

Spatial variability of tree height at treeline ecotones in the Pyrenees

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Abstract

We describe the spatial distribution of tree height of *Pinus uncinata* at two undisturbed altitudinal treeline ecotones in the southern Pyrenees (Ordesa, O, and Tessó, T). At each site, a rectangular plot (30 x 140 m) was located with its longest side parallel to the slope and encompassing treeline and timberline. At site O, height increased abruptly going downslope with a high spatial autocorrelation at short distances. In contrast, the changes of tree height across the ecotone at site T were gradual, and tree height was less spatially autocorrelated. These results can be explained by the greater importance of wind and snow avalanches at sites O and T, respectively.

Key words: fractal, height, *Pinus uncinata*, Pyrenees, semivariogram.

Resumen. Variabilidad espacial de la altura arbórea en ecotonos del límite del árbol en los Pirineos

Describimos la distribución espacial de la altura de individuos de *Pinus uncinata* en dos ecotonos del límite del árbol localizados en los Pirineos meridionales (Ordesa, O; Tessó, T). En cada sitio, situamos una parcela rectangular (30 x 140 m) con su lado mayor paralelo a la pendiente e incluyendo los límites altitudinales del árbol y del bosque. En el sitio O, la altura aumentó de forma brusca al descender en altitud mostrando una elevada autocorrelación espacial a pequeñas distancias. Por contra, los cambios de altura en el ecotono del sitio T fueron graduales, mostrando esta variable menor autocorrelación. Estos resultados pueden explicarse por la mayor importancia del viento en el sitio O y de los aludes de nieve en el sitio T.

Palabras clave: fractal, altura, *Pinus uncinata*, Pirineos, semivariograma.

Introduction

Recent regional climatic change has been described for the Central Pyrenees (Bücher & Dessens, 1991). Within this spatio-temporal context, altitudinal forest-pasture ecotones can be sensitive monitors of the effects of these changes on subalpine tree populations. These ecotones can respond to global change through

changes of: tree size and growth-form, demographic variables (recruitment, mortality), and ecotone position (Brubaker, 1986). An alpine forest-pasture ecotone (FPE) includes treeline (limit of arborescent growth forms) and timberline (limit of dense forest) separating alpine pasture and subalpine forest (Hustich, 1979). From an ecophysiological point of view, alpine treelines are dynamic zones basically controlled by the decrease of temperature with increasing altitude (Tranquillini, 1979, Grace 1989).

Much treeline research has focused on the relationships between regeneration and climate. Several studies have found changes of tree density with minor treeline shifts in response to climate warming (Payette & Filion, 1985; Szeicz & MacDonald, 1995). However, the change of tree form in response to climate has become a key aspect to understand the effects of climate on treeline populations (Lavoie & Payette, 1992). In addition, few treeline studies have considered the spatial variation of tree form and size within this ecotone as a main controlling factor of treeline dynamics (Weisberg & Baker, 1995).

The analysis of the spatial structure of treeline populations is basic to the understanding of their dynamics. The description of this pattern can serve to infer processes that produced it. We describe part of this variability considering the spatial structure of tree height because (1) this variable is the most widely used to define and locate treelines (Kullman, 1979); (2) its variation affects in turn tree microenvironment (Tranquillini, 1979); and (3) changes of this variable can reflect the effects of climatic change on tree growth.

We consider this detailed description of the FPE structure as a necessary step towards assessing its sensitivity to climatic change through future dendroecological studies. Our main objective was to describe the FPE structure in two contrasting alpine FPEs, mainly considering the spatial variability of tree height. The two studied sites were selected among a network of treeline sites in the Pyrenees that have not experienced many recent human disturbances, such as logging, overgrazing, or fires (Gil-Pelegrín & Villar-Pérez, 1988). The selected sites represent a major part of the great variability of Pyrenean FPEs because of their contrasting environmental characteristics.

Materials and Methods

Tree species

Pinus uncinata Ram. is the dominant tree species of most of the Pyrenean treelines and timberlines. It is a shade-intolerant conifer whose reproduction is mostly sexual (Cantegrel, 1983; Ceballos & Ruiz de la Torre, 1971). Currently, *P. uncinata* timberlines and treelines in the Pyrenees reach maximum altitudes of ~ 2500 and ~ 2700 m asl, respectively (Carreras et al., 1995). In the Pyrenees, some FPEs follow the typical structural sequence of growth forms from vertical uni-stemmed trees close to the timberline to shrubby multi-stemmed krummholz forms above the treeline (Gil-Pelegrín & Villar-Pérez, 1988). Few Pyrenean FPEs have not been affected by local anthropogenic disturbances (fires, and logging).

Pinus uncinata forests are now reported to be recolonizing many subalpine pastures in the Pyrenees due to grazing reduction and, possibly, improved climatic conditions (Camarero & Gutiérrez, 1999).

Study sites

The study sites are located in the Spanish Central Pyrenees and showed contrasting characteristics (table 1). The understory vegetation at the Ordesa site (hereafter site O) is dominated by *Festuca rubra* L. and *Calluna vulgaris* (L.) Hull. A dense understory, typical of longer and deeper snow cover sites and dominated by *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L. (de Bolós et al., 1993), appears at the Tessó site (hereafter site T). Both sites are located in the buffer zones of "Ordesa y Monte Perdido" (site O) and "Aigüestortes i Estany de Sant Maurici" (site T) National Parks, which we considered a guarantee that recent human activity would diminish further. In the Pyrenees, grazing pressure has fallen continuously since the 1950's (García-Ruiz & Lasanta-Martínez, 1990). The recent stocking rates at both parks are low. According to historical data (Bringue, 1995), site T has hardly been affected by local human disturbances (grazing, logging) since the end of the XVIIIth century. No evidence of recent fires (fire scars, charcoal) was found at either sites. The landscape around site T is composed of

Table 1. Characteristics of the studied treelines ecotones (O and T). At site O, the climate is continental (Góriz meteorological station, 2215 m, 42° 39' N, 0° 01' E; 1981-95). At site T, the climate is continental with a maritime influence (data from: Esterrí 1054 m, 42° 37' N, 1° 07' E, 1970-97; Cavallers 1733 m, 42° 34' N, 0° 51' E, 1955-72; Tredós-Baqueira 1800, 1880 m, 42° 42' N, 0° 57' E, 1968-87). The reported wind speeds are for the period of record december 1992-april 1995.

Characteristics	Site O	Site T
Latitude (N)	42° 37'	42° 36'
Longitude	00° 02' W	01° 03' E
Treeline / timberline elevations (m asl)	2110 / 2100	2360 / 2330
Slope (°) / Aspect	17 / S	27 / NE
Total annual precipitation (mm)	1700	1800
Maximum estimated snow thickness (cm)	150-200	250-300
Mean annual temperature (°C)	5	3
Lowest / highest mean monthly temp. (°C)	-2 / 13	-4 / 12
Maximum wind speed (m s ⁻¹)	26 (NW)	17 (W)
Main geological substrate	Limestone	shales
Mean (± SE) tree height (m)	1.56 ± 0.12	4.00 ± 0.29
Density of living individuals (ind. · ha ⁻¹)	1529	471
Basal area (m ² · ha ⁻¹)	8.87	12.10

forest corridors separated by avalanche paths located in concave surfaces and dominated by pasture. At this site, the risk of avalanches is high mainly because of its steep slopes (Furdada, 1996).

Field sampling

At each site a rectangular plot (140 m x 30 m) was placed in topographically uniform parts of the FPE, including treeline and timberline, with its longer side along the altitudinal gradient. The current mean altitude of the timberline was visually determined and measured in the field (altimeter calibrated against topography map, accuracy of ± 5 m). In each plot, we recorded the coordinates of each main stem for every *P. uncinata* individual. At both sites, point $(x, y) = (0, 0)$ is located in the upper right corner looking upslope.

For every *P. uncinata* individual within the plot, several variables were recorded. In this study, we will only consider: location of each tree in the plot (x and y coordinates of the main stem), diameters at the base (db) and at 1.3 m (dbh), and maximum stem height (h). All *P. uncinata* individuals were tagged to allow future monitoring. The heights of those individuals higher than 3 m were estimated visually. According to Kullman (1979) the measurement error is ~ 15 cm for stems 3 m in height. All individuals in the plot were grouped in five size classes following Bosch et al. (1992): adults, dbh > 17.5 cm; poles, $7.5 < \text{dbh} \leq 17.5$ cm; saplings, dbh ≤ 7.5 cm and h > 0.5 m; seedlings, h ≤ 0.5 m; and dead individuals. At site O, the dominant growth-form were krummholz individuals (h ≤ 0.5 m, shrubby development; Daly & Shankman, 1985). To check for spatial independence, we excavated several tree clumps at site O. At site T, we estimated nondestructively the ages of all poles, saplings and seedlings by counting the number of branch whorls and bud scars on the main stem. This method yields an age underestimation of 0-5 yr (McCarthy et al., 1991). This procedure was not carried out at site O because of the multi-stemmed character of most of the individuals.

Spatial analyses: semivariograms and fractal dimension

The (semi)variogram is one of the structure functions available to describe the surface pattern or spatial continuity of a data set (Isaaks & Srivastava, 1989). Spatial continuity is based on the assumption that, on average, the closer two sampling locations are, the more likely it is that their values will be similar (regionalized variable). The semivariance is half the average squared difference for a continuous variable calculated between all possible pairs of points separated by a given distance. The variogram measures the average dissimilarity between the values or the average rate of change as a function of the separation distance (Rossi et al., 1992). The variogram is a better tool than the spatial correlogram to describe the spatial variation of a variable when the variance is non-stationary (Burrough, 1995; Legendre & Fortin, 1989). We consider that the spatial variation is not the same in all directions, i. e. it is anisotropic.

We used variograms to describe the spatial structure and autocorrelation of tree heights in the FPE. Trees are discrete objects but their size can be assumed to be a consequence of the influence of continuous spatial variables such as wind, radiation, soil nutrients and moisture (Biondi et al., 1994, Kuuluvainen et al., 1996). If z_x and z_{x+i} are the heights (regionalized variable z) measured at points $(x, x+i)$ separated by a distance i (lag), and $n(i)$ is the number of pairs of data points separated by distance i , we can estimate the semivariance $\gamma(i)$ by:

$$\gamma(i) = \frac{1}{2 \cdot n(i)} \sum_1^{n(i)} (z_{x+i} - z_x)^2 \quad (1)$$

The experimental variogram is a plot of the values of the semivariance $\gamma(i)$ as a function of distance i . Usually, the last one-third of the variogram is not taken into account to describe the spatial structure due to low $n(i)$ for high i . The variograms calculated for any direction and its opposite direction are identical. We calculated two-dimensional variogram surfaces of tree height in both FPEs, obtaining semivariance values for distances of 6 m on both axes or 6 m x 6 m quadrats (these figures are symmetrical; Pannatier, 1996). To obtain reliable results, possible outliers of tree height were eliminated for those 6 m x 6 m quadrats containing *P. uncinata* individuals. Within each quadrat, outliers were regarded as those values greater than mean height at the quadrat plus three times its standard deviation. We obtained variogram surfaces (variogram where each cell represents a semivariance value revealing possible anisotropies) and directional (considering different trigonometric directions: 0° –perpendicular to the slope–, 45°, 90° –parallel to the slope– and 135°) variograms for different distances (2, 4, 5, 6, 7, 8, 10, 14 and 20 m), using Variowin 2.2 (Pannatier, 1996).

Noisy or “complex” processes where short-range effects dominate (high frequency variability or low autocorrelation) show high values of fractal dimension –FD– (Burrough, 1983). Small FD values correspond to processes where long-range systematic variation (low frequency variability, high autocorrelation) is more important. The FD measures the degree of spatial dependence of a variable, and its relationship with the sampling scale can reveal the spatial variation of the variable (Frontier, 1987; Phillips, 1985). For instance, it has been used to describe and quantify the complexity of the spatial patterns of vegetation (He et al., 1994; Leduc et al., 1994; Palmer, 1988). We estimated the FD of tree height for several directions and scales in order to measure the similarity of this variable to noise or “complexity” in both FPEs. In the case of transects, the FD can be calculated as a function of the slope (m) of the linear part of a variogram, near the origin, on a double logarithmic scale (Burrough, 1983). This approach has also been applied to three dimensions obtaining $FD = (6 - m) / 2$, where $2 \leq FD \leq 3$ (He et al., 1994). To describe the directional spatial dependence of tree height, we display the variation of the FD as a function of the inter-point or lag distance for several directions (fractogram, see Palmer, 1988).

Results

Spatial changes in tree height

We mapped and measured 692 and 259 *P. uncinata* individuals at sites O and T, respectively. The most abundant size and growth-form classes were krummholz ($n=404$, 58%) and saplings ($n=75$, 29%) at sites O and T, respectively. At site O, there was a trend of increasing height descending across the FPE which was characterized by a sharp change halfway through the plot (figure 1). At site T, this trend was much more gradual than at site O. The most abundant (krummholz at site O and saplings-seedlings at site T) and smallest ($h < 2$ m) individuals, located in the upper half of the plot (figure 1), produced reverse-J-shaped height distributions for all living individuals for both sites. Power functions explained well the height distribution of all living individuals at sites O ($a = 73.18$, $b = -1.72$, $r = 0.94$, $p < 0.001$) and T ($a = 50.73$, $b = -1.02$, $r = 0.94$, $p < 0.001$).

Site O showed greater spatial dependence (smaller increments of semivariance with increasing distance) than site T, but both variogram surfaces showed the presence of height gradients across the ecotone (figure 2). Several directional variograms (45° , 90° , 135° ; not shown) did not reach a plateau, indicating the absence of variance stationarity. The variogram surfaces of height showed obvious anisotropic variation for both sites (figure 2). Semivariance increased more along the altitudinal gradient (90° direction) than at similar elevations (0° direction; figure 2). At site T, there was more variability at similar elevations (x -axis) than at site O.

We used simple quadratic functions to remove the main spatial trend of decreasing height with increasing altitude at both sites. This step was necessary to look for structural changes masked by the long-range variation imposed by the altitudinal gradient. The fit of the quadratic function explained a larger amount of variance for site O ($a = 1.248$, $b = -0.075$, $c = 0.001$, $r = 0.87$, $p < 0.001$, $n = 636$) than for site T ($a = 1.311$, $b = 0.006$, $c = 0.0004$, $r = 0.57$, $p < 0.001$, $n = 197$). The same spatial analysis was applied to the residuals of the fits, and their variograms changed considerably. For site T, the height residuals gave no spatial structure (fractal dimension = 2.99 for the 90° directional variogram). However, for site O, the height residuals formed patches of similar heights with a mean size of ~ 60 m (figure 1).

Fractal dimensions were higher for site T than for site O for all directions (figure 3). Therefore, site T presented a more noisy (predominant short-range effects) height distribution across the ecotone than site O (as shown by the highest mean value of height variance for site T, figure 2). Again, site O presented the highest spatial autocorrelation (low fractal dimension values) along the slope (90°) due to the dominance of the altitudinal gradient (figure 3). Anisotropic spatial variation was evident in the fractograms, because those at similar elevations (0°) showed the effects of short-range variation, while those along the altitudinal gradient (90°) described the effects of long-range variation (lowest values of fractal dimension). The increase in the distance lag of the variograms (i) reduced slightly the fractal dimension for both sites. The reduction in fractal dimension for higher distances

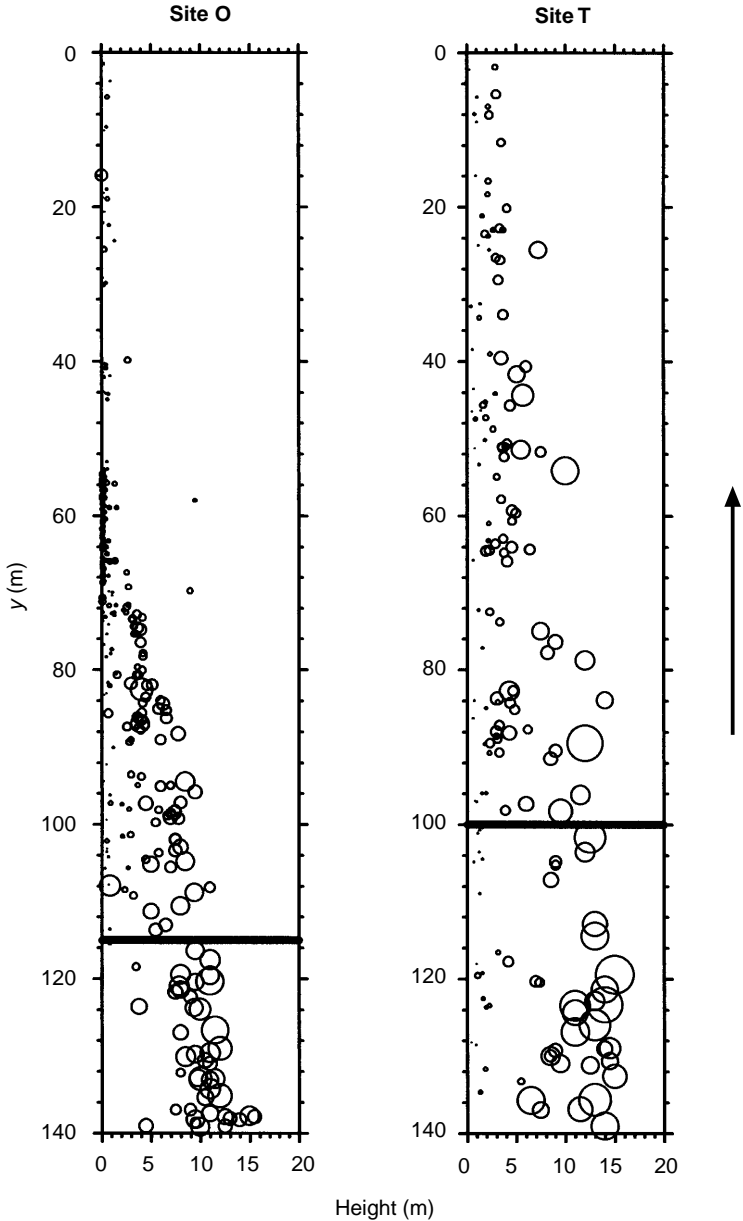


Figure 1. Height of living individuals in the alpine forest-pasture ecotone at sites O and T. Each individual is represented according to its position along the plot axis parallel to the slope (y) and its basal diameter (circle diameter is proportional to the diameter at the base in dm). The arrow parallel to the axis y points upslope, and the horizontal thick lines show the timberline at each site.

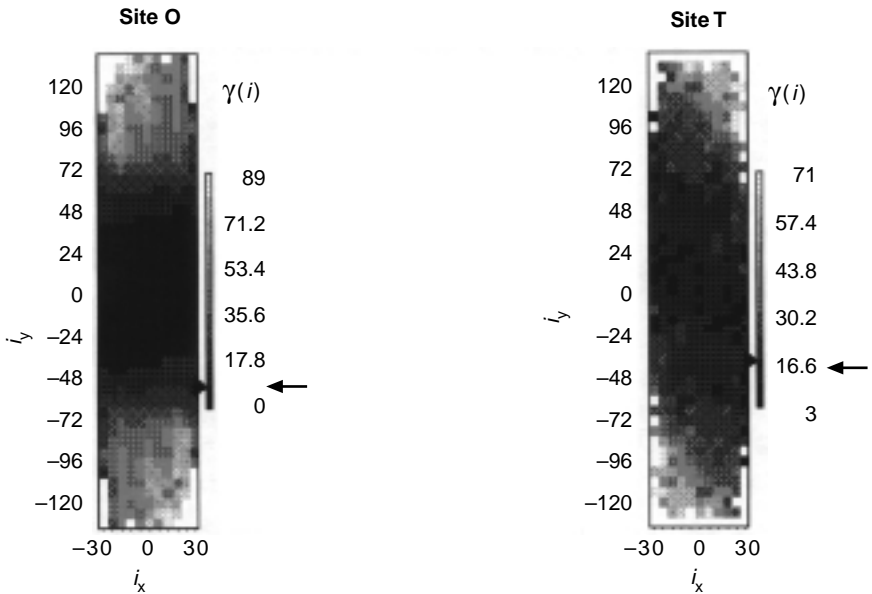


Figure 2. Variogram surfaces for height of all living individuals of the alpine forest-pasture ecotones at sites O and T. These surfaces are the plots of semivariance ($\gamma(i)$) values in all directions for 6 m x 6 m quadrats (lag distance $i = 6$ m, along the axes x , i_x , and y , i_y) in 30 m x 140 m plots. The central cell includes all pairs with a zero distance and represents $\gamma(i) = 0$. The lower and left halves of the plot are symmetric to the upper and right halves, respectively. Plot orientation as in figure 1. The gray scale shows the scale of increasing semivariance from low (black) to high (white) values. The arrow shows the value of variance of all data for each site.

and diagonal directions (45° , 135°) was greater for site O than for site T, indicating the existence of noisy processes for all distances along these directions at the second site.

Discussion

In a continental scale, the decline of tree height in temperate mountains is usually pronounced near the forest limit (Ohsawa, 1995). In this study, the increase in height descending across both ecotones was more sharp at site O and more gradual at site T, where multi-stemmed forms were absent (figures 1, 2 and 3). The treeline and the timberline at site O can be regarded as abrupt edges facing intense winds. These would create sharp microenvironmental changes near these boundaries. Grace (1989) suggested that the thermic difference between the surface of low plants (*e.g.*, krummholz) and that of higher plants (*e.g.*, trees) could explain the higher elevation of the first type of growth-forms, which reach higher

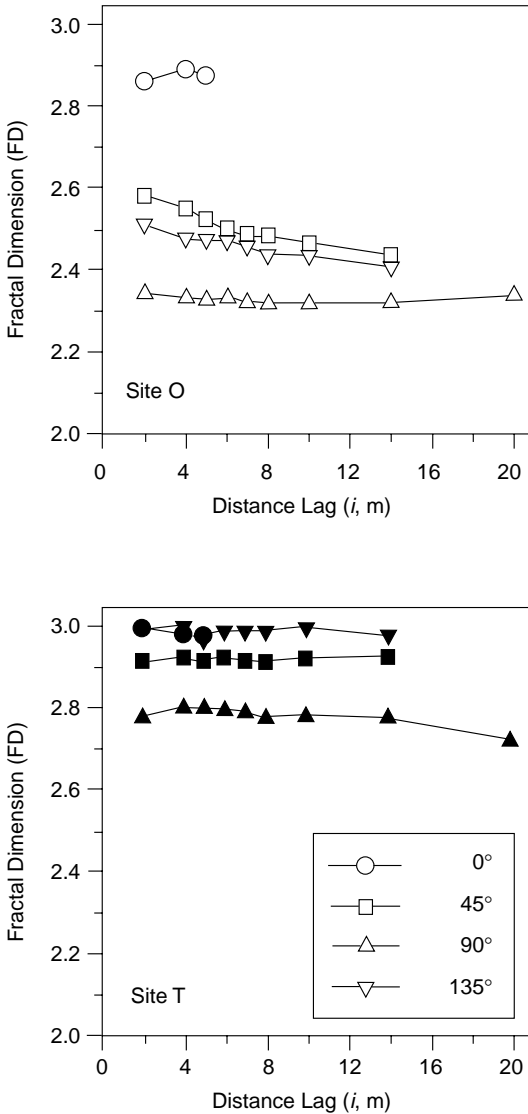


Figure 3. Fractograms (fractal dimension, FD against distance lag, i) for height of all living individuals of the alpine forest-pasture ecotones at sites O and T. The fractal dimension was obtained for several directions (0° –perpendicular to the slope, x axis–, 45° , 90° –parallel to the slope, y axis– and 135°) and distance lags in $30 (x) \times 140 (y)$ m plots.

temperatures in their apical meristems with bright sunshine. Körner (1998) has also suggested that the tree growth-form is adapted to grow vertically. However, the tree crown limits the amount of radiation received by the soil what could reduce soil temperature and root growth. At site O, treeline and timberline are nearby boundaries. Therefore, the pattern of tree height in this ecotone can partially be ascribed to pronounced thermic differences among meristems of shrubby and arborescent *P. uncinata* individuals. These contrasting microclimates can be greatly controlled by the intense winds at this area (table 1).

Overall, the ecotone at the exposed site O seems to be a local phenomenon due to the strong winds and the reduced snowpack. Snow abrasion and wind can generate shrubby forms (krummholz) and flagged krummholz as those observed in this site. Our data suggest that the local factors are more important to control treeline position than the altitudinal gradient at site O (Hansen-Bristow, 1986). This is also confirmed by the lower elevation of timberline at site O compared with site T (table 1), and maximum elevation of timberlines in the Pyrenees (~ 2500 m).

The variogram surfaces and fractal dimensions described a greater spatial autocorrelation for the height of living individuals at site O (figures 2 and 3). Removing the main trend of decreasing height across the ecotone, site O still displayed spatial structures due to its non-linear changes in height from shrubby krummholz forms to adult individuals (figure 1). The mean size of patch with similar tree heights corresponds well with the distance ($y = 140 - 80 = 60$ m) where arborescent individuals located near the forest disappeared and krummholz forms dominated. This situation is closer to a "false" gradient (heterogeneity of variances), where the spatial structure is the result of community interactions (e.g., local abundance of krummholz forms), producing the predominance of autocorrelation at small-scales (Legendre, 1993). However, the height of living individuals at site T formed a structure more similar to a "true" gradient (heterogeneity of means, large-scale trend, monotonic variation of height across the ecotone) where height is mainly explained by environmental variables (e.g., the decrease of air temperature) related to the altitudinal gradient (Dutilleul & Legendre, 1993). At this site, the greater spatial heterogeneity of tree height is partly explained by the importance of snow avalanches (Furdada, 1996). Snow avalanches slice the FPE and create forested strips along the slope increasing the spatial variability of the ecotone (Walsh et al., 1994).

The studied ecotones could be compared with the two types of community boundaries exposed by van der Maarel (1990): site O is closer to the ecotone concept, characterized by abrupt structural changes; while site T is an ecocline, where transitions are gradual (gradient zone) creating greater spatial heterogeneity. In both cases, the altitudinal gradient controls the distribution of the different size and growth-form classes, but local factors, such as wind at site O or avalanches at site T, greatly modify this pattern in different ways. We have shown how several statistical analyses help to describe complementary aspects of the structure of alpine FPEs. This structural approach should improve the monitoring through time of treeline ecotones to assess their response to climatic change.

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