# A broad-scale analysis of the main factors determining the current structure and understory composition of Catalonian sub-alpine (*Pinus uncinata* Ram.) forests.

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## Summary

A broad-scale analysis of the structure and understory composition of Pyrenean mountain pine (*Pinus uncinata* Ram.) stands was performed using data from the Spanish National Forest Inventory. Twelve structure-based forest typologies were defined from variables related to tree size, stand density, vertical structure and standing deadwood, using cluster analysis techniques. These typologies were adequately classified (accuracy >75%) by a dichotomous key obtained from classification and regression trees (CART). Multiple regression models were then used to analyze relationships between the main stand structural variables and a set of climatic and physiographic factors. The models showed significant correlations between winter temperature, slope and continentality (among other variables) and the current structure of mountain pine stands. The relationships between the understory composition of mountain pine forests and different environmental and structural overstory factors were found to be driven by an elevation-pH gradient and a stand density-soil stoniness gradient.

The results of this study can be directly used for forest planning at different scales, and could help forest managers to establish strategies designed to facilitate a given habitat for species of conservation interest.

## 1. Introduction

Mountain pine (*Pinus uncinata* Ram.) forests are distributed along the subalpine belt in the Eurosiberian biogeographic region, with their southernmost distribution limit near the Pyrenees (in the Iberian System). These ecosystems are considered as having high conservation interest as they shelter protected and endangered species such as the capercaillie (*Tetrao urogallus*) or Tengmalm's owl (*Aegolius funereus*) (Canut et al., 2011), and are functionally important for soil and water protection and scenic landscape values. There is a general consensus between conservationist and more productivist approaches that silvicultural practices in these forests need to maintain their multifunctionality (de Miguel et al., 2007; González, 2008). The combination of uneven- and even-aged management systems applied to each stand according to its particular characteristics (e.g. initial structure and site quality) together with the establishment of priority conservation areas appears the best way to meet these demands (González, 2008). However, the use of these stand-oriented management strategies requires tools able to facilitate a synthetic description of the stand structure. Forest typologies (FTs) can respond to this need, since they provide detailed and objective classifications of forest stands according to their structure that can be used as a basis to define different management alternatives (e.g. Herbert and Rebeirot, 1985; Aubury et al., 1990; Chauvin et al., 1994). In Spain, for example, FTs have recently been developed with success for silver fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* Matt.) stands using the National Forest Inventory as data source (e.g. Aunós et al., 2007; Gomez-Manzanedo et al., 2008; Reque and Bravo, 2008). The main interest of FTs is that they are based on the overstory structure, which is directly linked to many fundamental functions of forests (i.e. stability, soil protection, scenic landscaping, production) and is a key component in determining biodiversity (e.g. Kuuluvainen et al., 1996; Lindenmayer et al., 2000; Pommerening, 2002).

The overstory structure of forest ecosystems results from a combination of site variables (e.g. soil, climate, topography) (Lindenmayer et al., 1999), natural disturbances (Attiwill, 1994) and the effects of past management (Montes et al., 2005; Ameztegui et al., 2010). These components also have a direct impact on understory composition (Tarrega et al., 2006; Gracia et al., 2007), which is particularly relevant in mountain pine forests as it is one of the main elements defining habitat quality for species of conservation interest (Canut, 2007; Canut et al., 2011). The forest overstory-understory relationship is complex and two-sided, but is dominated by the strong influence of the overstory through its effects on litter, temperature and light quantity and quality (Messier et al., 1998; Legare et al., 2001; Coll et al., 2011). Although the relationship between the distribution of understory species and environmental factors has been widely investigated (e.g. Brosofske et al., 2001; Svenning and Skov, 2002; Kolb and Diekmann, 2004), few studies have analyzed how overstory structure modulates this relationship and its role in the assessment of the broad-scale ecological preferences of understory species (but Gracia et al., 2007; Gazol and Ibáñez, 2009, focused on a smaller scale).

In this study, we conducted a detailed analysis of the overstory structure of mountain pine forests in the Eastern Pyrenees with three different objectives: (1) to develop forest typologies that allow a rapid structural diagnostic of *P. uncinata* stands for subsequent management decision-making processes, (2) to assess the effect of different environmental and anthropogenic factors on the general structural pattern of the stands, and (3) to analyze the combined role played by structural overstory attributes and environmental factors in defining the understory composition of these forests.

## 2. Materials and methods

### 2.1 Study area

The study area is located in the subalpine belt of the Pyrenees, in the southeastern part of the axial zone of the Pyrenees mountain range, covering an area of over 65,000 ha of forest dominated by mountain pine (Figure 1) (Burriel et al., 2004). This area is placed almost entirely in the Boreo-Alpine phytogeographic region, and important physiographical differences cause strong variations in local climatic and soil conditions. Thus, the higher elevations are representative of a mountain climate (mean annual temperature below 3°C, precipitation over 1400 mm), while the valley bottoms present much more temperate conditions (mean annual temperature over 12°C, precipitation below 700 mm) and show certain traits of a Mediterranean climate, at least in the eastern zone. This area of the Pyrenees contains the largest concentration of mountain pine forests, of both Spain and France, and are taken to be highly representative of the total variability of mountain pine forests throughout its distribution area.

*Approximate position of Figure 1*

In this geographical context, mountain pine dominates the subalpine belt (1700-2400 m) upslope from villages and agricultural areas, showing optimum performance at about 1800 m (Blanco et al. 2005; Ruiz de la Torre 2006) and a preference for cold sites with a northerly or easterly aspect and precipitation over 900 mm (Lloret et al., 2009). In the subalpine belt, it forms mostly pure stands but in lower elevations it usually appears in mixture with silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris* L.), beech (*Fagus sylvatica* L.), silver birch (*Betula pendula* Roth.), rowan (*Sorbus aucuparia* L.) or aspen (*Populus tremula* L.) (Ruiz de la Torre, 2006).

## 2.2 Data preparation

### 2.2.1 *Stand structural attributes*

The dataset used to characterize the structure of Pyrenean *Pinus uncinata* stands is taken from the third Spanish National Forest Inventory (NFI3) (DGCN, 2005) and was generated using BASIFOR software (Bravo et al., 2002). The NFI data consisted of a systematic sample of permanent plots distributed over a 1 km square grid surveyed in 1989-1990 (NFI2) and 2000-2001 (NFI3). The NFI plots were circular, with radius dependent on tree diameter at breast height (dbh, 1.3 m): a 5 m radius was used for trees with a dbh of 7.5-12.49 cm; 10 m for 12.5-22.49 cm; 15 m for 22.5-42.49 cm, and 25 m for trees with a dbh of 42.5 cm or higher. NFI data for each sample tree included species, dbh, height, and distance and azimuth from plot centre. Shrubs were counted over the 10 m-radius plots. For each shrub species, mean height (in dm) and cover (in %) were estimated.

We focus our analysis on those mountain pine-dominated woodlands that are interesting from the perspective of wood production. For that, we selected the NFI3 plots dominated by *Pinus uncinata* (i.e. species occupancy > 80% of total basal area) fulfilling some criteria about the minimum stocking (canopy cover > 25%, basal area > 5 $m^2 \cdot ha^{-1}$ and stocking density > 50 $stems \cdot ha^{-1}$). In total, 431 plots fulfilled these criteria. For all these plots, different stand overstory variables were considered for use in the analysis of the structure of *Pinus uncinata* stands. A first group of variables described the main stand characteristics (classic forest inventory variables): tree canopy cover (TCC, %), stocking density (N, $stems \cdot ha^{-1}$ with dbh greater than 7.5 cm), basal area (G, $m^2 \cdot ha^{-1}$), volume with bark (V, $m^3 \cdot ha^{-1}$), mean diameter ($D_M$, cm), Assmann's dominant diameter ($D_0$, cm), mean height ($H_M$, m) and Assmann's dominant height ($H_0$, m). A second group of variables related to the distribution (percentage value) of basal area and stocking density into three diameter classes: fine wood (FW: with dbh between 7.5 and 22.49 cm); medium wood (MW: with dbh between 22.5 and 32.49 cm) and thick wood (TW: with dbh greater than 32.5 cm). A similar approach was used to describe the vertical stratification of the stands by calculating percentage of basal area included in three different height categories: Stratum 1 (STR1: tree height > 2/3 of $H_0$), Stratum 2 (STR2: tree height between 1/3 and 2/3 of $H_0$) and Stratum 3 (STR3: tree height < 1/3·$H_0$). We also assessed relative difference between Assmann's dominant height and mean height [RD-H, $\left(H_0 - H_M\right)/H_M$ ] for each plot, and calculated standing deadwood (ST-DW, %) using the percentage of basal area corresponding to dead trees (standing dead trees, without distinguishing deadwood decay classes) and presence/absence data for all understory species in the selected plots.

### 2.2.2 *Environmental factors*

Environmental variables selected according to their relevance to tree development (Table 1) included climatic variables (mean winter and summer precipitations, mean winter and summer temperatures, and continentality index) and site or geographical attributes (latitude, mean annual solar radiation, elevation, slope, aspect, terrain curvature, site stoniness, soil pH, soil organic richness, and position of the stand in the forest continuum). These variables were selected following a colinearity analysis performed with numerous other site and climatic variables. Site stoniness was recorded from NFI3 as a categorical variable with five percentage ranges of the plot surface covered by stones (Class 1: 0%; Class 2: 0-25%; Class 3: 25-50%; Class 4: 50-75%; Class 5: 75-100%). Then, the variable was reclassified to generate three dummy variables: lowSTO (classes 1 or 2), medSTO (class 3), highSTO (classes 4 or 5). Soil organic richness (a three-level categorical variable in NFI3 with values low, moderate and high depending on the depth and quality of the organic matter) was coded as a dummy variable (lowORG = 1 when the value of organic richness was low, with both other categories coded as 0). Furthermore, the position of the stand in the forest continuum (DISTFE) was assessed as the distance from the plot to the closest forest edge. A log transformation of the DISTFE (distance to forest edge) variable was applied in order to achieve the linearity assumption for linear regression procedures. Aspect was also pre-transformed into a Shade index to better reflect the variation between north and south aspects. Thus, Shade index increased from 0º on south slopes to 180º on north slopes, with east and west slopes given a value of 90º.

*Approximate position of Table 1*

## 2.3 Data analyses

### 2.3.1 *Forest structural typologies*

Principal component analysis (PCA) with a varimax rotation was performed to reduce the number of structural variables to be used for the assessment of forest typologies. After removing variables showing reiterative information, the PCA was conducted with 12 variables (Table 2). The Kaiser-Meyer-Olkin statistics (0.671) and the Bartlett's test of sphericity (rejected the null hypothesis with $p < 0.001$) were used to confirm the sampling suitability to the PCA technique (Hair et al., 2009). The components were selected according to the latent root criterion (Hair et al., 2009), dropping all components with eigenvalues under 1.0.

The different structural typologies of *Pinus uncinata* were determined by applying Ward's method with squared Euclidean distances over the PCA factor scores in the 431 plots selected. Number of clusters was selected according to the cut-off point of the hieratical tree when heterogeneity measure made a sudden jump (Hair et al., 2009). Classification and regression trees (CART) with binary recursive partitioning (p-level for split variable selection = 0.05; goodness of fit: Gini index) were used to assist classification of new stands into the previously-defined structural types. In the dichotomous classification key created by the CART method, the maximum variability between groups is assessed on each node of the decision tree through classification tree analysis so that the partitioning produced the largest improvement in goodness of fit. The final CART model was selected by estimating true prediction error through cross-validation implemented using *V*-fold cross-validation with $V = 10$ (Breiman *et al.*, 1984; De'ath and Fabricius, 2000).

### 2.3.2 *Forest structure and environmental variables*

Multiple regressions were used to evaluate the relationship between each selected component of the PCA and the environmental variables. There was a preliminary analysis of NFI3 plots to identify plots with no evidence of recent silvicultural interventions (presence of stumps, logs, branches, etc.) at the time of the NFI3 measure (n = 337 plots)**.** Recently-managed plots were excluded in order to focus our analysis on the effects of environmental variables and long-term management practices on forest structure, avoiding the possible strong but short-term effects of recent interventions. The model was estimated using the ordinary least squares (OLS) method (SPSS, 2007). From the large number of explanatory environmental variables (Table 1), we only selected those presenting a significant effect and no colinearity-related problems. Kolmogorov-Smirnov normality tests were applied to verify the normal distribution of the residuals for each model. Residual spatial autocorrelation of the models was tested using global Moran's *I* coefficients. ROOKCASE software was used to calculate Moran's *I* for eight equal distances with 1,500 meters as lag distance according to analysis of nearest neighbour statistics (Sawada, 1999).

Canonical Correspondence Analysis (CCA) was carried out to assess the effects of overstory structural variables in combination with environmental variables on the distribution of the most representative understory species in pure *Pinus uncinata* stands. Analyses used the counts of the 13 most common species (present in at least 5% of the 431 plots of our initial dataset) as well as the same environmental and structural components of the multiple regression described above. The set of understory species included shrub species but also regeneration of tree species with dbh < 7.5 cm. A Monte Carlo test (with 9,999 unrestricted random permutations) was executed to determine the significance of the eigenvalues, and semi-automated stepwise forward selection with manual choice of variables was used to select the environmental and structural variables that significantly explained the residual variation in species composition. Only significant variables (with $p < 0.05$) were included. Some strongly correlated variables (e.g. temperatures or precipitation, all highly correlated with elevation) were excluded by examining the Variance Inflation factors for each environmental variable to eliminate superfluous effects liable to generate an arch effect. The correlation threshold used to exclude those variables was the critical value of 0.8 proposed by Menard (2002). However, the existence of some correlations among environmental variables should not weaken the CCA ordination diagram (ter Braak and Prentice, 1988; Palmer, 1993). CCA analysis was performed using CANOCO 4.5 (ter Braak and Smilauer, 2002).

## 3. Results

### 3.1 Structural characterization of *Pinus uncinata* stands

Four PCA components presented eigenvalues above 1.0 and together expressed 85.43% of the variance in the original data (Table 2). The first component accounted for 37.35% of the variance and was constituted by variables related to mean tree size in the stand (mean diameter, Assmann's dominant diameter, mean height and the relative importance to stand basal area for FW and TW). The second component represented 23.99% of the variance and was dominated by different variables related to stand density (tree canopy cover, stand basal area, volume, stocking density, Assmann's dominant height). The third axis explained 15.06% of the variance and was constituted by two variables related to the vertical stratification of the stand (the relative importance on stand basal area for trees in vertical stratum 1 and the relative difference between Assmann's dominant height and mean height). Finally, the fourth axis explained 9.03% of the variance and was mainly dominated by standing deadwood. These PCA components are hereafter named trees size (1st component), stand density (2nd component), vertical stratification (3rd component), and standing deadwood (4th component).

*Approximate position of Table 2*

The cluster analysis was applied using the principal components' scores and classified the 431 plots into 12 structural typologies (Table 3). The cut-off point of the cluster analysis corresponded to a sharp increase in the linkage distances in clustering steps. Kruskal-Wallis non-parametric comparison tests on multiple independent samples ($p < 0.000$) and Mood's median test ($p < 0.000$) confirmed the independence between groups for the 12 structural typologies obtained.

*Approximate position of Table 3*

Forest types T1, T2 and T3 corresponded to young mono-stratified stands, in pole stage of growth, with dominancy of FW. Differences between these three types were mainly given by density, standing deadwood, and a slight size difference. Types T5, T6 and T7 corresponded to adult mono-stratified stands in different phases of timber stage, and differences between them were also given by density, size and standing deadwood. Type T8 corresponded to a bi-stratified stand, with a higher stratum in the medium-to-high timber stage and a lower stratum in the small pole stage. Finally, types T4, T9, T10, T11 and T12 corresponded to multi-stratified structures: type T9 matched to unbalanced irregular stands with excessive occupancy of the FW class while type T11 matched to unbalanced irregular stands with under-occupancy of the FW class but excessive occupancy of the MW and TW classes. T11 also showed a certain mono-stratification in height and increasing standing deadwood values, probably due to the high density. Types T4 and T10 matched to balanced irregular stands with a fairly balanced occupancy of FW, MW and TW classes. T4 corresponded to low-density (quite open) balanced stands, while T10 matched to the full-density ones. Finally, T12 type included adult stands of variable density (but normally low) and predominantly MW and TW. Moreover, T12 stands are characterized by high levels of standing deadwood that may point to partially damaged stands in particularly tough site conditions.

*Approximate position of Table 4*

The classification tool constructed with the CART method (Figure 2Figure 2) considered 9 variables, and performed 23 splits and 22 nodes. The resulting decision tree was able to classify the 431 plots in the 12 structural forest types of *Pinus uncinata* stands with 76.8% accuracy. T10 (balanced irregular stands) was the type showing less well-classified plots (52.4%). Nevertheless, in almost all cases misclassified plots were assigned into the structural types closest to the correct one (Table 4).

*Approximate position of Figure 2*

## 3.2 Forest structure and environmental factors

The correlation coefficients for the models relating the main parameters defining *P. uncinata* stand structure and different environmental variables were relatively low, ranging from 0.34 (**stand vertical stratification** parameter) to 0.61 (stand density parameter) (**Table 5**). Overall, tree size was found to be high in stands located in colder sites with lower continentality and away from the forest edge. Stand density followed a similar pattern, **being** positively correlated with winter mean temperature and distance from the forest edge but negatively affected by slope of the site. Interestingly, stand **vertical stratification** was positively associated with colder sites, lower latitudes, and steep and concave terrain. Finally, standing deadwood was positively correlated with elevation and south-facing slopes.

The models do not present heteroscedasticity or nonlinearity-related problems. Absence of high multicolinearity was tested by examining Variance Inflation Factor, which was never higher than 2. Both stand density and stand even-agedness showed significant but low positive spatial autocorrelation of residuals up to 4.5 km and 1.5 km, respectively (Table 5).

*Approximate position of Table 5*

### 3.3 Understory composition and *Pinus uncinata* stand structure

The first two CCA components accounted for 75.7% of explained species-environment relationships. For the 431 plots six variables contributed significantly to explain the distribution of understory species: elevation (ELE; F = 13.63, p = 0.0001), pH (F = 10.49, p = 0.0001), trees size (PC1; F = 5.84, p = 0.0001), shade index (SHADE; F = 5.01, p = 0.0001), stand density (PC2; F = 3.56, p = 0.0001) and low soil organic richness (lowORG; F = 2.71, p = 0.0025). The first axis was primarily related with an elevation gradient combined with pH, discriminating the more elevated and acidic habitats from other lower-altitude and more basic habitats. *Pinus sylvestris* and *Buxus sempervirens* were the most responsive species to this gradient, showing a clear preference for low-altitude and basic sites. Conversely, species such as *Rhododendron ferrugineum* and *Vaccinium myrtillus* presented a marked preference for higher or more acidic locations, whereas *Abies alba* or *Sorbus aucuparia* proved to be indifferent to this gradient. The second axis was more closely associated with trees size, stand density, aspect, and also low soil organic richness, separating the more shade-tolerant species (*Abies alba*) from the more intolerant ones (*Cytisus purgans*, *Calluna vulgaris*, *Arctostaphylos uva-ursi* and *Juniperus communis*). Other species such as *Sorbus aucuparia*, *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Betula sp*, *Pinus sylvestris* or *Buxus sempervirens* do not show any clear respond to this gradient. No evidence of an artificial arch effect was observed, so detrending was not necessary (Palmer, 1993).

*Approximate position of Figure 3*

## 4. Discussion

The analysis conducted with Spanish National Forest Inventory data allowed us to define a set of different mountain pine forest types. Our forest typologies were developed using stand density and tree size data (as previously done by Roig et al., 2007; Gomez-Manzanedo et al., 2008; Reque and Bravo, 2008) but also integrating the vertical structure of the stands and a simple approach of the standing deadwood, to better assess important characteristics tied to structural heterogeneity and habitat quality for singular species. All these components fully coincided with the factors other authors have defined as the main drivers of the stand structure in mountain pine-dominated forests (e.g. Gil-Pelegrin and Villar, 1988; Calama et al., 2004; González, 2008).

In general, the dichotomous key obtained from CART analysis classified well the 12 forest typologies (accuracy > 75%) using a handful of variables that can be easily obtained from classical forest inventories. Although some minor misclassification problems were found (particularly with the balanced irregular type (T10)) our results show that the use of forest typologies with their corresponding classification tool (dichotomous key) appears to be a useful technique for forest managers to objectively describe forest stands at much lower cost than traditional inventories (Reque and Bravo, 2008). In addition, they may also be used as a forest planning instrument as far as different management guidelines could be associated to them (as has already been done for other European mountain forests (e.g. Gauquelin et al., 2006)).

The analysis of forest structure was focused on mountain pine woodlands fulfilling a minimum cover criterion (25%) and thus excluding very sparse stands (e.g. timber-line, areas with incipient encroachment or forest edges with grasslands). The effect of human intervention was not explicitly considered as we could not find local-level data to adequately describe it. However, although our models used exclusively environmental factors to predict the structure of mountain forest stands, the mid- and long-term effects of human land use are also indirectly considered because the abovementioned environmental variables are highly correlated with them(GarciaRuiz et al., 1996; Lasanta-Martinez et al., 2005; Chauchard et al., 2007; Ameztegui et al., 2010) and in other mountain systems strongly influenced by anthropogenic uses (Coop and Givnish, 2007; Gellrich et al., 2007).

Between the 18th and 19th centuries, intensive land management in different European mountain areas (mainly grazing and logging) resulted in a significant loss of forest cover (Garcia-Ruiz et al., 1996; Lasanta-Martinez et al., 2005, Gellrich et al., 2007). As a result, mountain pine forests in the Pyrenees were mostly reduced to forest patches in areas where human activities were less viable (Jordana, 1869; Bosch, 1999). In contrast, during the last century there has been a significant expansion of mountain forests (e.g. European larch and the Swiss stone pine in the Alps (Didier, 2001)). In the Pyrenees, mountain pine encroachment was particularly important in the low-altitude north-facing slopes where economic imperatives led to a decrease in management intensity (Ameztegui et al., 2010). Our results showed that currently, tree size, stand density and vertical regularity tend to be greater in colder locations, which might be a consequence of the low historical incidence of human activities in these areas. Furthermore, these mature forests tend to be placed further inside the forest continuum, probably because the expansion of mountain pine forests began from the ancient forest patches that subsequently tend to be located deep inside today’s recovered woodland. The negative correlation between slope and stand density could also be explained by land-use patterns. Vicente-Serrano et al. (2004) reported that in the Pyrenees, the ancient agro-pastoral areas located on steeper slopes were among the first to be abandoned. Although these areas experienced a strong increase in vegetation cover over the past few decades (Ameztegui et al., 2010), at present they probably still present low stand density values.

Other environmental factors may reflect long-term and large-scale effects of silviculture. The positive relationship between the vertical regularity and the concavity of the terrain can be explained by the greater productivity of these stands, which has promoted their management (Calama et al., 2004). In fact, in the second half of 20th century, mountain pine forests in the Pyrenees continued to be managed as even-aged stands (Cano, 2003), and this may explain the observed higher regularity of the forests located in productive sites. The low but significant spatial autocorrelation exhibited by regression residuals of stand density and even-agedness for distances up to 4,500 meters pointed out the existence of small-scale processes that were not detected by our models. Some of these processes might be related to spatial variation in site quality or in small-scale structural attributes related to historical management or natural disturbances.

With independence of land use-associated patterns, environmental gradients have been proved to be good predictors of forest structure (e.g. Lindenmayer et al., 1999; Garbarino et al., 2009). The greater quantity of standing deadwood found in the higher elevations is probably a result of the effect of abiotic factors such as wind and snow (Martin-Alcon et al., 2010) or drought stress (Galiano et al., 2010) combined with a higher incidence of pathogens (Oliva and Colinas, 2007). Similarly, the decrease in tree size observed in more continental sites may also have a climatic explanation.

The general analysis of the main factors driving understory composition in Pyrenean mountain pine forests revealed the existence of two main gradients: an elevation-pH gradient and a stand structure-soil organic richness gradient. It has already been recognized that elevation influences understory cover and composition in mountain pine forests (Camarero and Gutiérrez, 2002a; Gracia et al., 2007; Coll et al., 2011). In general, variation in the presence of species along this gradient is related to their tolerance to low temperatures (e.g. *Pinus sylvestris, Buxus sempervirens*) but also their ability to cope with acidic soils. It should be noted that the elevation-pH gradient might include a precipitation gradient that was not integrated in the analysis due to its higher correlation with elevation. This may explain why *Rubus idaeus* is placed so leftward along this axis despite the fact that this species is not exclusively limited to high-altitude sites. Other studies conducted on a smaller scale identified site aspect as one of the most important variables determining species distribution due to its effect on microclimate or soil formation (e.g. Sternberg and Shoshany, 2001; Camarero and Gutiérrez, 2002b; Gracia et al., 2007). Here, the aspect effect was gathered in the second CCA axis which was related to a gradient of shading, where aspect was jointed with stand density and tree size. Some species that preferentially develop in north-facing slopes can also perform well in south-facing slopes if they grow under the protection of an overstory providing the necessary shading.

The main environmental requirements of the understory communities of mountain pine forests were adequately assessed by our analysis: *Calluna vulgaris, Arctostaphyllos uva-ursi, Cytisus purgans* or *Juniperus communis* were found to dominate in open stands located on south-facing slopes whereas *Rhododendron ferrugineum, Vaccinium* *myrtillus* and *Buxus sempervirens* showed a clear preference for more mature stands on north-facing slopes (Camarero and Gutiérrez, 2002b), with *R. ferrugineum* presenting slightly higher shade-tolerance than *V. myrtillus*. Interestingly, *Arctostaphyllos uva-ursi* is mainly distributed in north-facing slopes at lower elevation (where Scots pine or oaks are the dominant species (Gracia et al., 2007; Lloret et al., 2009) but showed preference for south-facing slopes or much more open stands on soils with low organic richness at higher elevations (where mountain pine dominates). Since our study was conducted on a large area by using National Forest Inventory and other data presenting broad spatial variability our analysis contains a large unexplained variance. This could be attributed to other factors acting at finer scales (e.g. livestock grazing and browsing by game) that may warrant to be studied with different methodological approaches.

In summary, in this study we have provided suitable analysis to assess forest typologies and adequately describe the main factors defining at regional scale the present-day structure of Pyrenean mountain pine stands and the main drivers of understory composition. We have observed some parallelisms with those processes that have occurred or are now occurring in subalpine forests from other mountain ranges (i.e. Alps or the Atlas). The findings reported here can be directly used for forest planning at different scales, and can be very useful to predict future dynamics in those mountain ranges that nowadays are experiencing those human impacts that European mountains suffered in the recent past. Moreover, our results provide valuable contributions to help managers establish strategies designed to facilitate a given habitat for species of conservation interest (e.g. promoting *Vaccinium myrtillus* over *Rhododendron ferrugineum* in areas frequented by capercaillie (*Tetrao urogallus*)).

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# Tables

**Table 1**: Descriptive statistics and sources of continuous environmental variables

| Group | Variable | Units | Source | Mean | S. D. | Min. | Max. |
|---|---|---|---|---|---|---|---|
| CLIMATE | Winter mean precipitation (PW) | mm | *(Ninyerola et al., 2000))* | 205.9 | 24.7 | 164.1 | 299.1 |
| | Summer mean precipitation (PS) | mm | *(Ninyerola et al., 2000))* | 323.7 | 38.4 | 241.0 | 454.0 |
| | Winter mean temperature (TWi) | °C | *(Ninyerola et al., 2000))* | -0.6 | 0.9 | -2.8 | 2.4 |
| | Summer mean temperature (TS) | °C | *(Ninyerola et al., 2000)* | 12.1 | 1.1 | 8.4 | 15.6 |
| | Continentality Index (IC) | - | *Based on (Conrad, 1946)* | 24.8 | 2.7 | 15.7 | 30.1 |
| LOCATION | Latitude (LAT) | ° | *DEM* | 42.4 | 0.2 | 42.1 | 42.8 |
| | Mean annual radiation (RAD) | 10 KJ·m$^{-2}$·day$^{-1}$ | *(Ninyerola et al., 2000)* | 1319.0 | 156.1 | 1000.0 | 1900.0 |
| | Elevation (ELE) | m.a.s.l. | *DEM* | 1916.2 | 181.4 | 1310.2 | 2477.0 |
| | Slope (SLP) | ° | *NFI3 (DGCN, 2005)* | 18.0 | 8.0 | 1.3 | 48.8 |
| | Terrain curvature (CUR) | - | *Based on (Moore et al., 1991)* | 0.05 | 0.37 | -1.20 | 1.51 |
| | Shade index (SHADE) | ° | *DEM* | 105.4 | 51.3 | 0.9 | 180 |
| | Soil pH (PH) | pH | *NFI3 (DGCN, 2005)* | 5.7 | 0.9 | 3.5 | 8.0 |
| | Distance to forest edge (DISTFE) | m | *Based on NFI3 (DGCN, 2005) and MCSC (Ibañez et al., 2002)* | 113.14 | 129.14 | 0.0 | 724.0 |

*Abbreviations: DEM: Digital Elevation Model; NFI3: Third National Forest Inventory; MCSC: Soil Cover Map of Catalonia*

**Table 2**: **Varimax rotated factor loadings and communalities for the forest structural variables of the 431 forest plots studied.**

| VARIABLES | Component | | | | Communalities |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | |
| **DM** | **0.926** | -0.157 | -0.092 | -0.077 | 0.896 |
| **FW (%G)** | **-0.902** | 0.192 | -0.202 | 0.027 | 0.892 |
| **DO** | **0.829** | 0.134 | 0.332 | 0.296 | 0.902 |
| **TW (%G)** | **0.805** | -0.282 | 0.287 | 0.168 | 0.838 |
| **HM** | **0.689** | 0.551 | -0.127 | -0.307 | 0.889 |
| **TCC** | -0.111 | **0.851** | -0.064 | -0.013 | 0.741 |
| **G** | 0.247 | **0.849** | 0.030 | 0.330 | 0.892 |
| **N** | -0.529 | **0.714** | -0.017 | 0.319 | 0.892 |
| **HO** | 0.496 | **0.624** | 0.369 | -0.309 | 0.867 |
| **RD-H** | -0.383 | 0.057 | **0.869** | 0.032 | 0.905 |
| **STR1 (%G)** | 0.403 | 0.200 | **-0.762** | -0.121 | 0.798 |
| **ST-DW (%G)** | 0.308 | -0.166 | -0.269 | **0.739** | 0.740 |

*Abbreviations: DM, mean diameter; FW (%G), basal area of fine wood; D0, Assmann's dominant diameter; TW (%G), basal area of thick wood; HM, mean height; TCC, tree canopy cover; G, basal area; N, stocking; H0, Assmann's dominant height; RD-H, relative difference in heights; STR1 (%G), basal area of height stratum 1; ST-DW (%G), basal area of standing deadwood.*

**Table 3**: Mean and standard deviation of the main forest variables used for each of the 12 structural types obtained for the *Pinus uncinata* stands in the Catalan Pyrenees.

| VARIABLE | STRUCTURAL TYPOLOGIES | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **T1**<br>(n = 40) | **T2**<br>(n = 30) | **T3**<br>(n = 36) | **T4**<br>(n = 63) | **T5**<br>(n = 47) | **T6**<br>(n = 71) | **T7**<br>(n = 35) | **T8**<br>(n = 15) | **T9**<br>(n = 25) | **T10**<br>(n = 21) | **T11**<br>(n = 31) | **T12**<br>(n = 17) |
| **TCC (%)** | 65.8 | 61.2 | 82.6 | 51.0 | 77.0 | 74.2 | 49.1 | 68.0 | 60.6 | 59.8 | 69.7 | 46.8 |
| | 16.1 | 12.5 | 9.1 | 15.2 | 8.4 | 10.1 | 10.3 | 10.7 | 14.8 | 12.3 | 12.2 | 12.4 |
| **N (trees·ha$^{-1}$)** | 1138 | 532 | 1709 | 349 | 1269 | 714 | 270 | 730 | 1069 | 819 | 803 | 440 |
| | 450 | 205 | 558 | 164 | 510 | 232 | 124 | 268 | 448 | 304 | 408 | 432 |
| **G (m$^2$·ha$^{-1}$)** | 20.7 | 14.3 | 39.2 | 13.9 | 37.2 | 35.9 | 23.0 | 29.6 | 23.3 | 26.8 | 40.5 | 18.8 |
| | 7.6 | 5.6 | 11.2 | 5.5 | 10.4 | 9.3 | 8.6 | 6.5 | 8.2 | 9.4 | 11.4 | 7.5 |
| **V (m$^3$·ha$^{-1}$)** | 98.5 | 70.7 | 232.9 | 68.0 | 211.2 | 223.6 | 107.8 | 180.2 | 118.2 | 121.7 | 200.9 | 64.3 |
| | 45.9 | 33.3 | 84.9 | 31.9 | 71.5 | 72.4 | 48.1 | 31.0 | 57.8 | 49.8 | 64.3 | 33.5 |
| **DM (cm)** | 14.4 | 18.0 | 16.6 | 21.2 | 18.2 | 24.3 | 31.6 | 20.5 | 15.3 | 18.2 | 24.4 | 23.8 |
| | 1.9 | 3.4 | 2.6 | 3.3 | 2.0 | 3.7 | 4.0 | 2.9 | 2.3 | 2.2 | 3.6 | 6.6 |
| **DO (cm)** | 25.5 | 25.8 | 27.5 | 30.9 | 33.8 | 37.7 | 41.9 | 39.9 | 32.8 | 36.6 | 41.6 | 36.1 |
| | 2.9 | 4.5 | 4.2 | 3.9 | 3.1 | 5.0 | 4.6 | 3.6 | 6.5 | 3.4 | 5.7 | 7.2 |
| **HM (m)** | 6.6 | 8.2 | 9.8 | 8.3 | 9.4 | 12.7 | 11.1 | 9.8 | 6.7 | 7.3 | 10.7 | 7.3 |
| | 1.4 | 2.0 | 2.0 | 1.6 | 1.3 | 2.3 | 1.9 | 1.1 | 1.2 | 1.0 | 1.8 | 1.1 |
| **HO (m)** | 9.0 | 9.4 | 11.1 | 10.6 | 13.1 | 15.3 | 12.1 | 16.5 | 11.6 | 10.4 | 12.0 | 7.7 |
| | 1.9 | 2.2 | 2.1 | 2.3 | 1.6 | 2.5 | 2.0 | 2.2 | 2.4 | 1.4 | 2.2 | 1.2 |
| **FW (%G)** | 71.3 | 60.5 | 70.5 | 29.6 | 44.6 | 21.0 | 6.1 | 22.6 | 51.4 | 33.7 | 20.3 | 23.9 |
| | 14.3 | 22.9 | 19.7 | 13.4 | 12.6 | 13.2 | 5.4 | 11.5 | 18.4 | 11.8 | 10.3 | 20.8 |
| **MW (%G)** | 24.4 | 33.2 | 25.7 | 37.8 | 37.5 | 43.8 | 22.4 | 26.6 | 22.2 | 30.8 | 34.9 | 28.2 |
| | 12.8 | 19.7 | 16.9 | 18.6 | 10.9 | 14.8 | 10.7 | 12.7 | 13.7 | 13.2 | 11.6 | 17.9 |
| **TW (%G)** | 4.3 | 6.3 | 3.8 | 32.6 | 17.8 | 35.2 | 71.5 | 50.8 | 26.4 | 35.5 | 44.8 | 47.9 |
| | 7.3 | 7.9 | 5.3 | 20.9 | 11.2 | 19.4 | 11.7 | 19.8 | 19.5 | 13.1 | 13.9 | 30.8 |
| **ST-DW (%G)** | 0.7 | 3.6 | 5.6 | 1.1 | 3.5 | 2.0 | 6.4 | 3.7 | 1.2 | 10.6 | 12.3 | 28.1 |
| | 1.7 | 5.3 | 6.3 | 2.8 | 3.1 | 3.5 | 4.6 | 3.8 | 2.8 | 6.1 | 7.7 | 7.9 |
| **RD-H** | 0.37 | 0.14 | 0.13 | 0.29 | 0.25 | 0.22 | 0.10 | 0.68 | 0.75 | 0.41 | 0.17 | 0.06 |
| | 0.10 | 0.09 | 0.09 | 0.14 | 0.11 | 0.12 | 0.09 | 0.17 | 0.20 | 0.10 | 0.12 | 0.10 |

*Abbreviations: TCC, tree canopy cover; N, stocking; G, basal area; V, volume with bark; DM, mean diameter; D0, Assmann's dominant diameter; HM, mean height; H0, Assmann's dominant height; FW (%G), basal area of fine wood; MW (%G), basal area of medium wood; TW (%G), basal area of thick wood; ST-DW (%G), basal area of standing deadwood; RD-H, relative difference in heights.*

Table 4: Classification table (confusion matrix) resulting from the CART analysis (percentages of well-classified observations are showed in bold).

| | | FOREST TYPE (from cluster analysis) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | T1 *(n=40)* | T2 *(n=30)* | T3 *(n=36)* | T4 *(n=63)* | T5 *(n=47)* | T6 *(n=71)* | T7 *(n=35)* | T8 *(n=15)* | T9 *(n=25)* | T10 *(n=21)* | T11 *(n=31)* | T12 *(n=17)* |
| FOREST TYPE (from CART) | T1 *(n=46)* | **87.5%** | 13.3% | 2.8% | 1.6% | 4.3% | 0.0% | 0.0% | 0.0% | 8.0% | 4.8% | 0.0% | 0.0% |
| | T2 *(n=27)* | 2.5% | **66.7%** | 5.6% | 4.8% | 2.1% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| | T3 *(n=34)* | 0.0% | 0.0% | **83.3%** | 0.0% | 6.4% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 3.2% | 0.0% |
| | T4 *(n=80)* | 0.0% | 13.3% | 0.0% | **90.5%** | 4.3% | 8.5% | 11.4% | 0.0% | 12.0% | 14.3% | 3.2% | 0.0% |
| | T5 *(n=36)* | 5.0% | 0.0% | 0.0% | 0.0% | **61.7%** | 0.0% | 0.0% | 13.3% | 4.0% | 4.8% | 3.2% | 0.0% |
| | T6 *(n=76)* | 0.0% | 3.3% | 8.3% | 1.6% | 12.8% | **78.9%** | 2.9% | 13.3% | 0.0% | 9.5% | 9.7% | 5.9% |
| | T7 *(n=31)* | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 1.4% | **80.0%** | 0.0% | 0.0% | 0.0% | 3.2% | 5.9% |
| | T8 *(n=11)* | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | **73.3%** | 0.0% | 0.0% | 0.0% | 0.0% |
| | T9 *(n=20)* | 5.0% | 0.0% | 0.0% | 0.0% | 2.1% | 0.0% | 0.0% | 0.0% | **68.0%** | 0.0% | 0.0% | 0.0% |
| | T10 *(n=16)* | 0.0% | 3.3% | 0.0% | 1.6% | 2.1% | 0.0% | 0.0% | 0.0% | 8.0% | **52.4%** | 0.0% | 0.0% |
| | T11 *(n=37)* | 0.0% | 0.0% | 0.0% | 0.0% | 4.3% | 11.3% | 5.7% | 0.0% | 0.0% | 4.8% | **74.2%** | 5.9% |
| | T12 *(n=17)* | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 9.5% | 3.2% | **82.4%** |

**Table 5**: Model performances, significant environmental correlates (with direction of correlation and level of significance), and residual spatial autocorrelation (with significant Moran’s I values marked with an asterisk)

| | **Trees size (PC1)** | **Stand density (PC2)** | **Vertical stratification (PC3)** | **Standing deadwood (PC4)** |
|---|---|---|---|---|
| *Correlation* | 0.41 | 0.61 | 0.34 | 0.38 |
| $R^2$ | **0.17** | **0.37** | **0.12** | **0.14** |
| *F-Ratio* | 22.2 | 64.4 | 8.7 | 27.8 |
| *d. f.* | 336 | 336 | 336 | 336 |
| *p-value* | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| **Multiple regression** | | | | |
| *Variable 1* | (-) TWi ** | (+) DISTFE ** | (-) CUR ** | (+) ELE ** |
| *Variable 2* | (+) DISTFE ** | (+) TWi ** | (-) TWi ** | (-) SHADE * |
| *Variable 3* | (-) IC ** | (-) SLP ** | (+) SLP ** | |
| *Variable 4* | | | (-) LAT ** | |
| *Variable 5* | | | (+) DISTFE ** | |
| **Moran’s I residuals distance classes (meters)** | | | | |
| *1,500* | 0.047 | 0.099* | 0.138* | 0.038 |
| *3,000* | 0.079 | 0.099* | 0.026 | 0.043 |
| *4,500* | 0.001 | 0.137* | -0.031 | 0.028 |
| *6,000* | 0.025 | 0.017 | 0.076 | 0.059 |
| *7,500* | 0.070 | 0.025 | 0.032 | 0.080 |
| *9,000* | 0.031 | 0.067 | 0.087 | 0.019 |
| *10,500* | -0.007 | 0.043 | 0.008 | 0.043 |
| *12,000* | -0.014 | -0.036 | 0.029 | 0.077 |

*Abbreviations: TWi, mean winter temperature; DISTFE, distance to forest edge; IC, continentality index; SLP, slope; CUR, terrain curvature; LAT, latitude; ELE, elevation; SHADE, shade index.*

## Figures

**Figure 1**: Location of the study area in Catalonia, in the north-eastern Iberian Peninsula. Elevation ranges are marked using a grey-scale. Distribution area of *Pinus uncinata* is indicated in black.

**Figure 2**: Dichotomous decision tree for the 12 structural forest types of *Pinus uncinata* stands in the eastern Pyrenees. Abbreviations: $D_M$, mean diameter; FW, basal area (%G) of fine wood; MW, basal area (%G) of medium wood; TW, basal area (%G) of thick wood; TCC, tree canopy cover; G, basal area; RD-H, relative difference in heights; ST-DW, basal area (%G) of standing deadwood. T1 – T12: forest structural types.

**Figure 3**: Relationship between understory species and the main environmental and overstory structural variables selected by the canonical correspondence analysis. Variables: PC1, tree size; PC2, stand density; SHADE, shade index; ELE, elevation; pH, soil pH; lowORG, low soil organic richness. Species: *Abies alba*, *Arctostaphyllos uva-ursi*, *Betula sp.*, *Buxus sempervirens*, *Calluna vulgaris*, *Cytisus purgans*, *Juniperus communis*, *Pinus sylvestris*, *Rhododendron ferrugineum*, *Rosa sp.*, *Rubus idaeus*, *Sorbus aucuparia*, *Vaccinium myrtillus*.

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