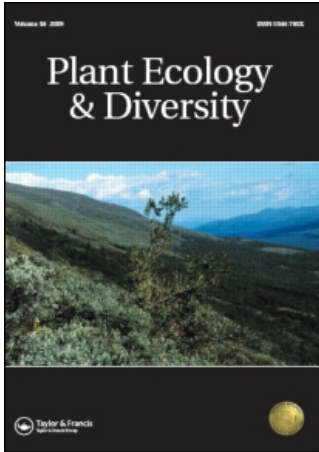


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Timberline structure and limited tree recruitment in the Catalan Pyrenees

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Background: Pyrenean timberlines, lowered to various extents through ancient land use, are expected to rise due to abandonment of land use and climate warming.

Aims: To provide a comprehensive survey of the timberline in the Catalan Pyrenees, at the landscape, plant community, and tree population levels.

Methods: We assessed the present location of timberlines by means of GIS techniques and characterised the treeline ecotone in 12 representative plots, where we took small phytosociological relevés (surface cover type, vegetation structure and species cover) and studied the regeneration of *Pinus uncinata* (seedlings and saplings).

Results: The potential timberline was mostly found between 2300 and 2400 m a.s.l., with complex variation in these values due to bioclimatic and topographic diversity. Most of the present timberline was found at far lower altitudes than its potential location. Present forests reached the potential timberline about 25% along its total length. At natural or semi-natural treelines, the transition from subalpine forest to open alpine landscapes was relatively sharp. It was formed by the irregular alternation of two or three contrasting plant community types (forest, dwarf-shrub, grassland). Most *Pinus* regeneration was recorded where vegetation mosaics occurred on a fine scale. The highest numbers of *Pinus* seedlings and saplings were found emerging from bare ground or litter in small vegetation gaps. Over recent years *Pinus* recruitment showed very slow growth and a strong limitation in reaching the pole stage.

Conclusions: In Pyrenean treeline ecotones situated near to their potential altitudes, recruitment and growth of existing *Pinus uncinata* seedlings and saplings is unlikely to produce pronounced infilling and thus perceptible changes in high-altitude forest cover.

Keywords: ecotone; high mountain; *Pinus uncinata*; treeline; vegetation dynamics

Introduction

The Pyrenean high mountain landscape includes a noticeable altitude zonation which shares many attributes in common with the western Alps (Braun-Blanquet 1948; Ninot et al. 2007). Where the landscape has been less modified by land use, there is a clear timberline or forest line followed by a marked ecotone extending upwards. There, an open pinewood gives way to treeless alpine vegetation intermixed with scarce, small pine trees or prostrate *Krummholz*. This ecotone is considered to extend to the treeline, the highest limit for trees reaching at least 2 m high (Kullman 2001).

Pinus uncinata forms most of the forests in the upper subalpine zone, irrespective of parent material (calcareous, acid) and of exposure. The structure of these upper subalpine *Pinus* stands reflects the limiting environmental conditions through altitude shifts in growth and morphology (Gil-Pelegrín and Villar 1988; Camarero and Gutiérrez 1999). However, the understorey on south-facing and north-facing slopes, and on acidic and lime-rich substrata is clearly differentiated. The plant communities have been classified in terms of their species composition (Braun-Blanquet 1948; Rivas-Martínez 1968; Vigo 1979).

The alpine zone is typically covered by contrasting mosaics, which include short meso-xerophilous grasslands of *Festuca airoides* (on acidic substrata) or *Kobresia myosuroides* (on carbonated soils), ericaceous dwarf-shrub (formed by, for example, *Rhododendron ferrugineum*, *Arctostaphylos uva-ursi*, *Vaccinium uliginosum*), and sparse vegetation on rocky substrata and scree (Braun-Blanquet 1948; Carrillo and Ninot 1992; Illa et al. 2006).

At the altitudes of the Pyrenean treeline, the growing period may be estimated as 90 to 68 d (from 2300 to 2450 m a.s.l., respectively), with mean temperatures averaging 10–12 °C over the growing season. Summer rainfall exceeds 300 mm, which is above the atmospheric water demand (Izard 1985; del Barrio 1990; Ninot 1998); therefore, summer drought does generally not limit plant growth. Regional variation in temperature and rainfall seasonality results in more continental bioclimates in the central and western parts of the south-facing valleys of the Catalan Pyrenees (from Cerdanya to Pallars) with respect to more maritime eastern and north-facing valleys (Izard 1985).

Based on extensive surveys and detailed vegetation mapping studies, Carreras et al. (1996) have proposed a model of the potential timberline for the Catalan Pyrenees

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on a scale of 1:50,000. The elevation of the potential timberline is mapped largely between 2200 and 2450 m, depending on continentality, exposure and landform. According to Körner and Paulsen (2004), the most basic ecological factor defining the location of timberlines is the mean temperature of the rhizosphere during the growing season (over 7 °C, as in the southern Alps and Apennines). However, traditional land use has lowered the timberline to its present location to varying extents, in order to enlarge the grazing areas. On the landforms that are most appropriate for pasturing (gentle relief, intermediate or south-facing exposures) forests have been cleared for most of the subalpine belt.

During the second half of the twentieth century, the abandonment of traditional land use may have caused noticeable reforestation of the subalpine landscape (Monje 2003; Ferré et al. in press). Forest recovery is particularly apparent in some lower subalpine locations, on mainly north-facing aspects. However, a general restoration locations of the timberline to its former position has not happened (Camarero and Gutiérrez 1999, 2004). In other alpine mountains, upward extension of the timberline has been described as particularly slow or inappreciable in areas where the timberline has been lowered least or soil has been eroded or transformed most (Körner 2003; Holtmeier and Broll 2005).

Previous work in the Pyrenees has shown a clear trend of *Pinus* seedlings and saplings becoming denser in the treeline ecotone during the second half of the twentieth century (Camarero and Gutiérrez 2004). At the population scale, the seedling stage is especially crucial over distributional boundaries such as alpine treeline ecotones (Hättenschwiler and Smith 1999). The spontaneous advance of juveniles of forest-forming trees into these ecotones and beyond the

tree limit is considered to be the best indicator of treeline sensitivity to environmental change (Holtmeier and Broll 2005).

The aim of this paper is to provide a comprehensive view of the timberline in the Catalan Pyrenees, bearing in mind its regional variation. We analyse (1) the status of the present timberlines by means of Geographic Information System techniques. We then describe (2) the main patterns of vegetation structure across the ecotone at the plot and community levels, and the (3) demographic structure of young individuals of *Pinus uncinata*.

Material and methods

The position of present and potential timberlines

The area studied is the transition zone between the subalpine and alpine belts found in the Pyrenees of Catalonia and Andorra (Figure 1). This includes the Iberian side of the eastern half of the axial range, one valley (the Aran valley) on the north side of the axial range of the Pyrenees, and detached ranges found southwards (the Pre-Pyrenees).

We performed a spatial analysis of the timberline, on the basis of the delimitation drawn by Carreras et al. (1996) and information from later work (Bolòs et al. 2004 and references therein). In all these vegetation maps and descriptions the potential location of the timberline is deduced from the highest locations of forest remains, with respect to exposure, landform, substrate and bioclimate. This yielded a potential timberline used as a frame of reference to evaluate the location of present timberlines, which are mainly affected by human activities. Differences were categorised into three conceptual states:

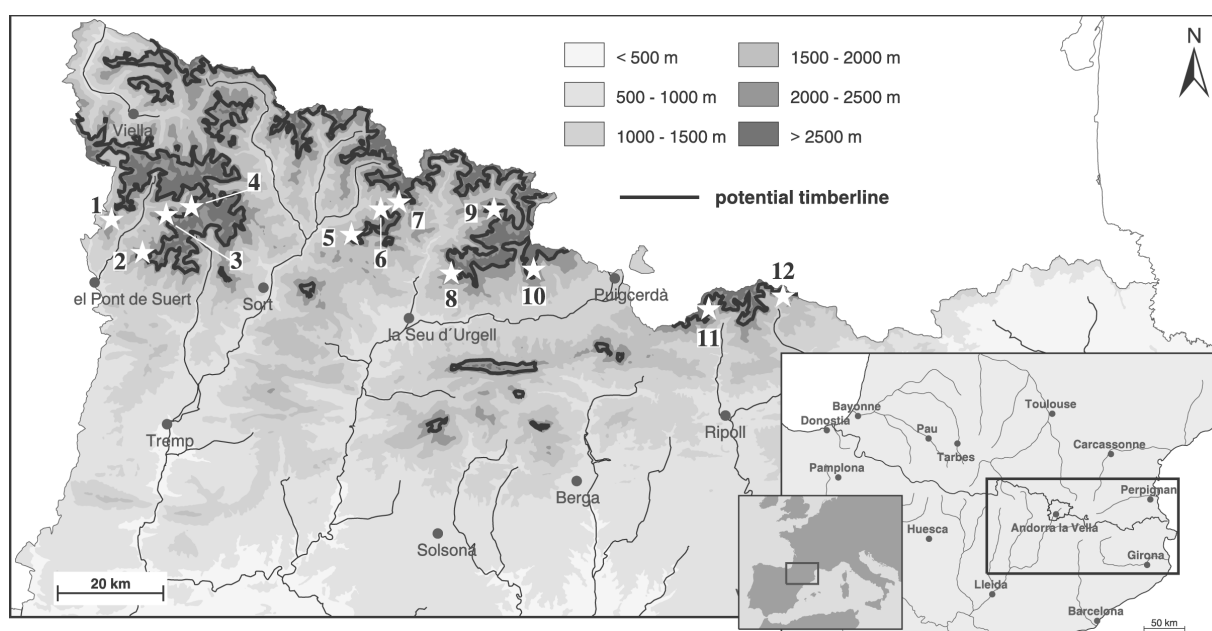


Figure 1. Potential timberline of the Pyrenees of Catalonia and Andorra and the location of the plots studied (see Table 1 for site codes).

- category a: the potential and present timberlines are approximately coincident (differences are estimated as not more than 100 altitude m);
- category b: the present timberline has been moderately displaced downwards (100–400 altitude m), but is still located in the mid or upper subalpine belt; and
- category c: the present timberline is now more than 400 m below its potential location.

We then analysed the occurrence of these states, according to their distribution within the area studied. The analysis was carried in ArcGIS by means of one DEM (Digital Elevation Model) with 20 m of resolution made from the contour lines given in the 1:50,000 maps of Carreras et al. (1996) and Bolòs et al. (2004).

Structure of the ecotone

We analysed in detail the timberline at the landscape and community levels, where the current timberline was identified to be within 400 m elevation of the potential timberline (categories a and b). A noticeable abandonment of land use has taken place in the Pyrenees during the twentieth century, particularly since the 1950s (García-Ruiz et al. 1996). Having this in mind, we focused on sites subject to low disturbance (low intensity grazing) during the last decades. Given the differences between north- and south-facing ecotones in terms of vegetation structure and available examples, we centred the study on north-facing aspects. We combined field visits with screening of aerial photographs taken in 1956 and in 2000 to select 12 plots, including a progressive – although relatively sharp – timberline zonation, as close to the potential timberline location as possible. The regional variation of north-facing ecotones along the axial Pyrenean range was therefore well represented in terms of parent rock material, landforms and plant communities (Table 1, Figure 1). At each site, the plot was placed on a homogeneous slope and avoiding avalanche paths, major rocky outcrops and other topographic irregularities. In each plot, we sampled the vegetation over a transect set along the altitude gradient

and encompassing the entire transition from forest to typical alpine vegetation mosaic. This resulted in 12 rectangles that were 10 m wide and had variable length (from 100 to 200 linear m), depending on the lengths of the ecotone. Since the slope angle was mainly between 21 and 30°, the mean altitude variation was 41 ± 6.2 m along 100 m transect length.

Population structure of *Pinus uncinata* along elevation transects

We described the population structure of *Pinus uncinata* in each transect plot, in terms of the precise location and size (height, crown size) of each individual. In this study we specially focus on the regeneration of pine of up to 50 cm tall. For each of these seedlings or saplings, we recorded surface properties around its stem (e.g. herbaceous or shrubby plant cover, stony, bare soil). We also estimated the age of individuals in the field by counting the whorls of branches and the scars left by them along the main stem. Since this method underestimates the age at the root collar (Camarero and Gutiérrez 1999), we collected 270 seedlings and small saplings in six of the plots to obtain age correction functions. A cross-section was cut at the base of each pine sampled containing root and stem tissue, and root collar was detected through successive sanding (Gutsell and Johnson 2002). The comparison of the age of the collected juveniles at the root collar with the age obtained with internode counting gave a mean error of 3.1 ± 0.15 years. Hence, for the demographic analysis of age structure we grouped the seedlings and saplings into 5-year classes, a period including the age determination error in the field. *Pinus* regeneration was typified in these terms for each plot, considering the 1969–2003 interval. The temporal pattern of recruitment among populations was analysed with Bonferroni adjusted Kolmogorov–Smirnov tests (Gamache and Payette 2005).

Altitude trends in the undergrowth and herb layer

Ground flora was recorded by phytosociological relevés in rectangular sample plots of 1 m × 0.5 m, at every 2 m

Table 1. Location and main features of the plots studied. Categories: a, treeline near its potential elevation (difference < 100 m); b, treeline suppressed by 100–400 m.

Code	Plot site	Altitude (m a.s.l.)	Bedrock	Category
1	Portell	2199–2268	Limestone	a
2	Durro	2010–2069	Limestone	b
3	Serrat del Contador	2270–2338	Limestone	a
4	Dellui	2299–2339	Granodiorite	a
5	Lo Covil	2363–2405	Slate	a
6	Serrat de Capifonts	2352–2435	Slate	a
7	Port de l'Ovella	2250–2297	Limestone	a
8	La Rabassa	2236–2271	Slate	b
9	Obac de Canillo	2266–2314	Limestone	b
10	Meranges	2312–2365	Slate	a
11	Ras de l'Ortigar	2241–2308	Slate	b
12	Serrat de la Balmeta	2184–2241	Slate	b

along the central axis of each transect plot. Percent cover of surface types (herbaceous, shrubby, stony, bare ground) was also estimated for each rectangle. This quantification yielded a good estimation of availability of sites suitable for seedling establishment and growth. Chi-squared test with continuity correction (Yates' correction) was performed to analyse the surface type preference of seedlings (in terms of significant difference between used and available surface types).

We analysed the vegetation relevés by using multivariate techniques, namely Fuzzy C-means partitions and Principal Component analyses, using the software package GINKGO (de Cáceres et al. 2007). Fuzzy analyses combine the advantages of numerical partitions with the evaluation of membership for each sample to the groups created. These techniques were appropriate, as we intended to evaluate the transitional status of the relevés between forest and alpine communities in terms of species composition.

Nomenclature for plants follows Bolòs et al. (2005).

Results

Present and potential location of the timberline

The potential alpine belt forms a discontinuous core in the main Pyrenean axis and a few small isolated areas in the Pre-Pyrenees (Figure 1). The total length of the potential timberline was estimated at 1110 km. Of this, 44.3% was on south-facing slopes (SE to SW), 33.6% on north-facing slopes (NE to NW), and 22.1% on intermediate exposures or flat surfaces.

The potential timberline was found between 2300 and 2400 m a.s.l. for half of its length (48%). However, there was a complex variation in these values, caused at the local scale by exposure and landform. As a general trend, the potential timberline is located at higher altitudes (mostly by between 50 and 150 m) on south-facing slopes than on north-facing ones. This is due to differences in thermal balance and dynamics in snow cover. This latter factor is also responsible for higher locations of the timberline on convex landforms, and lower locations on concavities and leeward positions (even on south-facing aspects) with higher snow accumulation.

At the regional scale, the potential timberline runs at higher altitudes in the axial part of the central Pyrenees, due to its more continental bioclimate. This altitude displacement, known as 'mountain mass elevation effect', is also known from other temperate mountain systems, and is related to cloudiness and radiation differences between maritime and central ranges (Ozenda 1985:90–98; Körner 2003:86–87). The potential timberline progressively descends toward the eastern valleys and the southern Pre-Pyrenees, and on the snowy north side of the axial range. Thus, between Andorra and the western border of the Catalan Pyrenees (the internal valleys of Ribagorça, Pallars, Alt Urgell and Baixa Cerdanya) the potential forest elevation reaches 2350–2500 m a.s.l., depending on the topographic

factors mentioned above. These potential altitudes decrease through intermediate areas to 2100–2350 m in the eastern valleys of the axial range (Alt Ter, Ribes), related to maritime influence. The potential timberline runs over similar altitudes in the steep south-eastern Pre-Pyrenees (e.g. Cadí, Port del Compte), due, in part, to topographic factors. Timberline altitudes are also similar in the north-western edge of the area studied (mid and lower Aran valley) as in the other valleys on the north side of the Pyrenees, which have a sub-Atlantic bioclimate.

Little modified timberlines (category a) account for 24.7% of the total length of the potential timberline. This includes 'pristine' sites, where the potential and present lines nearly coincide, and areas where forest lowering was estimated to be small. Approximately 10% of these little modified timberlines occur in rocky, abrupt places, where they are located at lower altitudes than expected due to topographic factors.

Most of the present timberline was found at far lower altitudes than its potential location. It was moderately lower (category b) than the potential timberline over 32.2% of the length of this potential limit, and much lower (category c) over 43% of this length.

South-facing slopes are clearly more deforested than north-facing areas (Figure 2). Almost half of these subalpine areas were highly deforested, while slight, moderate and heavy depression of the timberline occurred in similar proportions on north-facing slopes (Carreras and Diego 2007).

Vegetation structure across the ecotone

In the plots studied, the transition from subalpine to alpine landscapes was not a smooth, gradual ecotone, where plant species shifted individually from pinewood to grassland. Instead, two or three contrasting plant communities (pinewood, dwarf-shrub heath and grassland) replaced one another sharply and irregularly (Figure 3a,b; for details of plant communities, see Appendix 1). The *Pinus uncinata* forest found at the bottom of the transect plots gave way in small clearings to heath or grassland communities. Above this, heath and grassland alternated, together with small groups of pine (2–4 small trees) and isolated *Krummholz*. Upslope, the alpine grasslands acquired dominance, although heath, small pines and *Krummholz* still occurred sparsely. Clearly, the main protagonist of the vegetation shifts in the low and intermediate zone of the ecotone was *Pinus uncinata*, by modifying microhabitat conditions (shade and the associated dominance of a few tolerant species in the understory). Upwards, decreasing arboreal structure and density (Figure 3a) allowed ground heterogeneity to arise as the alternative vegetation driver. Microtopography, soil stoniness and sparser *Pinus* cover promoted dense vegetation patching up to the upper zone.

In addition to species replacement, the altitude shifts in plant communities were apparent in terms of dominant life forms, species richness and ground cover (Figure 4). These aspects showed noticeable interdependence, since strong dominance by phanerophytes (*Pinus*, *Rhododendron*)

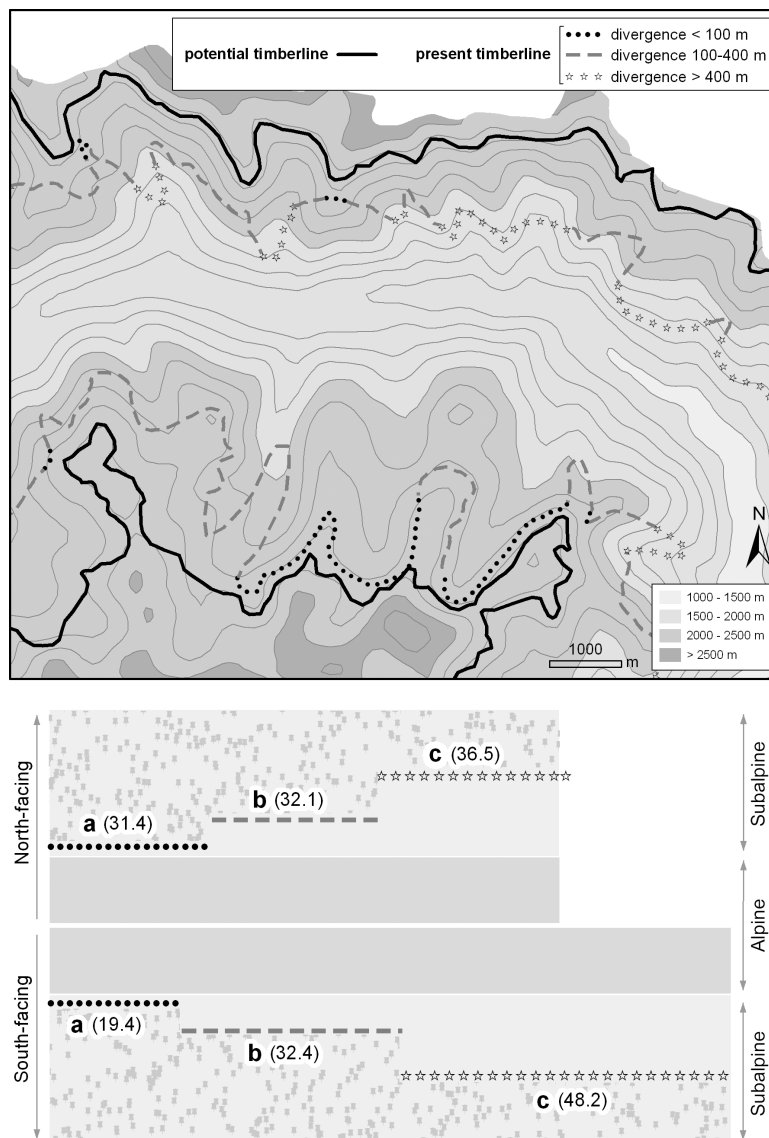


Figure 2. Location of potential and present timberlines, Catalan Pyrenees. Above: example from the central axial Pyrenees, where the potential and present timberlines differ in varying degrees. Below: schematic bird's-eye view of the whole area studied, where the location of the present timberline is evaluated in percentage (in brackets) on north- (upper half) and south-facing slopes (lower half). Note that more timberlines exist along south-facing than along north-facing slopes.

corresponded to the poorest relevés in terms of herbaceous species and to high cover of persistent litter. In grassland, co-dominance of graminoid and non-graminoid hemicryptophytes corresponded to the richest relevés and involved high percentages of bare surface (soil, gravel, small stones) in the form of small gaps interspersed among the grass turfs. Litter was here much less, connected with lower persistence of herbaceous debris. Despite large variation at the small scale (Figures 3a and 4) and of different patterns between transects, the trends described were general, mainly for litter and bare ground cover (Figure 5).

Tree recruitment in the ecotone

Small individuals of *Pinus uncinata* occurred abundantly across the ecotone in all the study sites. The overall

density was 971 individuals ha^{-1} , but large differences were observed among plots (range from c. 200 to $> 3400 \text{ ha}^{-1}$). A very general trend (Figure 3c) consisted of the absence or extreme scarcity of small pines in the lower and upper parts of the plots, and dense populations of seedlings and saplings (< 10 years) in the intermediate part of the plots (the true ecotone), particularly located in small vegetation gaps that had bare soil or were covered by gravel or litter (Figure 6).

Demography of seedlings and saplings

The populations of seedlings and saplings of *Pinus uncinata* showed similar age distribution in all the plots considered. Irrespective of their density and of vegetation differences, their age structure included a bell-shaped maximum of

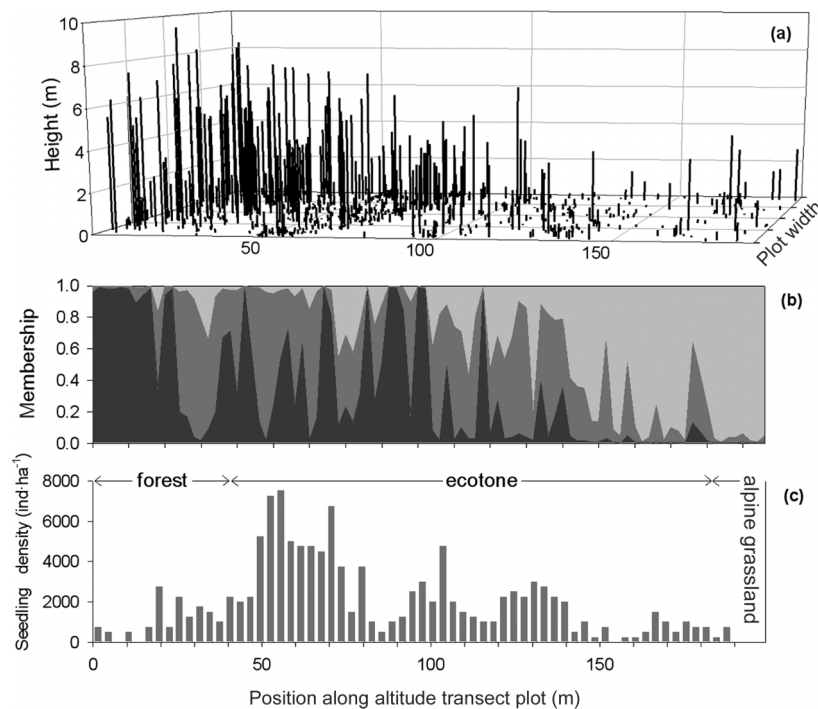


Figure 3. Vegetation structure in one of the plots (Serrat de Capifonts) from the upper subalpine forest (left) to alpine grassland (right). (a) Position and height of *Pinus uncinata* individuals, through decreasing height (and crown size). (b) Membership of the relevés taken along the plot to the three plant communities defined by means of a Fuzzy-C means analysis (dark grey, forest; medium grey, dwarf-shrub heath; light grey, grassland). (c) Density of small pines (individuals ha⁻¹) along the same gradient, grouped into 3-m intervals. The ecotone stands out as a dense alternation of contrasting communities and as a preferred location for *Pinus* regeneration.

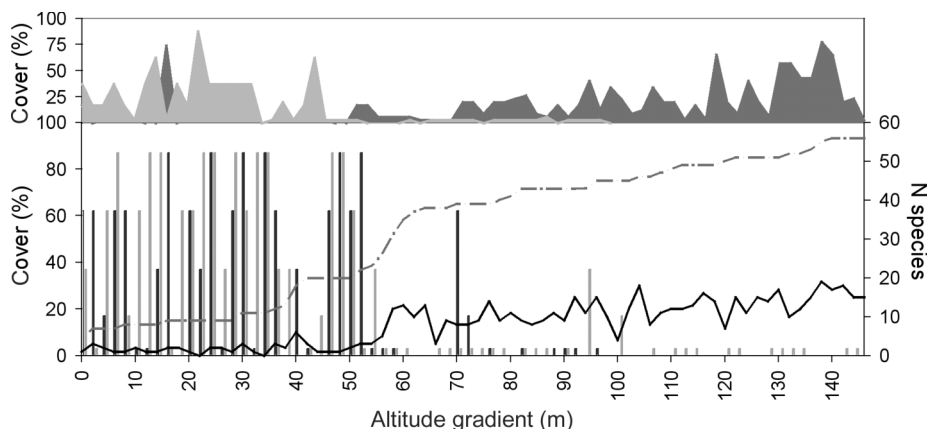


Figure 4. Varying aspects of vegetation structure along the ecotone in one of the plots (Ras de l'Ortigar) from the forest (left) to alpine grassland (right). Cover percentages of litter (light grey area, in the upper part of the figure) and bare ground (dark grey area) showed opposite trends with increasing altitude. In parallel, decreasing dominance of *Pinus uncinata* (dark bars, in the lower part of the figure) and *Rhododendron ferrugineum* (light bars) are related to increasing species richness at the small scale (solid line) and cumulative species richness (dashed line). The values used correspond to 0.5 m² sample plots.

individuals recruited during 1989–1993 (Figure 7, left). Despite the aforementioned limitations in determining age, we are confident that our data show a real decrease in the establishment of seedlings during the period 1994–2003.

The Kolmogorov–Smirnov tests indicated significant differences in the temporal pattern of recruitment among plots in 30 out of 55 comparisons (54.5%). When analysing

separately treelines at their potential altitude vs. moderately lowered treelines, the variability between sites was similarly high, with 46% of the ‘natural’ treelines showing comparable demographic structures for recent regeneration, and with 66% for moderately lowered treelines. However, looking at the time range of maximum recruitment two groups of populations may be distinguished (Figure 7, right), which may be connected with the naturalness of the ecotones.

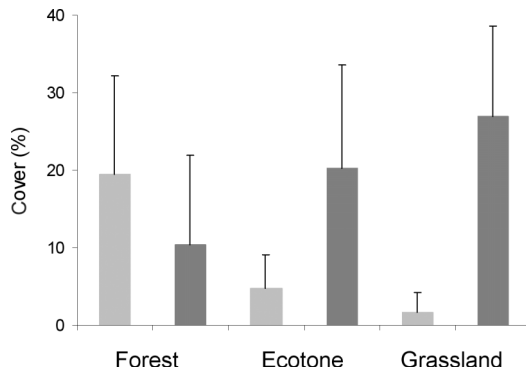


Figure 5. Mean cover percentages of litter (light grey) and bare ground (dark grey) in the three main vegetation formations. There is a general inverse trend in mean percentage values with distance from forest, in spite of noticeable variation at the small scale and across the 12 plots (vertical segments indicate standard deviation).

Accordingly, sites with older age range of recruits mainly coincided with the 'natural' treelines (67% of the plots studied) whereas populations with more recent age range of recruitment corresponded to more 'anthropic' examples (80%).

Discussion

Chances for forest regrowth to the potential timberline

Of little modified timberlines in the Catalan Pyrenees, about 10% are in places where the ecotone changes from irregular forest to rock outcrops. Since these areas are not suitable for human activities, they have remained in a largely natural state. Nonetheless, noticeable spontaneous

reforestation is not expected in such locations because of the lack of soil.

The ecotone noticeably changes along the gradient from near natural timberlines to those lowered more than 400 m altitude. At the most lowered timberlines the transition from forest to pasture includes less plant communities and proceeds through sharper shifts in vegetation structure (Batllori 2008), in accordance with Pignatti et al. (1988). Also, in these timberlines the spontaneous reforestation expected may proceed faster than in near natural timberlines, due to better growing conditions for *Pinus uncinata* (Gil-Pelegrin and Villar 1988; Ferré et al. in press).

There are large differences in timberline depression between north and south exposures. These are partly due to the fact that warmer exposures are more suitable for grazing use (Lasanta 1990). However, this difference may also be caused by summer water stress on *Pinus uncinata* juveniles on south-facing slopes that may limit regeneration (Cantegrel 1983).

There is a great variation in the landscape pattern related to subalpine deforestation. This is mainly due to the dominant landforms and to the socio-economic structure and tradition of the local societies. Cabdella Valley has the most deforested subalpine zone, associated with rather gentle relief and a strong grazing tradition. In contrast, other areas (Aigüestortes, Andorra) have notable areas of preserved upper subalpine forests. These areas have steep slopes and have perhaps been subjected to less human pressure since the 1950s. A typical subalpine landscape in the Catalan Pyrenees, which is somewhere between these cases, is that of a valley with varying degrees of deforestation on the north exposures, including noticeable, well-preserved upper subalpine

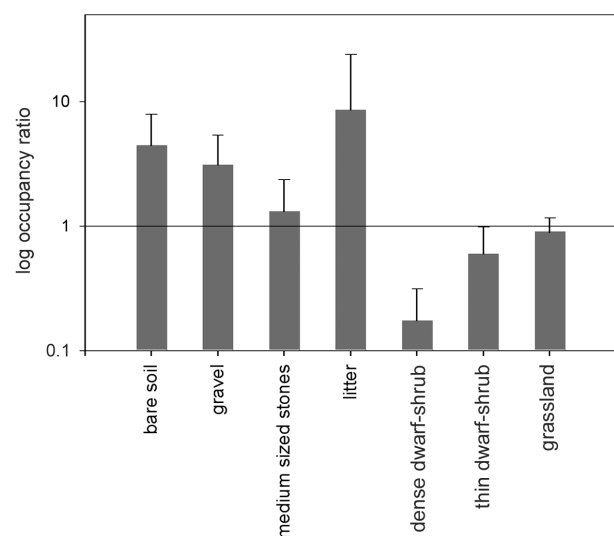
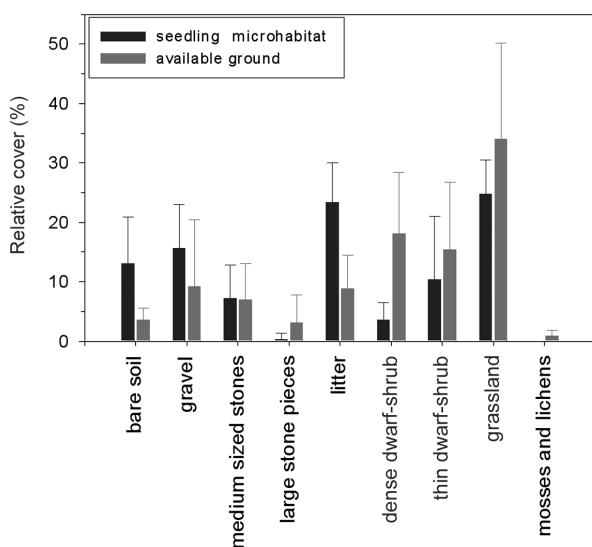


Figure 6. The relationship between surface cover type and their occupation by *Pinus uncinata* seedlings. Left: a comparison between mean percentage of seedling microhabitat (dark bars) and mean percentage of available ground (light bars), with standard deviation. Right: the ratio between seedling microhabitat and available ground on a logarithmic scale, with standard deviation. Note that the lowest categories (large stone pieces and mosses and lichens) are not displayed in the right graph, as they were not representative.

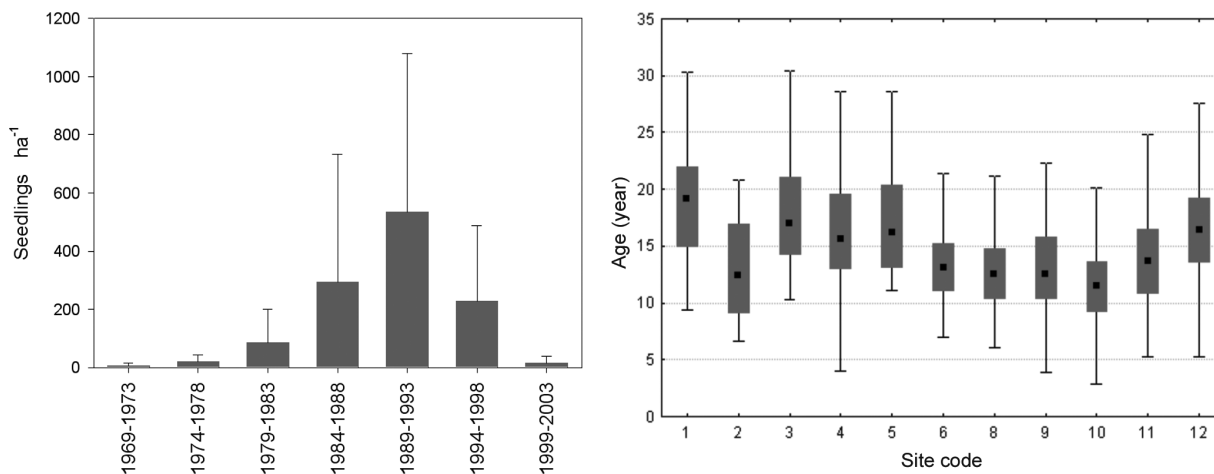


Figure 7. Age structure of the populations of small *Pinus uncinata* individuals. Left: mean density (bars) and standard deviation (vertical segments) for each 5-year age class over the 12 plots studied. Right: box-plot representing the 25–75% percentile (boxes), median value (small squares) and maximum and minimum values (vertical segments) of the ages of small pines for each plot.

forests, and south exposures with extensive areas of pastures and scrub (Figure 2).

Pinus uncinata recruitment in the transect plots

In the lower part of our transect plots (below the timberline) the irregular canopy cover of *Pinus uncinata* trees combined with dense patches of low scrubs (i.e. *Rhododendron ferrugineum*) create unfavourable light conditions for the regeneration of *Pinus uncinata*, a heliophilous species (Cantegrel 1983). At the upper end of the transects, in the alpine zone, the limiting factor cannot be light or lack of safe sites for germination, given that alpine pastures always have numerous small gaps (Illa et al. 2006). Therefore, low densities in the upper zone may be owing to a combination of factors, mainly poor seed rain, a lack of nurse effects from low shrubs or small pines (Ninot et al. in press) and perhaps connected to mycorrhization (e.g. Wiemken and Boller 2006). The intervening mid-transect zone, with alternating heath (including medium-sized gaps), open pastures, *Krummholz* and isolated small trees seemed to combine the appropriate conditions for tree recruitment. Thus, spatial distribution in the ecotone for *Pinus* regeneration during the last 30 years has led to a clear increase in density of juveniles below rather than at or above the actual treeline. This trend seems to be a common phenomenon during the twentieth century in northern and high-elevation treelines (Szeicz and MacDonald 1995; MacDonald et al. 1998; Stöcklin and Körner 1999; Payette et al. 2001; Juntunen et al. 2002; Shiyatov 2003; Camarero and Gutiérrez 2004; Kullman 2005).

Young *Pinus* individuals were mostly recorded from open surface types. In contrast, and in accordance with Pornon and Doche (1995), dense low shrubs (*Rhododendron ferrugineum* and *Juniperus communis* ssp. *alpina*) seemed to prevent tree recruitment. Alpine grasslands and dwarf-shrub heaths (*Loiseleuria procumbens*, *Calluna vulgaris*,

Vaccinium uliginosum, *Dryas octopetala*) had a moderate inhibiting effect on tree recruitment.

Thus, germination and seedling development seemed to require low competition for light and soil resources at the small scale, and it might be promoted by the mulching effect of litter or gravel. When higher than a few centimetres, small pines may benefit from topographic irregularities or neighbouring shrubs (Kitzberger et al. 2000; Resler 2006) or conspecific individuals (Holtmeier 2003; Smith et al. 2003). These elements promote snow persistence on and around seedlings, which protects them from wind abrasion and winter desiccation. Root competition with neighbouring shrubs and pines may become limiting in upper sub-alpine soils, which are mainly rocky and nutrient-poor. The combination of these factors makes the regeneration of arboreal *P. uncinata* a complex process, which may result in very small advances of the timberline when it is located near to its potential altitude. In Andean middle latitude ecotones the tree seedlings emerging above the treeline never grow into adults, but are kept as low shrubby forms by wind or ice damage (Young and León 2007).

Dynamics and role of *Pinus uncinata* juveniles at the Pyrenean treeline

The demographic analysis based on the morphology of small pines presented some difficulties. Age estimation was less precise for older individuals, since most of them had small, dense basal parts that obscured whorl scars. Moreover, some tiny individuals (1–2 years) may have escaped our detection and measures. Despite this, we are confident that the pattern we found represents real recruitment over the past decades. Climate variability affects production of viable seeds, dispersal, availability of adequate regeneration sites, germination and successful establishment of seedlings (Camarero and Gutiérrez 2004). This suggests that a complex combination of factors influences the observed trends in the regeneration dynamics.

The delayed response in recruitment in human affected ecotones may be related to time since land use abandonment. However, local interactions among micro- and macrotopography may cause differential treeline responses even between geographically close sites (Resler 2006). This may be the cause for no clear trends in the demographic structure of regeneration, even within each treeline types (near natural vs. moderately lowered).

The analysed time span does not permit an explanation of whether the low recruitment in the older age classes was due to few seedlings having become established, to mortality, or to the recruitment of seedlings to saplings or poles. However, the presence of old, small individuals (> 25 years old) showed that environmental limitations could prevent the vertical growth of small pines for decades at least. In addition to occasional browsing and spring fungal infections (by *Herpotrichia* sp.), climatic hazards can greatly influence seedling growth and survival (Camarero and Gutiérrez 2004). Small pines are mostly covered by snow during the coldest months. However, occasional strong winds may expose them to extreme cold and abrasion effects. For example, low pines lost a high proportion of leaves and branches in February 2005, while arboreal pines showed no cold injury (Ninot et al. in press). The combination of winter damage with other disturbance events (browsing, occasional summer drought) may kill some of these small pines.

In summary, our study of present timberlines and ecotones situated at slightly or moderately lower altitudes than potential timberlines suggested that there would be little or no upward displacement in the medium term. On the one hand, seedling emergence and establishment was reduced to the immediacy of the upper forest boundary, in relation to the occurrence of safe microsites and probably to seed rain, reinforcing the idea of ecotone densification rather than tree advance upslope. This and the very slow growth of small pines keep the forest advance at very low rates. On the other hand, vulnerability of regeneration to various stress and disturbance factors, including strong climate irregularities, makes the advance above the tree limit a hazardous process.

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Appendix 1. Plant communities identified over the transects, from forest (bottom) to alpine grasslands (top). In each transect, the vast majority of relevés (0.5 m²) belonged to two or three well-defined plant communities

Calcareous bedrock	Siliceous bedrock
Grasslands	
<i>Oxytropido–Elynetum myosuroidis</i> Chouard 1943 with <i>Dryas octopetala</i>	<i>Hieracio–Festucetum supinae</i> Br.-Bl. 1948
Patchwork of grassland including rich herbaceous (<i>Kobresia myosuroides</i> , <i>Oxytropis</i> spp., etc.) and dense dwarf-shrub heath (<i>Dryas</i>)	Short, open grassland formed by the tussocky <i>Festuca airoides</i> and small alpine herbs (e.g. <i>Minuartia recurva</i> , <i>Hieracium breviscapum</i>)
or	
<i>Arenario–Festucetum yvesii</i> Baudière et Serve 1975	
Open, xeromorphic grassland (of e.g. <i>Festuca gautieri</i> , <i>F. yvesii</i> , <i>Helictotrichon sedenense</i>)	
Ecotone	
<i>Festuco–Trifolietum thalii</i> Br.-Bl. 1948	<i>Cetrario–Loiseleurietum procumbentis</i> Br.-Bl. 1926
Rich, mesophilous <i>Festuca nigrescens</i> grassland with dwarf-shrub (<i>Salix pyrenaica</i> , <i>Dryas octopetala</i>) patches	Dwarf, open carpet of the creeping <i>Loiseleuria procumbens</i>
or	
<i>Oxytropido–Elynetum myosuroidis</i> Chouard 1943 with <i>Salix retusa</i>	<i>Saxifrago–Rhododendretum ferrugini</i> Br.-Bl. 1948
Patchy grassland (of <i>Kobresia myosuroides</i> , <i>Oxytropis</i> spp., etc.) including local dwarf-shrub (<i>Salix</i>) spots	Mosaic of low <i>Rhododendron</i> scrub, with herbaceous or chamaephytic (<i>Vaccinium uliginosum</i>) vegetation
Forest	
<i>Rhododendro–Pinetum uncinatae</i> (Br.-Bl.) Rivas-Mart 1968	
Open <i>Pinus uncinata</i> forest with undergrowth of dense low shrubby layer of <i>Rhododendron ferrugineum</i> interspersed with dwarf-shrubs and herbs (e.g. <i>Vaccinium myrtillus</i> , <i>Deschampsia flexuosa</i>)	