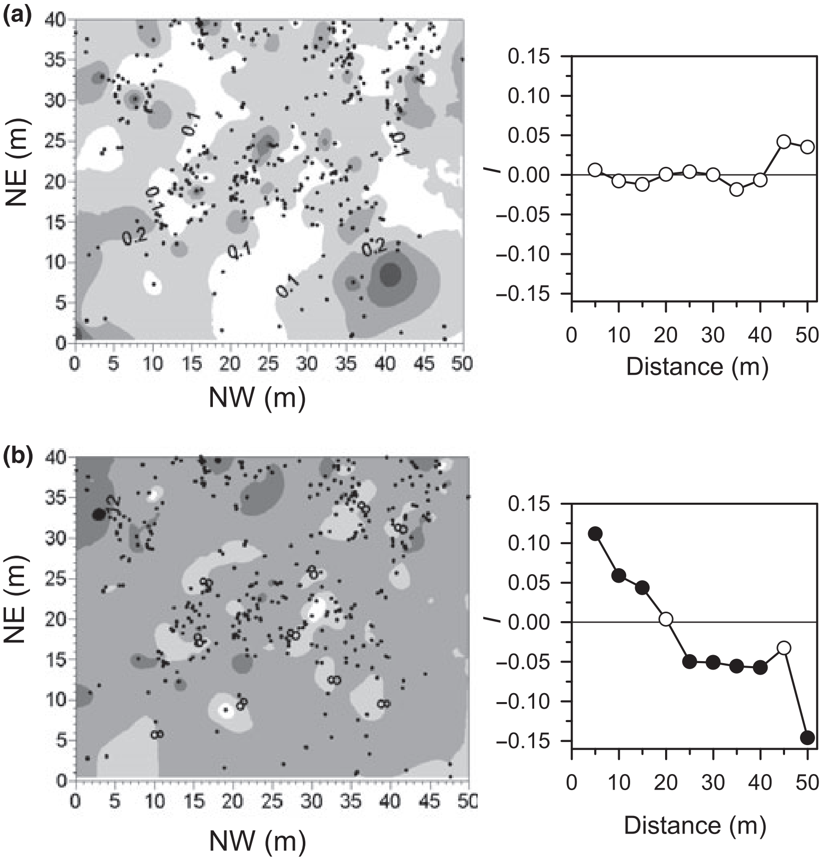

Figure 7 Surface pattern analyses based on all-directional correlograms (Moran's *I*) of height (a) and age (b) of *Pinus uncinata* seedlings and their corresponding surface maps (points in contour plots are seedlings). Black symbols, significant individual coefficients of spatial autocorrelation ($P \leq 0.05$). Only the age correlogram was globally significant ($P \leq 0.05$).

Table 1 Correlations (Pearson's coefficient) between variables measured for *Pinus uncinata* seedlings (density, age, height, basal diameter, maximum number of living needle-age classes), excluding r-trees (mean crown radius of adults, poles and saplings)

	Density	Age	Height	Basal diameter	Needle age
Density					
Age	0.53***				
Height	0.43***	0.85***			
Basal diameter	0.37**	0.74***	0.91***		
Needle age	0.50***	0.95***	0.86***	0.76***	
r-trees	−0.32**	−0.37**	−0.32**	−0.29**	−0.37**

Variables were averaged in 5 × 5-m quadrats ($n = 80$). Significance values: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 2 Correlation results (Pearson's coefficient) between variables measured for *Pinus uncinata* seedlings (density, age); *P. uncinata* mature individuals (mean crown radius of reproductive individuals, r-trees); substrate (herbs = basal parts of herbaceous plants, organic matter); and cover variables (*Cv*, *Calluna vulgaris*; *Pu*, *Pinus uncinata*)

	Density	Age	r-trees	*Cv*	Herbs	*Pu*
Density						
Age	–					
r-trees	–	–				
Cv	0.33**	0.23*	−0.29*			
Herbs	−0.36**	−0.35**	–	−0.39**		
Pu	–	−0.24*	0.38**	−0.40***	0.29**	
Organic matter	–	*0.29*	–	–	−0.24*	–

Significance values as in Table 1. Values in italics indicates loss of significance due to spatial autocorrelation. Values not reported are not significant or appear in Table 1. Variables were averaged in 5 × 5-m quadrats ($n = 80$).

between both conifers might explain their different regeneration niches, because *P. uncinata* is more shade-intolerant than *P. engelmannii*. Additional field data are required to know the time required by a seedling to emerge above the shrub canopy (e.g. shoot growth), which is critical in determining the rate of tree invasion (Hill *et al.*, 1995; Mitchell *et al.*, 1999).

Spatial patterns suggest a stratified-diffusion process

The spatial patterns of seedlings described here suggest a two-phase expansion process based on two scales of clustering. Most seeds travelled between 4 and 6 m, distances similar to the estimated radius of seedling clusters (6 m). The estimated mean dispersal distance based on seedling patterns was 27 m, a fairly typical value for winged-seed pines (Ribbens *et al.*, 1994). This distance may be due to rare dispersal events that occurred under eddies induced by strong wind (Horn *et al.*, 2001). Similar long distances have been travelled by winged seeds of

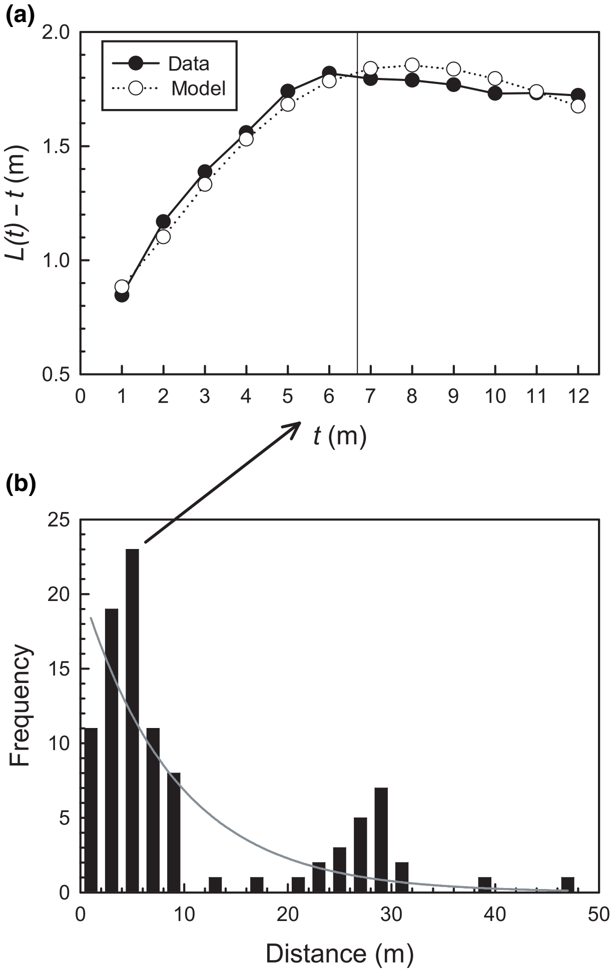

Figure 8 Comparison of spatial point pattern of *Pinus uncinata* seedlings and frequency of seed-dispersal distances. (a) Point-pattern analysis of seedlings showing the $L(t)$ function for field data and simulated values based on a Neyman–Scott process. Vertical line indicates fitted cluster size (6.7 m). (b) Frequency of seed-dispersal distances from a seed-release experiment and fitted exponential function (line). Arrow shows similarity between seedling cluster size and the most frequent dispersal distance (4–6 m).

other conifers (e.g. 39 m, *P. sylvestris*) under turbulent wind conditions (Hughes *et al.*, 1994). The 27-m scale corresponded to the size of the north to north-eastern front of expansion or large cluster detected in the middle of the study plot, which was paralleled by an eastward trend of increasing seedling age. The spread of introduced pines in New Zealand occurs in 'waves' oriented downwind (Ledgard, 2001). Seedlings recruited in the late 1980s dominated the north to north-eastern front of expansion, which might have been caused by rare medium-distance dispersal events related to the dominant north-westerly winds. Wind effects in the study plot are demonstrated by the eastward asymmetry in adult crowns, and north to north-eastern snow-accumulation patterns.

The strongly leptokurtic pattern typical of wind-dispersed seeds was also observed in this study (Portnoy & Willson, 1993). Wind is a common dispersal agent of many pine species (van der Pijl, 1982), but secondary seed dispersal by birds has also been described in species similar to *P. uncinata* such as *Pinus mugo* (Müller-Schneider, 1986). The pattern of low spatiotemporal variation in seed-dispersal rates near adult trees and high variation further away is common among wind-dispersed pines (Nathan *et al.*, 2000). High spatiotemporal variability of medium and long distances is expected, due to the rarity of long-distance dispersal events (Greene & Johnson, 1995). Indeed, rare long-distance dispersal events may critically affect the expansion of populations at their distribution limit (Clark, 1998). We suggest that the observed recruitment patterns were related to the spatial variation in seed dispersal. The spatial aggregation of different life stages (Wada & Ribbens, 1997), and the spatial position of reproductive individuals, are crucial for estimating potential range shifts of relict populations (Debain *et al.*, 2003). In the study case, *P. uncinata* saplings and seedlings were more widely dispersed from conspecific adult trees than were seeds.

Theoretically, isolated populations might act as invasion foci for rapid expansion under favourable conditions, as suggested by stratified-diffusion models (Shigesada *et al.*, 1995) and palaeoecological reconstructions (MacDonald & Cwynar, 1991). We suggest that a two-phase process produced the bimodal seed-dispersal curve, which might explain the two spatial scales of invasion. First, frequent short-distance dispersal events induced the primary spatial clustering of seedlings in safe sites. Second, wind turbulence caused rare medium-distance dispersal events. Dispersal curves with bimodal patterns of dispersal respond to diverse processes such as contrasting wind velocities (Clark *et al.*, 1999; Higgins & Richardson, 1999).

Consequences for the management of relict tree populations

Dispersal and biotic interactions may be as important as climate for predicting range shifts in response to climate warming (Davis *et al.*, 1998). The expanding *P. uncinata* relict population probably originated from seeds coming from old

Table 3 Parameter estimates and 95% confidence intervals (CI) obtained with RECRUITS

STR	Low-CI STR	High-CI STR	MDD (m)	Low-CI MDD (m)	High-CI MDD (m)	*N*
82.41	74.89	92.12	27.22	24.52	29.77	2555.23

Mean dispersal distance (MDD) is presented instead of the dispersion parameter (*D*) because of the more direct interpretation of the former. STR, standard total recruitment; *N*, normalizer (see equation 2).

individuals located near the summit. The expansion process was possibly enhanced by favourable climatic conditions, but the availability of suitable regeneration microsites determined its success. We did not find a low regeneration capacity by seeding in the relict population studied, despite it being a marginal stand, which underlines the importance of preserving reproductive adults to 'store' recruitment potential (Warner & Chesson, 1985). Quantitative description of the regeneration niche and the spatial patterns and modes of tree recruitment provides managers with specific information to enhance regeneration in relict tree populations. Monitoring of similar marginal populations is essential for predicting their responses to global change.

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