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

SANTIAGO MARTÍN-ALCÓN[1]*, LLUÍS COLL[1] AND ÁLVARO AUNÓS[2]

[1] Forest Sciences Center of Catalonia (CTFC), Ctra. Sant Llorenc de Morunys, km. 2, 25280 Solsona, Spain
[2] Department of Crop and Forest Science, University of Lleida, Rovira Roure 191, 25198 Lleida, Spain
*Corresponding author. E-mail: santiago.martin@ctfc.es

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 per cent) by a dichotomous key obtained from classification and regression trees. Multiple regression models were then used to analyse 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.

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 analysed 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 and 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 FTs 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 analyse the combined role played by structural overstory attributes and environmental factors in defining the understory composition of these forests.

Materials and methods

Study area

The study area is located in the sub-alpine 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 is taken to be highly representative of the total variability of mountain pine forests throughout its distribution area.

In this geographical context, mountain pine dominates the sub-alpine 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 sub-alpine belt, it forms mostly pure stands but in lower elevations, it usually appears in mixture with silver fir (*A. alba* Mill.), Scots pine (*Pinus sylvestris* L.), beech (*F. sylvatica* L.), silver birch (*Betula pendula* Roth.), rowan (*Sorbus aucuparia* L.) or aspen (*Populus tremula* L.) (Ruiz de la Torre, 2006).
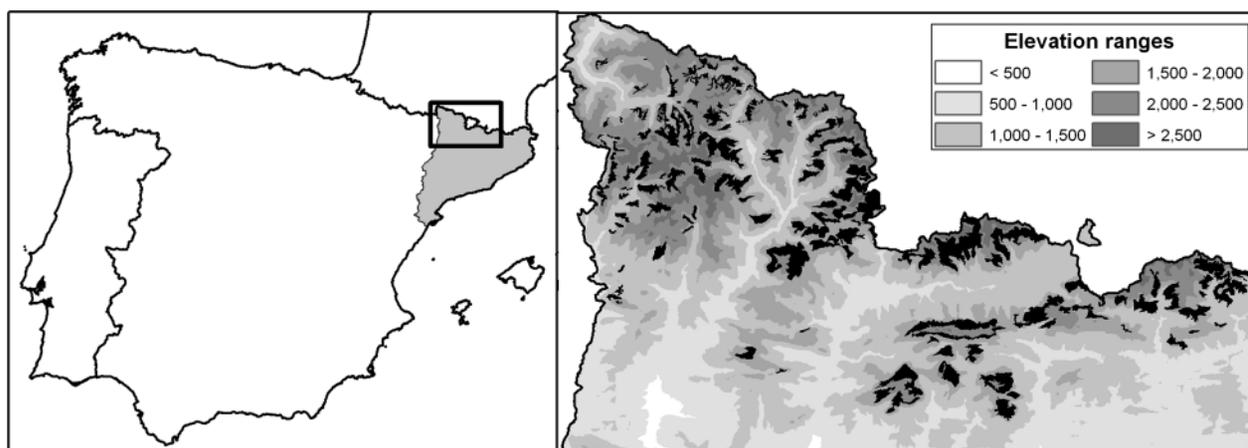

Figure 1. Location of the study area in Catalonia, in the north-eastern Iberian Peninsula. Elevation ranges are marked using a grey scale. Distribution area of *Pinus uncinata* is indicated in black.

Data preparation

Stand structural attributes
The dataset used to characterize the structure of Pyrenean *P. 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 (d.b.h., 1.3 m): a 5 m radius was used for trees with a d.b.h. 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 d.b.h. of 42.5 cm or higher. NFI data for each sample tree included species, d.b.h., height and distance and azimuth from plot centre. Shrubs were counted over the 10-m radius plots. For each shrub species, mean height (in decimeter) and cover (in per cent) 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 *P. uncinata* (i.e. species occupancy >80 per cent of total basal area) fulfilling some criteria about the minimum stocking (tree canopy cover, TCC >25 per cent, basal area >5 $m^2 \cdot ha^{-1}$ and stocking density >50 stems·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 *P. uncinata* stands. A first group of variables described the main stand characteristics (classic forest inventory variables): tree canopy cover (in per cent), stocking density (N,

stems·ha^{-1} with d.b.h. 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 d.b.h. between 7.5 and 22.49 cm); medium wood (MW: with d.b.h. between 22.5 and 32.49 cm) and thick wood (TW: with d.b.h. 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,$(H_0 - H_M)/H_M$] for each plot and calculated standing deadwood (ST-DW, per cent) 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.

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

Table 1: Descriptive statistics and sources of continuous environmental variables

Group	Variable	Units	Source	Mean	Standard deviation	Minimum	Maximum
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
	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	°	DEM	105.4	51.3	0.9	180
	Soil pH (PH)	pH	NFI3 DGCN (2005)	5.7	0.9	3.5	8.0
	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; MCSC = Soil Cover Map of Catalonia.

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 per cent; Class 2: 0–25 per cent; Class 3: 25–50 per cent; Class 4: 50–75 per cent; Class 5: 75–100 per cent). Then, the variable was reclassified to generate three dummy variables: lowSTO (Classes 1 or 2), medSTO (Class 3) and 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 0° on south slopes to 180° on north slopes, with east and west slopes given a value of 90°.

Data analyses

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 FTs. 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 eigen values under 1.0.

The different structural typologies of *P. 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 (CARTs) 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).

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 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

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	
D_M	0.926	−0.157	−0.092	−0.077	0.896
FW (%G)	−0.902	0.192	−0.202	0.027	0.892
D_0	0.829	0.134	0.332	0.296	0.902
TW (%G)	0.805	−0.282	0.287	0.168	0.838
H_M	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
H_0	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: FW (%G) = basal area of fine wood; TW (%G) = basal area of thick wood; N = stocking; RD-H = relative difference in heights; STR1 (%G) = basal area of height stratum 1; ST-DW = basal area of standing deadwood.

I coefficients. ROOKCASE software was used to calculate Moran's *I* for eight equal distances with 1500 m 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 *P. uncinata* stands. Analyses used the counts of the 13 most common species (present in at least 5 per cent 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 d.b.h. < 7.5 cm. A Monte Carlo test (with 9999 unrestricted random permutations) was executed to determine the significance of the eigen values, 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).

Results

Structural characterization of P. uncinata stands

Four PCA components presented eigen values above 1.0 and together expressed 85.43 per cent of the variance in the original data (Table 2). The first component accounted for 37.35 per cent 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 per cent of the variance and was dominated by different variables related to stand density (TCC, stand basal area, volume, stocking density and Assmann's dominant height). The third axis explained 15.06 per cent 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 STR 1 and the relative difference between Assmann's dominant height and mean height). Finally, the fourth axis explained 9.03 per cent of the variance and was mainly dominated by standing deadwood. These PCA components are hereafter named trees size (first component), stand density (second component), vertical

stratification (third component) and standing deadwood (fourth component).

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.

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.

The classification tool constructed with the CART method (Figure 2) considered nine 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 *P. uncinata* stands with 76.8 per cent accuracy. T10 (balanced irregular stands) was the type showing less well-classified plots (52.4 per cent). Nevertheless, in almost all cases, misclassified plots were assigned into the structural types closest to the correct one (Table 4).

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

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		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 ($n = 17$)
							Structural typologies						
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
D_M (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
D_0 (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
H_M (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
H_0 (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: N = stocking; 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.
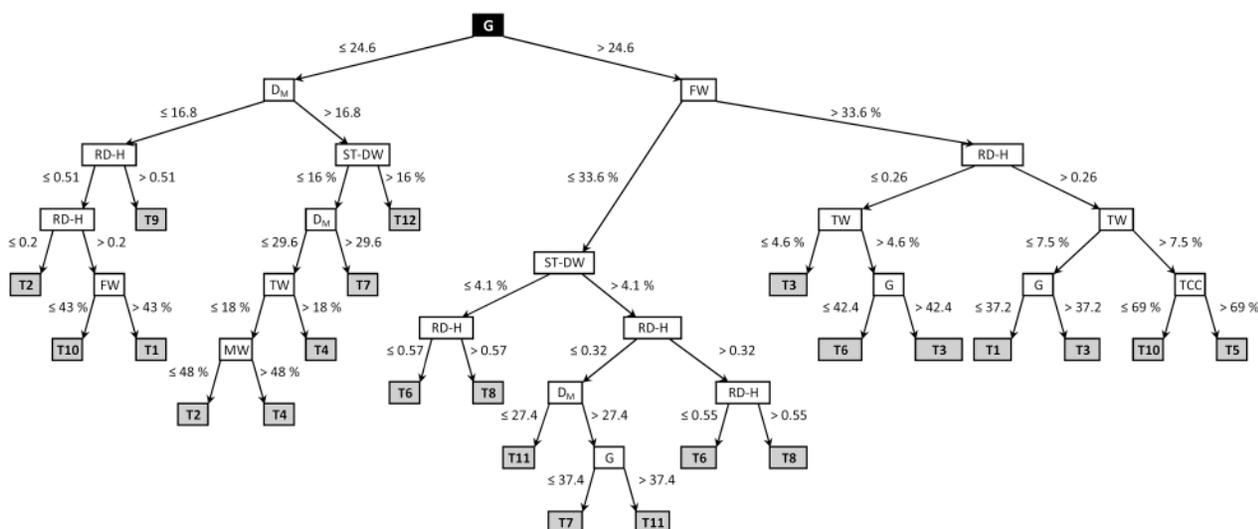
Figure 2. Dichotomous decision tree for the 12 structural forest types of *Pinus uncinata* stands in the eastern Pyrenees. Abbreviations: FW = basal area (%G) of fine wood; TW = basal area (%G) of thick wood; RD-H = relative difference in heights; ST-DW = basal area (%G) of standing deadwood; T1–T12 = forest structural types.

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 non-linearity-related problems. Absence of high multicolinearity was tested by examining variance inflation factor, which was never higher than two. Both stand density and stand even-agedness showed significant but low positive spatial autocorrelation of residuals up to 4.5 and 1.5 km, respectively (Table 5).

Understory composition and P. uncinata stand structure

The first two CCA components accounted for 75.7 per cent of explained species–environment relationships. For the 431 plots, six variables contributed significantly to explain the distribution of understory species (Figure 3): 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. *P. 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 *A. alba* or *S. 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 (*A. alba*) from the more intolerant ones (*Cytisus purgans*, *Calluna vulgaris*, *Arctostaphyllos uva-ursi* and *Juniperus communis*). Other species such as *S. aucuparia*, *R. ferrugineum*, *V. myrtillus*, *Betula* sp., *P. sylvestris* or *B. 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).

Discussion

The analysis conducted with Spanish National Forest Inventory data allowed us to define a set of different mountain pine forest types. Our FTs 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 FTs (accuracy >75 per cent) 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 FTs 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,

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)
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%**

Forest type (from CART)

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 and Courbaud, 2006)).

The analysis of forest structure was focused on mountain pine woodlands fulfilling a minimum cover criterion (25 per cent) and thus excluding very sparse stands (e.g. timberline, 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 above-mentioned environmental variables are highly correlated with them (Garcia-Ruiz 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; Hammi et al., 2010).

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 twentieth century, mountain pine forests in the Pyrenees continued to be managed as even-aged stands (Cano, 2003), and this may

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 (m)				
1500	0.047	0.099*	0.138*	0.038
3000	0.079	0.099*	0.026	0.043
4500	0.001	0.137*	−0.031	0.028
6000	0.025	0.017	0.076	0.059
7500	0.070	0.025	0.032	0.080
9000	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; IC = continentality index; SLP = slope; CUR = terrain curvature; LAT = latitude; d.f. = degrees of freedom.
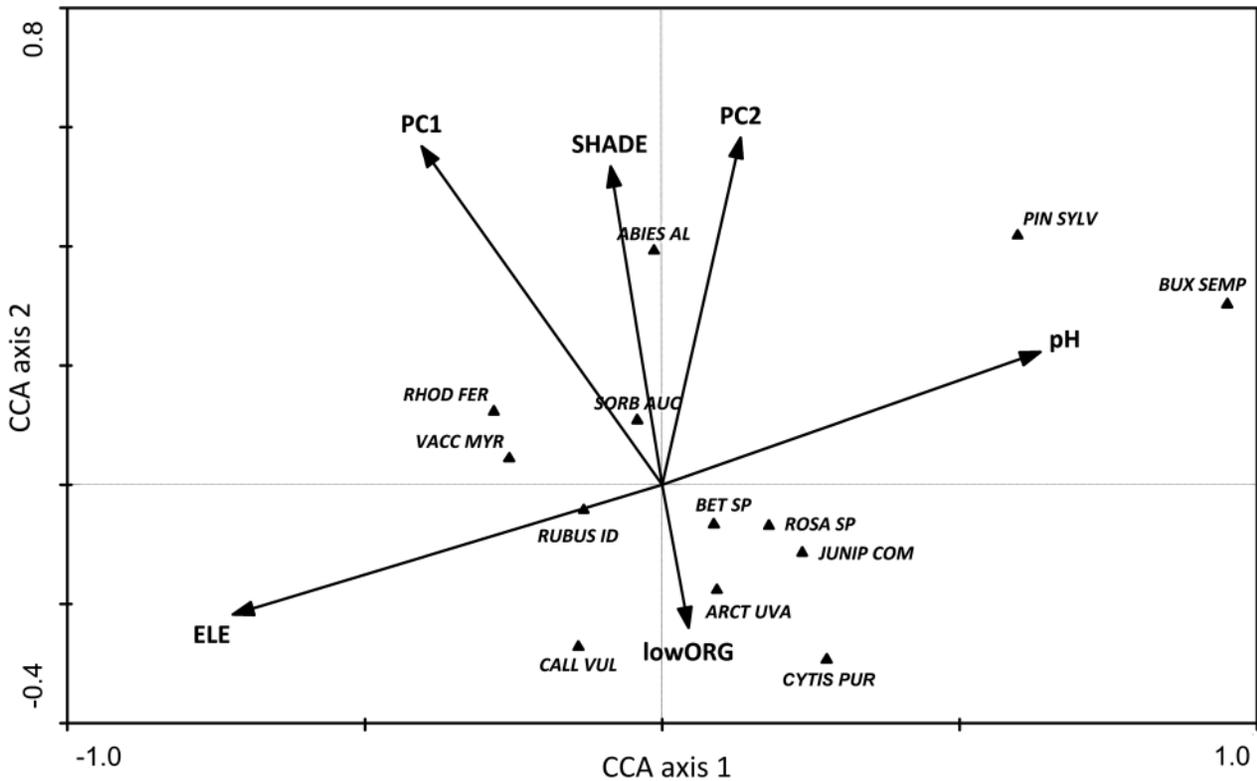

Figure 3. Relationship between understory species and the main environmental and overstory structural variables selected by the CCA. Variables: PC1 = tree size; PC2 = stand density; SHADE = shade index; ELE = elevation; pH = soil pH; lowORG = low soil organic richness. Species: *Abies alba*, *Arctostaphyllos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

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 4500 m 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*, *B. 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: *C. vulgaris*, *A. uva-ursi*, *C. purgans* or *J. communis* were found to dominate in open stands located on south-facing slopes, whereas *R. ferrugineum*, *V. myrtillus* and *B. 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, *A. 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 FTs and adequately described 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 sub-alpine 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 *V. myrtillus* over *R. ferrugineum* in areas frequented by capercaillie (*T. urogallus*)).

Conflict of interest statement

None declared.

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