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Spatial Patterns and Predictors of Forest Carbon Stocks in Western Mediterranean

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ABSTRACT

Mediterranean semi-arid forest ecosystems are especially sensitive to external forcing. An understanding of the relationship between forest carbon (C) stock, and environmental conditions and forest structure enable prediction of the impacts of climate change on C stocks and help to define management strategies that maximize the value of forests for C mitigation. Based on the national forest inventory of Spain (1997–2008 with 70,912 plots), we estimated the forest C stock and spatial variability in Peninsular Spain and, we determined the extent to which the observed patterns of stand C stock can be explained by structural and species richness, climate and disturbances. Spain has an average stand C stock of 45.1 Mg C/ha. Total C stock in living biomass is 621 Tg C (7.8% of the C stock of European forests). The statistical models show that structural richness, which is driven by past land use and life forest history including age, development stage, management activities, and disturbance regime, is the main predictor of stand tree C stock with larger C stocks in structurally richer stands. Richness of broadleaf species has a positive effect on both conifer and broadleaf forests, whereas richness of conifer species shows no significant or even a negative effect on C stock. Climate variables have mainly an indirect effect through structural richness but a smaller direct predictive ability when all predictors are considered. To achieve a greater standing C stock, our results suggest promoting high structural richness by managing for uneven-aged stands and favoring broadleaf over conifer species.

Key words: tree carbon stock; understory carbon stock; national forest inventory; conifer and broadleaf forests; structural richness; tree species richness; water availability; forest management; fire disturbance; Peninsular Spain.

INTRODUCTION

Knowledge of the patterns and ways to predict forest carbon (C) stocks are needed to determine the role of forests in the C cycle and in the provision of multiple ecosystem services which the wellbeing of societies depends upon. The current estimate of the world's forests C stocks is 861 ± 66 Pg C (1 Pg = 10^9 g, 1 Mg = 10^{15} g) with 363 ± 28 Pg C (42%) in above- and belowground live biomass (Pan and others 2011). The same forests were

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a net C sink of 1.2 ± 0.9 Pg C y^{-1} over the past decade (Pan and others 2011). On a global scale, forests dominate the terrestrial C sink which is responsible for removing 30% of all anthropogenic C emissions (Canadell and others 2007). However, uncertainty in these estimates and those of regional fluxes is large and the accurate quantification of forest C stocks is one of the main sources (Houghton and others 2009). The uncertainty also affects calculations of the potential capacity for C mitigation of forests and forestry, and the reporting commitments to the Ministerial Conference on the Protection of Forests in Europe, United Nations Convention on Climate Change, the Kyoto Protocol, and the Forest Resource Assessment with important management implications.

At large scales, the most influential drivers in determining stand C stocks are climatic variables, particularly temperature (Brown and others 1999; Houghton 2005; Zhao and Zhou 2006). However, in semiarid ecosystems, precipitation and potential evapotranspiration also play a key role (Kerkhoff and others 2004; Sankaran and others 2005; Huang and others 2009). At the local scale, soil properties (for example, texture, amount of organic matter, stoniness, soil depth) modulate soil water content and affect C stock, whereas topographic factors act in an indirect way by modifying local climatic patterns (Zhao and Zhou 2006; Huang and others 2009). Natural disturbances (for example, wildfires, wind, storms) and human-induced disturbances by means of management practices (for example, clearing, thinning, reforestation) are also important determinants of stand C stock due to changes in stand structure and diversity (Merino and others 2007; Nabuurs and others 2008). Temperate and Mediterranean forests were intensively managed for timber production over the last century. However, during the last decades there has been a process of forest expansion after agricultural abandonment and reduction in forest management now thought to be responsible for the increment of C stock in many forested areas (Houghton 2003; Friedlingstein and others 2010).

The above external factors lead to a particular forest structure and composition such as structural diversity (that is, the variation in tree size and height), and species and functional richness (McElhinny and others 2005; Lexerød and Eid, 2006) which can also be used to predict C accumulation (Kueppers and Harte 2005). Under similar environmental conditions different stand structures and species composition have different growth and mortality rates and these differences eventually lead to differences in stand C stocks. A positive relationship between structural diversity and stand C stock may be due to the fact that different horizontal and vertical layers enhance niche complementarities of resource use reducing competition among trees (Lei and others 2009). Additionally, there is evidence that forests with high species diversity may promote a more efficient use of resources and higher rate of C sequestration (Vandermeer 1989; Vilà and others 2007) compared with sites with a lower number of species or poor structural diversity. As a direct consequence, these stands can maintain higher living C stock. Moreover, some authors (for example, Lei and others 2009) recommend uneven-aged stand management in conjunction with selective or partial cutting to maintain high structural and species diversity.

There has been much attention on assessing C stocks of forests at the global scale (Goodale and others 2002; Nabuurs and others 2008; Pan and others 2011) as well as at regional scales (for example, Brown and others 1999; Dieter and Elsasser 2002; Kueppers and Harte 2005; Zhao and Zhou 2006; de Castilho and others 2006; Risch and others 2008) with little or no attention to semi-arid and Mediterranean regions. In this context, forest woodlands in Spain (Iberian Peninsula, SW Europe) represent well the influence of environmental and disturbance factors that have been dominant in semi-arid forest ecosystems of Southern Europe. Most of the region is under the influence of Mediterranean climate, with strong gradients in temperature and precipitation, it has high structural and tree species diversity that, combined with a long history of disturbances and human management, influence the current patterns of C stocks.

The objective of this study is to estimate the total forest C stock and its spatial distribution, and to determine the main predictive variables of the observed patterns of C stocks in conifer and broadleaf forests in Peninsular Spain. Our main hypothesis is that structural and species richness variables, rather than factors such as climate and local site variables are better predictors of C accumulation, because they integrate many of the above factors.

Materials and Methods

Study Area

The study area comprises the forested areas of Spain (SW of Europe, situated between 9°2′W and 3°2′E and 36°0′N and 43°5′N) excluding the Canary and Balearic Islands (ca. 49.35 million has). The climate is highly variable (Figure 1) due to topographic and continental gradients. Mean minimum temperature ranges from −2 to 14°C and mean maximum temperature from 9 to 25°C. Annual precipitation ranges from 100 to 2500 mm. There are two major climatic domains (Capel Molina 2000): the Mediterranean, which covers most of the Iberian Peninsula (except in the northwest and mountain regions) and is characterized by mild winters and hot and dry summers, and the temperate-oceanic, which covers the northwest of Spain and is characterized by a relatively wet and cold climate. According to the Forest Map of Spain (MFE50, MARM 2007), the forested area has 18.4 million ha or 37.3% of the whole area. Forests are mainly concentrated in the steeper areas, from 0 to 2500 m above-sea-level. Flat and low regions are mainly covered with croplands and urban areas. Forests are distributed in Mediterranean, sub-Mediterranean, Eurosiberian, and Boreoalpine areas. The national definition of forest in Spain also includes dehesas, a particular forest (ca. 2.2 million ha) of low tree cover (between 5 and 20%) and very low tree density (20–200 trees/ha), which allows the presence of pastures that maintain extensive livestock of either pigs or cows and has a high socioeconomic importance.

Dataset: The Third National Forest Inventory of Spain (IFN3)

In this study, the main data set used for computing stand C stock (Mg/ha) was the third National Forest Inventory of Spain (IFN3, Villanueva 2005), which was conducted from 1997 to 2008. The IFN is an extensive national database of forest surveys distributed systematically across the forested area of

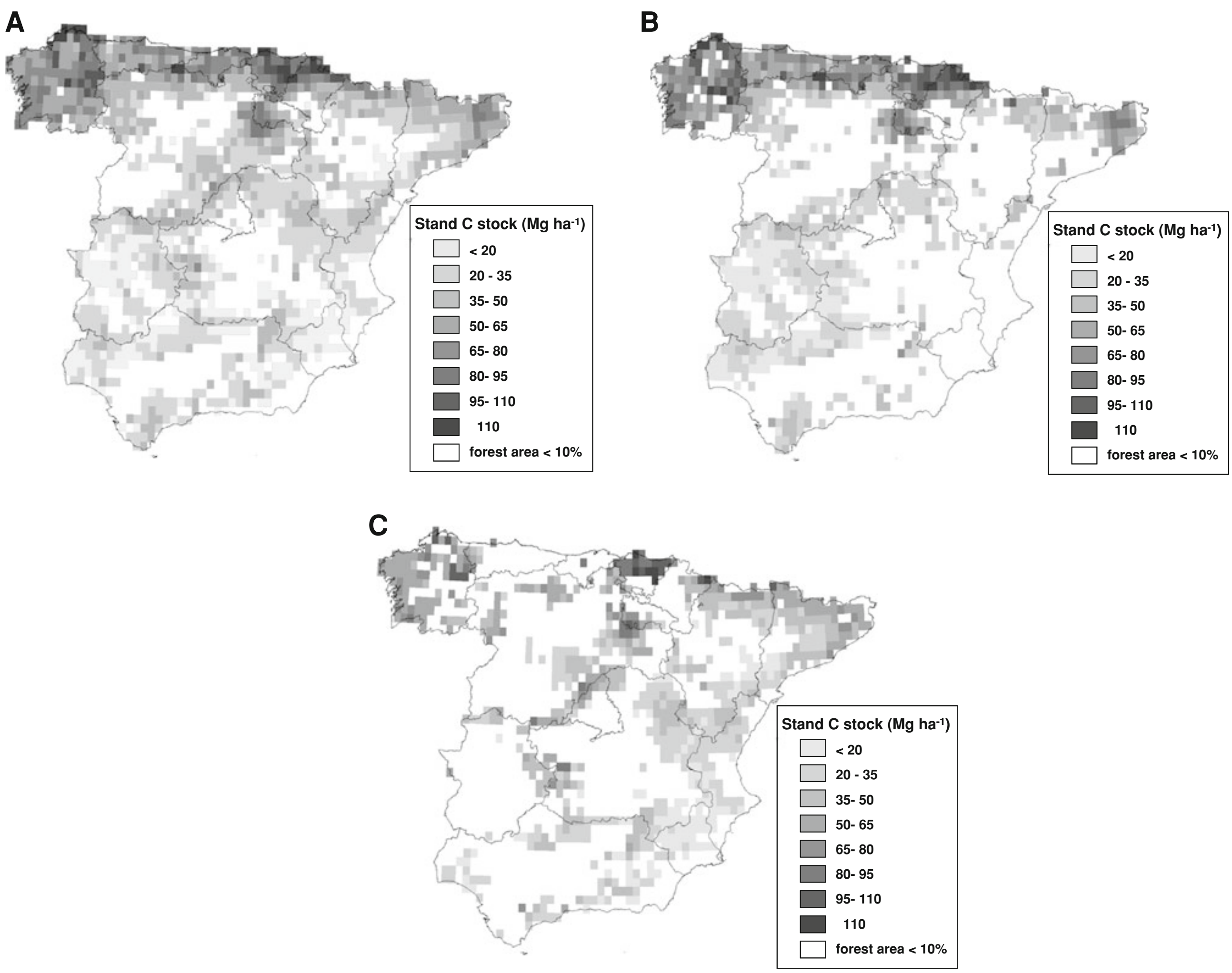

Figure 1. Map of mean stand C stock (sum of the two compartments—trees and understory—Mg/ha) in cells of 10′ × 10′ resolution in forests of peninsular Spain for **A** all species (number of plots = 70,912); **B** forests dominated by broadleaf species (number of plots = 34,334); and **C** conifer forests (number of plots = 36,578).

Spain. The IFN is based on a network of circular plots at a density of 1 plot per 200 ha, which allows forest characterization and includes exhaustive information on the structure and composition of canopy and understory woody species. There were 89,369 plots in the IFN3 and, from those, 70,912 had at least one adult tree (diameter at breast height, DBH ≥ 7.5 cm) (that is, 15.2 million ha, 30.8% of the whole area). According to data from IFN3, the ten most abundant species depending on the area occupied were: *Quercus ilex* (22.8%), *Pinus pinaster* (11.9%), *Pinus halepensis* (11.8%), *Pinus sylvestris* (9.1%), *Pinus nigra* (7.0%), *Quercus pyrenaica* (5.3%), *Pinus pinea* (3.9%), *Quercus suber* (3.8%) *Fagus sylvatica* (3.1%), and *Quercus faginea* (2.9%). These ten species represented 81.5% of all Peninsular Spain forests.

Tree sampling followed a nested design with plot size depending on tree DBH to guarantee the representative of tree size distribution. Thus, all trees with DBH at least 7.5 cm were measured within 5 m of the center of the plot, trees with DBH at least 12.5 cm were also measured between 5 and 10 m around the center of the plot, whereas trees with DBH at least 22.5 cm and DBH at least 42.5 cm were also considered within 10–15 and 15–25 m around the center of the plots, respectively. Species identity, DBH, and height of all living trees were recorded. In a radius of 5 m from the center of the plot, the number of small trees (from 2.5 to 7.5 cm DBH) and their mean height was recorded. The understory was sampled by identifying each species present in a radius of 10 m within the plot and annotating its fraction cover and mean height.

Calculations of Stand C Stock

We established and defined two different compartments to compute stand C stock (Mg/ha) for each plot: (1) *Tree biomass.* This compartment included the living biomass, both aboveground (trunks, branches, and leaves) and belowground (large roots and stumps) of individuals with DBH at least 7.5 cm sampled in each plot and; (2) *Understory biomass.* This component included the living biomass, both aboveground (trunks, branches, and leaves) and belowground (large roots and stumps) of the shrub stratum and of living small tree individuals with DBH between 2.5 and 7.5 cm sampled in each plot (additional details available in Appendix 1 of Supplementary material).

To upscale stand C stock (Mg/ha) to total C stock (Tg) we chose a very simple and direct method consisting of computing for each province (corresponding to the main administrative division in Spain) the ratio between the forest area (MFE50, MARM 2007) and the number of sampled plots. This factor is a measurement of the sampling effort and is equivalent to the forest area represented by each plot. The absolute C stock at the province scale was obtained as the sum of the C stock of each plot multiplied by the corresponding province factor. Finally, the sum of all values obtained at the province level was the absolute C stock for the whole peninsular Spain.

We produced stand C stock maps (tree + understory) (Mg C/ha) for conifers, broadleaf forests and forests as a whole (conifers + broadleaves) using MiraMon GIS software (Pons 2008). The map was obtained by dividing the territory of Spain in polygons of 10′ × 10′ resolution. For each of these polygons with forest area of at least 10% we computed the mean stand C stock of all plots included in the polygon. The polygons with forest surface below this threshold were included in the map as N/A (not available).

Predictors of Stand Tree C Stock

We analyzed the relationship between stand tree C stock (above- and belowground biomass) and structural and species richness, climate variables, local site characteristics, and recent disturbances. In these analyses we include the five main broadleaf species (*F. sylvatica*, *Q. faginea*, *Q. ilex*, *Q. pyrenaica*, and *Q. suber*) and the five main conifer species (*P. halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, and *P. sylvestris*). The dominant tree species of each plot (DBH ≥ 7.5 cm) was determined using basal area as criteria. We also exclude forest plantations and dehesas (open woodland forests). For each plot we obtained the following groups of predictor variables:

Climate

This information was obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola and others 2005), a collection of digital maps of 200 × 200 m resolution with annual and monthly information for cumulative rainfall, and maximum, mean, and minimum temperatures. Based on the geographic coordinates of each IFN3 plot we determined three climatic variables: (1) Mean annual temperature (MT, °C); (2) Mean annual thermal amplitude (or temperature range, TR) obtained from the annual difference between maximal and minimal temperature (°C); and (3) Annual water availability index (WAI) obtained at monthly level according to:

$$\mathrm{WAI} = ((\mathrm{P} - \mathrm{PET})/\mathrm{PET}) \times 100$$

where P is rainfall (mm/month) and PET is potential evapotranspiration (in mm/month) following Hargreaves and Samani (1982). Annual WAI was obtained as a sum of the WAI of 12 months. Negative values of WAI correspond to dry sites, and positive values to wet sites. The map of WAI (Figure A2.1 in Supplementary Material) indicates that 85% of the overall area of Spain has a water deficit and only 15% of the area has a water surplus throughout the year. The WAI values indicate a clear latitudinal gradient and a slight gradient from west to east.

Local Site Characteristics

We used four local site variables: (4) Soil type: it had two categories based on the reaction of mineral soil to hydrochloric acid: limestone (those that reacted with the acid) or siliceous (those that did not show any chemical reaction with the acid); (5) Soil texture: in each plot soil texture was estimated following a granulometric classification of three categories: sandy, loam and clay; (6) Stoniness: surface soil stoniness was estimated following a four-level ordinal classification: 0, 1–25, 26–50, and 51–75% of stones on the surface of the soil; (7) Slope: the only topographical variable considered was slope which was estimated as the maximum slope (°) in the center of the plot.

Recent Forest Disturbances

We used two categorical variables related to forest disturbances and included in the IFN3 dataset: (8) Forest management (Yes/No): we considered that there had been recent exploitation when there was any evidence of cutting or thinning in the plots; (9) Fire (Yes/No): evidence of severe damage caused by fire in the recent past.

Structural and Species Richness

These predictor variables were obtained from the living trees with DBH at least 7.5 cm: (10) Structural richness: number of diameter classes present in the plot for any species (each class was 5 cm of DBH wide); (11) Conifer species richness: number of conifer species present in the plot and; (12) Broadleaf species richness: number of broadleaf species present in the plot. To avoid the bias that could be produced in these variables due to low numbers of trees per plot, we only included plots with at least six trees sampled (that is, the threshold of the first quartile of the number of trees sampled in all plots).

Statistical Analyses

The total number of plots used in statistical analyses was 33,827. From those, 12,642 plots were dominated by one of the five broadleaf species and 21,185 plots were dominated by one of the five conifer species. We fitted separate models, using general linear models (GLM), for conifers and for broadleaves (see above) with stand tree C stock as response variable (previous log-transformation to satisfy the normality assumption). Species identity was included in each model as a fixed factor. The other predictor variables were described in the previous section. Stepwise model selection was applied starting from the saturated model (using all variables) and removing the least significant term until there was no further decrease in the Bayesian Information Criterion (BIC). We considered all models within 2 BIC units as equivalent in terms of fit. Given the large sample size, significance was accepted at $P < 0.01$. We checked if residuals of the models showed any spatial pattern using spherical spatial correlation structure by using generalized least squares (GLS). These models were similar in terms of the fitted coefficients to the equivalent GLMs. Given that the two types of models did not significantly differ (BIC values < 2 units) in the results we only included the models without spatial autocorrelation. Statistical analyses were carried out with the R software (package nmle, R 2.10.0, The R Foundation for Statistical Computing).

Structural equation modeling (SEM) was used to analyze the complex effects of the three groups of variables: climate, local site characteristics and richness, on stand tree C stock. We carried out different models with conifers and broadleaves and also in the plots affected or not by disturbances (both management and fire), that is, we carried out four models for the combinations of forest type and presence or not of disturbances. We tested a common conceptual model to explain the patterns of stand C stocks in these four combinations. This general model considered that climate and local site characteristics have indirect effects on the response variable through richness variables but also direct effects on stand C stocks. We fitted each ''saturated'' model including all possible directional relationships plus covariation between the climate variables and between the richness variables. Each model was simplified stepwise removing the least significant term until there was no further decrease in the BIC. We considered all models within 2 BIC units as equivalent in terms of fit. All SEM analyses were performed using the package AMOS 18

(Arbuckle 2009). In all cases, parameter significance was accepted at $\alpha = 0.05$.

Results

Patterns of Total C Stocks

The total C stock of forests in Peninsular Spain was 621 Tg (1 Tg = 10^{12} g) of which 547 Tg (88.1%) were in trees and 74 Tg (11.9%) in the understory. A significant fraction of this stock was belowground, with 29.5% for trees and 37.6% for the understory (Table 1). The mean stand C stock was 45.1 ± 0.16 Mg/ha, with 39.8 ± 0.15 Mg/ha (88.4%) for trees and 5.2 ± 0.002 Mg/ha for the understory (11.6%). Total C stock of broadleaf forests (trees + understory) was 330 Tg, whereas that of conifer forests was 291 Tg. Conifers had a lower value of stand C stock (41.8 ± 0.185 Mg/ha) than broadleaves (48.6 ± 0.254 Mg/ha). The mean stand C stock stored belowground on broadleaf forests was higher (36.5%) than on conifer forests (23.8%).

The spatial distribution of stand C stock in Peninsular Spain showed that forests with the highest values (>80 Mg/ha) were mostly concentrated in the north and the northwest regions by the Atlantic Ocean, Pyrenees, and other mountain regions (Figure 1A). Forests in the south and the east had the lowest stand C stocks, especially along the southern Mediterranean coast. The spatial distribution of broadleaf and conifer forests showed a similar pattern (Figure 1B, C). Broadleaf forests were mostly concentrated in the north, again with the highest values. The lowest values (<35 Mg/ha) were in the southwest where there are the major concentrations of dehesas (mainly *Q. ilex* and *Q. suber*). Similarly, the highest values of conifer forests were in the north but the major concentration, and also the lowest values, were located in the south-east (coinciding mainly to the forests of *P. halepensis*).

The lowest values of stand tree C stock (both above- and belowground) (Figure 2A) among broadleaf species corresponded to *Q. suber* (20.3 ± 0.37 Mg/ha), *Q. faginea* (22.9.0 ± 0.52 Mg/ha) and *Q. ilex* (26.2 ± 0.22 Mg/ha). Intermediate values are found for *Q. pyrenaica* (41.0 ± 0.67 Mg/ha) and very high values for *F. sylvatica* (105.4 ± 1.09 Mg/ha). Among conifers, the lowest values were for *P. halepensis* (19.2 ± 0.17 Mg/ha), followed by *P. pinea* (23.8 ± 0.36 Mg/ha) and *P. nigra* (32.7 ± 0.37 Mg/ha), whereas the highest mean values were those of *P. pinaster* and *P. sylvestris*, with 44.8 ± 0.38 and 48.7 ± 0.42 Mg/ha, respectively. The patterns of stand C stock for the understory were opposite to those found for trees: as stand tree C stock decreased,

Table 1. Mean and Standard Error (SE) of Stand C Stock (Mg/ha) by Fractions (Aboveground and Belowground) and Total, Percent of Each Compartment Related to Overall Stand C Stock and Total C Stock (Tg, 1 Tg = 10^{12} g) in (A) Compartments (Trees and Understory) and (B) Broadleaf and Conifer forests (Trees + Understory)

	Fraction	Stand C stock (Mg/ha)	SE	% Fraction	Total C stock (Tg)
(A)					
Trees	Aboveground	28.1	0.109	70.5	385
	Belowground	11.8	0.049	29.5	161
	Total	39.8	0.152	100.0	547
Understory	Aboveground	3.3	0.012	62.5	47
	Belowground	2.0	0.008	37.5	28
	Total	5.2	0.018	100.0	74
Total (Trees + understory)	Aboveground	31.3	0.109	69.5	432
	Belowground	13.7	0.052	30.5	189
	Total	45.1	0.156	100.0	621
(B)					
Broadleaves (Trees + understory)	Aboveground	30.8	0.166	63.5	210
	Belowground	17.7	0.092	36.5	120
	Total	48.5	0.254	100.0	330
Conifers (Trees + understory)	Aboveground	31.9	0.143	76.2	222
	Belowground	10.0	0.044	23.8	69
	Total	41.8	0.185	100.0	291

Total number of plots: 70,912; broadleaf forest: 34,334 and conifer forests: 36,578.

understory stand C stock increased and vice versa (Figure 3A, B). Hence, the highest proportion values in relation to the total stand C stock were in Mediterranean forests of *Q. suber* (24.7%), *P. halepensis* (23.2%), *Q. faginea* (20.2%), and of *Q. ilex* (16.7%). The mean values of stand C stock for conifers (mean of five conifer species) of the two compartments (trees and understory) were slightly lower than for broadleaves because conifer forests stored less biomass belowground (Figure 3A, B). The highest values of stand C stocks in natural forests in relation to reforestations was mainly due to the higher biomass stored in their understory (Figure 3B). The significant lower stand C stock found in dehesas was due to the fact that they stored less C in the two compartments (trees and understory) but, unlike the other forest types, the proportion of biomass stored belowground increased (Figure 3A, B).

Predictors of Stand Tree C Stock of Conifer and Broadleaf Forests

The two GLM proposed determining stand tree C stock explained 62% of variance for broadleaf species (Table 2A) and 53% for conifer species (Table 2B). The decomposition of explained variability (%) of stand tree C stocks (Mg/ha) to the different groups of variables showed that richness variables (both structural and species richness) showed the greatest effect in conifer and broadleaf forests (Figure 4). The effect of local site characteristics and variables concerning forest disturbances was lower than that of climatic variables. The highest effect was the strong and exponential positive effect of the number of diameter classes on stand C stock (Table 2A, B; Figure A2.3 in Supplementary Material). In broadleaf forests, the number of broadleaf species had a positive effect on stand tree C stock, whereas the presence of conifer species had a negative effect on it. In conifer forests, only the presence of broadleaf species had a positive effect on stand C stock whereas the presence of other conifers was not significant. Among climate variables, in the two groups of species WAI had a

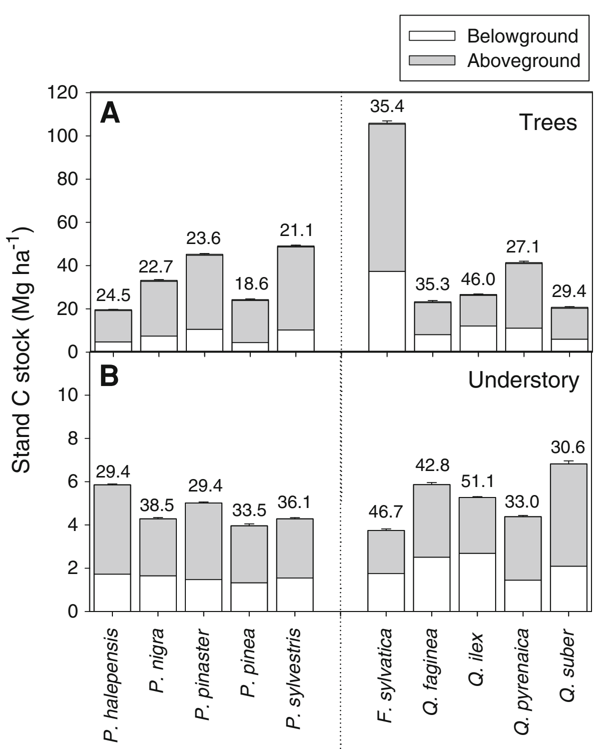

Figure 2. Mean (± standard error) of stand C stock (Mg/ha) for the five conifer species and for the five broadleaf species in **A** tree compartment (above- and belowground) and **B** understory (above- and belowground). Values indicated the percent of the total stand C stock of the compartment corresponding to belowground.

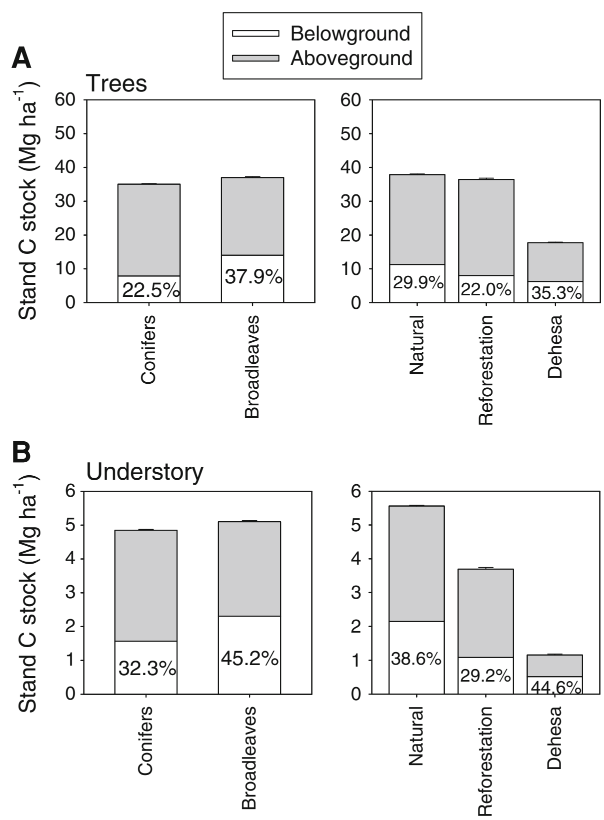

Figure 3. Mean (± standard error) of above- and belowground stand C stock (Mg/ha) by compartment (average of ten species analyzed) for **A** tree compartment (*left panel* by: conifer and broadleaf species; *right panel* by forest history: natural forests, reforestations or dehesas) and **B** understory compartment. Values indicated the percent of the stand C stock corresponding to belowground.

small and positive effect on stand tree C stock whereas mean annual temperature had a negative effect, stronger in broadleaf species. Finally, temperature range also showed a strong and negative effect on broadleaves, whereas in conifers was not significant (Table 2A, B). Among local site variables, stoniness had the most significant negative effect. Soil type showed opposite patterns: stand tree C stock in conifers was highest in siliceous soils whereas broadleaves showed the highest C accumulation in limestone soils. Soil texture had a low effect, whereas conifer forests showed the highest C accumulation on loam, intermediate on clay and the lowest on sandy soils; broadleaves showed the highest values on clay and the lowest in sandy and loam. Slope had a positive effect on broadleaf species but not in conifers. Managed conifer forest had higher stand C stock than unmanaged; in broadleaf forests this factor was not significant. Finally, fire disturbance lead broadleaf forests to accumulate less C.

Table 2. Summary of Stand Tree C Stock (Mg/ha) Models for (A) Broadleaves and (B) Conifers

	Estimate	*t* value
(A)		
Intercept	4.924 ± 0.071	69.0***
SP (*Q. pyrenaica*)		n.s.
SP (*Q. faginea*)	−0.423 ± 0.021	−20.2***
SP (*Q. ilex*)	0.070 ± 0.019	3.6***
SP (*Q. suber*)	−0.667 ± 0.025	−26.8***
WAI (%)	0.001 ± 0.0002	5.1***
MT (°C)	−0.066 ± 0.003	−24.8***
TR	−0.101 ± 0.005	−20.4***
Soil type (Limestone)	0.032 ± 0.011	2.9**
Texture (Loam)		n.s.
Texture (Clay)	0.042 ± 0.016	2.6**
Slope	0.004 ± 0.0004	8.7***
Stoniness	−0.042 ± 0.004	−9.5***
Fire (= yes)	−0.164 ± 0.030	−5.5***
Management (= yes)		n.s.
Number conifer species	−0.038 ± 0.008	−4.5***
Number broadleaf species	0.035 ± 0.005	7.2***
Number diameter classes	0.156 ± 0.002	70.7***
Degree of freedom	12,625	
Adjusted $-r^2$	0.62	
F value	<0.001	
(B)		
Intercept	2.811 ± 0.0309	90.9***
SP (*P. nigra*)	−0.047 ± 0.0126	−3.7***
SP (*P. pinaster*)	−0.058 ± 0.0135	−4.3***
SP (*P. pinea*)	−0.269 ± 0.0208	−12.9***
SP (*P. halepensis*)	−0.202 ± 0.0157	−12.9***
WAI (%)	0.001 ± 0.0001	7.5***
MT (°C)	−0.016 ± 0.0025	−6.5***
TR		n.s.
Soil type (Limestone)	−0.119 ± 0.0093	−12.8***
Texture (Loam)	0.043 ± 0.0104	4.1***
Texture (Clay)		n.s.
Slope		n.s.
Stoniness	−0.104 ± 0.0038	−27.2***
Fire (= yes)		n.s.
Management (= yes)	0.079 ± 0.0074	10.7***
Number conifer species		n.s.
Number broadleaf species	0.032 ± 0.0050	6.5***
Number diameter classes	0.220 ± 0.0019	115.7***
Degree of freedom	21,167	
Adjusted $-r^2$	0.53	
F value	<0.001	

SP, species factor; WAI (%), water availability index; MT (°C), annual mean temperature; TR (°C), temperature range.
*All values shown are significant at **P < 0.01, ***P < 0.001.*

The results of the path analyses for the different forest types with and without disturbances were essentially identical and we only show those without disturbances (Figure 5, Figure A2.4 in Supplementary Material the results of the other two models). All final four path models provided a good fit to the data indicated with a non significant Chi-squared value. The models captured a substantial proportion of the variance in stand C stocks, ranging from 42.3 to 47.6% for conifers and from 52.2 to 54.6% for broadleaves. The resulting models differed little from the saturated models, especially in the models of undisturbed forests, suggesting a complex network of direct and indirect relationships affecting stand C stocks. Structural richness was again the variable with the highest direct effect on stand C stock. The models indicated a higher effect of WAI on stand C stock to that shown in the GLM models, with a significant direct effect and an indirect effect through structural richness. Local site variables also showed both direct and indirect effects (through richness

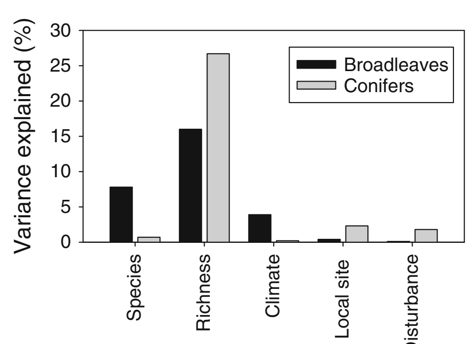

Figure 4. Decomposition of the explained variability (%) of tree C stock (Mg/ha) of the different group of variables for the models of broadleaves and conifers. The values indicate the percent of variance explained by each group of variables in the model.

variables) on stand C stocks, although lower than those of climatic variables.

Discussion

Patterns of Total C Stocks in Peninsular Spain

The total forest C stock (trees + understory) in Peninsular Spain was 621 Tg C, representing 8% of the C stock in Europe (Goodale and others 2002) and 0.17% of the world's C stocks. The use of ancillary data as topographic and climate variables to improve the upscaling of stand C stock to total C stock (Tg) (Table 1) and the maps of stand C stock (Figure 1) (Raupach and others 2005; Keith and others 2010) would have added little improvement to the accuracy of these estimates as a consequence of the low direct effect of topography (slope) and climate variables (mean annual temperature and WAI) on stand C stock (Figures 4, 5; Table 2). The spatial pattern of stand C stock (trees + understory) in Peninsular Spain follows a north–south gradient from high to low C accumulation (Figure 1A). This is especially true in the most arid areas of the Peninsula, where the severe climate prevents canopy closure and limits C accumulation (Sankaran and others 2005). The patterns obtained for the two groups of species were similar (Figure 1B, C). Mean stand C stocks (trees + understory) in forest of Peninsular Spain was low with an average of 45.1 ± 0.16 Mg/ha, or 40 ± 0.15 Mg/ha considering only the tree compartment. This stand C stock was less than half of that observed for more productive forest regions, such as tropical Amazonia (de Castilho and others 2006) or temperate regions (Brown and others 1999; Dieter and Elsasser 2002) where stand C stock is usually over 100 Mg/ha.

In contrast to the abundant information on stand tree C stock in Europe, estimates of forest understory are scarce (Risch and others 2008). This study presents extensive values for the understory of forests in Peninsular Spain. The understory stand C stock across all forests represents 11.9% of the C stock of the woody vegetation (Table 1). However, the fraction represented by the understory of most Mediterranean forests is particularly high, 17 and 23% of the stand C stock (trees + understory) for *Q. ilex* and *P. halepensis* forests, respectively (Figure 2A, B). Conifer and broadleaf forests maintained similar understory stand C stocks (Figure 3B). Understory stand C stock of reforested forests was two-thirds that of natural forests and in dehesas this value was reduced to one-fifth of natural forests (Figure 3B). In the two cases, and when the main purpose is to maximize wood production (reforestation) or pastureland and acorn production for livestock (dehesas; Linares 2007), the understory is periodically eliminated from these forests.

Predictors of Stand Tree C Stock Patterns

The results of the GLM were robust and roughly similar among groups of species, both in terms of their overall significance and the sign of the main effects (Table 2A, B). However, there were large differences in the magnitude of the effects of these predictive variables (Figure 4). Structural and species richness were the dominant predictors of stand C stocks in both forest types because these variables result from a number of important forest characteristics such as age, development stage, composition, and forest history (for example, management activities, disturbance regime) (Lei and others 2009; Keith and others 2009). The effect of species identity was high only in broadleaves, probably because, unlike conifers (all belonging to the genus *Pinus*), they show higher differences in architecture such as the branch:stem ratio (Keith and others 2009; Zhang and others 2011), root:shoot ratio (Montero and others 2005), and wood density (Baraloto and others 2011). Climatic variables had an important effect modifying spatial patterns, especially in broadleaf species, whereas they had almost no effect in conifers. In contrast, local scale factors—site characteristics and disturbances—had more effects in conifers. These differences between conifers and broadleaves suggest a different history of natural disturbances and human management, more intense in conifers, which lead to shorter time for the climate to influence stand C stocks (Sankaran and others 2005; Raich and others 2006; Keith and others 2009; Stegen and others 2011). The results obtained in the path analyses indicate that the effects of climate on stand C stocks are mainly through modifying species and structural richness (Figure 5).

Stand structure is a consequence of both autogenic development processes (that is, successional stage with regeneration, competition, and the consequent self-thinning effect) and past events such as forest management and disturbances (Lei and others 2009). In our study, the higher the number of classes, the higher the stand C stock (Table 2A, B; Figure A2.3 in Supplementary Material). This result is not necessarily obvious, because as forests grow, competition for resources also increases and this may favor the elimination of suppressed individuals (usually small ones) and,

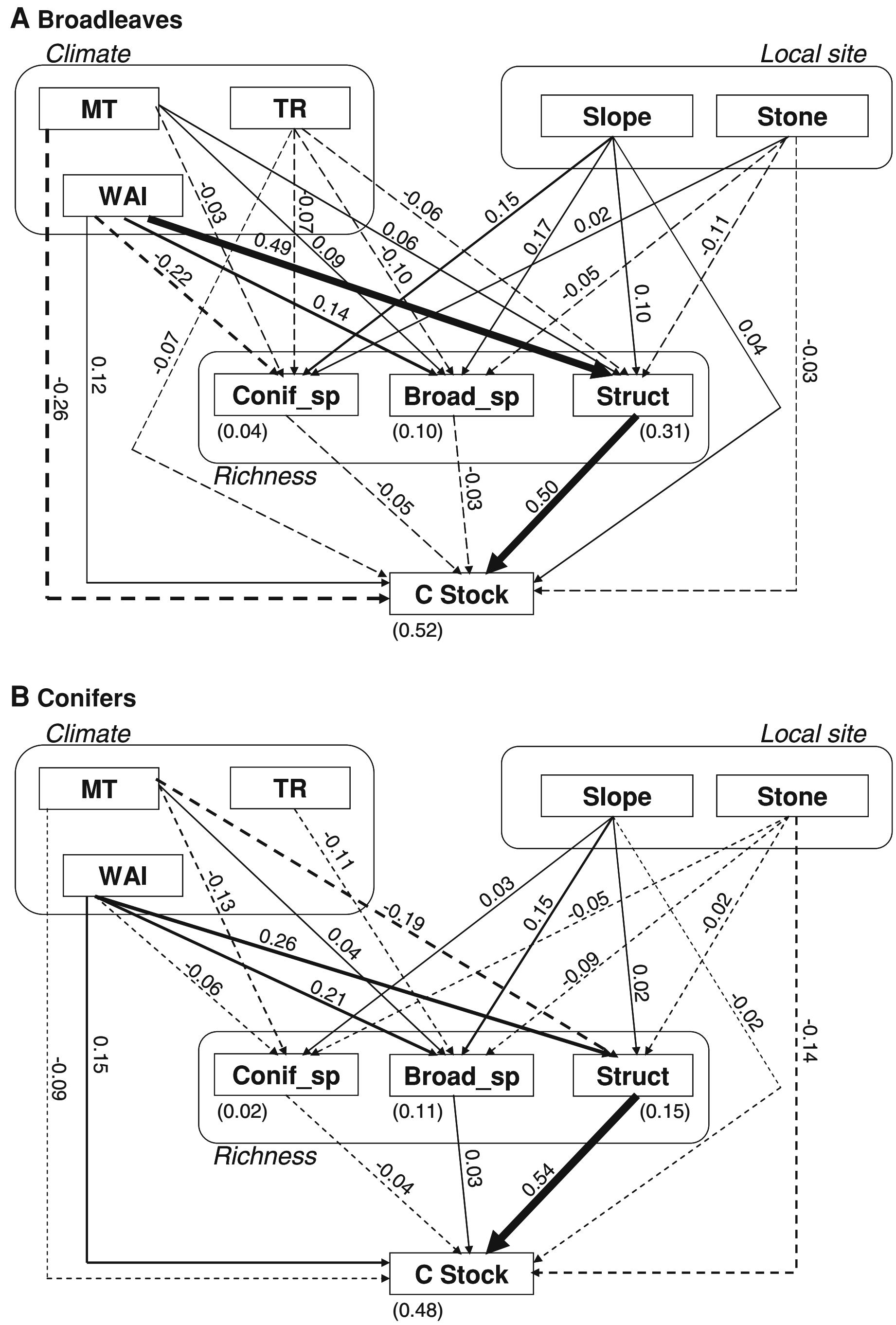

Figure 5. Path models relating tree C stock of natural forests (without recent disturbances) with groups of variables representing climate, local site characteristics and richness variables for **A** broadleaves and **B** conifers. Only *single-headed arrows* (directional paths) that are significant in the models are shown indicating the proposed links between variables. *Double-headed arrows* indicating covariances are not shown for clarity. Positive effects are indicated by *solid lines* and negative ones by *dashed lines*. *Arrow* thickness is proportional to the strength of the effect in terms of the absolute value of the standardized coefficients, indicated by the value close to each arrow. The number in *brackets* over a given endogenous variable corresponds to the R^2 value indicating the percentage of the variance in that variable that is accounted for by the model. Significance is accepted at $P < 0.01$. WAI (%), water availability index; MT (°C), annual mean temperature; TR (°C), temperature range; Stone, surface soil stoniness (%); Conif_sp, conifer species richness; Broad_sp, broadleaf species richness; Struct, structural richness; C_stock, tree C stock (Mg/ha).

thus, reduce the number of diametric classes (Keddy 2005; Healy and others 2008; Vance-Chalcraft and others 2010). The positive effect of the number of diametric classes on C accumulation for both conifers and broadleaves suggests that when trees occupy different horizontal and vertical layers, they can maximize the resources, whereas homogenous stand structure may reduce complementary effects (Lei and others 2009). Moreover, the almost exponential relationship between the number of diametric classes and stand C stock (Figure A2.3 in Supplementary Material) is consistent with the idea that stand tree C stock increases with stand age and with the presence of larger trees (Figure A2.2 in Supplementary Material) and highlights the important contribution of these trees to C storage in forests, such as has been suggested in other studies (Vanninen and others 1996; Baraloto and others 2011; Stegen and others 2011; Zhang and others 2011).

In mixed forests, there can be differences between the species in diametric classes when one species grows first and another is incorporated later. In such cases, structural richness incorporates in part the effect of species richness, explaining why the relationship between stand C stock and species richness is weaker than expected, but still significant in some cases. In this study, stand C stock of forests dominated by a conifer species increased if additional species were broadleaves, but not if they were conifers. These results agree with the niche complementarity hypothesis (Vandermeer 1989; Lei and others 2009) which stems from the different functional traits of the two groups of species. Thus, broadleaf species add new functional variation that enhances stand C stock when they share the plot with conifers and are able to access and utilize additional resources. This is particularly import for light, because they are more shade-tolerant species (Gravel and others 2010) and, for water, because they have more developed root systems than conifers (Montero and others 2005). It is also possible, as suggested by Caspersen and Pacala (2001), that causality runs in the opposite direction, that is, more productive stands may simply permit the coexistence of more species. If this was the case, then any increment in the number of species would have been positive. However, in our study only certain combinations of species are complementary in their patterns of resource use and can accumulate higher stand C stock by increasing the rate of productivity and nutrient retention or maintaining during more time stand C stock. In forests dominated by broadleaf species, the relationship with broadleaf species richness was also positive, but conifer richness had a negative effect, suggesting that stand C stock was also determined by the morphologic characteristics of the accompanying species (Zhang and others 2011). These results are analogous to those obtained in experimental biodiversity studies where particular species are better predictors for stand C stocks than overall species richness (Kahmen and others 2005). Several studies (Keddy 2005; Healy and others 2008) describe a potential decrease in species richness due to competition as biomass continues to slowly increase and resulting in a few dominant species excluding the others. But taking into account that many of the forests considered are still young, it has not been possible to determine the long-term trends of species richness.

Although with a weak direct effect, water availability had a positive effect on both groups of species. Interestingly, the results of path analysis revealed a strong and mainly positive indirect effect through richness variables. This result is relevant taking into account that 85% of Peninsular Spain is under a water deficit (Figure A2.1 in Supplementary Material). That water scarcity limits biomass in dry ecosystems is not surprising (Sankaran and others 2005; Kerkhoff and others 2004; Hicke and others 2007; Huang and others 2009), but may be relevant for understanding forest biomass dynamics in the context of changing precipitation regimes and increasing frequency of extreme droughts (for example, Goswami and others 2006; Stegen and others 2011). Temperature had also a weak direct negative effect on both groups of species, limiting stand C stock at high temperatures and exacerbating the adverse effect of water scarcity.

Among local site characteristic variables, different studies have described the effects of soil on trees and concluded that soil characteristics are among the most important factors describing stand C stock patterns at the local scale (for example, Clark and others 1999; de Castilho and others 2006). In our study, stoniness had the most strong and negative effect on stand C stock (Table 2A, B). This is an expected result because a higher amount of surface soil stones could be associated with low soil availability for plants, high erosion, and loss of fertile soil in the past. Unfortunately, the precision of the other soil variables considered was poor, reducing their potential effect in the full model. The unexpected, mainly indirect, positive effect of slope on stand C stocks of broadleaf forests (high slope has been traditionally associated with more stressed conditions—for example, shallow soils, high soil moisture variation, and pronounced soil erosion) (for example, Huang and others 2009) could be the result of the interaction with time since disturbance as suggested by Merino and others (2007). Stands confined to steep slopes, where access is difficult, have been maintained with little or no active management; in fact, this agreed with no effect of recent management in these forests. In contrast, recent management had a positive effect on stand C stocks of conifer forests, probably because managed forests occupy areas with higher site quality.

Implications for the Future

The low values of stand C stocks observed in Spain are due to a complex set of local and regional factors considered in this study, and particularly the legacy of land use and land-cover change, and past management practices and disturbances. A better understanding of the relationship between forest stand C stock, environmental conditions and forest structure is important to predict the impacts of climate change on C stocks and maximize the role of forests for C mitigation. This includes increasing the rate of C uptake, maintaining high stand C stocks and avoiding C loss through increasing their resilience. In this context, a comprehensive management approach is required that includes changes in the rotation length of harvest and the intensity of logging. Replacement of present species by others less vulnerable to climate change is another option that could be considered. In our study we have shown that structural richness is the main predictor of stand C, being a good indicator of past and recent land use and forest life history. We have also shown that a significant proportion of stand C stocks was stored in the larger trees and, whereas broadleaf species richness had a positive effect, conifer species richness showed no significant or even a negative effect on stand C stock. Thus, if the aim is to maximize stand C stocks, the first forest management option is to not log and allow the forest to regrow and reach maturity. The second management option is to lead forests to uneven-age stands combining selective or partial cutting to maintain high structural diversity and always favoring the maintenance of larger trees. In all cases, favoring late successional species, such as broadleaf species over conifers, with lower turnover rates will lead to more stable and longer residence times for stand C stocks.

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