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ORIGINAL PAPER

# Predicting understory maximum shrubs cover using altitude and overstory basal area in different Mediterranean forests

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**Abstract** In some areas of the Mediterranean basin where the understory stratum represents a critical fire hazard, managing the canopy cover to control the understory shrubby vegetation is an ecological alternative to the current mechanical management techniques. In this study, we determine the relationship between the overstory basal area and the cover of the understory shrubby vegetation for different dominant canopy species (*Pinaceae* and *Fagaceae* species) along a wide altitudinal gradient in the province of Catalonia (Spain). Analyses were conducted using data from the Spanish National Forest Inventory. At the regional scale, when all stands are analysed together, a strong negative relationship between mean shrub cover and site elevation was found. Among the *Pinaceae* species, we found fairly good relationships between stand basal area and the maximum development of the shrub stratum for species located at intermediate elevations (*Pinus nigra*, *Pinus sylvestris*). However, at the extremes of the elevation-climatic gradient (*Pinus halepensis* and *Pinus uncinata* stands), stand basal area explained very little of the shrub cover variation probably because microsite and topographic factors override its effect. Among the *Fagaceae* species, a negative relationship between basal area and the maximum development of the shrub stratum was found in *Quercus humilis* and *Fagus sylvatica* dominated stands but not in *Quercus ilex*. This can be due to the particular canopy structure and management history of *Q. ilex* stands. In conclusion, our study revealed a marked effect of the tree layer composition and the environment on the relationship between the development of the understory and overstory tree structure. More fine-grained studies are needed to provide forest managers with more detailed information about the relationship between these two forest strata.

**Keywords** Overstory · Basal area · Altitude · Shrub cover · *Pinaceae* · *Fagaceae*

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## Introduction

The understory stratum plays an important role in forest ecosystem functioning. It provides food and habitat for the fauna (González-Hernández et al. 1998; Yanai et al. 1998), protection from depredation and sun exposure to the regeneration (Kunstler et al. 2006), and it constitutes a major component of forest biodiversity (Kerns and Ohmann 2004; Aubin et al. 2009). It also competes for soil resources with the overstory trees (Coll et al. 2003, 2004) and represents, in some regions, a fire hazard (Fernandes and Rigolot 2007).

The forest overstory-understory relationship is complex and two-sided, but is nonetheless dominated by the strong influence of the overstory composition and structure through both its effects on the litter and light quantity and quality (Messier et al. 1998; Légaré et al. 2001; Aubin et al. 2009). Other factors such as climate, topography and the previous occurrence of natural disturbances or management practices also intervene (Roberts and Christensen 1988; Gilliam et al. 1995; Gràcia et al. 2007).

In the Mediterranean forests, controlling the understory (and particularly woody shrubs) is essential not only to reduce competition to the regeneration but also to prevent and reduce the occurrence of catastrophic fire events which are the main cause of forest lost (González et al. 2005). However, current management techniques do not adequately respond to this need. Mechanical treatment, which is at present the most widely used method to control the understory, provides a rather short-term solution because roots are left untreated and sprouting often occurs rapidly (Balandier et al. 2006a). Alternative methods such as the use of prescribed fires or grazing are more efficient, but their use is rather limited. In that context, controlling the development of the understory through an adequate control of the overstory canopy cover could represent an affordable ecological and economical alternative to the current management techniques.

This study was undertaken to determine the relationship between the overstory tree composition and basal area, and the cover of the understory shrubby vegetation along a wide altitudinal gradient. To that end, we used data provided by the third National Forest Inventory of Spain (IFN3) for the province of Catalonia (DGCN 2005). Although it is often assumed that taller trees determine the distribution and abundance of the understory shrubby vegetation (McKenzie et al. 2000), very few studies have examined these interactions at regional scales, particularly in Mediterranean areas. Given the topographical complexity and sharp variations in the climatic conditions that characterize these areas (Whiteman 2000; Lopez-Moreno et al. 2008), we expected the strength of the interactions between the two forest strata to strongly vary according to (1) the dominant species, (2) the abundance of that species and (3) the severity of the environment.

## Materials and methods

### Study area and species

Our study was conducted in the Catalonia region located in the north-east of Spain (Fig. 1). Forests in Catalonia are predominantly privately owned (around 80%) and mainly originate from natural regeneration. The heterogeneity, instability and low productivity that characterize Mediterranean forests together with the small size of forest holdings (average size 30 ha) has resulted in many cases in a lack of management (Saura and Piqué 2006).

Data on forest stands used in this study were obtained from the third Spanish National Forest Inventory (IFN3) (DGCN 2005). The IFN3 data consisted of a systematic sample of permanent plots, distributed on a square grid of 1 km throughout the territory (covering in Catalonia 32,114 km$^2$), which were remeasured after an interval of approximately 11 years. The sampling method used circular

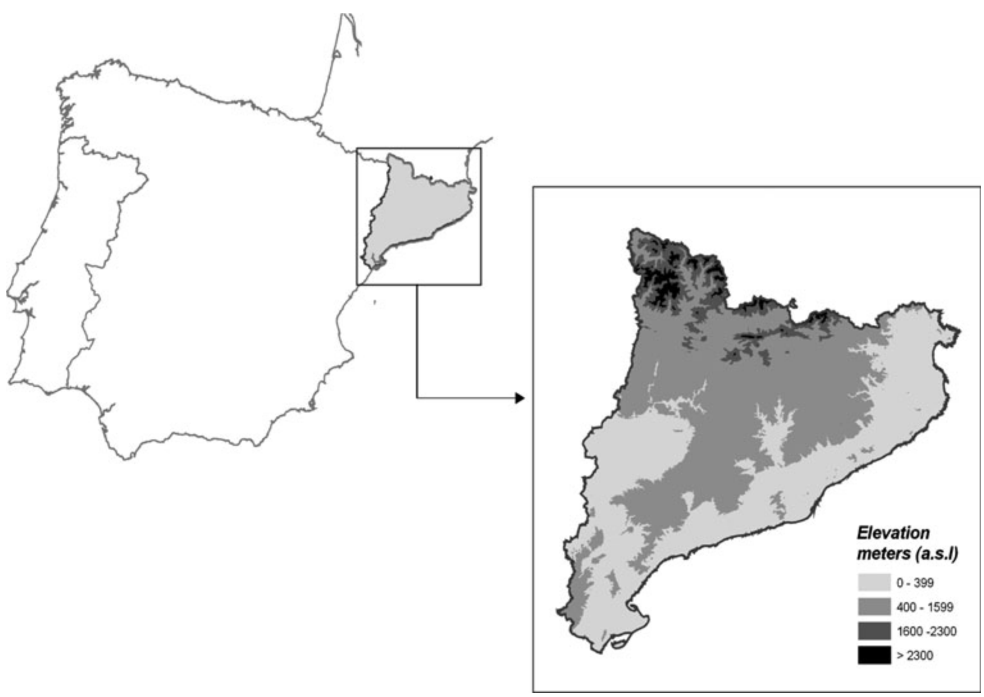



**Fig. 1** Location of the study area with altitude ranges according the altitudinal series of the National Forest Inventory of Spain

plots for which the radius varied according to the 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. IFN3 data for each sampled tree included species, dbh, height, and distance and azimuth from the plot centre. In each permanent plot, the composition of the woody shrub layer (non-herbaceous plants) was determined and the cover of each species (percentage of area occupied by the vertical projection of the whole foliage, %) was assessed visually in a circular plot of 10 m radius.

For this study, tree species that were dominant (i.e., occupancy >80% of total basal area) in at least 100 plots were selected: *Pinus halepensis* L. (*Pinhal*), *Pinus nigra* Arn. (*Pinnig*), *Pinus sylvestris* L. (*Pinsyl*), *Pinus uncinata* Ram. (*Pinunc*), *Quercus ilex* L. (*Queile*), *Quercus humilis* Mill (*Quehum*) and *Fagus sylvatica* L. (*Fagsyl*).

These species are distributed following a climatic gradient along the transition between Mediterranean and the Boreo-Alpine biogeographical regions (Table 1).

Within the *Pinaceae* species, *Pinhal*, predominantly found at low altitudes, is considered the most drought tolerant (see Fig. 2), whereas *Pinunc* is rather drought intolerant because mainly found at higher altitudes in Spain (subalpine zone) where annual rainfall is above 600–700 mm (Ceballos and Ruíz de la Torre 1979). *Pinnig* and *Pinsyl* grow at intermediate altitudes, the latter generally at a higher altitude. Both *Pinhal* and *Pinnig* (and in a lower extent *Pinsyl*) are recurrently affected by forest fires, some of them covering large areas (González-Olabarria 2006).

Among the *Fagaceae* species, the evergreen Holm oak (*Queile*) is the most drought tolerant and often forms mixed forests with *Pinhal*, whereas broadleaved oaks such as *Quehum* and, in particular *Fagsyl*, are generally distributed at higher altitudes in less water stressed sites. Most forests dominated by *Fagaceae* species have originated through resprouting after natural or anthropogenic disturbances (fire, wood extraction, charcoal production) (Gràcia et al. 2001; Saura and Piqué 2006). As a result of the abandonment of traditional coppice management, many of these forests now show high stand densities, stand decay, and absence of natural regeneration by seeds (Cañellas et al. 2004).

### Data preparation and shrub cover analysis

The following variables from the selected IFN3 plots were recorded: elevation (metres above sea level, m), diameter of each tree at breast height (dbh, cm), tree density (trees ha$^{-1}$)

**Table 1** Main ecological characteristics of the studied forest types: elevation (mean ± standard error; source: DGCN (2005)), climate (mean temperature of the coldest month, mean temperature of the warmest month and precipitation; source: Lloret et al. (2009)), aspect preference (source: Lloret et al. 2009), and list of the most common shrubby species of the understory (source: DGCN (2005) and Vigo et al. (2006))

| Canopy Sp. | Elevation | Climate | Aspect preference | Common understory species |
|---|---|---|---|---|
| *Pinhal* | 370 m (±180) | −1 → 3°C | Indifferent | *Quercus coccifera* |
| | | >28°C | | *Rosmarinus officinalis* |
| | | 500 → 750 mm | | |
| *Pinnig* | 690 m (±210) | −1 → 2°C | NE/N/NW | *Buxus sempervirens* |
| | | 26 → 30°C | | *Rosmarinus officinalis* |
| | | 650 → 850 mm | | *Thymus* sp. |
| *Pinsyl* | 1,160 m (±350) | <−1°C | NE/N/NW | *Buxus sempervirens* |
| | | 24 → 30°C | | *Rosa* sp. |
| | | 700 → 1,050 mm | | *Viburnum* sp. |
| *Pinunc* | 1,890 m (±180) | <−3°C | NE/N/NW | *Rhododendron ferrugineum* |
| | | <24°C | | *Vaccinum myrtillus* |
| | | >950 mm | | |
| *Queile* | 670 m (±280) | −2 → 3°C | Indifferent | *Erica arborea* |
| | | 26 → 30°C | | *Rhamnus alaternus* |
| | | 600 → 900 mm | | *Viburnum lantana* |
| *Quehum* | 840 m (±280) | <0°C | Indifferent | *Buxus sempervirens* |
| | | 24 → 30°C | | *Rosa* sp. |
| | | >600 mm | | *Rubus* sp. |
| *Fagsyl* | 1,080 m (±240) | −4 → −1°C | NE/N/NW | *Buxus sempervirens* |
| | | <26°C | | *Calluna vulgaris* |
| | | >1,000 mm | | *Daphne laureola* |

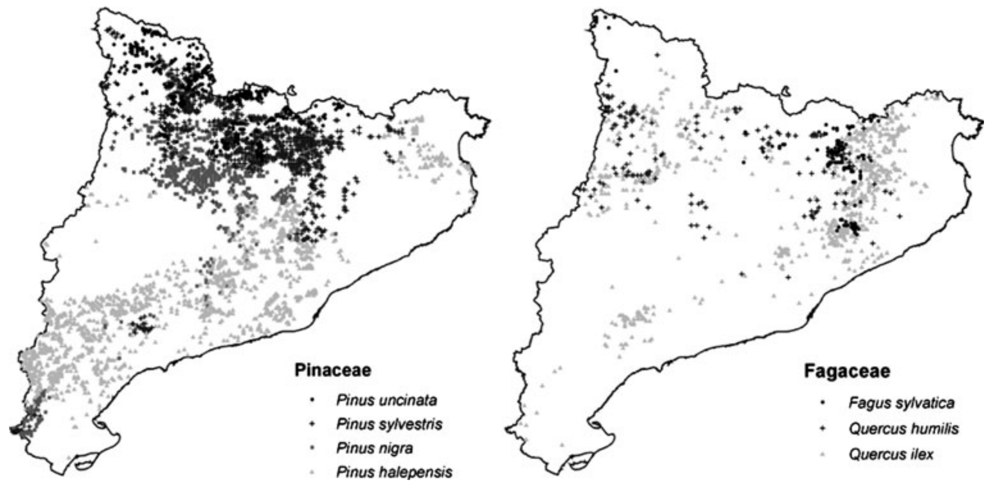



**Fig. 2** Distribution of the plots used in this study by dominant *Pinaceae* (*left*) or *Fagaceae* (*right*) species

and the sum of the cover of all shrubby species of the plot (%). Stand basal area (*BA*, $m^2$ $ha^{-1}$) was calculated for each plot from the measured diameters of all trees in the sampled surface area. For each canopy tree species, the mean shrub cover in the understory was calculated by groups of basal area of 5 $m^2$ $ha^{-1}$. We removed from the analysis plots in which signs of recent human activity (i.e., harvest residues) or fire occurrence were reported in the IFN3. A non-parametric Kruskall–Wallis test followed by a post hoc analysis of the median notches of the boxes was used to assess differences in shrub cover among canopy dominant species at a 95% confidence interval.

### Predictive maximum response models of overstory control

We built simple models using stand basal area (*BA*) and site elevation (*Ele*) as predictive parameters in order to test whether a significant correlation between the two forest strata exists for different dominant canopy species growing in contrasted environmental conditions. Stand basal area was used because it is the variable favoured by foresters to describe forest structure. Site elevation was used as a proxy for site environmental conditions since readily obtainable and of high correlation with climate variables which are in general those modulating forest development in Mediterranean areas (González et al. 2005). Other topographic variables such as aspect or slope were not included into the model either due to a lack of significance (aspect) or of a high correlation with elevation (slope). Maximum response models were developed to represent the potential effects of stand basal area and elevation on understory shrub cover. Such maximum response models have been successful for quantifying thresholds or limits, and the extent to which a predictor constrains a response variable (McKenzie et al. 2000).

For every tree species, all plots were grouped into basal area classes of 5 $m^2$ $ha^{-1}$. For each class, plots with the upper third shrub cover values were selected for modelling. That removes from the model a large part of those individual plots in which, for many potential reasons, the understory shrub layer have not yet reached its full potential (browsing, disturbances, human intervention, etc.).

The resulting shrub cover percentage was referred as the maximum shrub cover, abbreviated (*MaxSCov*). These plots were analysed using multiple regression analysis for each dominant canopy tree species relating *MaxSCov* with the overstory tree *BA* and associated *Ele*. As *MaxSCov* is expressed in percentage, the dependent variable was the logarithmic transformation of *MaxSCov*. The models included transformations of the predictors when violations of the normality occurred or when a transformation showed a higher predicting capacity, resulting in some cases in second order models. In the models, the selected predictors respect the following criteria: be significant at the 0.05 level, present a low RMSE (Fig. 3) and maximize the degree of explained variance.

The possible multicollinearity between the included variables was analysed by the estimation of the variance inflation factors (VIF). Finally, the models were evaluated by examining the magnitude and distribution of the residuals for the variables included in the models. This analysis enabled detection of any obvious dependencies or patterns indicative of systematic discrepancies, or unusual effects caused by outliers. The accuracy of the model predictions was estimated by calculating the absolute and relative root mean square errors (RMSE) as well as the coefficients of determination (Fig. 3).

## Results

### Stand structure and shrub cover

Among the monospecific stands, those composed by *Pinaceae* species dominate in Catalonia with *Pinhal* being

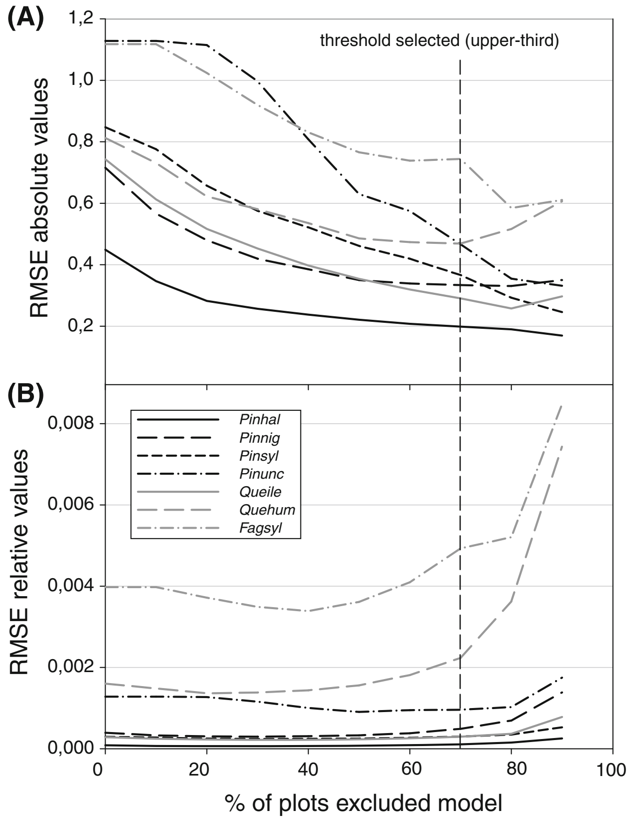



**Fig. 3** Variation of the absolute (**a**) and relative (**b**) Root Mean Square Error (RMSE) values of the models according to different percentages of plots excluded to build the models. The plots were first grouped by basal area classes, and then ranked by shrub coverage. Plots with low shrub coverage were systematically excluded to form the curves

the most abundant species followed by *Pinsyl*, *Pinnig* and *Pinunc*. *Pinhal* had the sparsest forests with a mean density lower than 500 trees $ha^{-1}$ whereas the rest of the *Pinaceae* species stands had mean densities around 800 trees $ha^{-1}$ (Table 2). Among the *Fagaceae* species, *Queile* was by far the most abundant species followed by other Mediterranean oaks (*Quehum*) and finally beeches (*Fagsyl*). *Queile* stands had the highest mean density of stems and the smallest mean diameter (around 15 cm), indicative of their sprouting origin. Mean shrub cover was rather variable within each stand type, ranging from 21.8 to 82.3%, the later corresponding to *Pinhal* stands and the former to beeches.

The mean shrub cover for the other overstory tree species was lower than 50% (although rather variable) with the exception of *Queile* at 62.4%. Mean shrub cover was found to be inversely correlated with mean elevation ($R^2 = 0.86$) when values from all stand types were put together in one model (Fig. 4). Elevation alone showed to be significantly and positively correlated for *Pinhal* and negatively for *Pinnig*, *Pinsyl*, *Queile* and *Quehum* stands (Table 3).

When differences on shrub cover among different stand types were analysed by *BA* classes, we found that *Pinhal* stands had the highest understory cover for all *BA* levels (Table 4). Both *Queile* and *Pinnig* stands had in general a sparser understory (mean values around 50%) but, due to high inter-stand variability, they did not show any significant difference in mean shrub cover with *Pinhal*.

**Table 2** Mean and standard error (in parenthesis) of the different tree and shrub variables used in the study in the upper 33% and total plots for each of the seven tree species analysed

| Canopy Sp. | *N* | Density (trees $ha^{-1}$) | Basal area ($m^2$ $ha^{-1}$) | Mean diameter (cm) | Mean shrub cover (%) |
|---|---|---|---|---|---|
| Upper 33% | | | | | |
| *Pinhal* | 439 | 467.73 (18.81) | 12.09 (0.42) | 19.66 (0.27) | 120.1 (1.31) |
| *Pinnig* | 180 | 899.74 (44.42) | 18.25 (0.82) | 17.23 (0.37) | 77.88 (2.05) |
| *Pinsyl* | 339 | 754.54 (26.31) | 22.19 (0.64) | 20.42 (0.26) | 63.19 (1.44) |
| *Pinunc* | 132 | 707.91 (47.19) | 24.69 (1.19) | 23.28 (0.63) | 64.91 (2.67) |
| *Queile* | 236 | 1074.99 (50.57) | 14.39 (0.61) | 13.83 (0.25) | 109.4 (2.37) |
| *Quehum* | 56 | 650.87 (66.53) | 14.14 (1.37) | 19.11 (1.24) | 67.75 (4.2) |
| *Fagsyl* | 47 | 794.55 (63.64) | 25.54 (1.55) | 21.99 (1) | 45 (4.85) |
| All the plots | | | | | |
| *Pinhal* | 1,273 | 491.17 (11.29) | 11.8 (0.24) | 19.05 (0.16) | 82.29 (1.07) |
| *Pinnig* | 506 | 845.17 (25.92) | 17.7 (0.46) | 18.03 (0.26) | 47.52 (1.37) |
| *Pinsyl* | 966 | 753.15 (16.12) | 22.11 (0.37) | 20.68 (0.17) | 33.1 (0.93) |
| *Pinunc* | 370 | 728.71 (27.56) | 24.83 (0.69) | 23.06 (0.37) | 29.08 (1.75) |
| *Queile* | 683 | 1149.57 (30.47) | 14.24 (0.35) | 13.22 (0.15) | 62.37 (1.65) |
| *Quehum* | 154 | 746.64 (48.83) | 12.94 (0.71) | 17.11 (0.62) | 38.73 (2.5) |
| *Fagsyl* | 125 | 796.94 (42.83) | 24.9 (0.85) | 22.3 (0.65) | 21.8 (2.49) |

*N* number of plots

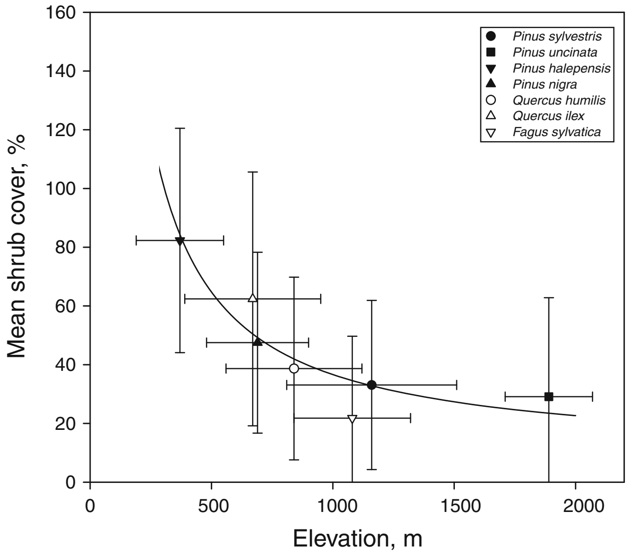



**Fig. 4** Relationship between the mean understory shrub cover (%) and the elevation (metres above sea level) in the study area. Each point is the mean and standard deviation value of each variable for a given dominant canopy species

**Table 3** Table of correlations between the elevation and the maximum shrub cover (%) present in the understory of the stands analysed in this study

| Canopy Sp. | *R* | *P* value |
|---|---|---|
| *Pinhal* | 0.198 | 0.000 |
| *Pinnig* | −0.292 | 0.000 |
| *Pinsyl* | −0.325 | 0.000 |
| *Pinunc* | 0.093 | 0.291 |
| *Queile* | −0.160 | 0.014 |
| *Quehum* | −0.386 | 0.003 |
| *Fagsyl* | −0.206 | 0.164 |

The significance of the correlation was based on a t-test

On the contrary, the understory was far less developed under *Pinsyl*, *Pinunc*, *Quehum* and *Fagsyl* stands at comparable *BA* values; *Fagsyl* having the sparsest understory cover (mean values under 30% for all *BA*).

### Shrub cover models

The linear regression models relating *MaxSCov* with *BA* and *Ele* (Table 5) showed $R^2$ above 30% for *Pinnig, Pinsyl, Quehum* and *Fagsyl* stand and close to zero per cent for *Queile*, *Pinunc* and *Pinhals* stands (Fig. 5). Stand basal area was significantly related to *MaxSCov* in all species with the exception of *Queile* stands. For a given basal area, *MaxScov* decreased with elevation in *Pinsyl*, *Pinnig* and *Queile* stands, though the opposite trend was observed in *Pinhal* stands.

There were no strong relationships between the predictor variables studied (basal area and elevation) that could cause multicollinearity in the models. The maximum variance inflation factor was 1.0322 ($R^2 = 0.031$) corresponding to *Pinsyl*. This was the only case where the relationship was significant ($P$ value $= 0.001$). The analysis of the residuals of the seven models showed no trends when displayed as a function of the variables studied (Fig. 6).

## Discussion

### Overall analysis

Our analysis was based on data from the National Forest Inventory of Spain and covers a large geographical area extending from typical Mediterranean forests (e.g., *Queile* or *Pinhal* stands) to the southern distribution limit of European temperate forests (*Pinunc*). At the regional scale, when all stands are analysed together, a strong negative relationship was found between mean shrub cover and site elevation. Although the mean understory shrub cover was rather variable within all stand types, it was generally highest under the drought-tolerant Mediterranean *Pinhal* and *Queile* stands at low to mid altitudes. Stands located at higher altitudes were usually dominated by *Pinsyl, Pinunc*, *Fagsyl* and *Quehum*, and presented a sparser shrubby understory. Several possible reasons could explain these

**Table 4** Mean shrub cover (%) present in the understory of the seven tree species analysed, in this study, by stand basal area (*BA*) classes

| Canopy Sp. | Mean shrub cover (%) by *BA* classes ($m^2$ $ha^{-1}$) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 0–5 | 5–10 | 10–15 | 15–20 | 20–25 | 25–30 | 30–35 | 35–40 | 40–45 | 45–50 |
| *Pinhal* | 80 a | 82 a | 89 a | 83 a | 75 a | 85 a | 70 a | 91 a | – | – |
| *Pinnig* | 62 ab | 55 ab | 46 b | 50 ab | 43 ab | 35 b | 46 ab | 34 ab | 43 a | – |
| *Pinsyl* | 40 b | 43 b | 41 b | 33 bc | 37 b | 32 b | 23 bc | 23 bc | 21 a | 12 a |
| *Pinunc* | 34 b | 22 b | 39 b | 37 abc | 28 b | 32 b | 23 bc | 25 bc | 21 a | 18 a |
| *Queile* | 66 ab | 65 ab | 65 ab | 64 ab | 55 ab | 54 ab | 54 ab | 51 ab | – | – |
| *Quehum* | 50 ab | 37 b | 45 b | 34 bc | 22 b | 26 b | – | – | – | – |
| *Fagsyl* | – | – | – | 22 c | 18 b | 29 b | 18 c | 10 c | – | – |

Different letters indicate significant differences (95% confidence interval) among dominant species for a given *BA* class

**Table 5** Maximum response models relating maximum understory shrub cover (*MaxSCov*, %) with stand basal area (*BA*, $m^2\ ha^{-1}$) and elevation (*Ele*, m × 100) for the seven different tree species analysed in this study

| Canopy Sp. | Variable | Parameter | Coefficient | Std error | Sig | $R^2$ | *P* value |
|---|---|---|---|---|---|---|---|
| *Pinhal* | | $B_0$ | 4.6333 | 0.0293 | <0.00005 | 0.062 | <0.001 |
| | *BA* | $B_1$ | 0.0085 | 0.0030 | 0.0050 | | |
| | $BA^2$ | $B_2$ | −0.0002 | 0.0001 | 0.0038 | | |
| | *Ele* | $B_3$ | 0.0235 | 0.0054 | <0.00005 | | |
| | $\ln(MaxSCov) = B_0 + B_1\ BA + B_2\ BA^2 + B_3\ Ele$ | | | | | | |
| *Pinnig* | | $B_0$ | 4.9023 | 0.0901 | <0.00005 | 0.484 | <0.001 |
| | $BA^2$ | $B_1$ | −0.0005 | 0.00005 | <0.00005 | | |
| | *Ele* | $B_2$ | −0.0597 | 0.0138 | <0.00005 | | |
| | $\ln(MaxSCov) = B_0 + B_1\ BA^2 + B_2\ Ele$ | | | | | | |
| *Pinsyl* | | $B_0$ | 4.5781 | 0.0640 | <0.00005 | 0.327 | <0.001 |
| | $BA^2$ | $B_1$ | −0.0004 | 0.00003 | <0.00005 | | |
| | *Ele* | $B_2$ | −0.0297 | 0.0060 | <0.00005 | | |
| | $\ln(MaxSCov) = B_0 + B_1 BA^2 + B_2\ Ele$ | | | | | | |
| *Pinunc* | | $B_0$ | 4.1681 | 0.0630 | <0.00005 | 0.047 | 0.012 |
| | $BA^2$ | $B_1$ | −0.0001 | 0.00006 | 0.0125 | | |
| | $\ln(MaxSCov) = B_0 + B_1\ BA^2$ | | | | | | |
| *Queile* | | $B_0$ | 4.742 | 0.003 | <0.00005 | 0.037 | 0.008 |
| | $Ele^2$ | $B_1$ | −0.0021 | 0.001 | 0.003 | | |
| | $\ln(MaxSCov) = B_0 + B_1\ Ele^2$ | | | | | | |
| *Quehum* | | $B_0$ | 4.3485 | 0.0774 | <0.00005 | 0.399 | <0.001 |
| | $BA^2$ | $B_1$ | −0.0009 | 0.0001 | <0.00005 | | |
| | $\ln(MaxSCov) = B_0 + B_1\ BA^2$ | | | | | | |
| *Fagsyl* | | $B_0$ | 4.3661 | 0.1785 | <0.00005 | 0.483 | <0.001 |
| | $BA^2$ | $B_1$ | −0.0012 | 0.0002 | <0.00005 | | |
| | $\ln(MaxSCov) = B_0 + B_1\ BA^2$ | | | | | | |

pattern. First, drought-tolerant species present, in general, low leaf area indices (LAI), as to limit transpiration and maintain a positive water balance (Grier and Running 1977; Gholz 1982). Light transmission is higher under low LAI canopies, which favours the development of a denser understory shrub cover. Furthermore, *Pinhal* and *Queile* forests tend to have small basal areas (<15 $m^2\ ha^{-1}$), suggesting more open overstory conditions. For oak stands this is in part the consequence of the abandonment of the traditional coppice management of these systems during the last decades (Valladares and Guzmán 2006). The relatively higher recurrence of anthropogenic and natural disturbances (e.g., fires) that occurred in these stand types can also explain their sparse and rather open overstory canopy structure.

Finally, changes in the composition or the life history strategy of the understory, which have not been assessed in this study, can also partly explain the shrub cover differences found among different stand types in different elevations. A negative impact of elevation on plant diversity has already been pointed out by a recent study conducted in the same region (Solé et al. 2007).

## Analysis per dominant canopy species

Within stand types, *MaxSCov* decreases with elevation in *Queile, Pinnig,* and *Pinsyl* stands, following the same pattern observed at the regional scale. However, an opposite trend was found in the *Pinhal* forests. This species occupies the most xeric areas and is exposed to severe water stress periods, which are less marked under higher altitudes, thus probably favouring the development of a denser understory shrub cover in higher elevation. In contrast, elevation was not correlated with shrub cover in stands dominated by *Fagsyl, Quehum* and *Pinunc*. Overall, at the stand scale, the effect of elevation on *MaxScov* appears to be rather species-specific. Furthermore it is difficult to separate the effect of elevation and overstory composition on *MaxScov* because both factors are correlated (Kerns and Ohmann 2004).

The predictive power of the various regression models relating *BA* and *Ele* with *MaxSCov* for the different forest types was in the range of those presented by Kerns and Ohmann (2004) and slightly lower than those obtained by McKenzie et al. (2000) that used similar variables and

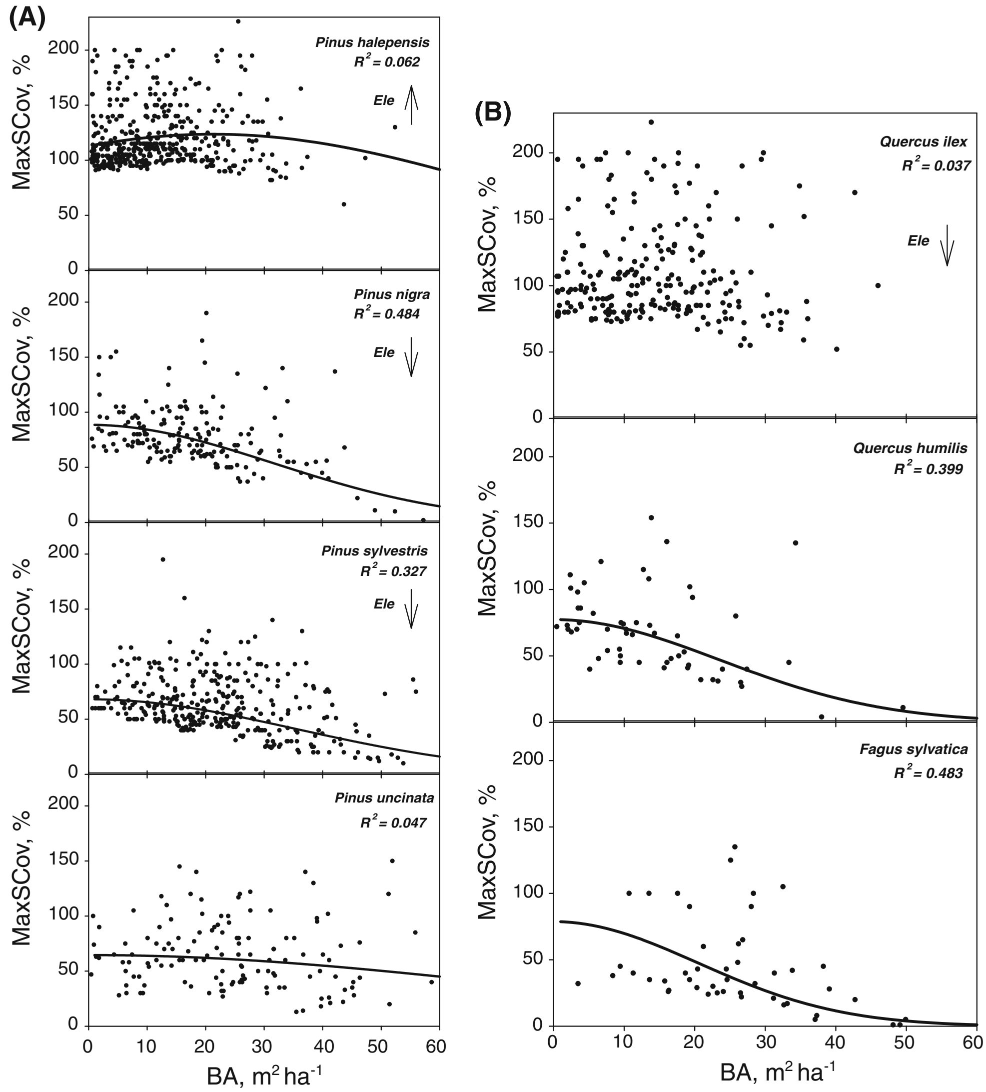
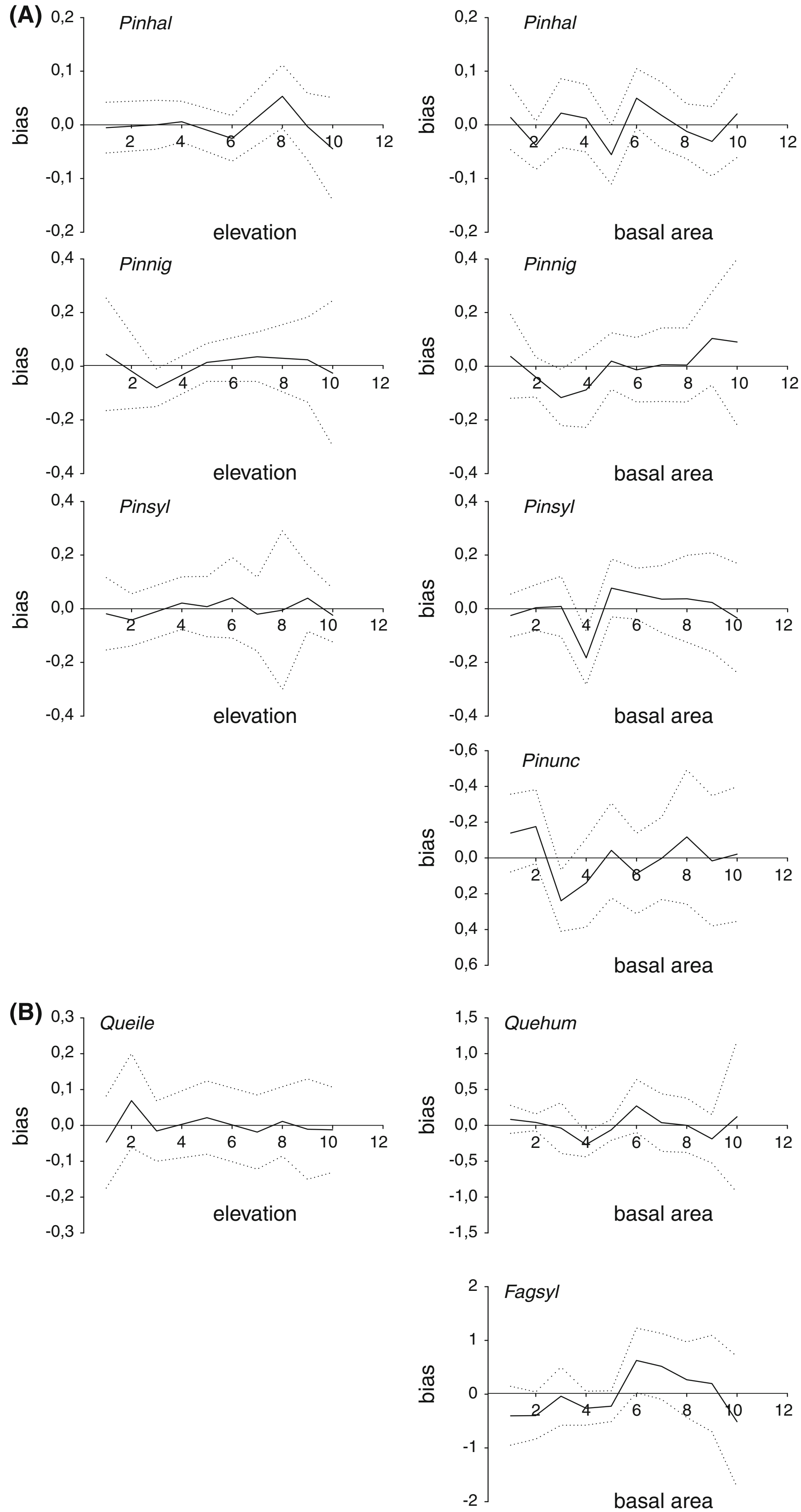



**Fig. 5** Regression models relating maximum understory shrub cover (*MaxSCov*. %) and stand basal area (*BA*, m$^2$ ha$^{-1}$) by dominant *Pinaceae* (**a**) or *Fagaceae* (**b**) species. For each species, models were represented at their mean elevation value (according to Table 1). The absence of the regression line (*Q. ilex*) means non-significant relationship ($P$ value $< 0.05$) between both variables. Captions with an arrow indicate a significant ($P$ value $< 0.05$) effect of the elevation on *MaxSCov* and the direction of the *arrow* indicates if this effect is positive (*up*) or negative (*down*)

approaches. We employed maximum response models in this study because they are more useful at assessing the extent at which a predictor (i.e., *BA* or *Ele*) constrains a response variable such as *MaxSCov*, and hence directly relate to the main objective of our study. Then the analysis was restricted to stands presenting a thick shrub understory, associated with favourable environmental conditions or particular land-use dynamics. That corresponded to the areas where the control of the understory strata (to help regeneration or reduce fire risk) could be needed. From the modelling point of view, the use of a 66% threshold for the exclusion of plots is justified as it clearly enhances the effects of the basal area and elevation, according to RMSE. In general, absolute values of RMSE do not seem to decrease further this threshold, whereas the relative RMSE clearly increases. However, models with higher predictive power would demand the inclusion of additional specific variables, which may vary depending on the main species. Overall, we found maximum shrub development to be mainly constrained by stand basal area and elevation, although the relationships were somewhat affected by canopy species as found by Brosofske et al. (2001) and Légaré et al. (2001). Among the *Pinaceae* species, we found that stands presenting a fairly good relationship between *BA* and the maximum development of the shrub strata were those located at intermediate elevations (i.e., *Pinnig, Pinsyl*) that do not suffer from major growth constraints associated with climate. In contrast, the development of the understory was poorly correlated with stand *BA* in those species that dominate the sites located in the extremes of the elevation-climatic gradient (i.e., *Pinhal* and *Pinunc*). These results seem to reflect higher competitive interactions and one-sided competition when abiotic stress is low (Bertness and Callaway 1994; Brooker et al. 2008).

**Fig. 6** Estimated mean bias of the models of maximum shrub coverage for the tree species studied as a function of the variables included. *Dotted lines* indicate the standard error of the means multiplied by a factor of 2. The values of the variables (elevation and basal area) have been grouped in 10 tiles of approximately equal number of plots



On the other hand, at both extremes of the severity gradient one would expect a neutral relationship between stand basal area and shrub development because both competition and facilitation might be occurring, as suggested by our results. Among the *Fagaceae* species, the maximum shrub cover sharply decreases with increasing *BA* under both *Quehum and Fagsyl* stands. The canopy structure and leaf morphology of these two species confer them with a high light interception potential (Planchais and Sinoquet 1998; Balandier et al. 2006b). Such stands are normally characterized by a highly shaded understory with very sparse vegetation (Watt 1924). On the other hand, *Queile* stands were the only ones that did not show a significant correlation between basal area and maximum understory cover. These stands have been actively managed by clearcuts and selection cutting for fuelwood purposes until the end of the 1960s resulting in rather open stands with a well developed shrubby understory of evergreen shrubs such as *Viburnum* sp., *Arbutus unedo, Erica arborea, Rhamnus alaternus* and *Pistacia lentiscus* (Jiménez Sancho et al. 1996; Gràcia and Ordóñez 2009). These shrubs are probably still present in those stands even though tree density has increased rapidly as a consequence of the abandonment of traditional management (Valladares and Guzmán 2006). This can explain the lack of correlation between *BA* and *MaxSCov*.

## Conclusion

Our study used national forest inventory data which present large variation in the studied variables. As stated by Bergstedt and Milberg (2001), studies like ours are useful for assessing the general patterns in a large geographical area. Although our analysis did not consider the species composition of the understory and the management history of the sites, we found a general significant negative relationship between stand basal area and understory shrub cover. However, this relationship varied with the dominant overstory tree species and the altitudinal gradient. Weak relationships were found for species located at both ends of the climatic gradient, whereas significant responses appeared at intermediate levels. Managing the canopy cover to control the development of the shrubby vegetation should therefore focus on stands dominated by species such as *Pinnig, Pinsyl, Quehum* or *Fagsyl* for which overstory effects are not overridden by other climatic or microsite factors and possibly facilitation effects. We believe that additional detailed studies in these stands are needed to provide greater fine-grained and useful predictions for forest managers regarding the relationships between the overstory and understory strata.

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