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ORIGINAL ARTICLE

Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime

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ABSTRACT

Aim Impacts of global change, such as land-use and climate changes, could produce significant alterations in the elevational patterns of alpine tree line ecotones and their adjacent vegetation zones. Because the responses of the tree line to environmental variations are directly related to successful tree regeneration, understanding recruitment dynamics is an indispensable step in tree line research. We aimed to compare potential ecological limitations on recent tree line regeneration in undisturbed and disturbed sites by analysing the demographic structure and spatiotemporal patterns of recruits and large trees.

Location Alpine tree line ecotones comprising *Pinus uncinata* in the Catalan Pyrenees (north-east Spain) and Andorra.

Methods We assessed the demographic structure and spatial pattern of recent recruitment using techniques of point-pattern and autocorrelation analyses. A total of 3639 *P. uncinata* individuals were mapped, measured and aged at 12 sites. To evaluate the effects of past disturbances on recent tree line response we compared tree lines that had either been recently affected by human-induced disturbances or had remained undisturbed for many years.

Results The age structure of the tree lines, together with the lack of an age gap between seedlings and saplings, did not indicate recent episodes of high seedling mortality and suggest that recruitment has been frequent under current climate conditions. Seedlings appeared highly aggregated at short distances (up to 3 m), irrespective of disturbance history, and were spatially segregated with respect to large trees. However, we found no evidence of patches of even-aged seedlings, and our results suggest that dispersal events at intermediate distances (10–17 m) may be frequent. Autocorrelation analyses revealed different patterns of density and age of recruits between disturbed and undisturbed tree lines, but the strength and small-scale clustering of seedlings and saplings were very similar between sites.

Main conclusions We found no recruitment limitation on recent tree line dynamics in the Pyrenees. Furthermore, processes affecting tree recruitment seem to be similar among populations regardless of their past disturbance regime. Our results suggest that constraints on tree line dynamics causing differential responses between sites may operate on older life stages and not upon recruits, and that such constraints may be more contingent on local site conditions than on disturbance history.

Keywords

Alpine tree line, disturbance, global change, Moran correlogram, pair-correlation function, *Pinus uncinata*, Pyrenees, recruitment.

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INTRODUCTION

The alpine tree line ecotone represents the upper elevational limit of forest and tree growth in mountains, forming a distinct transitional boundary between subalpine forest and alpine communities (Holtmeier & Broll, 2005; Körner, 2007). This boundary is considered to be thermally limited (Körner & Paulsen, 2004), and thus climate has been proposed to be one of the main factors governing the geographical distribution and dynamics of such tree populations (Daniels & Veblen, 2004). Consequently, tree line ecotones are assumed to be useful indicators of the effects of climate change on forest ecosystems (Körner, 2007). Furthermore, impacts of global climate change could bring significant alterations in the elevational patterns of high-elevation forests and the adjacent alpine zones (Smith *et al.*, 2009).

Many tree line ecotones are not in equilibrium with climate because they are limited by additional factors such as natural or anthropogenic disturbances. Hence, climate change is only one aspect of environmental change that may affect the current and future location of tree lines. Furthermore, the after-effects of historical disturbances may override the effects of climate change (Hofgaard, 1999; Holtmeier & Broll, 2005). Apart from the correlative relationships between high-elevation limits of forest and upright trees and climatic conditions, more mechanistic approaches for understanding current tree line dynamics have been proposed (e.g. Smith *et al.*, 2003). Such approaches are focused on the recruitment processes involved in the formation of new forests above current tree line positions (i.e. facilitation processes through life stages), which together with limited invasibility of alpine communities (i.e. microsite availability) or seed dispersal constraints can rival climate changes in controlling tree line shifts (Dullinger *et al.*, 2004).

In the context of global warming, many studies have reported an increased density of pre-existing tree populations at latitudinal and alpine tree lines during the 20th century, accompanied in some cases by changes in the position of the tree line (e.g. Holtmeier & Broll, 2007, and references therein). However, the presence of differential tree line dynamics in many regions in spite of the ubiquity of warming trends (Dalen & Hofgaard, 2005; Payette, 2007) highlights the fact that the pattern and pace of changes to the tree line may be contingent on local, landscape and regional-scale factors, as well as dependent on the biology of different tree species (Danby & Hik, 2007; Batllori & Gutiérrez, 2008).

Processes of tree line afforestation are directly related to successful tree regeneration and survival of recruits rather than on increasing growth rates of mature trees (Smith *et al.*, 2003; Holtmeier & Broll, 2007). This reflects the sensitivity of recruits to environmental variation (Lloyd, 1997), which makes the spontaneous advance of forest tree species into present treeless areas at the tree line (within or beyond it) a key indicator of responsiveness of the tree line to environmental change (Holtmeier & Broll, 2005). However, few studies have examined how environmental change affects regeneration and tree line dynamics at small spatial scales, which would be the most relevant scale for understanding recruitment processes (Veblen, 1992). Because the spatial structure of an ecosystem, i.e. the way its individuals are organized in space, plays an important role in its functioning and dynamics (Wiegand *et al.*, 2007), an analysis of recent spatial patterns of recruitment at the tree line ecotone could further our understanding of the mode and tempo of recent changes to the tree line in the context of global change. Furthermore, the world-wide documentation of the spatial patterns and development of the tree line (e.g. changing population densities) has been noted as an indispensable step in future tree line research (Holtmeier & Broll, 2007). Because the impacts of global change vary in importance in different mountain regions, studies are required in different regions and at different spatial scales, from whole catchments to the plot level (Becker & Bugmann, 2001).

Understanding current tree line dynamics is essential for forecasting the effects of ongoing changes to climate and land-use on such marginal tree populations and the potential alterations in adjacent alpine vegetation zones. The Pyrenees encompass the southernmost distribution range of many European alpine species, including endemic and threatened species, and are thus an excellent example in this sense (Carreras *et al.*, 1996a). Recent dendrochronological reconstructions have revealed increased density of alpine tree line ecotones at a regional scale in the Pyrenees since the mid 20th century, in parallel with the human abandonment of land in mountain areas and warming trends across southern Europe (Batllori & Gutiérrez, 2008). Hence, the Pyrenees provide a good system for evaluating whether, as a result of the after-effects of anthropogenic disturbances, tree lines that have recently been influenced by humans are responding to climate warming differently from tree lines that have remained undisturbed for longer periods.

In this study we assess the relevance of ecological constraints on tree recruitment in alpine tree lines. Our main objective is to evaluate whether the factors driving recent tree line responses (climate or land-use changes) cause distinct short-term recruitment dynamics in disturbed and undisturbed stands in the Spanish Pyrenees and Andorra, which in turn may determine future responsiveness of the tree line to environmental changes. To achieve this we test several hypotheses related to the potential constraints on recent tree line dynamics, namely: (1) seed production, (2) seed dispersal, (3) seedling mortality, and (4) the distribution and spatial pattern of recruits. Furthermore, we evaluate (5) if the recent (past 50 years) recruitment dynamics at the tree line reflect infilling processes (increased density) or tree line shifts. Objectives (1) and (3) are addressed by means of demographic analyses. Static demographic structures (age distributions) are not a suitable basis for the inference of detailed population dynamics (Johnson *et al.*, 1994), but they can be used to detect variation in recruitment and/or mortality processes through time. Thus, both temporal variation in seed production (e.g. masting) and/or episodes of high seedling mortality might produce uneven-aged stands. Objectives (2), (4) and (5) are

Table 1 The main hypotheses of ecological constraints on tree recruitment dynamics in alpine tree lines tested in this study, together with their expected patterns, the analyses applied and the relevant figures illustrating the results obtained.

Hypotheses	Expected patterns	Analyses	Figures
(1) Seed production limitation	Temporal variation in seed production may result in uneven-aged stands (periods of low establishment of recruits)	Demographic analysis, dendrochronological reconstruction	Fig. 2
(2) Seed dispersal limitation	(2a) Seedling recruitment significantly correlated with the distribution of reproductive trees (bearing cones)	Bivariate point-pattern analysis [($g_{12}(t)$]: pattern 1 = reproductive trees; pattern 2 = seedlings	Figs 1, 3 & 5
	(2b) Positive spatial association between even-aged seedlings	Surface pattern analysis of recruit ages (Moran's correlograms of age data)	Fig. 4
		Spatially corrected correlation coefficients between consecutive recruitment periods	Fig. 6
(3) Episodes of high seedling mortality	There is likely to be an age gap between seedlings and saplings (uneven-aged frequency distribution of the recruits)	Demographic analysis, dendrochronological reconstruction	Fig. 2 (inset)
(4) Seedling survival enhanced by microsite conditions (importance of feedback processes)	Fine-spatial aggregation of early life stages (seedlings and saplings). Subsequent density-dependent mortality is expected	Univariate point-pattern analysis [$g(t)$] applied to consecutive life stages	Figs 1, 3 & 5
		Surface pattern analyses of the abundance of recruits (Moran's correlograms of density data)	Fig. 4

addressed by means of spatial (point- and surface-pattern) analyses. We examine the spatial pattern of consecutive life stages (seedlings, saplings and large trees) and assess changes from one class to another (univariate point-pattern analyses). Further, we analyse the spatial interaction between life stages (bivariate point-pattern analyses) to determine if they are primarily positive (aggregation) or negative (segregation). Comparison of clustering among size classes allows exploration of whether, and at which life stage, survival constraints appear (Moeur, 1997), whereas the presence of spatial interaction between size classes provides indirect evidence of facilitative or competitive processes. Finally, we assess if the spatial correlation between recent recruitment periods (1950–74 and 1975–99) corresponds to changes in the position of tree line ecotones or to increased tree line density (spatial segregation between cohorts or not, respectively). Our hypotheses, respective analyses and associated figures are summarized in Table 1. Overall, our spatiotemporal approach should reveal the relative contribution of the mentioned constraints on recent tree line dynamics depending on the main driving factor (climate or land-use changes), thus furthering our understanding of the controls of current and future responses of the tree line to environmental changes.

MATERIALS AND METHODS

Study area and data collection

The studied tree lines are dominated by *Pinus uncinata* Ramond ex DC., and they are located in the eastern range of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Table 2). A combination of field visits and interpretation of aerial photographs was used to select 12 sites where a rectangular plot, its longer side parallel to the elevational gradient, was set up from the closed forest to the treeless alpine communities. Thus, the forest limit (maximum elevation of forest with cover of at least 30–40% given by trees > 5 m high) and the tree limit (uppermost elevation of upright trees ≥ 2 m high) were included in each plot. We established two large plots, with areas of 6000 and 7600 m^2 (40 m wide × variable length), and ten small plots, ranging between 940 and 1650 m^2 (10 m wide × variable length). The plot length depended on the characteristics of each tree line transition. This sampling design represents a trade-off between regional coverage, sufficient sample sizes and the detail required for fine-scale spatial analyses. First, we focus on the recruitment dynamics in the two large plots (stand-scale processes), then the insights gleaned from these analyses are used to evaluate whether there are generally similar patterns within the 10 smaller plots (region-wide processes).

Pinus uncinata is a shade-intolerant conifer that dominates most of the subalpine forests in the Pyrenees, and its potential tree line elevation is between 2200 and 2450 m a.s.l. depending on continentality, exposure and landform (Carreras *et al.*, 1996b; Ninot *et al.*, 2007). The study sites comprise a wide range of slope gradient, bedrock and plant communities (i.e. short meso-xerophilous pastures, ericaceous dwarf shrubs), and as such constitute a good representation of the *P. uncinata* tree line ecotones in the Pyrenees. All sites had uniform topography and no avalanche paths or evidence of recent fires, and there was no evidence of current human use (i.e. no longer intensively grazed). The 12 sites can be classified in two groups according to

Table 2 Characteristics of the 12 alpine *Pinus uncinata* tree lines studied in the Catalan Pyrenees, north-east Spain, and Andorra. Sites recently affected (since the 1950s) by anthropogenic disturbance (logging, grazing) were regarded as those with step-like transition patterns in age and/or size along the tree line ecotone, whereas sites with gradual tree-size and age transitions were considered as undisturbed.

							Transition pattern*	
Site (code)	Latitude (N)/longitude (E)	Plot size (m^2)	Elevation (m a.s.l.)	Slope (°)	Aspect	Bedrock	Tree age	Tree size
El Portell (PU)	42°31′/0°45′	6000	2199–2268	28	N	Lime	Step-like	Gradual
Durro (DU)	42°28′/0°49′	1200	2010–2069	30	N	Lime	Gradual	Gradual
Serrat Contador (SU)	42°32′/0°53′	1500	2270–2338	27	NW	Lime	Gradual	Gradual
Delluí (EU)	42°33′/0°56′	940	2299–2339	24	W	Granodiorite	Step-like	Gradual
Lo Covil (LU)	42°31′/1°21′	1180	2363–2405	21	N	Slate	Gradual	Gradual
Serrat Capifonts (FU)	42°33′/1°23′	7600	2352–2435	24	NW	Slate	Gradual	Gradual
Port Ovella (CU)	42°33′/1°25′	1160	2250–2297	26	NW	Lime	Step-like	Gradual
La Rabassa (RU)	42°26′/1°32′	1650	2236–2271	24	W	Slate	Gradual	Gradual
Obac Canillo (NU)	42°34′/1°37′	980	2266–2314	29	N	Lime	Gradual	Gradual
Meranges (GU)	42°27′/1°44′	1500	2312–2365	16	NE	Slate	Gradual	Gradual
Ras Ortigar (OU)	42°23′/2°08′	1500	2241–2308	27	N	Slate	Step-like	Step-like
Serra Balmeta (BU)	42°24′/2°19′	1500	2184–2241	22	N	Slate	Step-like	Step-like

*The transition pattern was determined by means of linear and smooth-spline regressions between the relative elevation and tree age and size (see Batllori & Gutiérrez, 2008).

their recent (*c.* 50 years) disturbance regime as inferred from tree age and size transition patterns along the ecotone (Batllori & Gutiérrez, 2008) (Table 2). Because these tree lines are not affected by major natural disturbances (e.g. extreme topography-induced winds, snow avalanches, rockfalls), step-like transition patterns in tree size and/or age along the ecotone may indicate recent human-induced perturbations (i.e. logging or pasture enlargement). Hence, the dynamics of tree lines with step-like patterns of transition were considered to be influenced by the after-effects of human perturbations (i.e. past changes in land-use, such as logging or grazing; hereafter disturbed sites). In contrast, gradual transitions of tree size and age along the ecotone may indicate no recent human-induced disturbances and, thus, the dynamics of tree lines exhibiting such patterns were considered to be climatically driven (hereafter undisturbed sites). The two large plots studied were representative of a disturbed and an undisturbed tree line ecotone (PU and FU, respectively; Fig. 1). Similarly, six of the small plots were regarded as undisturbed sites whereas the other four sites were considered disturbed tree line ecotones (Table 2).

Field sampling

The location of all tree stems in each plot, using rectangular coordinate axes, was noted for analysis of the tree spatial pattern. The positions of all living trees were recorded in Cartesian coordinates using tapes along the shorter (x-axis) and longer (y-axis) sides of the plot. Point $(x,y) = (0,0)$ was located in the lower left corner looking upslope. Additional tapes were placed every 5 m to subdivide the plot and measure the coordinates of the centre of each tree to the nearest 0.1 m. Basic biometric measurements (diameter at breast height, d.b.h.; total tree height, Ht) and the presence of cones were recorded for 3639 *P. uncinata* trees. Trees were classified by size as follows: large upright trees (d.b.h. > 7.5 cm), saplings (d.b.h. < 7.5 cm and Ht > 0.5 m) and seedlings (Ht < 0.5 m). Those trees bearing cones were considered to represent potentially reproductive individuals.

All trees of sufficient size (basal diameter > 10 cm) were cored at the base to determine age, whereas seedlings and small saplings were aged by counting the terminal bud scars (internodes) along the main stem (see Batllori & Gutiérrez, 2008, for details). Field sampling was conducted during the summers of 2003–06.

Demographic and spatial pattern analyses

Reconstructions of stand structure were developed to determine whether the stands contained trees of all ages or were reflective of episodic recruitment (uneven-aged). Age–frequency distributions covering the period 1801–2000 were generated in 5-year classes. However, due to uncertainties in age determination, some trees had a dating error of more than 5 years, and these individuals were classified separately in the demographic reconstructions. Furthermore, recent recruitment events were analysed on the basis of the tree size classification used (seedling and sapling classes).

We analysed the spatial pattern of tree distributions using the pair-correlation function $g(t)$, which is a second-order statistic suitable for characterizing a point pattern (Wiegand & Moloney, 2004). Unlike the more widely used Ripley's $K(t)$, $g(t)$ is not cumulative and is better suited to the evaluation of whether individuals are clustered/aggregated or regular/segregated at small spatial scales. Nevertheless, $g(t)$ might be noisier and more sensitive to small sample sizes than Ripley's $K(t)$ (Wiegand & Moloney, 2004). Hence, we only analysed those continuous areas within each plot where density was > 200 individuals ha^{-1} of recruits and 100 large

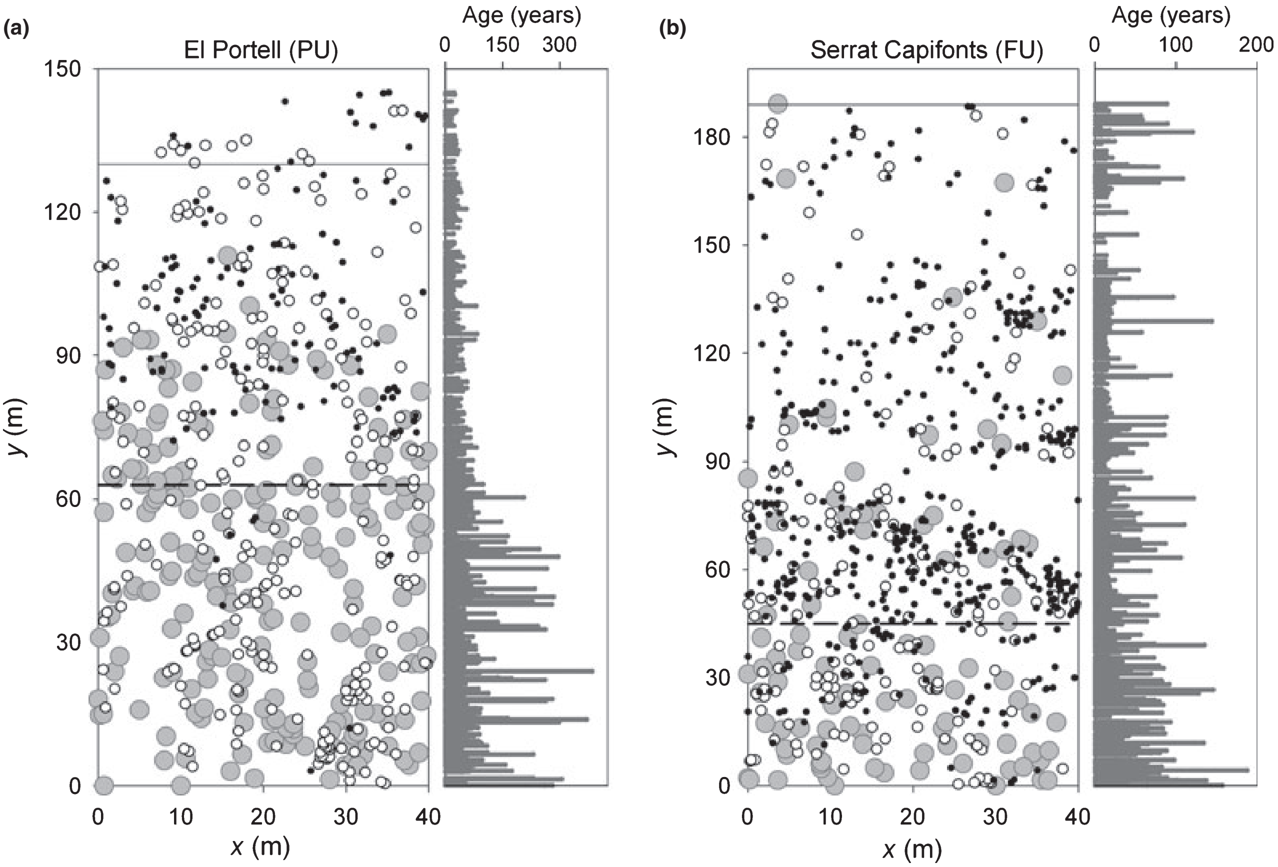

Figure 1 Mapped point patterns of *Pinus uncinata* individuals (left subplots) and transition patterns of tree age along the elevational gradient (right bar subplots) in the two Pyrenean tree line ecotones studied using large plots: (a) PU, a disturbed site; (b) FU, an undisturbed site (see Table 2 for site characteristics). The y(m) and x(m) axes represent, respectively, the longer and shorter side of each plot in metres. Symbols represent the defined tree size classes corresponding to: grey filled circles, large, upright trees; empty circles, saplings; black dots, seedlings. Solid and dashed lines correspond to the current tree limit and forest limit positions, respectively, at each site.

trees. For instance, this corresponds in the PU plot to y = 0–100 m for large trees, y = 0–150 m for saplings and y = 70–150 m for seedlings. In the FU plot the area analysed was y = 0–190 m for all size classes (see Fig. 1). Furthermore, $g(t)$ assumes first-order homogeneity, and thus we also delineated homogeneous areas for each tree class within each plot (Perry *et al.*, 2006).

We performed univariate [$g(t)$] and bivariate [$g_{12}(t)$] point-pattern analyses to characterize the spatial distribution of the different classes of individuals (large trees, reproductive trees, saplings and seedlings) and the relationship between them. We carried out the spatial analyses up to 20 m or up to 5 m in the large and smaller plots, respectively; the maximum distance that may be analysed using $g(t)$ is half the shortest side of the plot. The spatial resolution used in these analyses was 1 m for the large plots and 0.5 m for the smaller plots. In the univariate case we analysed the extent to which events show departure from complete spatial randomness (CSR), which corresponds to the homogeneous Poisson process. In the case of spatial randomness, $g(t) = 1$. Values greater or less than 1 indicate that inter-point distances (t) are more or less frequent than expected under CSR, illustrating clustering or segregation, respectively. In the bivariate case [$g_{12}(t)$], we assumed that pattern 2 did not influence the development of pattern 1, but pattern 2 might have been influenced by pattern 1. For example, for investigating the relationship between large trees [$g_{1*}(t)$] and seedlings [$g_{*2}(t)$], the locations of the seedlings were randomized while keeping the locations of large trees fixed. Values of $g_{12}(t)$ greater or less than 1 and located outside the confidence intervals indicate significant positive (attraction) or negative (repulsion) spatial interactions. Because first-order effects due to environmental heterogeneity may obscure second-order effects related to tree-to-tree spatial interactions, the selection of a null model is necessary (Wiegand *et al.*, 2007). We used heterogeneous Poisson processes as null models because they retain the large-scale structure of the pattern but remove its local heterogeneity (Stoyan & Stoyan, 1994). Finally, significance tests were constructed using 999 Monte Carlo simulations based on the null hypothesis of CSR, estimating the rejection limits as the 5 lowest and 95 highest simulated values for each distance. All point-pattern analyses were performed using the software Programita (Wiegand & Moloney, 2004).

To describe the spatiotemporal patterns of tree recruitment we analysed the spatial autocorrelation of density and age of

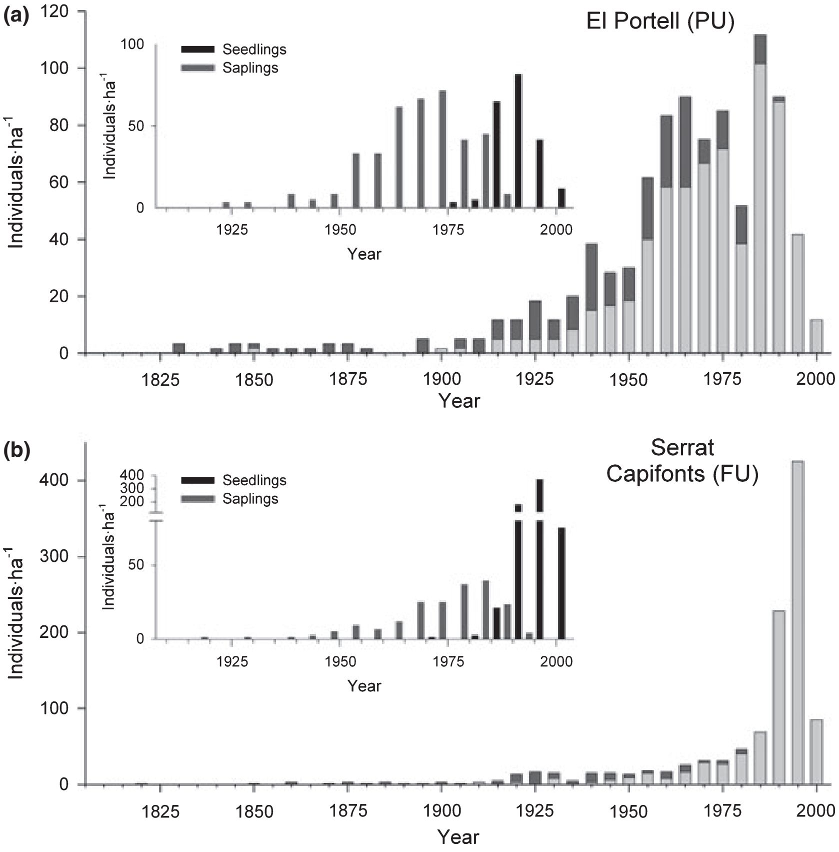

Figure 2 Age–frequency distributions in 5-year classes for all living *Pinus uncinata* individuals in the two Pyrenean tree line ecotones studied using large plots: (a) PU, a disturbed site; (b) FU, an undisturbed site. Light grey bars indicate individuals with a dating error of < 5 years; dark grey bars indicate individuals with a greater dating error. Inset figures correspond to the age–frequency distribution of recruits (seedlings and saplings) at each site. Note that vertical scales vary between populations (figure modified from Batllori & Gutiérrez, 2008).

recruits (seedlings and saplings) with Moran's correlograms, where Moran's *I* coefficients are plotted against distance (Legendre & Fortin, 1989, and references therein). The significance of Moran's *I* coefficients was calculated by comparing them with those obtained with 999 Monte Carlo simulations. Furthermore, the significance of each entire correlogram was tested at the 5% level using a Bonferroni correction (Fortin & Dale, 2005). In these analyses, original *x–y* point data were gridded; the total number of recruits and mean age were calculated for every quadrat. We used 5-m distance classes discarding those classes with < 20 point pairs. Spatial autocorrelation analyses were not performed for the smaller plots because of the small sample sizes and analysis area. The autocorrelation analyses were performed using passage v. 1.1 (Rosenberg, 2002).

Finally, we used spatially corrected correlation coefficients (SCC) to examine the spatial relationship at the plot scale between the densities of two regeneration periods (1950–74 and 1975–99) covering the period of increased density of the studied tree lines that began in the 1950s (Batllori & Gutiérrez, 2008). To perform this analysis we used the gridded density data from the autocorrelation analyses. We used the Spearman rank correlation coefficient because the data did not fit a normal distribution. SCC coefficients were calculated using the program Spatial Analysis in Macroecology (sam) (Rangel *et al.*, 2006). We used the SCC coefficients between the two recruitment periods to evaluate whether recent recruitment dynamics may reflect shifts of the tree line or infilling processes.

RESULTS

The two large plots (PU and FU) showed major increases in the frequency of recruits since the 1950s, which, as discussed in Batllori & Gutiérrez (2008), is a common feature at a regional scale in Pyrenean tree line ecotones (Fig. 2). Furthermore, despite the assumed episodic character of recruitment dynamics at the tree line, the all-aged structure of seedlings and saplings (Fig. 2) may indicate a rather continuous mode of recent recruitment at the tree lines. The absence of a clear age gap between seedlings and saplings did not reflect recent episodes of high seedling mortality. Further, recent recruitment in both ecotones showed an acceleration period followed by a decline in tree establishment in the last 10–15 years. At both sites seedling establishment mainly occurred above the forest limit and below the tree limit (Fig. 1), whereas saplings were abundant across the entire ecotone. Despite a general similarity in the distribution of seedlings and saplings between sites, small-scale distribution patterns of the two classes differed (Fig. 3). At the disturbed PU site, seedlings exhibited no significant departures from the CSR, whereas saplings showed a clustered distribution up to 2 m. Conversely, at the undisturbed FU site, seedlings appeared strongly clustered at small scales (1–3 m), whereas saplings had a distribution not significantly different from CSR. Despite these differences, the strength of small-scale clustering (0.5 m) of seedlings and saplings was very similar between sites, and the range of clustering extended only up to short distances (3 m) irrespec-

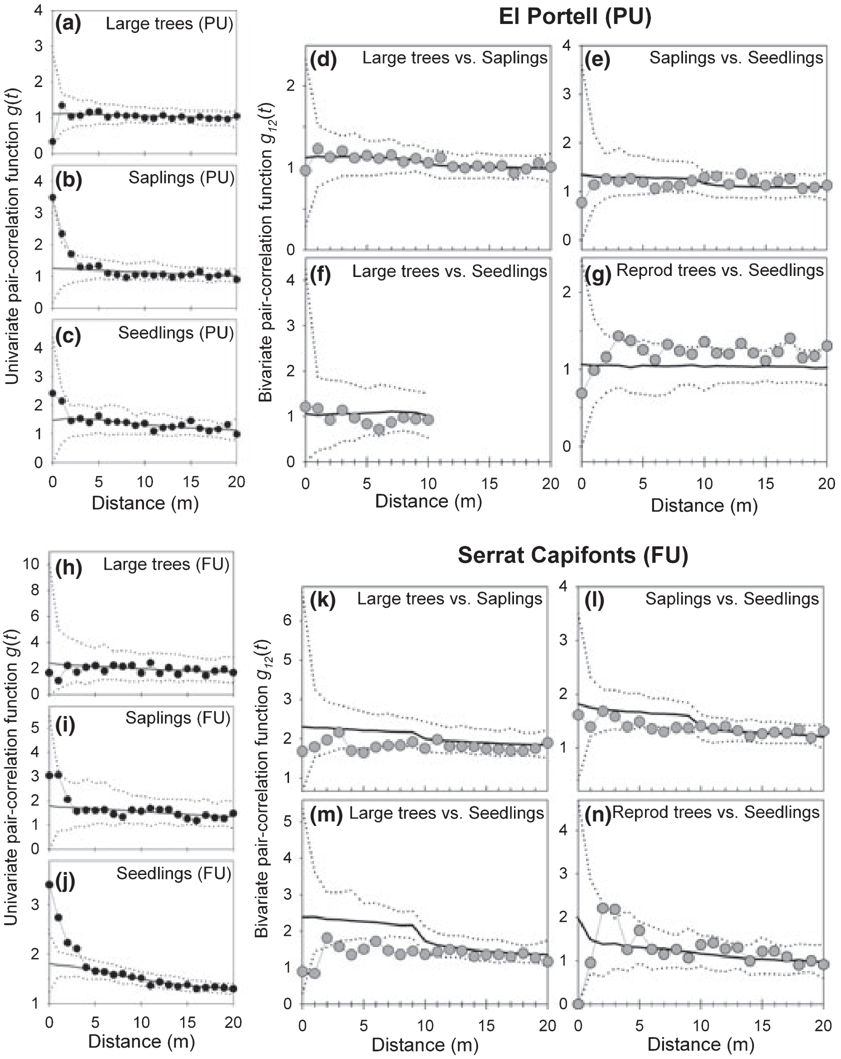

Figure 3 Univariate and bivariate point-pattern analyses of *Pinus uncinata* spatial distribution in the two Pyrenean tree line ecotones studied using large plots based on the pair-correlation functions [$g(t)$, $g_{12}(t)$]. (a–c) Univariate and (d–g) bivariate cases at PU, a disturbed site; (h–j) univariate and (k–n) bivariate cases at FU, an undisturbed site. Tree classes used in the analyses are: seedlings, saplings, large upright trees and reproductive individuals. The different lines correspond to the calculated $g(t)/g_{12}(t)$ (line, filled symbols) and the expected $g(t)/g_{12}(t)$ functions under the heterogeneous Poisson null model (thick lines), and the simulation envelopes (dotted lines) corresponding to the 5% and 95% confidence intervals.

tive of tree class (Fig. 3). Finally, the spatial distribution of large trees within the tree line ecotone was not significantly different from CSR at both sites (Fig. 3), and the spatial pattern of reproductive trees (bearing cones) was similar to those detected for large trees (results not presented). Hence, small-scale spatial patterns of tree classes in disturbed and undisturbed tree lines were similar.

The spatial relationships among seedlings, saplings, large trees and reproductive trees revealed similar patterns in the disturbed (PU) and undisturbed (FU) large study plots (Fig. 3). Seedlings and saplings were spatially independent, as illustrated by their spatial interaction being not significantly different from the CSR through the range (up to 20 m) in the two plots. Significant repulsion was detected only at 6–7 m in the FU plot. However, non-significant departures from the CSR towards repulsion were present up to 10 m at both sites. In contrast, repulsion between seedlings and large trees was apparent when considering the entire ecotone and also at smaller spatial scales (i.e. including the zone where most regeneration occurred). For example, in the FU plot the negative spatial relationship between recruits and large trees was significant at distances up to 10 m (Fig. 3). At the PU site, the spatial segregation of seedlings and large trees was evident at the plot scale (Fig. 1). Thus, we did not perform the bivariate analysis at the 20-m scale due to the lack of representative areas where both classes overlap. However, the results found at smaller scales (10 m range) also indicated spatial segregation between seedlings and large trees. In contrast, the spatial relationship between seed bearers and seedlings (Fig. 3) showed significant attraction effects at short (3 m) and intermediate distances (up to 10–17 m) at both sites.

The Moran's correlograms of seedling and sapling density and age within the tree line ecotone revealed different patterns in the disturbed (PU) and undisturbed (FU) tree lines (Fig. 4). However, the degree of autocorrelation of age and density of each of the two classes appeared to be independent of each other at both sites. Whereas seedling ages were not autocorrelated at the disturbed PU site, a gradual and significant decrease of seedling age with elevation (y-axis) was apparent at the undisturbed FU site, indicating the presence of an age gradient (Fig. 4). For seedling density, a large patch (*c.* 50 m) was detected at the PU site, whereas the pattern of seedling density at the FU site corresponded to an upward gradient with sharp steps (Fig. 4; see also Fig. 1). Conversely, sapling

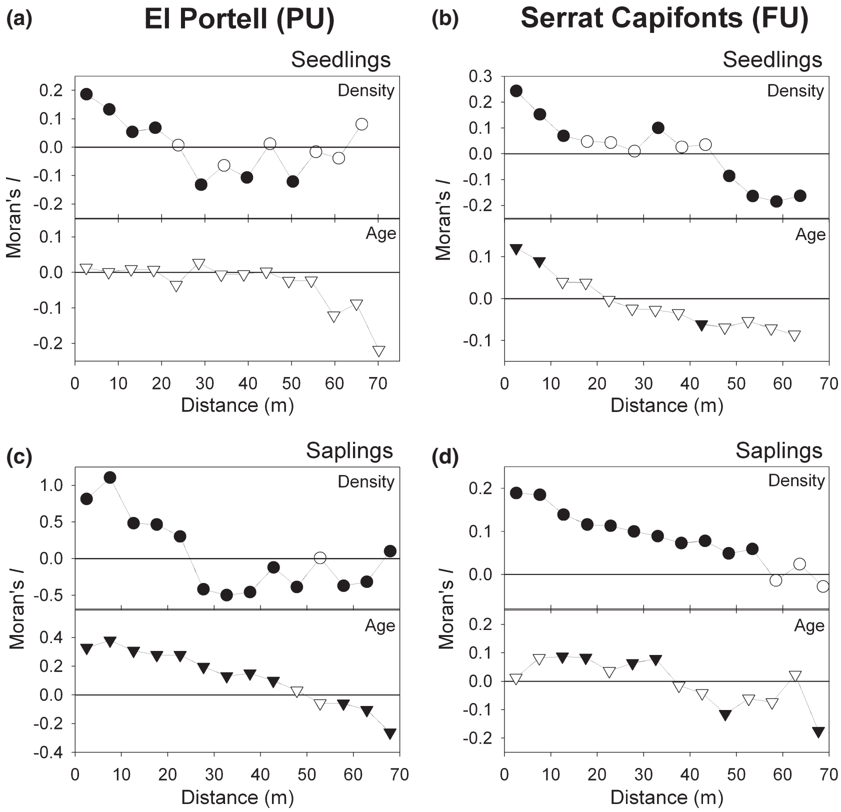

Figure 4 Spatial correlograms based on Moran's *I* index for density (circles) and age (triangles) of *Pinus uncinata* seedlings and saplings in the two Pyrenean tree line ecotones studied using large plots: (a) and (c) PU, a disturbed site; (b) and (d) FU, an undisturbed site. Solid symbols indicate significant values at $P < 0.05$, and open symbols indicate non-significant values. All correlograms, excepting the one corresponding to the age of seedlings at PU, are globally significant ($P < 0.05$).

age at PU decreased gradually with elevation, whereas sapling age had a patchy distribution at FU. Finally, the pattern of sapling density corresponded to a large patch at PU (*c.* 50 m) and to an upward gradient of decreasing sapling density at the FU site (Fig. 4).

The smaller plots, including both disturbed and undisturbed tree lines, had similar small-scale distribution patterns of tree classes (Fig. 5; and see Appendix S1 in Supporting Information). Seedlings were spatially aggregated (up to 2.5 m) in 70% of the stands, whereas sapling aggregation was found at 20% of the sites. Furthermore, non-significant departures from the CSR towards aggregation in seedling spatial pattern were found in the other 30% of the plots. Finally, none of the smaller plots had a spatial distribution of the large tree class significantly different from CSR. The spatial relationship between tree classes in the smaller plots indicated that the patterns detected in the larger plots are the most common in Pyrenean alpine tree lines, both at disturbed and undisturbed sites. In all smaller plots seedlings were spatially segregated from large trees, and patterns for seedlings and saplings also tended to be repulsed (Fig. 5). Finally, large trees and saplings mainly had repulsed patterns.

No spatial segregation at the plot scale between the two recruitment periods (1950–74 and 1975–99) was detected by SCC analyses in the PU and FU plots (Fig. 6). Furthermore, five of the smaller plots had slightly negative but non-significant SCCs between recruitment periods, whereas values for the other five were positive but mostly non-significant. Hence, no significant spatial segregation between recruitment periods was detected in any of the tree lines studied, irrespective of recent anthropogenic disturbances.

DISCUSSION

Irrespective of tree line attributes (disturbed or undisturbed), the recruitment of *P. uncinata* was characterized by a strong clustering of seedlings at small distances (0–3 m). Saplings showed clustering at the same scale range and strength as seedlings, but to a lesser degree. In contrast, large trees were not clustered. Differential aggregation patterns according to the stage of the life cycle have been described at the alpine tree line (Mast & Veblen, 1999; Camarero *et al.*, 2000; Srutek *et al.*, 2002). These can, for example, result from establishment in similar favourable microhabitats, followed by density-dependent mortality that reduces the degree of spatial association over time (Humphries *et al.*, 2008). Despite the lack of explicit measures of mortality rates in the study plots, both the proportion of dead seedlings at the time of sampling (Batllori & Gutiérrez, 2008) and the absence of a clear age gap in the demographic structures between seedlings and saplings fail to indicate high mortality rates under current climatic conditions. Furthermore, the all-aged frequency distribution of recruits suggests that recruitment is not limited and is continuous. This illustrates that constraints on tree survival, explaining the reduction of spatial association over time (i.e. seedlings versus large trees), may affect older classes more than seedlings.

As expected, due to the shade intolerance of *P. uncinata*, as indicated by its dependence on disturbance for regeneration

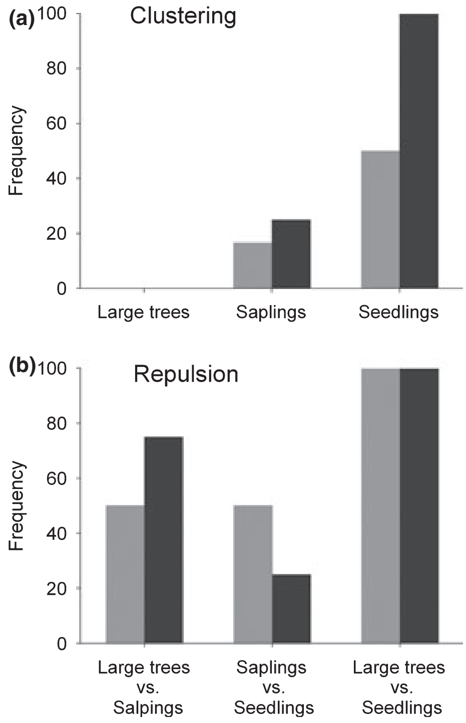

Figure 5 Summary of the univariate and bivariate point-pattern analyses in the 10 *Pinus uncinata* tree line ecotones studied in the Pyrenees using small plots. The frequencies of (a) significant clustering in at least some analysed distance for each tree class and (b) the negative spatial relationship (repulsion) between tree classes are illustrated. Light grey bars correspond to the undisturbed sites and dark grey bars correspond to the disturbed sites (see Table 2 for details).

(Bosch & Gutiérrez, 1999; Camarero *et al.*, 2005), we found evidence of spatial segregation between large trees and seedlings and saplings. First, this reinforces the idea that *P. uncinata* recruits establish predominantly above the forest limit, where favourable microsites for regeneration occur (Batllori *et al.*, 2009). Second, the weak support for positive spatial interactions between large trees and seedlings indicates that facilitation among these classes is weak, at least at these sites. This contrasts with the positive influence of tree islands and krummholz individuals on seedling abundance reported at other alpine tree lines, which has been attributed to facilitation (Hättenschwiler & Smith, 1999; Camarero *et al.*, 2000; Germino *et al.*, 2002). However, facilitation at the tree line has been related to protection by snow cover, among other factors (Smith *et al.*, 2003). Because isolated trees, krummholz individuals and tree islands have different effects on wind-blown snow cover accumulation (Scott *et al.*, 1993), the absence of such facilitation at the tree lines of this study may be attributable to the upright structure of the large trees that are rarely grouped in islands.

Seedlings and reproductive individuals exhibited peaks of aggregation at short and intermediate distances (3, 10–13 and 17 m), covering the entire range of scales studied in both disturbed and undisturbed tree line ecotones. Although highly variable spatial patterns in seed-dispersal rates are common in wind-dispersed pines (Nathan & Muller-Landau, 2000), our results showed strikingly similar intermediate-distance aggregation at the two large plots. The most frequent dispersal distance for *P. uncinata* seeds, estimated from the spatial pattern of seedlings in a relict population in northern Spain as well as in release experiments, was reported as being between 4 and 30 m (Camarero *et al.*, 2005). *Pinus uncinata* produces small winged seeds, which are primarily dispersed by wind in early spring, with large crops occurring every 2–4 years (Cantegrel, 1983). Furthermore, the mode of seed dispersal directly affects the spatial pattern of tree regeneration and the spatial interactions with conspecific individuals (Seidler & Plotkin, 2006). In all the tree lines studied, reproductive individuals showed significant attraction with large upright trees (mean SCC = 0.72 ± 0.13 SD), thus indicating that seed release may usually occur above a certain height. Bearing in mind that high wind speeds are typical of mountain environments (Barry, 1992), we suggest that in *P. uncinata* tree lines dispersal at medium distances may be more effective than in lower subalpine forest populations. Thus, we hypothesize that the intermediate-distance aggregation pattern detected at the tree lines reflects frequent dispersal events at these distances, and that rarer long-distance events might include greater distances than those detected in our analyses. Furthermore, we found no evidence of even-aged regeneration patches and no significant spatial segregation between the recruits of the periods 1950–74 and 1975–99. In accordance with Dalen & Hofgaard (2005), these results may indicate, together with the all-aged structure of the tree lines, that seed dispersal, seed quality and germination are unlikely to be limiting factors in current tree line dynamics. Overall, our results do not identify recruitment limitation as a constraint on recent tree line dynamics in either disturbed or undisturbed sites.

The spatial autocorrelation analyses of recruit age and density (seedlings and saplings) revealed distinct patterns between disturbed and undisturbed tree lines. However, the patterns of saplings in the disturbed site were very similar to the patterns of seedlings in the undisturbed site. Furthermore, the strength and range of small-scale clustering of saplings and seedlings were very similar between the disturbed and undisturbed sites, respectively. We suggest that this reflects, in accordance with the demographic structure at the two sites, an earlier response of the tree line (i.e. ecotone afforestation) to changing conditions in the disturbed site than in the undisturbed site. This may be related to the past disturbance regime of each site, which, as argued by Holtmeier & Broll (2007), may produce a complex spatiotemporal mosaic of tree line ecotones at different successional stages. The importance of microenvironmental conditions for recruit survival at the tree line has been recognized (e.g. Smith *et al.*, 2003; Körner, 2007), and we found very similar small-scale spatial distributions of the recruits in all the tree lines studied. Hence, consistent with Resler (2006), our results point to the similarity of the microtopographical conditions at the tree lines irrespective of disturbance history. This may indicate that the underlying

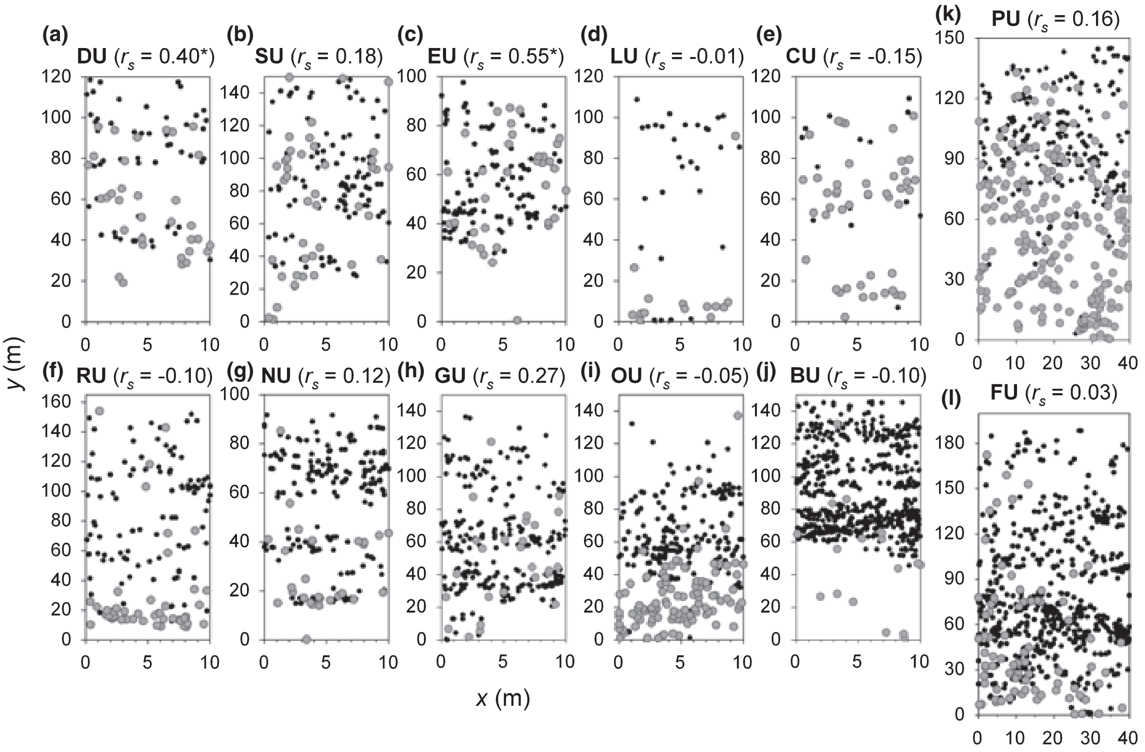

Figure 6 Mapped point patterns of recent *Pinus uncinata* recruitment in the twelve tree line ecotones studied in the Pyrenees: (a)–(j) small plots and (k)–(l) large plots (see Table 2 for site details). Two recruitment periods are illustrated: 1950–74 (grey circles) and 1975–99 (black dots). The *y*(m) and *x*(m) axes represent the longer and shorter side of each plot, respectively, in metres. The spatially corrected Spearman's correlation coefficient (r_s) between the two recruitment periods is noted for each site. *Significant ($P < 0.05$) r_s coefficients.

processes influencing short-term tree regeneration at undisturbed and disturbed tree line ecotones are similar; recruits that invade former pastures after human-induced disturbances are more strongly restricted by unfavourable site conditions (e.g. a lack of safe sites for regeneration) than in low-elevation forests (Holtmeier & Broll, 2005). Thus, our results do not indicate a faster short-term response of the tree line to climate in human-disturbed sites, once disturbance has ceased, compared with undisturbed sites.

The small-scale spatial clustering of recruits detected in all the ecotones studied, irrespective of tree line type (disturbed or undisturbed), in conjunction with the temporal recruitment pattern (acceleration and decline periods), may indicate positive feedback (Alftine *et al.*, 2003). Snow is an important factor in feedback processes at the tree line. Tree clumping promotes a more favourable microenvironment by enhancing snow retention, which increases recruit survival (Smith *et al.*, 2003). However, as suggested by Alftine *et al.* (2003), winter climatic variability may disrupt the establishment and survival of recruits, also limiting feedback processes, which may explain the recruitment drop observed in the study plots in the last decade. The effects of climatic conditions and their variability on *P. uncinata* recruitment at the Pyrenean tree line remain to be described.

Feedback processes and the spatial distribution of suitable sites for regeneration (determined in part by feedbacks) may exert a strong influence on spatial patterns of the tree line, and also modulate population responses of the tree line to environmental change (Alftine & Malanson, 2004; Bekker, 2005). However, the spatial pattern at any given time is only indicative of recent dynamics, and this distribution can potentially be affected by several factors (Malanson, 1997; Malanson *et al.*, 2006). Thus, differences in local conditions due to the macrotopography may result in medium-term variability in tree line dynamics among sites owing to local interactions between micro- and macrotopography. Such interactions may be of great importance in tree line ecotones where upright trees are constrained by different factors from recruits, which are more influenced by microsite conditions (Holtmeier & Broll, 2007, and references therein; Körner, 2007). We believe this is illustrated in our sites. The absence of spatial segregation between the 1950–74 and 1975–99 recruitment periods suggests that during the last 50 years tree line dynamics have mainly corresponded to a continuous infilling process rather than upward shifts of the tree line in both disturbed and undisturbed sites. However, previous studies at the same sites suggested upward shifts in several tree lines (including both undisturbed and disturbed sites) based on the uppermost elevation of 2 m tall upright trees, i.e. rises of the tree limit (Batllori & Gutiérrez, 2008). This may indicate that since the 1950s, the environmental conditions that promoted widespread, increased tree density of the tree line, which resulted in more favourable microenvironmental conditions for recruit survival, also enhanced the vertical growth of established trees in some sites (raising the tree limit position). However, new recruits have not successfully established in treeless alpine communities far above the current position of the tree line. Our results also highlight the importance of standardizing the methodology to compare studies dealing with the rate of shift of the tree line. For instance, it is not appropriate to compare rates of change in position of the tree line derived from determination of tree age at a certain height (e.g. 2 m) with those derived from analyses of recruitment dynamics. Overall, patterns of abundant recruitment within the ecotone may serve as an early signal of conspicuous future changes in position of the tree line (tree line shifts) if the predicted increase in extreme climatic events does not distort current tree line trends (Camarero & Gutiérrez, 2004; Meehl *et al.*, 2007).

Given the absence of recruitment limitation found in both disturbed and undisturbed tree lines, we propose that under current climate conditions the constraints on tree line dynamics triggering differential responses may operate upon growth and survival of upright trees rather than on recruits. Furthermore, such constraints may include processes more contingent on local environmental conditions than on the recent disturbance history. Finally, our findings suggest that the value of recruitment patterns for assessing rates of change of the position of the tree line may be limited.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Spatial patterns of *Pinus uncinata* at the alpine tree line in the Pyrenees.

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