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RESEARCH PAPER

Spatial patterns of plant richness across treeline ecotones in the Pyrenees reveal different locations for richness and tree cover boundaries

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ABSTRACT

Aim To forecast the responses of alpine flora to the expected upward shift of treeline ecotones due to climatic warming, we investigated species richness patterns of vascular plants at small spatial scales across elevational transects.

Location Richness patterns were assessed at local scales along the elevational gradient in two undisturbed treeline ecotones and one disturbed treeline ecotone in the Spanish Pyrenees.

Methods We placed a rectangular plot (0.3–0.4 ha) in each treeline ecotone. We estimated and described the spatial patterns of plant richness using the point method and Moran's *I* correlograms. We delineated boundaries based on plant richness and tree cover using moving split windows and wavelet analysis. Then, to determine if floristic and tree cover boundaries were spatially related, overlap statistics were used.

Results Plant richness increased above the forest limit and was negatively related to tree cover in the undisturbed sites. The mean size of richness patches in one of these sites was 10–15 m. Moving split windows and wavelets detected the sharpest changes in plant richness above the forest limit at both undisturbed sites. Most tree cover and plant richness boundaries were not spatially related.

Main conclusions The upslope decrease of tree cover may explain the increase of plant richness across alpine treeline ecotones. However, the detection of abrupt richness boundaries well above the forest limit indicates the importance of local environmental heterogeneity to explain the patterns of plant richness at smaller scales. We found highly diverse microsites dominated by alpine species above the forest limit, which should be monitored to describe their response to the predicted upward shift of forests.

Keywords

Boundaries, correlogram, elevational gradient, forest limit, *Pinus uncinata*, species diversity, wavelet analysis.

INTRODUCTION

Mountains contain several ecotones between different vegetation types under steep climatic gradients. This large environmental variation within a small geographical area makes elevational gradients ideal for investigating spatial patterns in species richness (Körner, 2000). Climatic warming might cause an upslope ascent of treeline ecotones in temperate and cold mountains and the consequent contraction and fragmentation of alpine areas (Brubaker, 1986; Theurillat & Guisan, 2001). Although recent warming has also induced upward migrations of herbaceous plants, many plant species might be unable to migrate upward rapidly enough (Grabherr *et al.*, 1994). Alpine floras may be highly sensitive to the upward displacement of forests because these floras have a high proportion of endemic species restricted to open microsites. Nevertheless, some species may persist as fragmented populations in favourable non-forested sites such as cliffs (Bruun & Moen, 2003). The displacement of bioclimatic limits would promote the upward shift of the two limits that define the treeline ecotone, i.e. the forest limit (uppermost location of sites where tree cover is above 50%) and the treeline (uppermost locations of trees at least 2 m tall). Recent findings have shown, however, that the spatiotemporal variability of these ecotones may mask their response to climatic warming (Daniels

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& Veblen, 2003), thus making it difficult to forecast how treeline dynamics will affect alpine flora.

To define the susceptibility of alpine grasslands to tree colonization, we need a precise description of the spatial pattern of plant communities across treeline ecotones at local scales, i.e. how and where plant richness changes abruptly along the elevational gradient (Hofgaard, 1997). The classical edge-effect hypothesis predicts that plant richness should increase within treeline ecotones (ecotone effect) in comparison with adjacent communities due to the interchange of species between forest and alpine communities (Stevens, 1992; Lomolino, 2001). Specifically, plant richness might peak at or near the forest limit where many plant species have their uppermost or lowermost populations (Hofgaard & Wilmann, 2002). However, the lack of studies at small spatial scales has precluded the detection of this richness pattern and hypothesis testing of factors causing the richness increase across treeline ecotones (Grytnes, 2003).

The definition of the forest limit relies on changes in tree cover and density, which should be among the main causal factors of the richness patterns within the treeline ecotone. Nevertheless, the scarcity of quantitative descriptions of tree cover and plant richness boundaries (abrupt changes) limits our ability to predict the interactions between them (Camarero *et al.*, 2000). The colonization of alpine grassland by trees may affect plant species in different ways according to their life traits. Many alpine species are adapted to high levels of radiation (Ellenberg *et al.*, 1991), and might be very susceptible to increasing tree cover. If plant richness patterns are controlled mainly by changes in tree cover and radiation at local scales across treeline ecotones, the boundaries of both variables should appear in nearby locations, i.e. the plant richness and tree cover boundaries should overlap.

To predict the response of local alpine flora to treeline shifts, we have to understand how the spatial patterns of plant richness across the treeline ecotone are influenced by the spatial patterns of tree cover at local scales. Specifically, this study addressed the following objectives: (i) to characterize the structure and spatial pattern of vascular plant richness across contrasting treeline ecotones along the elevational gradient; and (ii) to detect and relate boundaries of tree cover and plant richness within these ecotones. We hypothesized that vascular plant richness should increase above the forest limit, but not necessarily near this limit, in undisturbed treeline ecotones due to the reduction in tree cover. This hypothetical negative relationship between tree cover and plant richness at the ecotone scale does not imply similar and coherent spatial patterns for both variables if additional factors operate at local scales (e.g. soil features, competition, facilitation, dispersal). Therefore, we hypothesized that the main boundaries of plant richness and tree cover will appear in nearby locations if cover is the main factor controlling richness patterns at local scales.

MATERIALS AND METHODS

Alpine treeline ecotones in the Pyrenees

In the central Pyrenees, there has been a +0.8 °C increase in mean temperature during the 20th century (Bücher & Dessens, 1991). Assuming an elevational thermal lapse rate of 0.6 °C per 100 m, this warming would elevate bioclimatic limits by *c.* 130 m, which agrees with recent estimates of treeline shifts (1–2 m yr^{-1}; Camarero & Gutiérrez, 2004). *Pinus uncinata* Ram. dominates most alpine treelines in the Pyrenees. This shade-intolerant conifer colonizes all kinds of soils, and shows several attributes typical of good invaders such as light-winged seeds, short pre-reproductive period and frequent large crops (Ceballos & Ruiz de la Torre, 1979). Current mean elevations of undisturbed forest limits and treelines in the study area are 2300–2400 m a.s.l. and 2600–2700 m a.s.l., respectively. However, most forest limits have been depressed by man to 2000–2200 m a.s.l.

Study sites

To describe the spatial pattern of vascular plant richness at the local scale, we selected three sites that represented the environmental variability of Pyrenean treeline ecotones (Table 1). Sites Ordesa (hereafter O) and Tessó (hereafter T) are located in the buffer zones of National Parks. This fact, the comparison of current (1988) and previous aerial photographs (1946), and historical data led us to consider both sites as undisturbed at least during the past century. The present levels of livestock in nearby areas are not high (8–24 and 2–6 sheep month ha^{-1} for sites O and T,

Table 1 Geographic, topographic and structural characteristics of the studied ecotones (O, Ordesa; T, Tessó; E, Estanys de la Pera). Structural variables refer to *P. uncinata*

Characteristics	O	T	E
Latitude (N)	42°37′	42°36′	42°28′
Longitude	00°02′ W	01°03′ E	01°38′ E
Treeline/forest limit elevation (m a.s.l.)	2110/2100	2360/2330	2430/2400
Mean slope (°)/aspect	17/S	27/NE	19/SW
Main bedrock type	Limestones	Shales	Granites
Density (stems ha^{-1})	9548	476	963
Basal area (m^2 ha^{-1})	8.87	12.10	10.62
Mean (± SE) height (m)	1.56 ± 0.12	4.00 ± 0.29	2.39 ± 0.11
Mean (± SE) patch size (m)	4.49 ± 0.57	4.14 ± 0.54	3.11 ± 0.56
Cover (%)	40.90	24.94	13.37
S (plant richness)	40	25	16
Human disturbances	Undisturbed	Undisturbed	Disturbed

respectively; Aldezábal *et al.*, 1992; Bas *et al.*, 1994). The available historical documentation shows relatively few local anthropogenic disturbances at either site during the last 200 years. In site O, we found some burnt stems due to a fire during the 1930s that affected the lower subalpine forest. Site T is not appropriate for logging because of poor access and has not been subject to local human disturbance such as grazing since at least the 1790s (Bringue, 1995). Sites O and T also showed contrasting structures because the former has a locally depressed treeline due to the effects of intense winds, while the latter is more affected by snow effects (Camarero & Gutiérrez, 2002). The structure of site O was characterized by the sharp decrease in tree height, whereas site T showed a more gradual upward decrease of tree height. At site O, multistemmed krummholz individuals are dominant. We also studied a disturbed site in Estanys de la Pera (hereafter E), where signs of intense grazing were observed (Table 1). The most prominent feature of site E was the presence of scattered 'tree islands'.

Field sampling

We placed a rectangular plot in each site (30 m × 140 m in sites O and T; 30 m × 100 m in site E because a rocky cliff located downslope did not allow us to extend the plot up to 140 m) with its longest side parallel to the slope and encompassing treeline and forest limit. To estimate plant species richness (S) and *P. uncinata* cover (%), we used the point method (Barbour *et al.*, 1987). A sampling grid design, formed by six transects along the maximum slope (y axis, elevation), was used to record plant richness (Fig. 1). Transects were located every 6 m perpendicular to the slope along the x axis ($x = 0, \ldots, 30$ m) going from the lower ($y = 0$, forest) to the upper edge of the plot ($y = 140$, above treeline). We counted the number of contacts of understorey plants recorded individually and pine canopies with a metal rod (diameter = 2 mm) placed every 1 m along the y axis. We regarded the 1-m spacing as an appropriate scale to capture most of the variability in plant richness across the ecotone. Then, the number of vascular plant species for each 1-m elevational band was obtained combining the data of all transects. We acknowledge the fact that richness estimates based on the point method depend on plant size, which affects the probability of occurrence. However, plant size did not change greatly within the study plots as a function of elevation or tree cover, which makes our richness estimates comparable between the study sites and with other studies using number of species per plot of a given area. Finally, the location and size [diameter at breast height (d.b.h.) and height (h)] of all *P. uncinata* individuals located within each plot were recorded. Botanical nomenclature follows de Bolós *et al.* (1993).

Ecotone structure

To determine how the structure of treeline ecotones affected changes in plant richness, we related several characteristics defining ecotone structure and plant richness using the non-parametric Spearman's rank correlation coefficient (r_s). As environmental heterogeneity changes greatly at small scales near treelines (Hansen-Bristow, 1986), we used summary statistics to capture the main vertical and horizontal changes that may affect changes in plant richness. For instance, sites under dense tree cover or near krummholz individuals should show contrasting plant richness. To quantify the vertical and the horizontal heterogeneities across the treeline ecotone we used the mean tree height and the mean patch size of pine cover at different locations, respectively. A patch was defined as a set of contiguous positions with pine cover located at 1-m spaced points along the elevational transects. Preliminary analyses showed that plant richness was autocorrelated spatially at least up to 10 m in sites O and T. To avoid spurious correlations due to autocorrelated data, we used this distance to average or sum the compared variables. We compared plant richness with descriptors of the structural heterogeneity of the ecotone every 10 m along the slope following the y-axis ($n = 14$, O, T; $n = 10$, E).

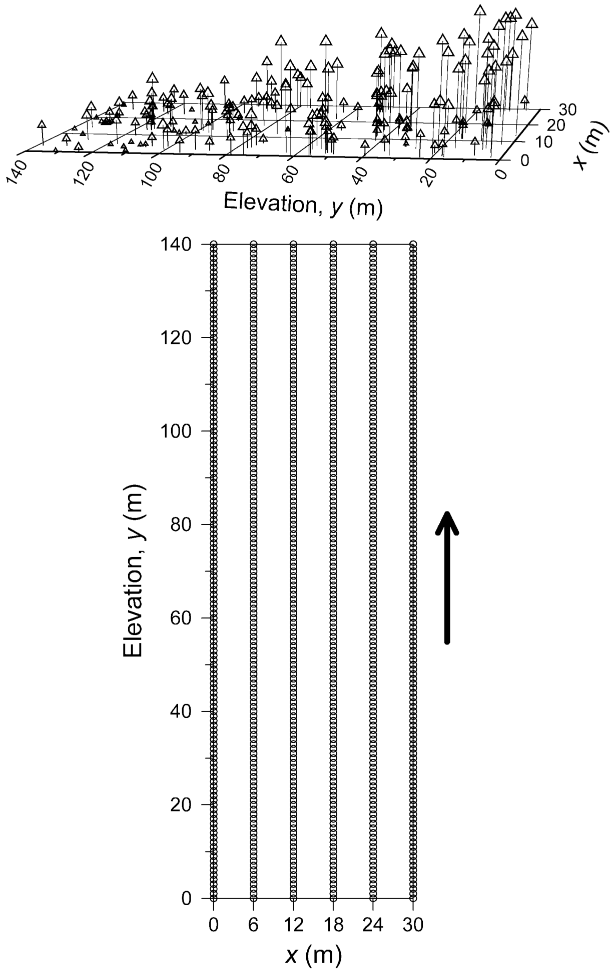

Figure 1 Schematic diagram illustrating the sampling point method used to estimate plant richness and tree cover changes across treeline ecotones. The upper figure shows the spatial distribution of *P. uncinata* individuals in the plot from site T. The lower figure shows the point method which was based on six transects located every 6 m perpendicular to the slope along the x axis ($x = 0, \ldots, 30$ m) going from the lower ($y = 0$, forest) to the upper edge of the plot ($y = 140$, treeline).

Spatial analyses

To characterize the spatial pattern of cover and plant richness across the three treeline ecotones, we used Moran's *I* correlograms (Legendre & Fortin, 1989). First, for each site we calculated the plant richness every 1 m along the slope considering the richness data across the six elevational transects. Second, we obtained a correlogram (a plot of distance vs. autocorrelation) based on this transect of plant richness across the ecotone. Correlograms were based on both raw richness values and the residuals by considering if the richness–elevation fits after detrending the elevational gradient. To describe the spatial pattern of *P. uncinata* cover, we calculated similar correlograms based on Moran's *I* for cover residuals extracted from elevation–cover linear regressions. Moran's *I* coefficient ranges from –1 (negative spatial autocorrelation) to +1 (positive spatial autocorrelation), 0 being the expected value for complete spatial randomness. The point at which the value of the autocorrelation coefficient crosses the abscissa in a correlogram provides an estimate of the mean size of the zone of influence of the variable in question. We used equal distance classes (5 m) with at least 30 values per class to calculate the correlogram. The global significance of the correlogram at the 5% level was tested using a Bonferroni procedure (Manly, 1997).

Detection of boundaries using moving split windows and wavelets

To detect boundaries in tree cover and plant richness within treeline ecotones we used: (i) the moving split windows technique to detect boundaries in *P. uncinata* cover; and (ii) wavelet analysis to detect plant richness boundaries. In both cases, we eliminated the large-trend spatial autocorrelation in a two-step process. First, we removed the linear trend of the raw richness data with respect to elevation through linear functions, which explained a high proportion of the variance for both variables (Table 2). Then, we used the residuals of the linear fits as input data for boundary analyses.

The use of moving split windows to detect boundaries along one-dimensional transects consists of: (1) defining a window with a predefined width; (2) dissecting the window into two equal halves; and (3) comparing the two halves through some dissimilarity metric (Whittaker, 1960). The window is moved along the transect and the locations of maximum rate of change in the analysed variable are identified (Ludwig & Cornelius, 1987). The window width must be large enough to detect boundaries and small enough to detect complex edges. After preliminary tests with different window widths (2–20 m), we selected a 10-m window as the most appropriate resolution for identifying boundaries at small spatial scales. Smaller windows detected multiple boundaries in areas where richness changes were subtle. Boundary locations were defined as those locations where the difference values were in the upper 10th percentile (Fortin, 1999). Boundary locations were compared with absolute change in tree cover (% m^{-1}) going downslope.

Table 2 Results of linear regressions fit to *P. uncinata* cover (*Pu*) or plant richness (*S*) and elevation (*y*) at three treeline ecotones (O, Ordesa; T, Tessó; E, Estanys de la Pera). The relative elevation varies from $y = 0$ (forest, lower edge of the plot) to $y = 140$ (treeline, upper edge of the plot). The values of *a* and *b* correspond to the constant and the slope of the linear regressions ($Pu = a + by$; $S = a + by$). Parameter estimates are presented with their SE and significance level

Site/variable	*a*	*b*	r^2
Pu			
O	87.84 ± 2.98**	–0.67 ± 0.04**	0.70
T	51.63 ± 2.79**	–0.38 ± 0.03**	0.47
E	32.47 ± 4.46**	–0.21 ± 0.05**	0.17
S			
O	1.62 ± 0.24**	0.03 ± 0.01**	0.46
T	3.17 ± 0.19**	0.02 ± 0.01**	0.24
E	2.35 ± 0.42**	0.01 ± 0.01	0.01

*$0.01 < P \leq 0.05$; **$P \leq 0.01$.

As moving split windows can ignore minor changes at smaller scales (Choesin & Boerner, 2002), we analysed plant richness data from the undisturbed sites O and T using wavelet analysis to detect abrupt changes in richness along the elevational gradient. Wavelets are similar to moving window analyses, but the wavelet functions are also robust against nonstationarity (Bradshaw & Spies, 1992). The wavelet function allows the detection of edges along a data series and the characteristic scales (patterns) of the analysed series. If the shape of the wavelet function is similar to the shape of the underlying data series, the wavelet variance has a higher value. Where there is a sharp change in adjacent values along a data series (boundary), there will be a relatively large increase in the wavelet variance indicating the presence of a boundary (Dale & Mah, 1998). We performed wavelet analysis on the residuals of linear fits between plant richness and elevation. To check if variance peaks matched sharp changes in plant richness, they were compared with original data and with boundaries detected using moving split windows. We selected the Haar wavelet because it is the most appropriate for detecting discontinuities in a spatial data series (Bradshaw & Spies, 1992). We used a continuous wavelet transform at a maximum scale of 10% (14 m). To estimate confidence intervals, we performed wavelet analyses on 99 randomizations of the original data set. The 95th highest value of wavelet variance was considered for each position to determine significant values at the 0.05 level (Manly, 1997). We performed a one-tailed test as we were testing if closer boundaries were influencing one another spatially. We assumed that the spatial autocorrelation of the analysed residual values did not affect our results greatly because the residuals were not highly autocorrelated. However, future analyses should be based on restricted randomizations based on the degree of autocorrelation in the observed data, which would provide more conservative estimates of the confidence intervals (Fortin & Jacquez, 2000). Spatial analyses were carried out using the software *PASSaGE* (Rosenberg, 2002).

Overlap statistics

To investigate if boundaries of *P. uncinata* cover and plant richness occur in nearby positions, we used overlap statistics based on mean nearest-neighbour distances (Fortin *et al.*, 1996). Following Jacquez (1995), four overlap statistics are defined when comparing two sets of boundaries (G and H, i.e. plant richness and tree cover boundaries): O_S, the number of boundaries found in both sets of variables; O_G, the mean distance from any boundary location for G to the nearest boundary location for H; O_H, the mean distance from any boundary location for H to the nearest boundary location for G; and O_{GH}, the mean nearest-neighbour distance from one boundary location in either variable to the nearest boundary location in the other. We expressed the overlap statistics O_G, O_H, and O_{GH} as standardized statistics, with positive values indicating boundary overlap and negative values indicating boundary avoidance. To determine the significance of the overlap statistics we performed 999 randomizations (Manly, 1997). As null hypothesis, we assumed the complete spatial randomness of the original observations. In this analysis, we considered that the plant richness boundaries were influenced by the *P. uncinata*-cover boundaries (and not vice versa). Therefore, we randomized only the original values of richness while preserving the location of pine-cover boundaries. When $O_S = 0$, its value and its associated significance level can be discarded. Boundary analyses were carried out using the software BoundarySeer (Greiling *et al.*, 2002).

RESULTS

Ecotone structure and plant richness at local scales

At the undisturbed sites (O, T), plant richness increased linearly upslope (Table 2). Although second-order functions also gave acceptable fits for the elevation–richness relationship ($r^2 = 0.27$–0.46, $F = 25.1$–59.1), linear functions captured a similar amount of variance in the richness data and showed higher F values (Table 2). The elevational decrease of *P. uncinata* cover at these sites was explained more effectively by logarithmic ($r^2 = 0.63$–0.77) than by linear functions ($r^2 = 0.40$–0.70).

Vascular plant richness increased above the forest limit at both undisturbed sites O and T (Fig. 2). Plant richness was related negatively and significantly to tree cover and basal area at these sites (Table 3). At site O, plant richness was related significantly ($P < 0.01$) and negatively to tree height and patch size. However, the latter two variables decreased upslope as richness increased at this site. At the disturbed site E, most structural variables did not covary with elevation, and they did not show any significant relationship with plant richness.

Spatial analyses of plant richness patterns

The Moran correlograms of plant richness revealed spatial patterns indicating the presence of diversity gradients in the undisturbed sites O and T, whereas the disturbed site E did not show any significant pattern (Figs 2 and 3a). However, the analyses of the residuals extracted from elevation–richness regressions indicated the existence of richness patches in site T, whose mean size was 10–15 m (Figs 2 and 3b). The examination of tree cover correlograms suggested a similar size for *P. uncinata* patches at this site (results not presented). The upslope increase in plant richness and the presence of gradients at the undisturbed sites suggested that their plant richness patterns were related to the increase in light availability above the forest.

Table 3 Correlation coefficients (r_s) between structural variables and plant richness for two undisturbed sites (O, T) and one disturbed site (E). Abbreviations: DIST, distance to the forest limit; SEEDL, *P. uncinata* seedling density (ind. ha^{-1}); COV, *P. uncinata* cover (%); DENS, *P. uncinata* density (ind. ha^{-1}); BASA, *P. uncinata* basal area (m^2 ha^{-1}); and *S*, plant richness. Correlations correspond to sites O, upper line; T, lower line (values above the diagonal); and E (values below the diagonal)

	DIST	SEEDL	COV	DENS	BASA	*S*
DIST	—	0.25	–0.88**	0.19	–0.95**	0.92**
		0.45	–0.88**	0.06	–0.97**	0.62*
SEEDL	–0.44	—	–0.40	0.71**	–0.36	0.19
			–0.44	0.54*	–0.43	–0.16
COV	–0.65*	0.15	—	–0.23	0.83**	–0.81**
				0.16	0.90**	–0.54*
DENS	–0.84**	0.72*	0.60	—	–0.34	0.14
					0.09	–0.50
BASA	–0.67*	0.28	0.76*	0.69*	—	–0.80**
						–0.68**
S	–0.24	0.15	–0.03	0.21	–0.24	—

*0.01 < $P \leq 0.05$; **$P \leq 0.01$.

Tree cover and plant richness boundaries

In both undisturbed sites O and T, tree cover boundaries appeared clustered near the forest limit (Figs 2 and 4). Some boundary locations of tree cover residuals appeared isolated below the forest limit at these sites, indicating the presence of gaps, especially in site T. Isolated boundary locations were also detected above the forest limit, except in disturbed site E where they were clustered. Wavelet analysis of plant richness detected significant sharp changes in richness within the ecotone at the undisturbed sites O and T (Fig. 5), but these changes were located away from the forest limit. In fact, most peaks of wavelet variance were located near the treeline (e.g. $y = 122$ at site O, and $y = 114$ at site T). Plant richness boundaries detected through wavelet analyses were located in similar positions as boundaries identified using moving split windows (results not presented). Spatial dissociation between tree cover and plant richness boundary locations was found at all sites, but only undisturbed sites O and T showed significant overlap statistics (Table 4). The boundaries of tree cover and richness occurred at distant locations (Figs 4 and 5). The detection of abrupt richness boundaries above the forest limit and the low overlap between tree cover and richness boundaries at the undisturbed sites indicate

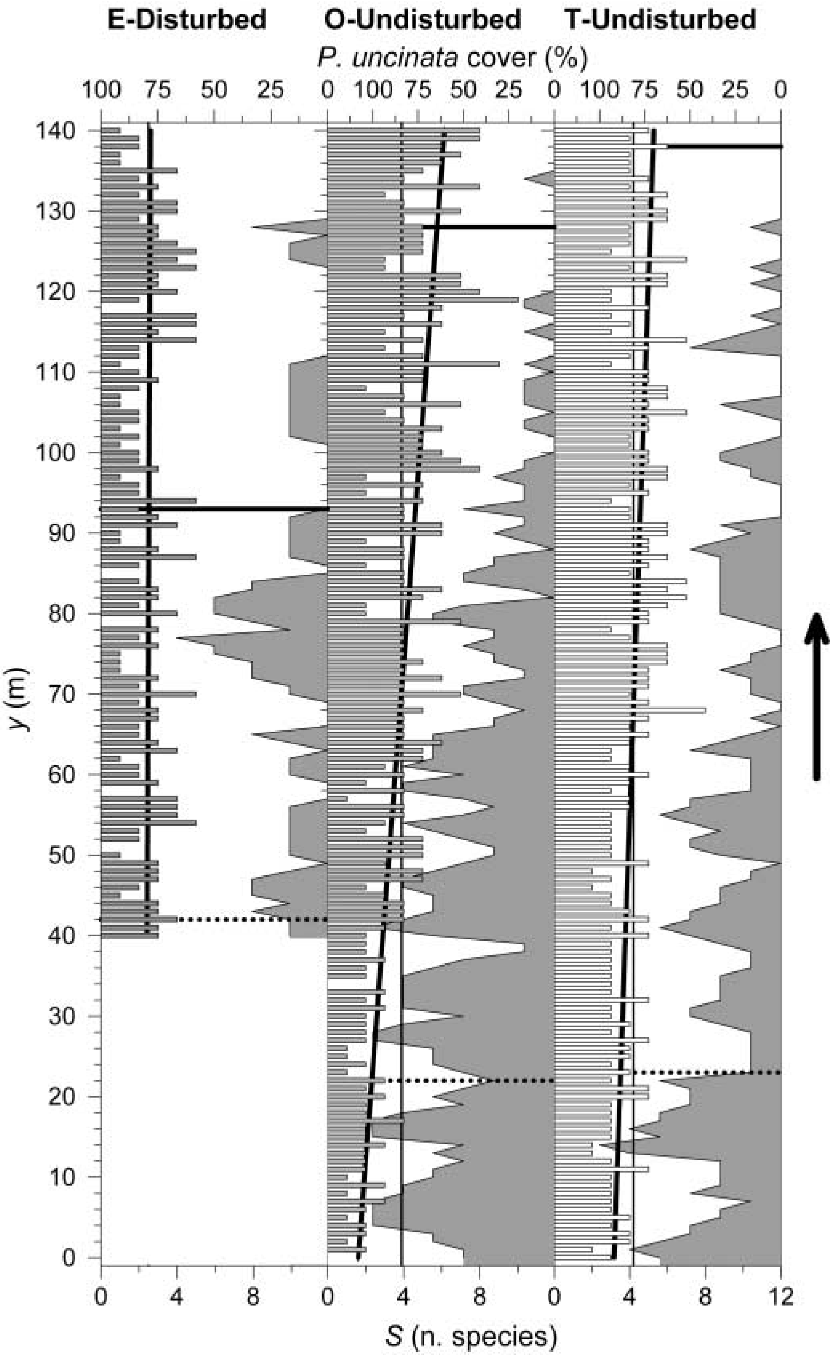

Figure 2 Changes in plant richness (*S*, bars) and *P. uncinata* cover (%, area graphs), along the elevational gradient (*y*) across three treeline ecotones (O, T, E). The thin vertical lines correspond to the mean richness value for each site, and the thick lines represent the linear *S*–*y* functions (Table 2). Horizontal lines correspond to the forest limit (dotted line) and the treeline (continuous line). The values of *P. uncinata* cover are indicated in the upper *x* axis (note the reverse scale).

the significance of local environmental heterogeneity to explain the patterns of plant richness at small scales.

DISCUSSION

At the regional scale, the forest limit may be regarded as a soft boundary, over which plant colonization can take place and hence create an ecotone effect. Grytnes (2003) detected an increase in plant richness well above the forest limit along elevational gradients. We did not detect any richness peak near the forest limit, which does not support the presence of feedback effects among the two neighbouring communities (alpine grassland, forest). Contrastingly, biogeographical comparisons of Asiatic forests revealed a sharp decline in plant richness above the forest limit, which was explained by lower winter temperatures upslope (Ohsawa, 1995). Nevertheless, the authors mentioned did not consider the radiation increase above the forest limit, which may enhance herb diversity at local spatial scales.

Grytnes (2003) suggested that the increase in species richness above the forest limit might be enhanced by a mass effect from forest taxa. The patterns of plant richness in this study corresponded to gradients, suggesting that the upslope increase in plant richness at the undisturbed sites was related to a greater light availability. As Grytnes (2003) pointed out, forest vascular

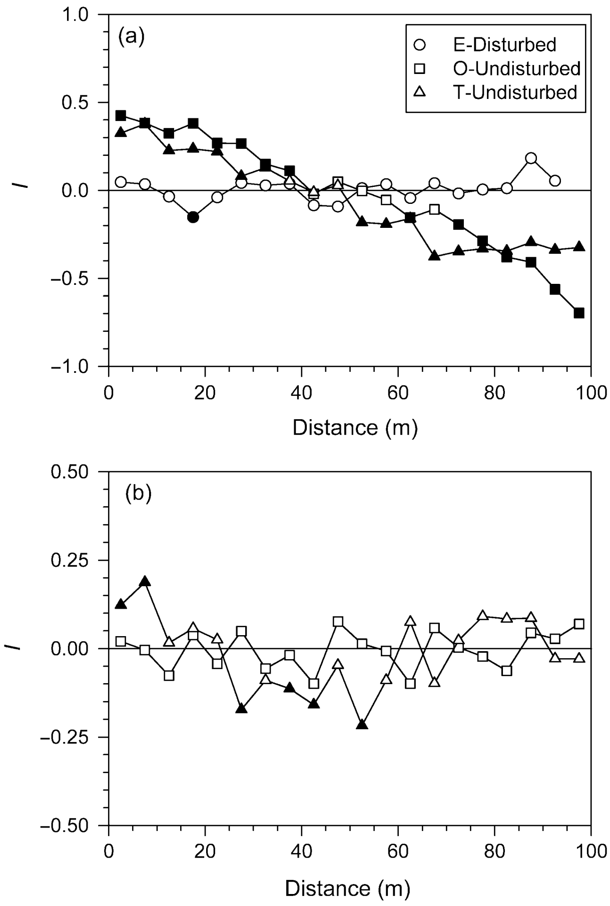

Figure 3 Spatial autocorrelation of understorey plant richness across three treeline ecotones (O, T, E) based on Moran's *I* correlograms. The correlograms were calculated using (a) raw richness data or (b) the richness residuals after extracting the elevational effects. The correlograms for sites O and T were globally significant ($P \leq 0.05$) in (a), while only that for site T was globally significant in (b). Filled symbols were significant ($P \leq 0.05$).

Table 4 Summary of overlap statistics (O_S, O_G, O_H, O_{GH}) computed between the boundary locations detected for *P. uncinata* cover (%) and plant richness across three elevational treeline ecotones (O, Ordesa; T, Tessó; E, Estanys de la Pera). The three last overlap statistics (O_G, O_H, O_{GH}) are displayed as standardized values, i.e. positive values indicate boundary overlap and negative values correspond to boundary avoidance. Abbreviations are as in Tables 2 and 3, except for *S*resid (residuals of the linear fit between position along the ecotone and plant richness at sites O and T; see Table 2)

Site	Pair of variables	O_S	O_G	O_H	O_{GH}
O	*Pu*–*S*	0	–2.35*	–7.29**	–5.87**
	Pu–*S*resid	0	–2.50*	–5.44**	–5.02**
T	*Pu*–*S*	2	–0.08	–1.61	–1.53
	Pu–*S*resid	2	–1.85	–1.20	–1.82
E	*Pu*–*S*	2	0.35	–3.11*	–2.55*

*$0.01 < P \leq 0.05$; **$P \leq 0.01$.

plants may be able to survive in open areas above the forest limit, whereas alpine plants will perish in shaded sites within the forest. However, the upslope increase in richness might also be related to a greater environmental heterogeneity above the forest limit. This might explain the underlying richness patches detected at site T and the spatial dissociation between tree cover and plant richness boundary locations. Our field observations support this view because the richness peaks above the forest limit in both undisturbed sites were caused mainly by the presence of typical alpine species, which were restricted to open microsites within the ecotone (Camarero & Gutiérrez, 2002).

A sharp change in species composition is one of the most characteristic features of ecotones (Van der Maarel, 1990; Walker *et al.*, 2003). Plant richness increased above the forest limit at the two undisturbed treelines so our data support an ecotone effect at the local scale. This increase in plant richness at the local scale may not be explained by the elevational climatic gradient (e.g. temperature decrease) or by differences in sampling area (Rosenzweig, 1995). The significant negative relationships between tree cover and plant richness agrees with other studies in temperate mountains (Dolezal & Srutek, 2002). In addition, several authors have described unimodal relationships between plant richness and cover at small scales (Grytnes, 2000; Grytnes & Birks, 2003). No unimodal relationship was observed between structure variables and plant richness. Perhaps a larger scale would have been more appropriate at both undisturbed sites to detect whether elevation is related curvilinearly to plant richness.

We found no spatial structure of plant richness in the disturbed site (E) where richness did not increase upslope. These two features might be expected for similar disturbed alpine treelines. The spatial changes of plant richness across treeline ecotones also differed between both undisturbed sites (O, T). The monotonous increase in richness at site O going upslope was steeper and more dependent on the location within the ecotone than the pattern detected at site T. Richness differences between both sites might be due to the size of species pool (Ricklefs, 1987). However, the different species pools of both undisturbed sites will not affect the negative relationship between tree cover and species richness. The contrasting patterns of plant richness might be due to different environmental conditions (Grytnes & Birks, 2003). Historical factors might also explain the different richness patterns of the two undisturbed treelines (Hofgaard & Wilmann, 2002). Furthermore, the different location, size and growth-form of trees of both ecotones might explain the divergent relationships between plant diversity and tree density. Site O was dominated by krummholz individuals forming a dense 'krummholz-belt' above the treeline but with low cover values. At this site, plant diversity was also high upslope because of the environmental variability generated by soil conditions and krummholz patches, i.e. horizontal heterogeneity prevailed. However, site T was characterized by a more gradual upward decrease in tree cover. The presence of significant relationships among variables describing the ecotone structure (e.g. tree cover) and plant richness may be a characteristic feature of undisturbed treelines. Relationships for the disturbed site were not significant, but showed the same direction as the undisturbed sites. This might

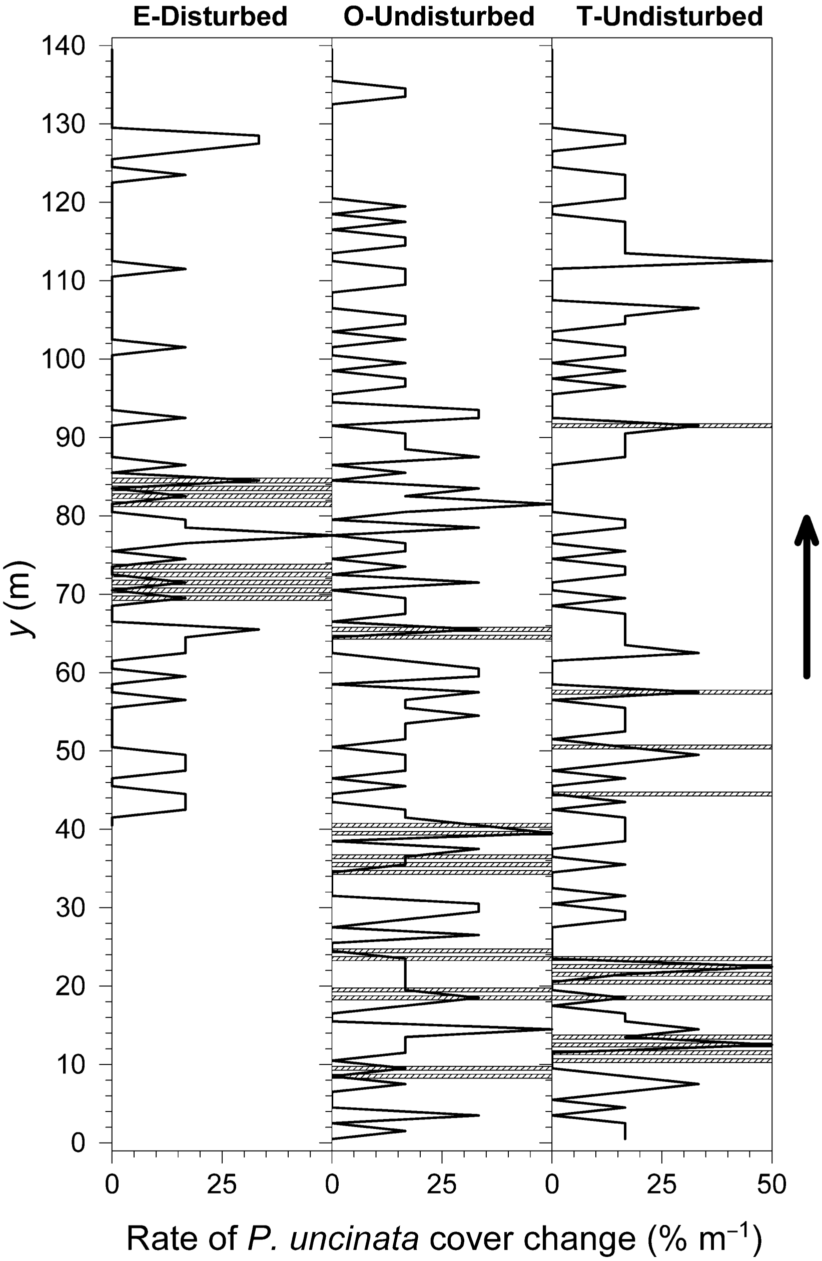

Figure 4 Comparison between tree cover boundaries (horizontal bars) and the rate of change of tree cover (% m^{-1}, lines) going downslope along the elevational gradient in three treeline ecotones (O, T, E).

be because the disturbed site was dominated by 'tree islands', whose presence masked any elevational trend in tree cover or richness.

The analyses of the elevation–richness residuals indicated the existence of richness patches in site T, whose size was similar to the scale of tree cover (10–15 m). Previous studies showed how snow avalanches created gaps with a mean size of 10–15 m in site T (Camarero *et al.*, 2000; Camarero & Gutiérrez, 2002). The richness pattern in site T implied that snow-mediated effects generated horizontal heterogeneity within this ecotone. Indeed, boundary locations of tree cover were frequent within the forest. Besides, dense mats of *Rhododendron ferrugineum* become dominant near the forest limit and prevent high-radiation levels in the understorey, thus reducing plant richness there. Although Vetaas & Grytnes (2002) found a reduction in habitat heterogeneity above the forest limit in Nepal, further studies should quantify how environmental variation changes at local scales across treeline ecotones.

Moving split windows and wavelet analyses based on the Haar wavelet, which is a split window, were efficient methods to detect plant richness boundaries at local scales. Sharp richness changes, as detected by wavelet analysis, were frequent above the forest limit. Overlap statistics confirmed that most tree cover and plant richness boundaries were located at distant positions. Thus, these statistics indicated that other factors in addition to tree cover influence the patterns of plant richness at smaller scales, for instance soil nutrients at site O or competition for light with the understorey at site T.

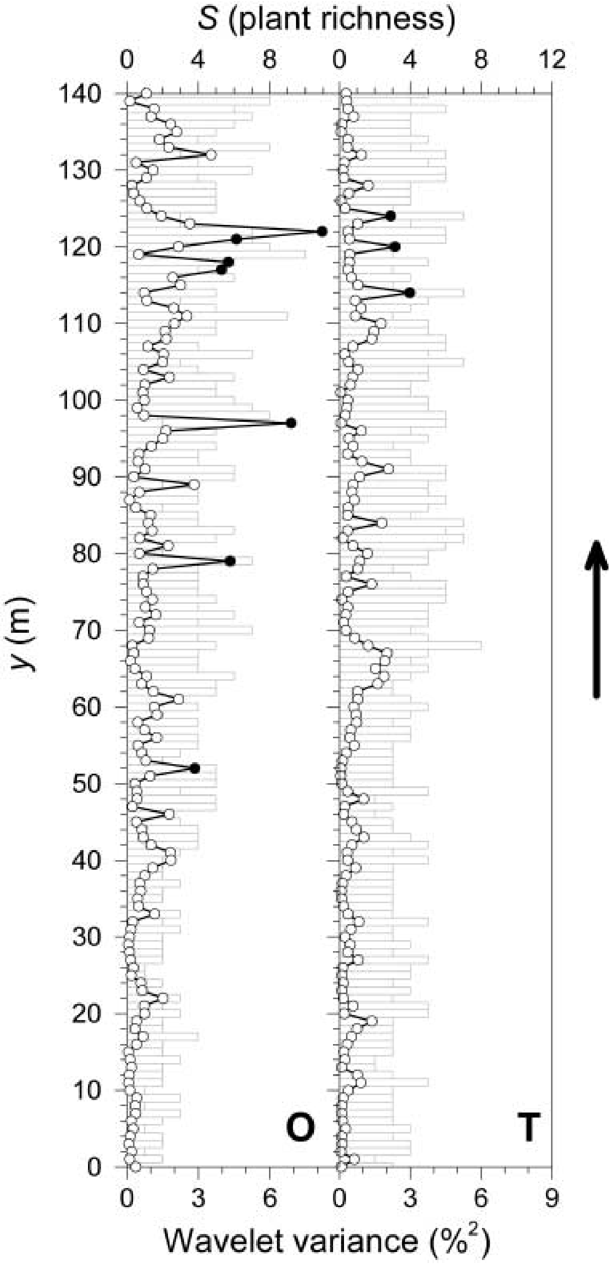

Figure 5 Comparison between plant richness boundaries based on wavelet analyses (lines, wavelet variance) and plant richness values (bars) in two undisturbed treeline ecotones (O, T). Filled symbols correspond to significant variance values ($P \leq 0.05$).

The trend of *P. uncinata* cover at the two undisturbed sites agrees with models predicting an upslope shift of tree species through rapid spread of isolated individuals (Kullman, 2002). Therefore, alpine flora might have to face nonlinear changes of upward tree expansion above the current forest limit. To address the impact of upslope treeline shifts on alpine vascular plant species, we should assess how the increase of tree cover affects those populations of alpine species at the lower margin of their distribution range. Nonlinear declines of plant richness above a certain threshold of tree cover might also be expected, but inertia in plant composition must not be disregarded.

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