



## A multivariate approach to the study of the spatial structure of treeline ecotones

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**Abstract:** We study the structure of two contrasting alpine forest–pasture ecotones located in the Central Pyrenees (sites Ordesa and Tessó). We define ecotone structure as the spatial distribution of trees of different size classes and growth-forms, and the relationship between these aspects and the spatial distribution of understory vegetation and substrate. The studied ecotones are dominated by *Pinus uncinata* and have been little affected by recent anthropogenic disturbances (logging, grazing). One rectangular plot (30 x 140 m<sup>2</sup>) was located within each site encompassing treeline and timberline with its longest side parallel to the slope. The distribution of size and growth-form classes at Ordesa followed a clear sequence of increasing size downslope, from shrubby krummholz individuals to bigger arborescent trees. At Ordesa, regeneration was concentrated near the krummholz area and over rocky substrates. At Tessó, regeneration was abundant above the treeline, where the cover of the dominant understory shrub (*Rhododendron ferrugineum*) decreased. Detrended canonical correspondence analysis of tree and plant cover data, with respect to spatial location in the ecotone and substrate cover, demonstrated that elevation was an important factor controlling the distribution of trees and understory plants in both ecotones. Finally, *k*-means clustering with spatial constraint revealed abrupt spatial clusters along the slope at Ordesa. However, the ecotone at site Tessó was composed of elongated downslope spatial clusters suggesting greater spatial heterogeneity and subtle gradual changes due to other factors in addition to the altitudinal gradient (snow avalanches). These contrasting structures correspond well with the ecotone (sharp boundary, Ordesa) and ecocline (gradual transition, Tessó) concepts. This suggests the dominant role of different local environmental factors: wind at site Ordesa and avalanches at Tessó. Positive feedbacks, like facilitation among *P. uncinata* individuals (nurse effect), may maintain and intensify the sharpness of the ecotone at Ordesa.

**Abbreviations:** A-adults, CCA- Canonical Correspondence Analysis, D-dead individuals, db-diameter at stem base, dbh-diameter at breast height, DCCA-Detrended Canonical Correspondence Analysis, FPE-Forest Pasture Ecotone, h-tree height, K-krummholz, KM- flagged krummholz, NDST-number of dead stems per individual, NLST-number of living stems per individual, NST-total number of stems per individual, O- Ordesa site, P-poles, S-saplings, SE-seedlings, T-Tessó site.

**Nomenclature follows:** de Bolòs et al. (1993)

### Introduction

Several components of global change (Houghton et al. 1996), such as climate change and land-use modifications, are influencing the dynamics of tree populations, especially at their distribution margins (Brubaker 1986). An ecological boundary potentially sensitive to these changes is the alpine forest-pasture ecotone (FPE), which is bounded by the treeline, usually defined as the maximum elevation of living individuals with stems at least 2 m high and the timberline, defined as the maximum elevation of a closed forest (Kullman 1991). However, there is certain controversy on the suitability of FPEs to detect the effects of climate change due to the treeline inertia (Noble 1993). A better knowledge of the spatial structure

of FPEs would improve the assessment of these ecotones as potential monitors of climate warming effects.

There is still a bad need of quantitative studies characterizing the FPE structure (tree density and spatial location; tree size, age and growth-form; understory vegetation; substrate type). It has been described how tree regeneration and growth-form at treeline ecotones are affected by different climatic variables (Payette and Filion 1985, Kullman 1991). In turn, these changes in response to climate variability and their corresponding spatial pattern also affect the microenvironmental conditions within the ecotone (Weisberg and Baker 1995, Lloyd 1996). Microenvironmental conditions, including understory composition and substrate availability, modulate the climatic control of tree regeneration at treeline ecotones (Earle

1993). In spite of the importance of the FPE structure to understand the mentioned feedbacks, relatively few detailed attempts have been made to describe it (Habeck 1969, Veblen 1979, Payette 1983, Gil-Pelegrín and Villar Pérez 1988, Tomback et al. 1993, Titus 1999, Barrera et al. 2000, Camarero et al. 2000).

The description of the spatial pattern of the plant community is a necessary step to infer the processes implicated in its dynamics (Watt 1947). The analysis of spatial pattern can generate hypotheses as to causative processes, even if different processes can produce similar patterns (Legendre and Fortin 1989). Nevertheless, the studies on treeline dynamics have rarely considered the FPE spatial pattern as a product of abiotic controlling factors such as climate and disturbances (see, however, Camarero et al. 2000). In this study, our main objective was to describe the spatial changes of tree size and growth form, and the understory plants through the FPE. We regard this as the first necessary step to fully understand treeline dynamics in response to climate change. A specific ecotone structure may be used to infer the causal processes of this pattern.

## Study area and methods

### Site selection

The studied ecotones are dominated by *Pinus uncinata*, which forms most of treelines at the Spanish Pyrenees. Two sites – Ordesa (O) and Tessó (T) – were selected among a network of undisturbed treeline ecotones in the central Pyrenees in Spain (Gil-Pelegrín and Villar Pérez 1988). They showed contrasting characteristics (topography, climate, vegetation, soil) within this set of ecotones (Table 1). Both sites were located in the buffer zones of two National Parks (Ordesa-Monte Perdido, site O; Aigüestortes-Estany de St. Maurici, site T) which we considered a guarantee that recent human activity would diminish further in comparison with neighboring unprotected areas.

We consider that the ecotone structure has not been affected by recent (last 50-100 yrs) local human disturbances in both sites. In fact, their present stocking rates are below  $24 \text{ sheep} \times \text{month} \times \text{ha}^{-1}$  due to a 50% reduction during the last 50 years (Aldezabal et al. 1992, Bas et al. 1994). At site O, only 14 (2.2% of all living trees) krummholz pines close to treeline pasture showed signs of grazing. In addition, site T has hardly been affected by logging since the end of the eighteenth century, according to local historical documentation (Bringue 1995). No evidence of recent fires (fire scars, charcoal) was found at either site. In addition, no treeline shift could be discerned

on comparing aerial photographs of the two sites from the last 50 years.

Climatic conditions were estimated for both sites (Table 1). For site O, the data from the nearby Góriz meteorological station were used (2215 m asl,  $42^{\circ} 39' \text{ N}$ ,  $00^{\circ} 01' \text{ E}$ ; 1981-99 data). For site T, the climatic values were estimated using data from Esterri station (1054 m,  $42^{\circ} 37' \text{ N}$ ,  $01^{\circ} 07' \text{ E}$ , 1970-97 data). Both meteorological stations were located at ~6 km from the sampling sites. Overall, the climate at sites O and T is regarded as continental with mediterranean influence and continental but characteristic of a subalpine area, respectively. At site T, the probability of avalanches is quite high (Furdada 1996). Avalanches have affected the current structure of *P. uncinata* stands at site T. These form altitudinal “stripes” of forests separated by avalanche paths dominated by herbs and shrubs.

### Sampling *Pinus uncinata* treeline ecotones

At each site, a rectangular plot (30 m x 140 m) was placed in topographically uniform parts of the FPE with its longest side parallel to the maximum slope ( $y$ -axis). The plot included current treeline and timberline. In each plot, we recorded the locations of the centre of each main stem for every *P. uncinata* individual following a Cartesian coordinate system. At both sites, point  $(x, y) = (0, 0)$  is located in the upper right corner when seen from below. The  $y$ -axis was placed parallel to the maximum slope, i.e., following the S and NE directions at sites O and T, respectively. The shortest  $x$ -axis was perpendicular to the  $y$ -axis. At site T, the  $(30, y)$ -side was located near an avalanche gully. The current altitudes of the treeline and timberline were measured in the field (altimeter calibrated against topography map, accuracy of  $\pm 5 \text{ m}$ ).

For every *P. uncinata* individual within the plot the following measurements were made: location in the plot ( $x$  and  $y$  coordinates), diameter at stem base (db), diameter at 1.3 m above the base (diameter at breast height, dbh), maximum stem height (h), crown projection in four radii along the two directions marked by the plot axes, height of the insertion of the lowest living branch in the trunk, number of living needle cohorts retained in the branches (estimated by examining 4 mid-canopy branches), and number and type (arborescent or stunted, living [NLST] or dead [NDST]) of stems per individual (NST, total number of stems per individual). All *P. uncinata* individuals were tagged to allow future monitoring. We mapped and measured 692 and 259 *P. uncinata* individuals at sites O and T, respectively.

**Table 1.** Contrasting characteristics of the studied treelines ecotones (sites O and T).

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 / 186	27 / 42
Total annual precipitation / maximum winter-spring snow thickness (mm)	1700 / 2000	1800 / 3000
Mean annual temperature (°C)	5	3
Lowest / highest mean monthly temp. (°C)	-2 / 13	-4 / 12
Main geological substrate	limestone	shales
Mean ( $\pm$ SE) tree height (m)	1.56 $\pm$ 0.12	4.00 $\pm$ 0.29
Mean ( $\pm$ SE) number of stems per tree	5.00 $\pm$ 0.25	1.00 $\pm$ 0.06
Most abundant tree class (number)	K (404)	S (75)
Density of living / dead individuals (ind. $\cdot$ ha <sup>-1</sup> )	1529 / 119	471 / 145
Basal area (m <sup>2</sup> $\cdot$ ha <sup>-1</sup> )	8.87	12.10
Cover of the main substrate (%)	Organic matter (50.13)	Organic matter (44.51)
Main understory plant (%)	<i>Festuca rubra</i> (27.35)	<i>R. ferrugineum</i> (20.57)
Understory plant richness (n. species)	40	25

All individuals in the plot were grouped in five size classes following Bosch et al. (1992): adults (A), dbh >17.5 cm; poles (P), 7.5 < dbh  $\leq$  17.5 cm; saplings (S), dbh  $\leq$  7.5 cm and h >0.5 m; seedlings (SE), h  $\leq$  0.5 m; and dead individuals (D). Two additional growth-form classes were specified for site O: krummholz (K) and flagged multistemmed krummholz with arborescent stems (KM). We considered as stems all trunklike woody structures above the ground directly connected with the base of the individual. Flagged krummholz forms develop arborescent shoots above the snowpack and maintain a dense mat-like infranival growth composed of shrubby stems. At site O, we considered K individuals as being those with h  $\leq$  0.5 m that showed multistemmed development (Daly and Shankman 1985). To check for spatial independence, we excavated several tree clumps at this site. At site T, we estimated nondestructively the age of young individuals (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 multistemmed character of most of the living individuals (59% of them had more than 2 stems per individual).

#### Sampling understory vegetation

To estimate vegetation and substrate cover, we used the point method (Barbour et al. 1987). We laid over the ground a sampling grid formed by 6 altitudinal transects along the maximum slope ( $y$  axis). Transects were located every 6 m perpendicular to the slope ( $x$  axis; i.e., at  $x = 0, 6, 12, 18, 24$  and  $30$  m) going downslope from the upper edge of the plot ( $y = 0$ , above treeline) to the lower edge ( $y = 140$ , forest). Cover was estimated from the number of contacts of *P. uncinata* (overstory), understory vegetation (shrub and herbaceous species recorded individually) and substrate with a metal rod placed every 1 m along the  $y$  axis. At both sites, we recorded all plant species encountered in point sampling. In site O, we grouped all shrub and herbaceous species to obtain a plant cover value for later analyses because of the high diversity and relatively low cover values of the understory species (94% of the species showed cover values < 5%). At this site, understory and substrate types were grouped into five classes: vegetation (shrubs and herbs), rock (diameter > 1 dm), gravel (diameter  $\leq$  1 dm), bare soil, and organic matter (mainly, pine needles and wood). These last four classes were considered as abiotic variables in the ordination

analyses. The same classes were used at site T, but considering those understory species whose cover values were  $> 3\%$ .

### *Ordination analyses*

One of the objectives of ordination is to highlight the prominent features of a data set, including spatial gradients (Legendre 1990, ter Braak 1995). To relate biotic or dependent variables (tree data including density, size, growth form, estimated age, and understory data including herb and shrub cover) to the abiotic or independent variables (spatial coordinates, percentage cover of rock, soil and organic matter), we chose a direct gradient analysis. Exploratory analyses (plots of dependent *vs.* independent variables) indicated unimodal responses of most dependent variables (e.g., the distribution of tree size and growth-form classes *vs.* elevation  $-y$ -axis; see Camarero and Gutiérrez 1999). As an evident arch-effect appeared in preliminary ordinations, we used Detrended Canonical Correspondence Analysis (DCCA) because detrending prevents the second axis from being obscured by dependence on the first axis and removes the arch effect (Gauch 1982, ter Braak 1986). We chose detrending by 2nd order polynomials. DCCA usually gives results similar to CCA if the data are not complicated (ter Braak 1986). No significant differences appeared when DCCA was applied instead of CCA. The eigenvalues of the first two axes, and the scores of sites and species were similar in both analyses. Even if the arch is not regarded as a mathematical artifact (Wartenberg et al. 1987), detrending and rescaling may facilitate the ecological interpretation of the ordination diagram (Peet et al. 1988).

To build the space matrix (spatial locations of gridded tree and understory data), we used the Trend-Surface Analysis described by Legendre (1990) because: (i) it captures most of the spatial structure of the data, and (ii) it is able to describe broad-scale spatial trends. First of all, tree data and transect data (percentage cover of shrubs, herbs, and type of substrate) were transformed into lattice data for both sites using 115 quadrats 6 m x 6 m each to make the variables comparable. The extra 2 m of the longer  $y$ -axis was discarded. To transform the cover data into lattice data, each point was attributed to one of its neighboring 36 m<sup>2</sup> quadrats (5 per each 6 m altitudinal belt) starting at  $x = 0$  m. As the first or the last columns of quadrats would have received two transects instead of one, we discarded the last altitudinal transect ( $x = 30$  m). The original data were gridded by counting the number of individuals per quadrat (density) or summing size data (db, dbh, height, etc.) for each size and growth-form class. The space matrix of two-dimensional geographical coordinates

( $x, y$ ) was built using the centres of the 115 quadrats and completed by adding all terms for a cubic (third-degree polynomial) surface regression ( $x, y, x^2, xy, y^2, x^3, x^2y, xy^2, y^3$ ) as suggested by Legendre (1990, 1993). All data in the matrix of dependent variables were standardized to make the variables dimensionally homogeneous (Legendre and Legendre 1998).

The ordination axes computed by DCCA are new synthetic variables that can be mapped to indicate the presence of spatial groups (Legendre 1990). The geographic variability of a multivariate data set can be mapped through the computation of a canonical ordination of the multivariate data constrained by the space matrix (cubic surface equation formed by the coordinates of the 115 quadrats). Then, the resulting canonical synthetic variables are mapped (Legendre 1990). We used this to represent the geographic variability of the dependent multivariate data set (tree and vegetation data).

The space matrix (independent variables) was composed of the significant ( $p \leq 0.05$ ) terms of a cubic surface regression. These terms were forward selected in previous DCCAs between this matrix and the tree-understory data (dependent variables). There were 5 such terms ( $x, y, x^2y, y^2, y^3$ ) for site O, and 3 ( $y, y^2, y^3$ ) for site T. The forward-selected abiotic variables (substrates) were the cover values of soil and organic matter, and organic matter for sites O and T, respectively. The forward selected input matrix of abiotic factors was composed of the following variables:  $x, y, x^2y, y^2, y^3$ , cover of soil, rock and organic matter for site O;  $y, y^2, y^3$ , and cover of organic matter for site T. All ordination analyses were performed with CANOCO 3.11 (ter Braak 1988ab). The significance of the overall ordination axes and of each forward-selected explanatory variable was assessed using 999 Monte Carlo permutations (ter Braak 1988a).

### *Spatial analyses: k-means clustering with spatial constraint*

To map the geographic variability and to describe the spatial structure of the tree data, we used a clustering technique to separate homogeneous groups (Legendre and Fortin 1989). We used the gridded tree data set previously described. For both sites, we considered the following multivariate set of variables: density and size (db, dbh, height, eastern and southern crown radii, maximum number of needle cohorts) data for all size and growth-form classes of living individuals; and density, basal diameter (db) and NDST for dead individuals. In addition, multitemmed individuals (K, KM) were characterized only at site O using density and size variables, and data of number and type of stems per individual (NLST, NDST

and NST). For site T, we used density and size variables, and the estimated age of the younger individuals (P, S and SE). Overall, 49 and 32 variables were selected for sites O and T, respectively.

We chose *k*-means clustering with spatial constraint to produce and map homogeneous multivariate groups (Legendre 1987, Legendre and Fortin 1989). This method creates homogeneous groups (*k*), according to the multivariate data, composed of adjacent quadrats inside the plot. The number of groups was selected according to the previously defined number of size and growth-form tree classes (*k* = 7 and *k* = 5 for sites O and T, respectively). These initial numbers of clusters produced compact clusterings according to the Calinski-Harabasz criterion (Milligan and Cooper 1985). The *k*-means algorithm is based on an iterative procedure of quadrat reallocation to minimize the amount of within-group variation. We selected the clustering iteration, out of 10, that minimized the sums of squared distances within clusters. Quadrats without trees were excluded from the analysis, leaving 113 and 97 objects (quadrats) for sites O and T, respectively. The first step was the computation of a matrix of dissimilarity among quadrats using the Bray-Curtis coefficient (Legendre and Legendre 1998):

$$d_{jk} = 1.0 - 2W / (A + B)$$

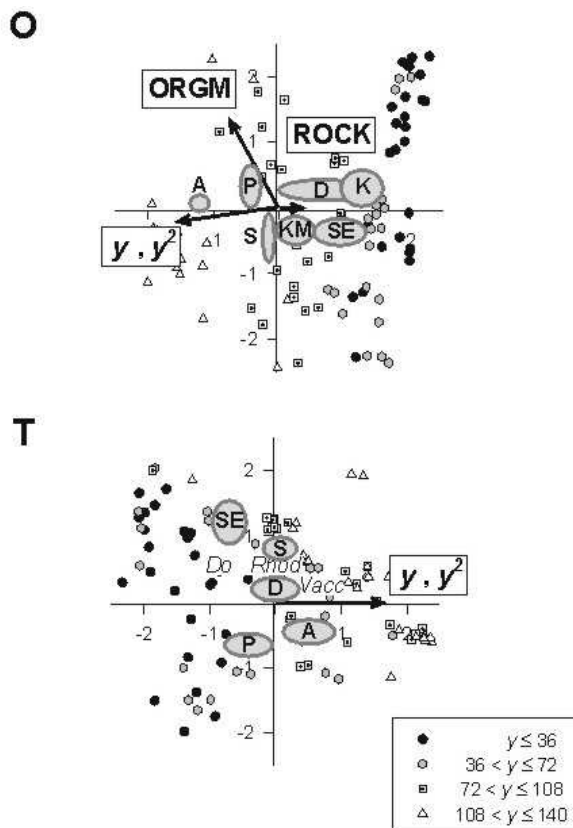
where *W* is the sum of the minimum abundance of all species; and *A* and *B* are the sums of the abundances of all species in sites *j* and *k* being compared.

Then, we conducted a Principal Coordinates Analysis from the dissimilarity matrix to create new synthetic variables. We selected all those eigenvectors –the coordinates of the objects in reduced space– with positive eigenvalues (15 coordinates). The spatial contiguity constraint is provided by the list of links obtained that connect neighbouring quadrats in all 8 directions ('king's move', Cliff and Ord 1981). Using as input data the link matrix and the 15 principal coordinates, the *k*-means clustering with spatial constraint produces a set of homogeneous groups composed of contiguous 6 m x 6 m quadrats. For the initial configuration, we used a random input matrix. For both sites, we selected the clustering result that showed the minimum amount of within-group variation. We performed the *k*-means clustering and its related analyses using the R-package version 3 (Legendre and Vaudor 1991).

**Results**

*Spatial variation of tree, substrate and understory along the FPE*

At site O, the presence of organic matter, altitude (*y*, *y*<sup>2</sup>), and rock cover influenced the ecotone structure (Fig. 1). Dead individuals occupied a portion of the multivari-



**Figure 1.** Ordination diagram based on Detrended Canonical Correspondence Analysis (DCCA) of the size and growth-form tree classes and understory plants (plants only at site T) with respect to spatial location and substrate cover along two alpine forest–pastures ecotones at sites O and T. Only the most significant abiotic or environmental variables are shown inside boxes for each site (*y*, *y*<sup>2</sup>-altitude factors, ROCK-rock cover, ORGM-organic matter). The symbols show site scores for the 115 quadrats of size 6 m x 6 m in each plot, grouped into four 36-m altitudinal bands of decreasing elevation (increasing *y*) along the ecotone (*y* ≤ 36, etc.). For each size and growth-form class, the ellipses join standard deviations of variable scores of both axes and are centred on the mean values of the scores. Abbreviations for size and growth-form classes: krummholz (K), seedlings (SE), dead individuals (D), flagged krummholz (KM), saplings (S), poles (P), and adults (A). The two arrows for *y* and *y*<sup>2</sup> are shown as one because they almost coincide. Plant cover data (dependent variables) appear in italics and underlined: *Do* - *Dryas octopetala*, *Rhod* - *Rhododendron ferrugineum*, and *Vacc* - *Vaccinium myrtillus*. The first axis is horizontal for both sites. Only highly significant (*p* ≤ 0.01) variables are reported.

ate space between krummholz and flagged krummholz. Most regeneration was concentrated near krummholz. The sets of quadrats from different elevational bands were well segregated along the ecotone and formed distinct groups (Fig. 1).

At site T, altitude ( $y$ ,  $y^2$ ) affected the distribution of trees and plants along the ecotone, and was highly related to axis I. The different size and growth-form classes were distributed along this altitudinal gradient but overlapped more than at site O (Fig. 1). Only adults and seedlings were located at opposite ends of the ecotone. Seedlings were associated with low cover values of *Vaccinium myrtillus* and *R. ferrugineum* but high cover values of *Dryas octopetala* and higher altitude (Fig. 1). For both sites, a non-linear altitudinal factor ( $y^2$ ) was related to the distribution of trees.

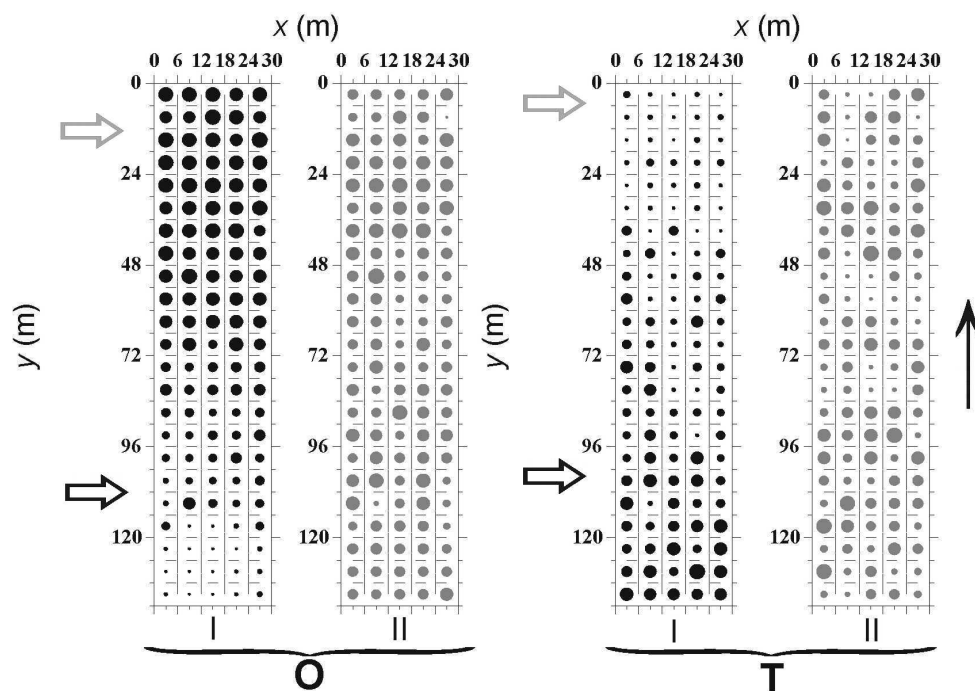
The overall amount of explained variation was greater for site O (38.3%) than for site T (13.7%). For both sites, the first axis (I) of the ordinations corresponded to the altitudinal gradient along the ecotone (Fig. 1). For site O, this axis was negatively related to altitude and positively related to rock cover, while the second axis (II) showed higher values in those quadrats with a high presence of organic matter (Fig. 1). For site T, the gradient of the sam-

ple scores of axis I was not as neat as for site O (Fig. 2). The values of the sample scores of this axis increased downslope (higher values of  $y$ ) while *V. myrtillus* and *R. ferrugineum* increased in abundance, and *D. octopetala* decreased (Figs 1 and 2). Axis II for site T was positively related to regeneration but negatively related to the presence of bigger trees (Fig. 1).

When space is used as a covariable, the altitudinal gradients disappeared (Fig. 3). In the case of the DCCA constrained by the space matrix, higher scores of axis I for site O corresponded to high densities of saplings (mean  $y \pm$  standard error =  $90.8 \pm 3.0$  m) and seedlings ( $58.6 \pm 1.8$  m), presence of soil substrates and absence of organic matter. Axis II was related to high densities of krummholz ( $47.1 \pm 0.8$  m) and seedlings. For site T, axis I of the spatially constrained DCCA was inversely related to the abundance of organic matter but positively related to plant cover. Sample scores for axis II for site T showed similar results when compared with the unconstrained DCCA (Figs 2 and 3).

#### Spatial clusters of multivariate tree data

Clusters at site O were mostly distinct along the slope ( $y$ -axis), producing a neat and sharp gradient (Fig. 1). For



**Figure 2.** Spatial variation of the sample scores of the DCCA for multivariate tree data of two tree ecotones (O, T) for the first two axes (see Fig. 1). The sample scores are plotted in 6 m x 6 m quadrats as circles whose size is proportional to the score value. Black and gray circles show scores for axes I and II, respectively. The horizontal arrows indicate the approximate location of the forest limit (black arrow) and the treeline (gray arrow). The vertical arrow points upslope.

site T, the spatial clusters formed sinuous contact borders suggesting the existence of more gradual changes along this ecotone (Fig. 4). Most clusters for site T were more elongated along the slope than in site O.

To characterize the groups formed by *k*-means clustering, the classifications obtained were compared to the raw density data of the size and growth-form classes. For site O, the upper groups were dominated by krummholz and seedlings (Fig. 4). Going downslope, an intermediate group was dominated by flagged krummholz. Lower groups close to the timberline and in the forest were composed of middle-size individuals above the timberline, and adults and dead individuals in the forest.

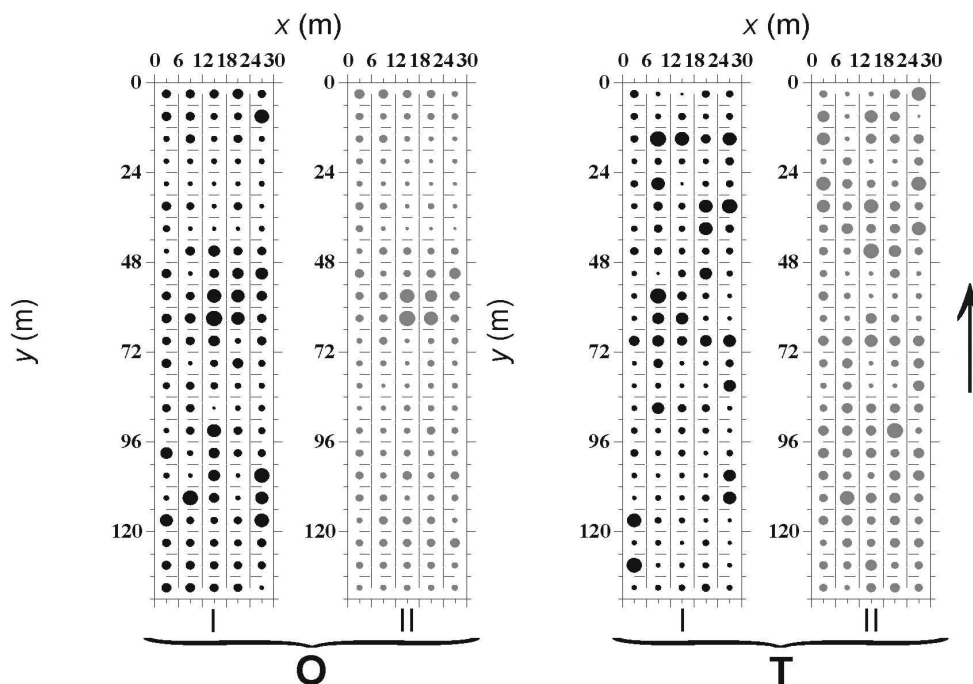
At site T, the seedlings formed the most elevated group followed by a lower elongated group dominated by saplings and dead individuals. The poles and saplings were abundant in middle positions. Again, the lowest group was characterized by high densities of adults below the timberline (Fig. 4).

**Discussion**

Both sites showed contrasting environmental conditions (Table 1) and ecotone structures (Figs. 1-4). Site O was characterized by the ordered arrangement of the dif-

ferent size and growth-form tree classes (going upslope: A → P → S → KM → D → SE → K). These changes could represent an analogue of temporal processes as the different growth forms evolve in response to climatic conditions. Similar cases of orderly spatial pattern under directional environmental stress are subalpine wave-generated *Abies balsamea* forests in NE America (Sprugel 1976). The regeneration of *P. uncinata* was abundant in the area where krummholz individuals were dominant and over rocky substrates. The spatial proximity between seedlings and krummholz could indicate a facilitation process (nurse effect). Environmental conditions at treeline ecotones are harsh for survival and growth. Krummholz individuals may modify microenvironment conditions to the benefit of regeneration, forming compact clusters that enhance snow accumulation, thus reducing wind abrasion (Holtmeier and Broll 1992). This kind of positive-feedback switches can produce and maintain abrupt transitions or ecotones between different plant communities (Wilson and Agnew 1992), such as that described for site O.

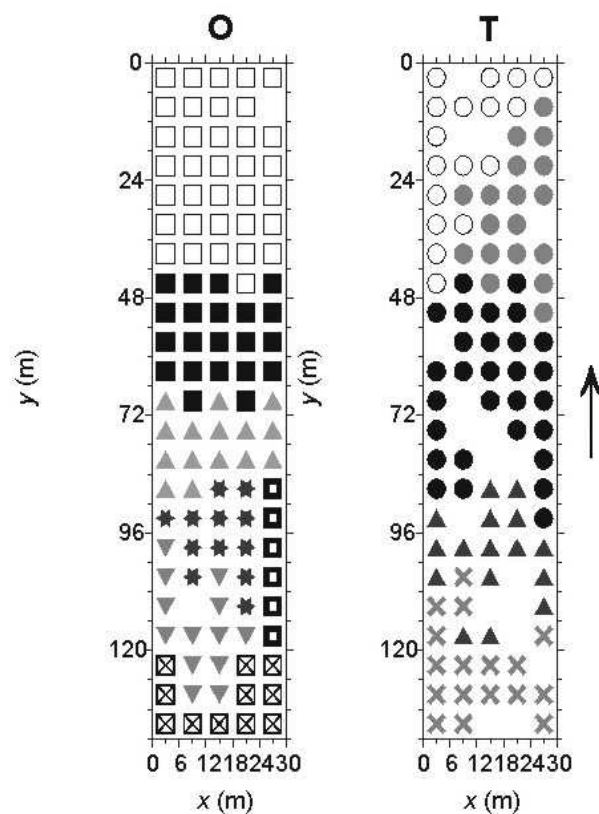
Contrastingly, site T showed an overlapping distribution of the size and growth-form classes (going upslope: A → S → D → P → SE) along the ecotone (Figs 1 and 4). The type of understory was related to the spatial distribu-



**Figure 3.** Spatial variation of the sample scores of the DCCA for multivariate tree data of two treeline ecotones (O, T) constrained by the space matrix for the first two axes. This representation does not take into account the spatial variability due to the altitudinal gradient. The vertical arrow points upslope.

**Figure 4.** Spatial clusters of tree multivariate data (density, size, growth-form, estimated age) obtained by  $k$ -means clustering with spatial constraint for the alpine forest–pasture ecotones of sites O (number of groups,  $k = 7$ ) and T ( $k = 5$ ). To characterize the groups formed by  $k$ -means clustering, the classifications obtained were compared to the raw density data of the size and growth-form classes. The different symbols indicate the cluster to which each 6 m x 6 m quadrat belongs. For site O, the two upper groups were composed of krummholz (empty squares) and very dense quadrats dominated by krummholz and seedlings (filled squares). Going downslope, a group in intermediate areas (upright triangles) was dominated by flagged krummholz. Lower groups close to the timberline and in the forest (stars, thick-line squares, downright triangles) were composed of middle-size individuals above the timberline (flagged krummholz, saplings and poles), and big arborescent adults and dead individuals located in the forest (squares with sails). At site T, the seedlings formed an upper group (empty circles) followed by an elongated group (gray circles) with saplings and dead individuals. The poles were abundant in a middle group (black circles). A lower group (upright triangles) formed by saplings was located near the timberline. Again, the lowest cluster (sails) was characterized by high densities of adults.

The clusters were obtained using 49 variables and 113 objects (quadrats) and 32 variables and 97 quadrats for sites O and T, respectively. Quadrats without symbols contain no trees (2 at site O and 18 at site T). The vertical arrow points upslope.



tion of regeneration at site T (Fig. 1). At this site, *P. uncinata* regeneration was negatively associated with *R. ferrugineum* cover but positively related to the presence of *D. octopetala*. The competitive effect of the dense *R. ferrugineum* mats can prevent the establishment of the pine, a shade-intolerant species (Bosch et al. 1992). Future studies should characterize with detail the regeneration niche of *P. uncinata* within these treeline ecotones.

The greater importance of the spatial component at site O compared with site T can be explained because of the local character of the first site (Gil-Pelegrín and Villar Pérez 1988). Site O is located on a gentle slope where intense NW-W winds blow downslope and can clean the snow present during winter and early spring. At this site, tree height decreases abruptly upslope and krummholz individuals are dominant tree (Table 1). The elevations of treeline and timberline at this site are much lower than the mean values recorded at undisturbed sites in the Pyrenees (e.g., site T; Table 1). For all these reasons, we regard wind as the main environmental factor producing the sequential arrangement of the different size and growth-form classes of *P. uncinata* at site O. Spatial changes at site T are more gradual (e.g., the overlap of tree classes), thus reducing the spatial component of its structure. This spatial heterogeneity and the elongation of the clusters is

partly explained by the importance of snow avalanches at this site.  $k$ -means clustering with spatial constraint clearly summarized the two contrasting ecotone structures (Fig. 4). Most clusters at site O were compact and perpendicular to the slope, creating a sharp gradient. The spatial clusters at site T were elongated along the slope forming sinuous boundaries, and indicating the existence of more gradual changes.

This study has allowed us to characterize the structure of two contrasting forest-pasture ecotones using multivariate and spatial techniques. These fit quite well within the two opposite community boundaries proposed by van Leeuwen (1966) and van der Maarel (1990): site O is an ecotone, where structural changes are abrupt and produce distinct altitudinal belts (Camarero and Gutiérrez 1999); while site T is an ecocline, where transitions are gradual and the different size and growth-form classes overlap. These contrasting structures are the product of: (i) historical factors (regeneration, mortality, disturbances, treeline dynamics), and (ii) environmental variables modulating the altitudinal gradient (mainly wind at site O and avalanches at site T).

The spatial description of ecotone structure is necessary but not sufficient to explain the processes determining the environment-vegetation relationships (Czárán and

Bartha 1992). It should be extended to include demographic studies to determine how regeneration and mortality respond to climate fluctuations in ecotones and ecoclines (Payette and Filion 1985). For instance, a demographic survey of the studied plots combined with a multivariate analysis of similar data should allow to quantify how the structure of treeline ecotones is responding to recent climate variability.

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