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Vegetation patterns at the alpine treeline ecotone: the influence of tree cover on abrupt change in species composition of alpine communities

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Abstract

Aims: The upper elevation limit of forest vegetation in mountain ranges (the alpine treeline ecotone) is expected to be highly sensitive to global change. Treeline shifts and/or ecotone afforestation could cause fragmentation and loss of alpine habitat, and are expected to trigger considerable alterations in alpine vegetation. We performed an analysis of vegetation structure at the treeline ecotone to evaluate whether distribution of the tree population determines the spatial pattern of vegetation (species composition and diversity) across the transition from subalpine forest to alpine vegetation.

Location: Iberian eastern range of the Pyrenees.

Methods: We studied 12 alpine *Pinus uncinata* treeline ecotones. Rectangular plots ranging from 940 to 1900 m^2 were placed along the forest-alpine vegetation transition, from closed forest to the treeless alpine area. To determine community structure and species distribution in the treeline ecotone, species variation along the forest-alpine vegetation transition was sampled using relevés of 0.5 m^2 set every 2 m along the length of each plot. Fuzzy C-means clustering was performed to assess the transitional status of the relevés in terms of species composition. The relation of *P. uncinata* canopy cover to spatial pattern of vegetation was evaluated using continuous wavelet transform analysis.

Results: Vegetation analyses revealed a large degree of uniformity of the subalpine forest between all treeline ecotone areas studied. In contrast, the vegetation mosaic found upslope displayed great variation between sites and was characterized by abrupt changes in plant community across the treeline ecotone. Plant richness and diversity significantly increased across the ecotone, but tree cover and diversity boundaries were not spatially coincident.

Conclusions: Our results revealed that no intermediate communities, in terms of species composition, are present in the treeline ecotone. Ecotone vegetation reflected both bedrock type and fine-scale heterogeneity at ground level, thereby reinforcing the importance of microenvironmental conditions for alpine community composition. Tree cover did not appear to be the principal driver of alpine community changes across the treeline ecotone. Microenvironmental heterogeneity, together with effects of past climatic and land-use changes on ecotone vegetation, may weaken the expected correlation between species distribution and vegetation structure.

Keywords: Community structure; Ecotone; *Pinus uncinata*; Plant diversity; Pyrenees; Vegetation analysis; Wavelets.

Plant nomenclature: Bolòs et al. (2005).

Introduction

The Pyrenees, like other mountain systems, are characterized by altitudinal zonation formed by contrasting vegetation belts. In the upper parts of the Pyrenees, a subalpine (or highest forest) belt and an alpine (supraforest) belt have been traditionally distinguished (Braun-Blanquet 1948; Ninot et al. 2007). At higher altitudes, the potential upper limit of the forest – treeline ecotone – coincides, by definition, with the boundary between the subalpine and alpine belts. Ecotones are defined as transition zones between adjacent ecological systems (Hansen et al. 1988; van der Maarel 1990), and two types have been differentiated, (1) *ecotones* in the strict sense, where strong fluctuations create contrasting environments that are individually relatively homogeneous, and (2) *ecoclines*, where gradual differences in at least one major environmental factor allow transitional states. In this study, we use the term treeline ecotone (or treeline) in a broad sense to describe the transition between the subalpine forest and alpine vegetation (Körner 1998; Holtmeier & Broll 2005). This transition occurs through an elevational gradient of increasingly adverse conditions that leads to the altitudinal limit of closed forest stands (forest limit) and, finally, to the limit of tree growth (tree limit), which marks a combined biotic and abiotic threshold for arboreal lifeforms (Körner 2003, 2007).

Tree populations at the treeline ecotone are highly sensitive to climatic variation (Hansen & di Castri 1992; Theurillat & Guisan 2001; Grace et al. 2002). Körner (1998) and Körner & Paulsen (2004) presented data supporting the hypothesis for a common thermal threshold that might explain limits to forest and tree growth at high elevations. Thus, in the context of global warming, the responses of polar and altitudinal treelines have become of major concern worldwide (Callaghan et al. 2002), and several studies reported substantial changes in treeline populations during the 20th century (e.g. Daniels & Veblen 2004; Kullman 2005; Danby & Hik 2007; Gehring-Fasel et al. 2007; Payette 2007; Batllori & Gutiérrez 2008). Structural changes at the treeline ecotone, including growth and regeneration responses, can not only lead to treeline shifts but are expected to trigger alterations in alpine vegetation (Holtmeier & Broll 2005). For example, several alpine plant species that are restricted to above the treeline would experience severe habitat fragmentation and reduction, resulting in an increased risk of regional extinction (Dirnböck et al. 2003). However, climatic change is only one aspect of environmental variations at the treeline (Holtmeier & Broll 2005). In the Pyrenean range, as in many other Eurasian mountain systems, human activities (e.g. seasonal farming) were common at the treeline until the onset of the 20th century, when dramatically decreased, particularly from the 1950s onwards (García-Ruiz et al. 1996). Consequently, since the second half of the 20th century, climate changes have been accompanied by changes in land use, which may have contributed to the spatiotemporal variability in treeline response to local environmental conditions (Daniels & Veblen 2004; Dalen & Hofgaard 2005).

Given the scarcity of quantitative descriptions of tree cover and plant richness boundaries at the treeline (Camarero et al. 2000), a better understanding of the influence of tree cover on spatial patterns of plant richness is required to predict the response of local alpine flora to potential treeline shifts (Camarero et al. 2006). Hence, plant diversity and community structure should be examined together to assess the potential role of key structuring species (e.g. tree species) that may have directional effects on the entire community (Hofgaard & Wilmann 2002). For example, individual trees change environmental conditions under their canopy by decreasing light availability and also modify soil nutrient and moisture conditions (Kembel & Dale 2006).

Although the Pyrenees encompass the southernmost distribution of many European alpine species, including endemic and endangered species (Ozenda 1985; Bolòs et al. 2005), only local studies on vegetation structure have been performed in this treeline ecotone (Camarero & Gutiérrez 2002; Camarero et al. 2006). Here, we analyse community structure and species distribution in the treeline ecotone of the Pyrenees at a regional scale, and examine to what extent *Pinus uncinata* canopy cover determines the spatial pattern of vegetation across the forest-alpine transition. The objectives were to: (1) describe vegetation patterns in 12 treeline ecotones; (2) evaluate plant richness, diversity and tree cover across the treeline; (3) characterize relationships between plant richness and diversity with tree cover; and (4) evaluate the coincidence between species diversity changes and boundaries of the treeline ecotone (forest limit and tree limit).

Methodology

Study area

In the study range of the Pyrenees there is essentially one tree species that inhabits the upper subalpine area: mountain pine (*Pinus uncinata*). This species forms most alpine treeline ecotones on all substrates and at all exposure levels (Ninot et al. 2007). Other species, such as silver fir (*Abies alba*), birch (*Betula pubescens*) and beech (*Fagus sylvatica*), are present in the subalpine belt but rarely dominate the treeline ecotone (Carrillo & Vigo 2002). Thus, we performed our study at the treeline ecotone of the eastern half of the Spanish Pyrenees (Catalan Pyrenees) and in Andorra (Fig. 1) that is dominated by *P. uncinata*. This pine is highly frost-resistant and tolerant to low nutrient and water supply (Ceballos & Ruiz de la Torre 1979), features that have made it a widespread alpine treeline species (Erschbamer & Wallnöfer 2007). Early phytosociological studies (Braun-Blanquet 1948; Rivas-Martínez 1968) described major differences in species occurrence between *P. uncinata* forests, depending on aspect (north- and south-facing) and substrate (acidic and lime-rich). Pine forests on acidic north-facing slopes are characterized by a dense understorey of the low shrubs *Rhododendron ferrugineum* and *Vaccinium myrtillus* (*Rhododendro-Pinetum uncinatae* Rivas-Mart. 1968), whereas, on lime-rich substrata, these

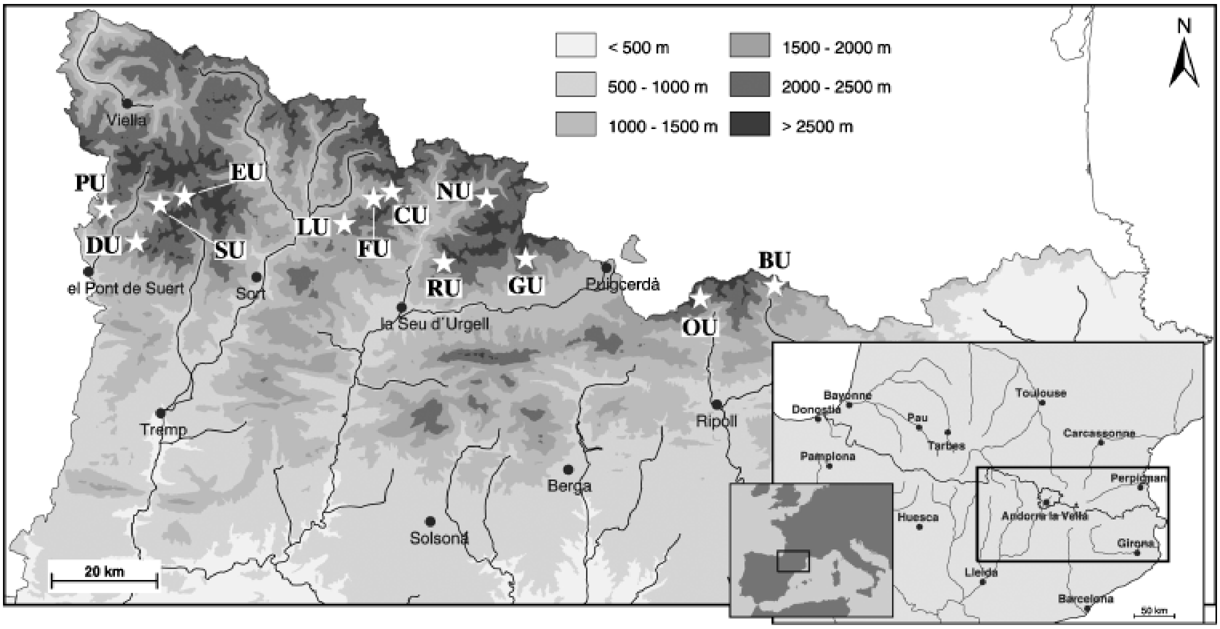

Fig. 1. Location of study sites in the Catalan Pyrenees and Andorra (NE Iberian Peninsula).

low shrubs are mostly replaced by a grass stratum with *Pulsatilla alpina* (*Pulsatillo-Pinetum uncinatae* Vigo 1974). On south-facing slopes, the forest communities are open, irregular pinewoods with a xerophilous subshrub layer of the low shrubs *Juniperus communis* subsp. *nana* or *Arctostaphylos uva-ursi* (*Arctostaphylo-Pinetum uncinatae* Rivas-Mart. 1968).

Detailed vegetation mapping and field surveys performed by Carreras et al. (1996) provided a potential treeline elevation for the Catalan Pyrenees of mostly between 2200 and 2450 m a.s.l., depending on continentality, exposure and landform. At the treeline ecotone, open woods give way to a patchy area with small areas of dwarf scrub, grassland, tree islands and isolated trees. The vegetation above the forest limit, in the alpine zone, forms a small-scale mosaic of structurally and floristically distinct plant communities (Illa et al. 2006; Vonlanthen et al. 2006) that include short grasslands of *Festuca airoides* or *Carex curvula* (on acidic substrata) and grasslands of *Kobresia myosuroides* or *Festuca gautieri* (in carbonated soils), ericaceous dwarf scrub (formed by *R. ferrugineum, Vaccinium uliginosum* ssp. *microphyllum*, *Loiseleuria procumbens, Dryas octopetala*, etc.), and sparse vegetation on rocky substrata and scree (Braun-Blanquet 1948; Carrillo & Ninot 1992).

Field methods

We combined field visits with aerial photographs (taken in 1956 and 2000) to select 12 sites (Fig. 1) that include a progressive – though relatively sharp – transition from subalpine forest to alpine vegetation. At each site, we placed a rectangular plot at the treeline ecotone parallel to the main slope (a transect 10-m wide×variable length). Plot area varied from 940 to 1900 m^2, depending on the characteristics of each transition (Table 1), so as to include the forest limit and the tree limit that corresponds to the line connecting the uppermost upright trees with a minimum height of 2 m (Kullman 2002). Keeping in mind the characteristics of the high subalpine Pyrenean forests of *P. uncinata*, we defined the forest limit position as a coverage threshold of 30-40% (Holtmeier 2003) of arboreal (at least 5-m high) pines (Smith et al. 2003).

The study plots were placed on homogeneous slopes, avoiding major rocky outcrops, avalanche paths and other topographic irregularities. None of the areas studied had been intensively grazed in recent decades, and five of them are located in protected areas subject to almost no human use. We restricted our study to examples of the *P. uncinata* ecotone on north-facing aspects, since north- and south-facing ecotones vary greatly in terms of vegetation structure and composition.

In each plot, the location of all *P. uncinata* stems was noted using rectangular coordinate axes (x, y). For each tree, an estimation of crown size was obtained by measuring four crown radii. Major and minor crown radii and their opposite radii, as well as aspect for each radius, were noted. Using ArcInfo (ArcGis 9.2), we calculated the crown projection

Table 1. Characteristics of examples of the *Pinus uncinata* treeline ecotone sampled in the Catalan Pyrenees and Andorra (NE Iberian Peninsula). *Altitudinal range represented by the plots.

Code	Site	Latitude	Longitude	Plot size (m^2)	Altitude* (m a.s.l.)	Slope (°)	Aspect	Bedrock
PU	Portell	42°31′	0°45′	1400	2199–2268	28	N	Lime
DU	Durro	42°28′	0°49′	1200	2010–2069	30	N	Lime
SU	Serrat del Contador	42°32′	0°53′	1500	2270–2338	27	NW	Lime
EU	Delluí	42°33′	0°56′	940	2299–2339	24	W	Granite
LU	Lo Covil	42°31′	1°21′	1180	2363–2405	21	N	Slate
FU	Serrat de Capifonts	42°33′	1°23′	1900	2352–2435	24	NW	Slate
CU	Port Ovella	42°33′	1°25′	1160	2250–2297	26	NW	Lime
RU	La Rabassa	42°26′	1°32′	1650	2236–2271	24	W	Slate
NU	Obac de Canillo	42°34′	1°37′	980	2266–2314	29	N	Lime
GU	Meranges	42°27′	1°44′	1500	2312–2365	16	NE	Slate
OU	Ras de l′Ortigar	42°23′	2°08′	1500	2241–2308	27	N	Slate
BU	Serra de la Balmeta	42°24′	2°19′	1500	2184–2241	22	N	Slate

area for each tree, properly orientated, and crown cover estimates were then computed every 1 m along the length of each plot.

Finally, we sampled species variation along plots by means of relevés, since plant richness estimates based on the point method (absence/presence measures) depend on plant size, thereby affecting the probability of occurrence and leading to underestimations of species diversity (Fortin et al. 1999). Thus, given the characteristics of the alpine vegetation, we used relevés of 0.5 m^2 (1×0.5 m) set at every two lineal meters on the central axis of each plot. In each relevé, lists of all plant species present and their cover/abundance were noted using the Braun-Blanquet scale (Choesin & Boerner 2002). Plants were identified to species in the field or collected and identified in the laboratory when necessary. Field sampling was conducted in summer between 2003 and 2006.

Data analysis

We analysed the vegetation relevés using multivariate techniques, namely Fuzzy C-mean (FCM) partitions (Bezdek 1981) and principal coordinate analyses (PCoA), using the GINKGO package (Cáceres et al. 2007). FCM is an iterative procedure that minimizes within-cluster variability but allows clusters to overlap (Bezdek 1981); such analysis combines the advantages of numerical partitions with an estimate of membership of each sample to the groups created. To perform FCM partitions, the relevé data in each plot were converted to a distance matrix using the chord distance to take advantage of the fact that the original data referred to relative species cover. Relevés were then partitioned into two, three or four groups using a fuzzy exponent of 1.2 (Cáceres 2005). We evaluated species composition and membership of the groups created in order to determine the transitional status of the relevés and the number of communities present at the treeline for each study site. Finally, we constructed a new matrix containing the abundance data of species present in the communities identified for all studied plots. This matrix was converted to a distance matrix with the chord distance, and PCoA analyses were used to evaluate the uniformity of forest and alpine communities in the 12 study plots. Two PCoAs were performed, one including all communities identified in the transects and one only for the alpine communities.

Linear regression methods were used to ascertain trends in tree cover, plant richness and diversity (Shannon index) across the treeline (increasing altitude gradient) as well as relationships between plant richness and diversity with tree cover. Tree cover and diversity regressions were computed by means of linear models, whereas plant richness regressions used generalized linear models with a Poisson error distribution (Faraway 2006). Finally, we analysed relationships between the spatial pattern of crown cover and species diversity variation in each plot using the continuous wavelet transform method (CWT). CWT analysis has several advantages over other spatial methods; for instance, moving split windows can ignore minor changes at small scales (Choesin & Boerner 2002), and the wavelet functions are also robust against nonstationarity (Bradshaw & Spies 1992). CWT analysis consists of a particular wave form in a moving window of fixed dimensions (windowing function or "wavelet"), which travels along the data sequence to assess the match between the analysing wavelet and the data for each point (Bradshaw & Spies 1992). This process is repeated for a range of wavelet sizes, thereby providing a transformation of the data by the wavelet function at several scales. The CWT method permits data analysis using distinct wavelet forms; in this study we chose the Haar wavelet since, given its resemblance to a step function, it is most appropriate to detect edges and gradients (Bradshaw & Spies 1992). We examined the relationship between tree cover and species diversity at several spatial scales, up to a maximum wavelet size equal to 10% of the length of the area sampled in each plot (Camarero et al. 2006). The CWT was computed over the transects using signal reflection to avoid edge effects, and a two-relevé buffer was used to prevent spurious significance at the extremes of each transect (Addison 2002). The wavelet coefficients were averaged over all scales for any particular position along each transect to obtain a position variance (Dale & Mah 1998). The position variance allowed us to identify abrupt diversity changes and density transitions in crown cover for the treeline ecotone. Given the lack of tests of statistical significance for CWT, we calculated wavelet variance from 1000 randomizations of the original data on diversity and crown cover. The 95th highest value of the position variance for each position along the treeline ecotone was used to ascertain the significance of the detected peaks at $\alpha = 0.05$ (Manly 1997). Following Kembel & Dale (2006), we calculated covariance between the CWT of tree cover and species diversity at each scale in each plot. Linear regression and wavelet analysis were carried out in R 2.6.1 (R Foundation 2007), using the wavCWT function of the wmtsa package (Constantine & Percival 2007) for the latter.

Results

Vegetation patterns

Two or three communities in the forest-alpine transition in each plot were determined by means of FCM analysis (Fig. 2). We identified species that were faithful to communities in each transect (Supporting Information, Appendix S1), some of which coincided with the characteristic taxa inferred by phytosociologists (Carrillo & Ninot 1992; Bolòs et al. 2005) whereas others reflected local conditions. In spite of noticeable crown heterogeneity between plots and a relatively poor understorey, the subalpine forest in all study sites was representative of the calcifuge subalpine *Rhododendro-Pinetum uncinatae* (Br.-Bl.) Rivas-Mart. (1968) in terms of structure and species composition.

In the stands on siliceous bedrock, the alpine community was short, tussock-like grassland of *Hieracio-Festucetum supinae* Br.-Bl. 1948 (LU, FU and OU) or open grassland of *Arenario grandiflorae-Festucetum yvesii* Baudière & Serve 1975 (GU and BU), both of which had similar floristic trends (Fig. 2, Appendix S1). Between pinewood and alpine grassland, two of these ecotone examples (LU, FU) included small patches of *R. ferrugineum*, dwarf formations of *V. uliginosum* ssp. *microphyllum* or patches of the creeping dwarf shrub *Loiseleuria procumbens*. The alpine community in EU, where upper parts of the treeline are dominated by granitic rocky outcrops, was tussock-like grassland of *Hieracio-Festucetum supinae* with high coverage of heather (var. of *Calluna vulgaris*). In lime-rich plots (PU, DU, SU, CU, NU), only the pinewood was calcifuge, while the alpine communities were clearly calcicole (Fig. 2, Appendix S1). In PU and RU, the alpine community was open grassland of *Arenario grandiflorae-Festucetum yvesii*, and in DU mesophilous grassland of *Festuco-Trifolietum thalii* Br.-Bl. 1948. In SU, CU and NU, two alpine communities were identified, where the alpine grassland in these three stands was short grassland mixed with patches of *Dryas octopetala* carpet (*Oxytropido-Elynetum* with *Dryas* Chouard 1943). Between the forest and this alpine community, the NU site presented large patches of *Salix retusa* whereas SU and CU included rich mesophilous grassland of *Festuco-Trifolietum thalii* Br.-Bl. 1948.

The PCoA analysis of all plant communities identified in the stands discriminated between forest and alpine communities (Fig. 3a). Furthermore, the described uniformity of pinewoods in the lower part of plots and the high variability of alpine vegetation mosaics were clearly reflected. The first two PCoA coordinate loadings were significant, and explained 27% and 14.7% of total variance. The PCoA analysis of alpine communities (without the forest) revealed three groups of communities dependent on species composition (Fig. 3b). The first three PCoA coordinates were significant, explaining 20.2%, 17.1% and 14% of total variance, respectively, with acidophilous and calcicole communities clearly separated, and the third group corresponding to the dwarf shrub carpet.

The frequency of alpine species in forest relevés did not exceed ca. 15%, except in LU where *Luzula lutea* and *Festuca airoides* were present in ca. 30% of forest inventories. Species of closed forest were detected only in some study sites and accounted for between 3.5% and 16.4% of the forest inventories. Finally, montane and subalpine grassland species (e.g. *Alchemilla hybrida*, *Carex mixta*, *Carlina acaulis*, *Trifolium pratense*) were detected at very low

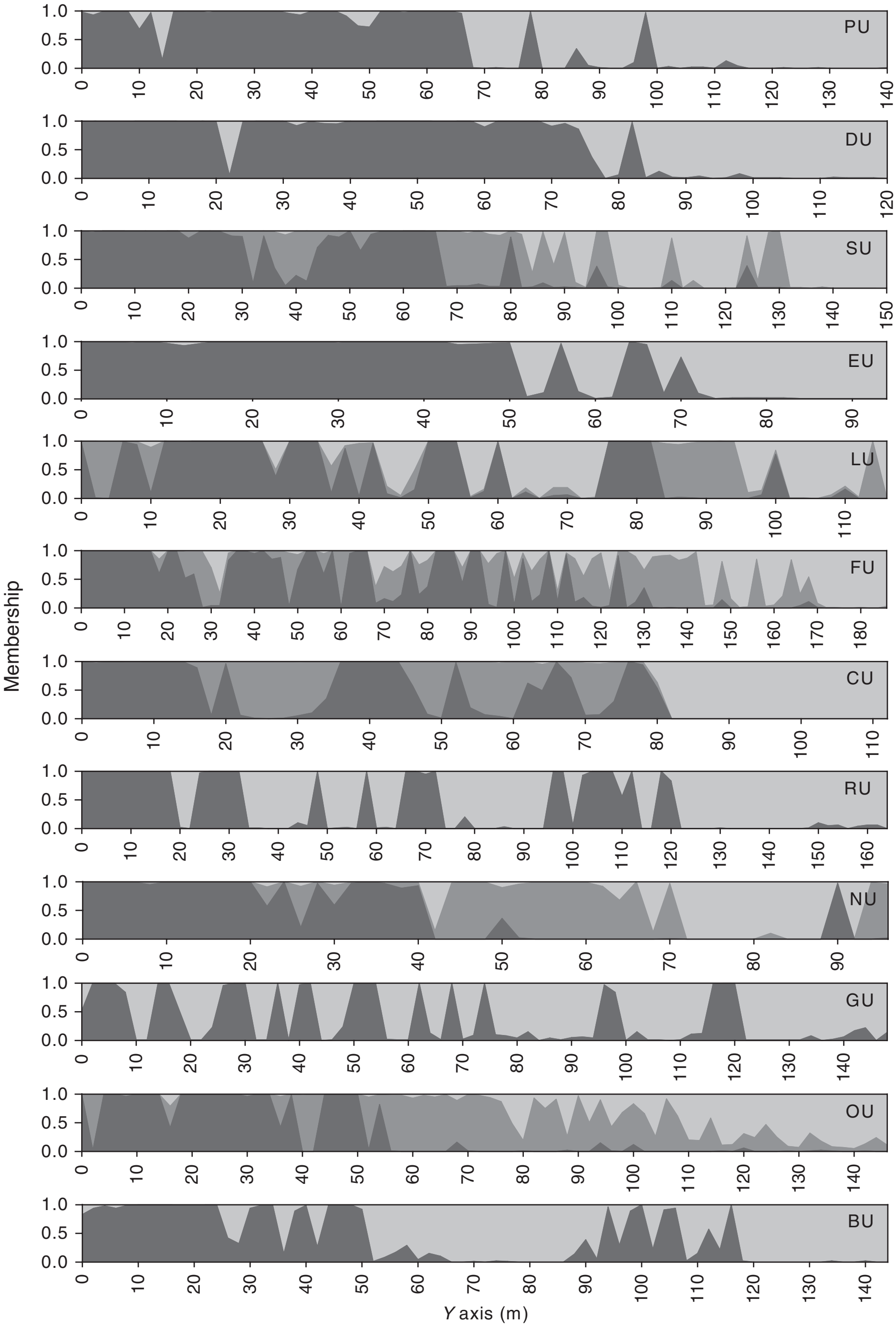

Fig. 2. Vegetation structure across the treeline ecotone in the 12 study plots, from subalpine forest (left) to alpine vegetation (right), evidenced by membership of the relevés defined by Fuzzy C-means analysis. Grey intensity (from dark to light) represents pinewood, dwarf heath and grassland, respectively. See Appendix S1 for a more detailed description of communities at each site.

frequency (<5% of forest relevés) in four of the treelines studied (DU, CU, RU and BU). These results indicate an interchange of species between subalpine forests and adjacent non-forest communities.

Tree cover and diversity variations

Linear regression showed that plant richness and diversity increased significantly along the altitudinal gradient in most study sites (Table 2). As

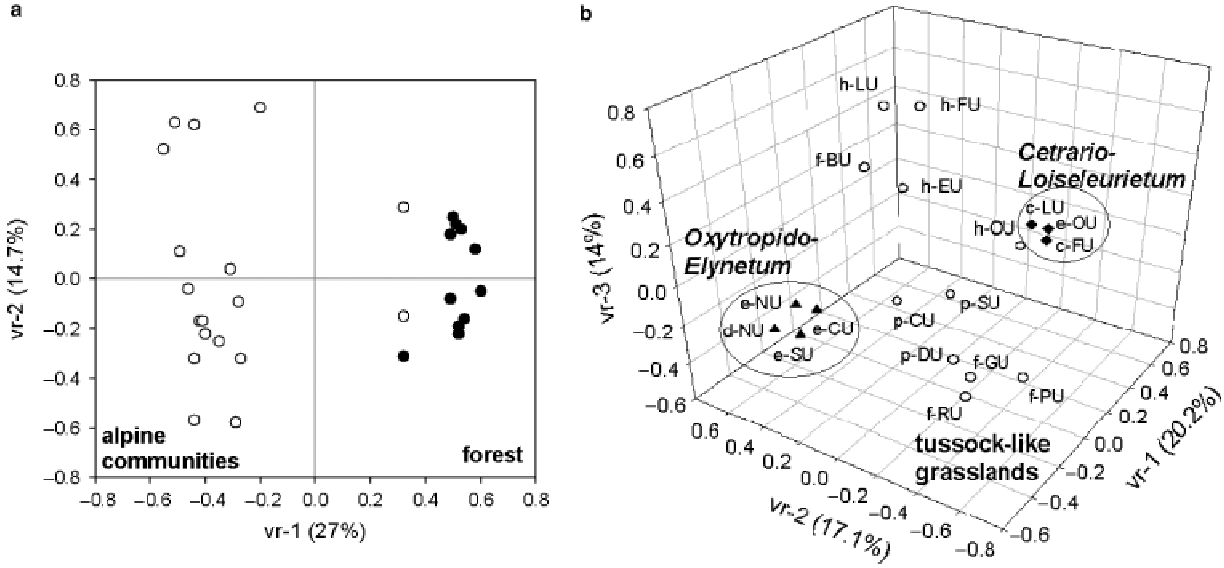

Fig. 3. Scatter plots of PCoA coordinate loadings of the plant communities identified in the 12 study plots. (**a**) Two first PCoA loadings for all plant communities; solid symbols represent forests and open symbols alpine communities. (**b**) Three first PCoA loadings of the alpine communities; symbols represent the group of relevés corresponding to: circles – tussock-like grasslands; diamonds – *Cetrario-Loiseleurietum*; triangles – *Oxytropido-Elynetum*. In the codes, lower-case letters indicate the plant community: c, *Cetrario-Loiseleurietum*; d, *Oxytropido-Elynetum* with *Salix retusa*; e, *Oxytropido-Elynetum* with *Dryas*; f, *Arenario grandiflorae-Festucetum yvesii*; h, *Hieracio-Festucetum*; p, *Primulion*. Capital letters identify the study site (see Table 1 for codes).

Table 2. Results of linear regression fits to tree cover, plant richness or diversity versus altitude across the ecotone at the 12 studied treeline plots. Values of *a* and *b* correspond to intercept and slope of the linear regression (e.g. tree cover = $a+b\cdot$ altitude). Tree cover and diversity regressions were computed using linear models, whereas plant richness regressions were calculated using generalized linear models with a Poisson error distribution. $^{***}P<0.001$; $^{**}P<0.01$; $^{*}P<0.05$.

Site code	Tree cover			Plant richness			Diversity		
	a	*b*	R^2	*a*	*b*	R^2	*a*	*b*	R^2
PU	31.41***	– 0.56***	42.84	1.802***	0.013***	30.50	1.396***	0.026***	35.66
DU	48.40***	– 0.83***	34.28	1.532***	0.019***	34.86	1.588***	0.035***	38.03
SU	29.35***	– 0.45***	35.46	2.165***	0.008***	13.65	2.687***	0.015***	16.01
EU	31.76***	– 0.58**	16.19	1.408***	0.016**	21.10	1.505***	0.014	4.82
LU	13.65***	– 0.34***	18.18	1.753***	0.016***	21.97	2.312***	0.024***	19.38
FU	10.97***	– 0.16***	16.04	1.732***	0.011***	35.38	1.627***	0.016***	21.17
CU	38.43***	– 0.77***	30.9	1.972***	0.019***	36.84	1.526***	0.041***	47.25
RU	42.27***	– 0.76***	45.56	1.562***	0.012***	26.23	1.491***	0.019***	18.36
NU	38.12***	– 0.95***	35.56	1.973***	0.011***	15.56	1.852***	0.016	5.89
GU	27.00***	– 0.88***	28.33	1.096***	0.020***	10.09	0.958***	0.032**	11.36
OU	21.99***	– 0.44***	59.88	1.557***	0.022***	66.35	1.062***	0.040***	70.86
BU	29.37***	– 0.63***	36.4	2.112***	0.003	3.48	1.946***	0.010*	5.90

expected, *P. uncinata* tree cover showed a significant reduction with altitude in all treeline ecotones (Table 2). Although 87.5% of the linear fits were significant at $P<0.001$, the proportion of variance explained by the models was low. The relationship between plant richness and diversity with tree cover was significant and negative in all study plots except for BU and SU, where the same negative relation was observed but was not significant at $\alpha = 0.05$ (Table 3).

Wavelet analysis of *P. uncinata* crown cover along the altitudinal gradient showed that none of the plots had a single, clear tree cover boundary coincident with the forest limit location (Fig. 4). Instead, multiple significant crown cover fluctuations were observed in the lower and middle part of plots, of which one (not necessarily the strongest or widest) corresponded to the forest limit position. Upslope, above the forest limit, isolated significant crown cover fluctuations observed throughout the

Table 3. Results of linear regression fits to plant richness or diversity versus tree cover at the 12 treeline studied ecotone plots. Values of *a* and *b* correspond to intercept and slope of the linear regression (e.g. plant richness = $a+b \cdot$ tree cover). Diversity regressions were computed using linear models, whereas plant richness regressions were calculated using generalized linear models with a Poisson distribution. ***$P<0.001$; **$P<0.01$; *$P<0.05$.

Site code	Plant richness			Species diversity		
	a	*b*	R^2	*a*	*b*	R^2
PU	2.469***	– 0.019***	36.86	2.601***	– 0.028***	28.75
DU	2.462***	– 0.015***	31.17	3.201***	– 0.024***	32.99
SU	2.493***	– 0.004	2.57	3.304***	– 0.007	1.11
EU	1.993***	– 0.012**	16.90	2.119***	– 0.016**	14.95
LU	2.205***	– 0.016**	11.58	2.983***	– 0.020*	6.57
FU	2.285***	– 0.020***	12.26	2.393***	– 0.026**	7.29
CU	2.705***	– 0.014***	31.90	2.995***	– 0.024***	29.81
RU	2.122***	– 0.009***	15.07	2.424***	– 0.018***	20.51
NU	2.393***	– 0.011***	26.16	2.420***	– 0.012*	9.73
GU	1.548***	– 0.014**	10.59	1.724***	– 0.018**	9.74
OU	2.586***	– 0.042***	54.52	2.765***	– 0.052***	38.69
BU	2.234***	– 0.004	7.29	2.322***	– 0.008	3.12

ecotone revealed the presence of sparse individuals forming tree islands in the transition zone. Except for GU, the tree limit position was not associated with significant cover fluctuations in any of the plots. Wavelet analysis of species diversity across the treeline ecotone revealed significant sharp changes in species composition in the majority of study sites (Fig. 4). Only DU, EU and OU did not present abrupt and significant changes in species diversity; nevertheless, considerable fluctuations in species richness were also observed in these ecotones. Multiple significant changes in community diversity that were not aggregated in space were detected in seven of the 12 plots (PU, SU, LU, FU, RU, NU, BU) (Fig. 4). Most of these changes in species diversity (74%) occurred in the area between the forest limit and tree limit. However, in three study sites (PU, FU and RU), significant changes were observed beneath the forest limit, and only in NU did an abrupt diversity shift occur above the tree limit. Patterns of wavelet covariance between tree canopy cover and species composition (Table 4) revealed weak relations, and no general trends were apparent across the range of scales studied.

Discussion

Vegetation patterns

Our analyses revealed a considerable degree of uniformity in the subalpine forest for the 12 treeline ecotone areas studied, irrespective of bedrock type of each site. But, in accordance with well-known differences between alpine communities on siliceous and lime-rich bedrocks in terms of species composition (Braun-Blanquet 1948), the alpine vegetation mosaics above the forest limit described in this study presented considerable differences in relation to the main substrata of the studied sites. Furthermore, large variation was observed among sites in the mosaic found upslope, which may reflect micro-scale heterogeneity in environmental conditions at ground level (Körner 1995). At alpine treeline locations, exposure, soil, mineral nutrients, water availability and microclimate change over short distances. This translates into small-scale mosaics of varying environmental conditions (environmental micro-fragmentation). Moreover, a complex pattern of interferences between species may also contribute to contrasting local vegetation changes (Grabherr et al. 1995). Accordingly, our results from the clustering analyses (FCM) for the set of relevés of each plot revealed that the transition from subalpine to alpine communities is not a smooth and gradual process where plant species shift individually from subalpine forest to alpine communities. In all ecotone areas studied, this was reflected by the very high membership values of the vast majority of relevés to only one of the detected plant communities. Two or three contrasting plant communities (pinewood, dwarf heath and grassland) replaced one another sharply and irregularly along the altitudinal gradient. Thus, there were no typical intermediate communities in terms of species composition along the forest-alpine vegetation transition.

Tree cover and diversity variations

The presence of multiple canopy gaps beneath the forest limit, as shown by the CWT analysis, is reflected by the presence of alpine grassland species (e.g. *Festuca airoides*, *Helictotrichon sedenense*, *Leontodon pyrenaicus*, *Luzula lutea*) in the lower part of ecotones (forest relevés) and the low presence of species indicative of closed forest environments (e.g. *Hieracium murorum*, *Oxalis acetosella*, *Pyrola secunda*). Overall, these observations reflect the low-canopy cover typical of *P. uncinata* forests that extend up to the treeline (Ninot et al. 2007). Furthermore, our results indicate an interchange of species between subalpine forests and adjacent non-forest communities.

Plant richness increased significantly across the treeline ecotone in all stands studied, except BU. However, large differences in number of species

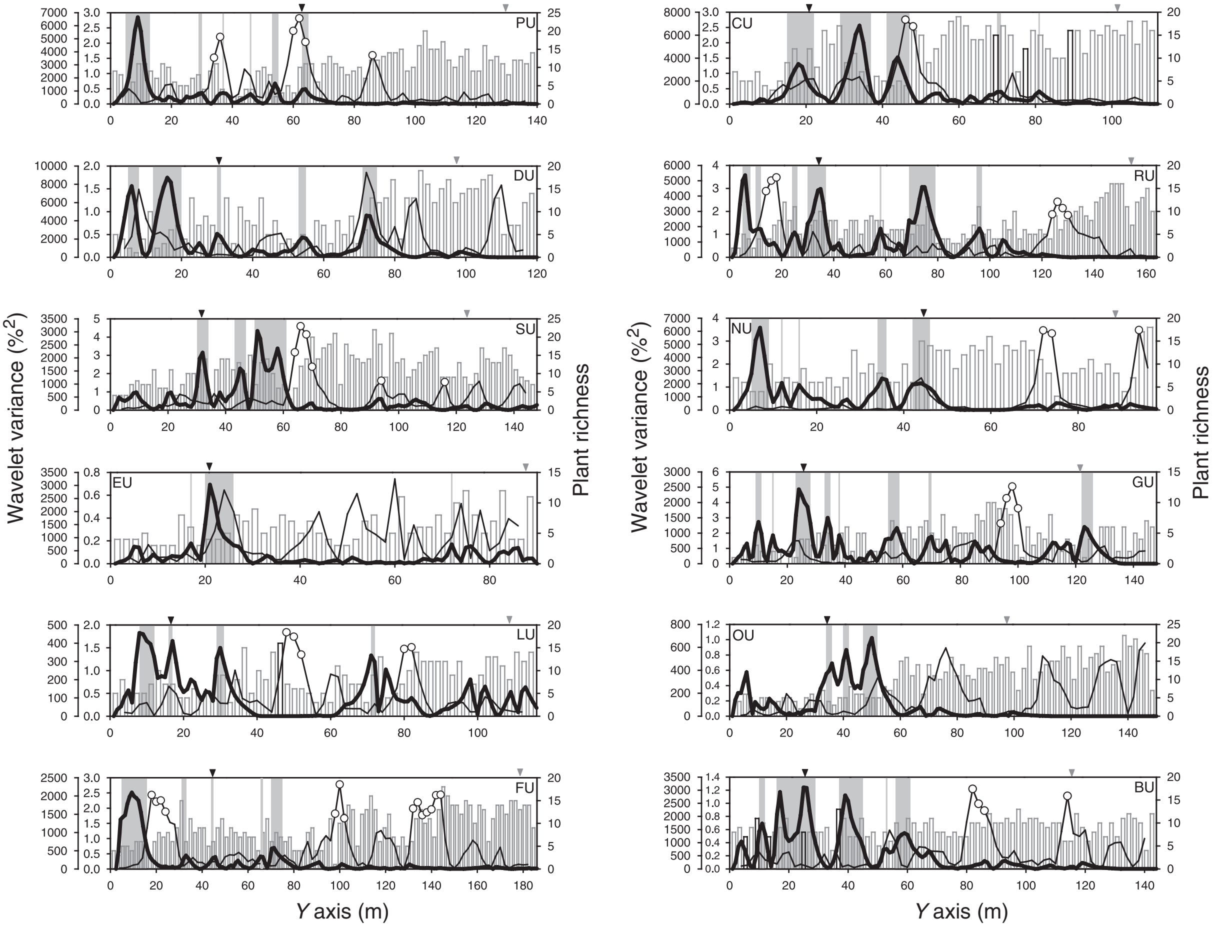

Fig. 4. Results of continuous wavelet transform analysis on tree cover and diversity at the 12 treeline study sites. Thick black line, wavelet position variance (WPV) for tree cover (left offset axis); black line, wavelet position variance for diversity (left axis); grey areas, significant values of WPV for tree cover; open symbols, significant values of WPV for diversity; bars = plant richness; upper black arrow, forest limit position; upper grey arrow, tree limit position.

Table 4. Wavelet covariances versus spatial scale for the relationships between tree cover and alpine community diversity in the 12 studied treeline plots.

Site code	CWT scale of analysis								
	1	2	3	4	5	6	7	8	9
PU	– 0.561	– 2.901	– 5.429	– 6.810	– 4.281	– 2.527	–	–	–
DU	0.457	1.392	2.493	4.352	7.723	12.132	–	–	–
SU	0.379	0.763	0.762	1.045	1.333	1.543	1.698	1.524	–
EU	1.199	2.359	1.965	2.685	3.403	–	–	–	–
LU	0.120	0.333	0.785	1.035	1.215	1.223	–	–	–
FU	– 0.173	– 0.543	– 0.435	– 0.069	0.142	– 0.189	– 0.873	– 1.782	– 2.755
CU	– 0.513	– 2.869	– 5.681	– 7.952	– 10.004	– 10.928	–	–	–
RU	– 0.882	– 3.584	– 6.208	– 6.704	– 4.959	– 3.157	– 2.382	– 2.635	–
NU	0.101	0.937	2.941	5.129	6.983	–	–	–	–
GU	0.259	1.107	2.529	4.173	4.866	4.741	4.488	–	–
OU	0.013	0.097	0.277	0.409	0.386	0.148	– 0.204	–	–
BU	0.321	1.027	0.596	– 0.251	– 0.486	– 0.542	– 0.818	–	–

were observed among contiguous relevés, thereby reinforcing the pronounced small-scale shifts in vegetation composition. Since alpine species are generally of small stature, fine-scale environmental heterogeneity can cause abrupt differences in plant richness (Körner 2003). Similarly, species diversity in the treeline ecotone varied with altitude, increasing from forest to alpine vegetation. Furthermore, CWT analysis of diversity variation showed considerable fluctuations across the treeline ecotone that were linked to small-scale variations in plant richness. The diversity patterns described are not consistent with an overall reduction of species richness with increasing altitude (Grabherr et al. 1995); although the small scale and grain of our study did not reflect forest heterogeneity, rapid shifts in alpine community composition were recorded with greater precision.

The relationship between tree cover and plant richness and diversity presumably reflects not only a variation in physical environment along the elevation gradient, but also the negative influence of tree cover on the occurrence of alpine species. Plant community diversity and composition at small spatial scales is controlled by numerous factors related to microtopography, light availability, temperature, snow distribution, wind, soil nutrients, moisture availability, pH, dispersal limitation, competition and herbivory (Ehrlén & Eriksson 2000; Hofgaard & Wilmann 2002; Kembel & Dale 2006; Vonlanthen et al. 2006). These multiple factors may explain the general low variance accounted for by the linear fitted models used to ascertain relationships between tree cover and plant richness and diversity. We suggest that our models, which mainly indicate increasing light availability along the altitudinal gradient, reflect the presumed importance of light availability in determining species richness patterns in alpine vegetation (Grytnes 2000).

Despite the general negative relation between tree cover and plant richness and diversity across the treeline ecotone, wavelet analysis revealed that tree cover is not closely associated with abrupt changes in alpine community composition at the treeline. Furthermore, the absence of clear peaks or shoulders in the covariance between tree canopy cover and species composition indicates that there is no clear relationship between spatial patterns of the variables analysed. Thus, in accordance with Camarero et al. (2006), significant changes in tree cover were not spatially coincident with abrupt changes in species diversity. Hence, the forest limit position, in most study sites, did not involve significant abrupt changes in species diversity. Factors responsible for environmental heterogeneity at the treeline ecotone, including the spatial pattern of low shrubs (e.g. *R. ferrugineum*) and microtopography, which have the potential to modify microenvironmental conditions (Akhalkatsi et al. 2006; Resler 2006), may weaken the relationship between tree cover and species diversity. Furthermore, since structural and compositional adjustments of ecosystems to environmental changes may present considerable temporal lags, community responses to past climatic and land-use changes may have contributed to weaken the expected correlation between species distribution and vegetation structure (Hofgaard & Wilmann 2002).

Armand (1992) argues that "any natural boundary is in reality a transition zone." From this viewpoint, the exact location of a natural border is, in principle, inexact and largely determined by convention. Moreover, detection of a distinct natural boundary line becomes more difficult as change becomes more gradual (Choesin & Boerner 2002). This is the case for the treeline ecotone, where the boundary between subalpine forest and alpine vegetation is often gradual and fragmented over several tens of meters in altitude (Körner 1995). The inherent arbitrariness in boundary delineation may also partly explain why the forest limit and tree limit presented a weak correlation with plant richness and community diversity. Our results highlight the occurrence of a gradual transition of the tree population from forest to alpine vegetation, coinciding with a general increase in harshness of climatic conditions. This transition is coupled with large fluctuations in environmental conditions at ground level, thereby creating great variability in microclimate, which, in turn, triggers abrupt plant richness and diversity variations. Hence, although the general view of the studied plots gave the impression of a gradual transition, and thus the treeline areas studied could be regarded as *ecoclines*, the sharp and irregular oscillations in contrasted communities, and the lack of intermediate communities in terms of species composition observed at a finer scale, are more associated with the features of *ecotones* (van der Maarel 1990). Although we did not specifically address the scale problem in our study, our findings reinforce the importance of scale when analysing and interpreting transition characteristics.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Communities identified in each transect, with the species with higher membership and behaving as faithful to each community.

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