

How does forest landscape structure explain tree species richness in a Mediterranean context?

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Abstract Although the strong relationship between vegetation and climatic factors is widely accepted, other landscape composition and configuration characteristics could be significantly related with vegetation diversity patterns at different scales. Variation partitioning was conducted in order to analyse to what degree forest landscape structure, compared to other spatial and environmental factors, explained forest tree species richness in 278 UTM 10 × 10 km cells in the Mediterranean region of Catalonia (NE Spain). Tree species richness variation was decomposed through linear regression into three groups of explanatory variables: forest landscape (composition and configuration), environmental (topography and climate) and spatial variables. Additionally, the forest landscape characteristics which significantly contributed to explain richness variation were identified through a multiple regression model. About 60% of tree species richness variation was explained by the whole set of variables, while their joint effects explained nearly 28%. Forest landscape variables were those with a greater pure explanatory power for tree species richness (about 15% of total variation), much larger than the pure effect of environmental or spatial variables (about 2% each). Forest canopy cover, forest area and land cover diversity were the most significant composition variables in the regression model. Landscape configuration metrics had a minor effect on forest tree species richness, with the exception of some shape complexity indices, as indicators of land use intensity and edge effects. Our results highlight the importance of considering the forest landscape structure in order to understand the distribution of vegetation diversity in strongly human-modified regions like the Mediterranean.

Keywords Forest diversity · Landscape ecology · Tree species richness · Pattern metrics · Variation partitioning

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Introduction

Understanding the factors that determine the patterns of biodiversity is one of the core objectives for ecologists and biogeographers (Huston 1994; Begon et al. 1999; Gaston 2000). The increasing trend in biological diversity from polar to equatorial regions (i.e. latitudinal gradient) is a widely recognized pattern (see Willig et al. 2003), particularly for plant species (Huston 1994). Different hypothesis have been proposed to explain latitudinal gradients of richness (reviewed in Willig et al. 2003; Huston 1994); in particular, correlations between global patterns in species richness and climate are widely known, and climatic factors as predictors of plant distributions have been analysed by a large number of studies (e. g. Heikkinen and Birks 1996; Field et al. 2005). Relationship between species diversity and the size of the sample area has also generated great interest in ecological studies; for example, Nogués-Bravo and Araújo (2006) have recently studied the correlations between species richness and both the size of the sample area and climatic characteristics. However, biodiversity patterns are strongly influenced by multiple factors, both biotic and abiotic, at multiple scales (see Huston 1994; Begon et al. 1999). In this context, factors operating at the landscape level could be related with vegetation spatial distribution at different scales, although there is a considerable lack of knowledge in this respect, particularly in human-modified areas like the Mediterranean. In fact, the impact of landscape structure has been comparatively less explored in this context, mainly because of the perceived difficulty of conducting broad-scale studies (Fahrig 2005). From a landscape ecology approach, the effects of landscape structure on the abundance and distribution of organisms can be explored, focusing on much larger spatial extents than those traditionally studied in ecology (Turner 1989; Fahrig 2005).

A considerable number of studies have analysed the effects of landscape structure on different taxons such as plants or birds (McGarigal and McComb 1995; Metzger 1997; Dauber et al. 2003; Heikkinen et al. 2004; Fisher et al. 2005; Hernandez-Stefanoni 2005; Mitchell et al. 2006; Simmering et al. 2006). Besides, several studies have evaluated how configuration indices can contribute to explain biodiversity distribution, with forest landscape fragmentation being considered in some cases a major determinant of biodiversity loss (see Forman 1995; Fahrig 2003; Hernandez-Stefanoni 2005). Other authors have analysed the effect of landscape shape on species, more frequently in agricultural landscapes (Hamazaki 1996; Moser et al. 2002; Honnay et al. 2003; Saura and Carballal 2004; Økland et al. 2006). Moser et al. (2002) found a positive relationship between landscape shape irregularity and plant species richness in rural landscapes in Austria, as a result of the degree of land use intensity, which both decreased richness and simplified the landscape shape. Saura and Carballal (2004) noted that forest types with higher species richness presented more irregular boundaries, and found that some landscape shape complexity indices were able to discriminate native and exotic forest patterns and were potentially related to forest naturalness. Honnay et al. (2003) also used landscape complexity indices as predictors for plant species diversity. In summary, previous studies suggest that landscape structure could be used as an effective biodiversity indicator (Lindenmayer et al. 2000; Dauber et al. 2003).

Here we investigated to what degree forest landscape structure can explain forest tree species richness distribution, including both variables related to landscape composition (forest area, forest canopy cover (FCC), forest development stage and land cover diversity) and to landscape configuration (fragmentation and shape irregularity), some of them rarely analysed in previous studies despite their potential interest in this context. We evaluated how much of the variation in species richness can be exclusively attributed to landscape

structure compared to other environmental (topography and climate) and spatial factors. We used partial linear regression (Legendre and Legendre 1998) and the variation partitioning method proposed by Bocard et al. (1992), widely applied in previous studies on the diversity and composition of different taxons (e.g. Aude and Lawesson 1998; Boone and Krohn 2000; Lobo et al. 2001; Vandvik and Birks 2002; Heikkinen et al. 2004; Nogués-Bravo and Martínez-Rica 2004; Svenning and Skov 2005; Kivinen et al. 2006; Økland et al. 2006). To refine the analysis for the forest landscape structure variables, we explored the relative contribution in this respect of landscape composition and configuration variables.

Our study was conducted in the Mediterranean region of Catalonia (NE Spain) using a UTM 10 × 10 km cells grid, and with the recent Spanish Forest Map (SFM) at 1:50,000 (developed within the Third Spanish National Forest Inventory) as the information source for the forest landscape variables. Mediterranean climate zones are characterized by a high plant diversity and also by a high number of endemic species, providing an Earth's biodiversity hotspot (Reid 1998; Médail and Quezel 1999; Myers et al. 2000); however, they have received little attention compared to other regions like Northern Europe or tropical regions (e.g. Heikkinen 1996; Hernandez-Stefanoni 2005). This study intends to provide further insights into the understanding of Mediterranean tree species richness patterns from a landscape ecology perspective, considering that in the Mediterranean the potential patterns of diversity have been considerably modified by a strong and long-lasting human influence, which may result in a lower predictive power of climatic models compared to other study areas.

Material and methods

Study area and scale of analysis

Our case study was carried out in the region of Catalonia (NE Spain), located within 0°15' E and 3°15' E longitude and 40°30' N and 42°40' N latitude, and with a total extension of 32,098 km². The climate is Mediterranean in the majority of the territory, with also some subtropical, temperate and Atlantic influences that make Catalonia a climatically singular region. In addition, a great contrast in altitude, a complex relief and other geographic factors favour climate diversity at the micro-scale. About one third of the territory of Catalonia is comprised between an altitude of 600 and 1,000 m, one tenth between 1,000 and 2,000 m, and nearly 7% above 2,000 m in the Pyrenees. According to the Land Cover Map of Catalonia (CREAF-DMA 1993) the dominant cover types are forests (occupying about 38% of the territory), cultivated lands (35%), and natural grasslands and shrublands (23%), with the remaining 4% corresponding to urban and artificial areas. The main forest tree species are *Pinus halepensis*, *Pinus sylvestris* and *Quercus ilex* representing about 20%, 18% and the 16% of the total forested area respectively (Gracia et al. 2000–2004), followed by *Pinus nigra*, *Quercus humilis*, *Quercus suber*, *Pinus pinea*, *Quercus cerrioides*, *Pinus uncinata*, *Fagus sylvatica*, *Quercus faginea*, *Pinus pinaster*, *Abies alba*, *Quercus petraea*, *Castanea sativa*, *Betula pendula*, *Acer opalus* and other species with lower importance.

The analysis was performed in a grid of UTM 10 × 10 km cells, considering only those cells with at least 90% of its area falling within the territory of Catalonia and excluding those that covered no forest area or that had recently suffered forest fires (for which we did not have updated data as for the rest of the study area), resulting in 278 cells. This was an

important aspect to allow linking our results with other ongoing researches and monitoring projects, since numerous biodiversity monitoring schemes in Catalonia and the rest of Spain use the same UTM 10×10 km grid, as is the case of the Spanish Breeding Bird Atlas (Martí and Del Moral 2003), the Spanish Terrestrial Mammal Atlas (Palomo and Gisbert 2002) or the Catalan Breeding Bird Atlas (Estrada et al. 2004). Tree species richness and forest and environmental variables were estimated for each of those 278 UTM 10×10 km cells, as described next.

Tree species richness data

Tree species richness data were obtained from the recent SFM developed within the Third Spanish National Forest Inventory (Ministerio de Medio Ambiente 2006). The SFM has a vector data structure and a scale of 1:50,000, and has been developed in Catalonia from the interpretation of aerial photographs combined with pre-existing maps and field inventory data. The minimum mapping unit is in general 6.25 ha, but lowering to 2.25 ha for forest patches embedded in a non-forest land use matrix. The SFM provides detailed information on each patch, including the cover type, presence and abundance of tree species (only up to the three most abundant species in each patch), the total FCC, and the forest development stage. Tree species richness in each UTM 10×10 km cell was obtained from the SFM by counting all the different species present in all the patches within each cell. The SFM only gathers information on a maximum of three different tree species in each forest patch; therefore, additional and less abundant species that may be present in a particular forest patch were not considered in the analysis. However, the impact and possible bias of this limitation at the patch level is considerably low at the 10×10 km level, since each UTM cell contains a large number of different forest patches (40 on average). As a result, the mean and maximum species richness for the 10×10 km cells were 16 and 34 respectively, and a total of 104 different species were recorded for the entire Catalonia from the SFM, which is consistent with previous data coming from field inventories in Catalonia that estimated about 90 different tree species in 10,644 forest inventory plots (Gracia et al. 2000–2004).

Forest landscape, environmental and spatial variables

Forest landscape structure in each UTM cell was estimated from the SFM considering variables related to both forest composition and configuration. Forest composition variables included total area covered by forests, mean FCC, mean forest development stage, and diversity of FCC, development stages and land cover types (considering the 28 land cover types classified in the SFM for Catalonia). Nine different forest area variables were computed as the area of land with a forest tree canopy cover above different FCC thresholds ranging from 5% to 90%. Forest landscape configuration was quantified through a wide set of metrics related to fragmentation and shape irregularity. The calculated fragmentation metrics were number of patches, edge length, edge density, arithmetic and quadratic mean patch size, patch size standard deviation, and the percentage of core area at 100 and 300 m from forest edge (for a description of these indices see McGarigal and Marks 1995). Shape irregularity or complexity was measured through the perimeter-area ratio, area-weighted perimeter-area ratio, mean shape index, area-weighted mean shape index, elongation index, number of shape characteristic points (SCP), density of SCP (SCP

divided by the total perimeter of forest patches) and the minimum circumscribing circle index (see Moser et al. 2002; Saura and Carballal 2004), all of them computed in the original vector format of the SFM.

Environmental variables included topographic information derived from the official Spanish Digital Elevation Model (DEM) at the resolution of 25 m (Ministerio de Fomento 1999) and climatic information obtained from the Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005). Topographic variables were related to elevation and slope, both summarised as the mean, maximum, minimum, range, standard deviation and aspect diversity in each cell. Climatic variables were mean annual precipitation, mean summer precipitation, mean annual radiation, mean annual temperature, mean temperature of the coldest (January) and the hottest (July) month, mean annual maximum and minimum temperature, mean maximum temperature of the hottest month and mean minimum temperature of the coldest month.

The variables representing diversity within the 10 × 10 km cells (land cover diversity, aspect diversity, FCC diversity, development stage diversity) were all calculated through the Shannon diversity index (see Marrugan 1989): $H' = -\sum p_i \ln p_i$, where p_i is the proportion of each of the categories described in Table 1 for the corresponding variables.

Finally the spatial factors were analysed through the geographic coordinates of the centre of each UTM 10 × 10 km cell and the nine terms of the third-degree polynomial of a trend surface analysis (Legendre 1993). Geographic coordinates were centred and rescaled between -1 and 1.

Data analysis

Prior to the analysis, all the explanatory variables were standardized and some of them discarded because of its high Pearson's correlations with other variables within its group (landscape or environmental factors). When the correlation coefficient between two variables was higher or equal than 0.8, one of them (the one with the lowest correlation with tree species richness) was discarded for subsequent analyses. Regarding the spatial variables, we performed a multiple linear regression (backward stepwise) for tree species richness against the nine terms of the third-degree polynomial of the cell coordinates; only the variables that were significant in that regression were selected for further analyses (see Legendre 1993; Legendre and Legendre 1998). Table 1 shows the landscape, environmental and spatial variables finally selected for subsequent analyses.

We performed a partial linear regression analysis (Legendre and Legendre 1998) to decompose the variation in tree species richness among the three groups of explanatory variables: landscape composition and configuration (L), environmental (E) and spatial variables (S). This resulted in seven different non-overlapping fractions (Fig. 1), apart from the unexplained variation (Bocard et al. 1992):

- (a) pure effect of landscape factors
- (b) pure effect of environmental factors
- (c) pure effect of spatial factors
- (d) the joint effect of landscape and environmental factors
- (e) the joint effect of landscape and spatial factors
- (f) the joint effect of environmental and spatial factors
- (g) the joint effect of the three groups of explanatory variables

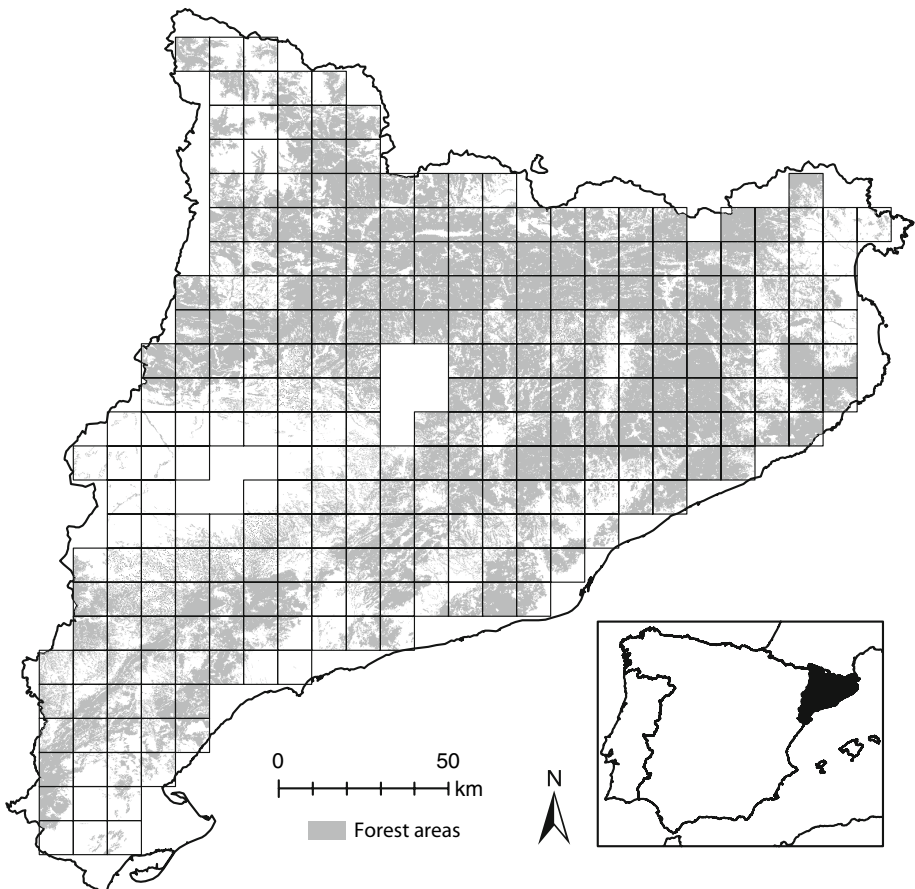
Table 1 Explanatory variables finally considered in the analysis

Abbreviation	Description
<i>Forest landscape</i>	
<i>Composition</i>	
Area	Total area covered by forests, defined as those lands where the forest canopy cover is above 5%.
Mean-FCC	Mean forest canopy cover in the forest lands.
Div-FCC	Forest canopy cover diversity quantified through the Shannon index for five different forest canopy cover classes (5–20%, 20–40%, 40–60%, 60–80%, 80–100%).
Mean-STAGE	Mean forest development stage, computed as the area-weighted average for each forest patch by assigning a numerical value ranging from 1 to 4 to the four different development stages discriminated in the SFM: just regenerated (1), thicket (2), trees with diameter at breast height (DBH) below or equal to 20 cm (3) and trees with DBH > 20 cm (4).
Div-STAGE	Development stage diversity, quantified through the Shannon index for the four categories described above.
Div-COVER	Land cover diversity, quantified through the Shannon index for the 28 cover classes discriminated in the SFM for Catalonia.
<i>Configuration</i>	
<i>Fragmentation</i>	
Num-PATCH	Number of forest patches.
Mean-SIZE	Mean size of the forest patches.
Len-EDGES	Edge Length of the forest patches.
<i>Shape complexity</i>	
MSI	Mean shape index, computed as an arithmetic mean of the shape index of all forest patches, where the shape index is computed as $SI = p/2\sqrt{\pi}\sqrt{a}$ (being p and a the perimeter and the area of the patches, respectively). It attains a minimum value of 1 when patches are circular and increases (with no theoretical upper limit) for more irregular or elongated shapes (see Saura and Carballal 2004).
AW-MSI	Area-weighted mean shape index, similar to MSI but with the patch shape index weighted by the patch area for the average (see Saura and Carballal 2004).
Sum-NSCP	Total number of shape characteristic points, based in the minimum number of points necessary to describe a patch boundary and computed on vector data as the number of vertices of the polygons with a minimum vertex angle of 160° (Moser et al. 2002).
DSCP	Density of shape characteristic points, resulting from dividing Sum-NSCP by the total perimeter of the forest patches.
MCC	Minimum circumscribing circle index, based on the ratio between the area of the patch and the area of the minimum circumscribing circle around the patch. This index attains a minimum value ($MCC = 0$) for circular patches and increases for more elongated and narrow patches, up to a maximum value of $MCC = 1$ (Saura and Carballal 2004).
<i>Environmental</i>	
Mean-PREC	Mean annual precipitation.
Mean-RAD	Mean annual radiation.
Mean-ELEV	Mean elevation.
Div-ASPECT	Aspect diversity, quantified through the Shannon index for the eight aspects defined by the cardinal points.

Table 1 continued

Abbreviation	Description
<i>Spatial</i>	
X	X coordinate of the grid cell centre.
Y	Y coordinate of the grid cell centre.
XY	
X ³	

Tree species richness was first regressed with the whole set of selected variables for the three groups of explanatory variables together (Table 1), which yielded the total explained variation ($a + b + c + d + e + f + g$). Subsequently, regressing tree species richness with each of the explanatory variable groups separately yielded the variation explained by L ($a + d + e + g$), E ($b + d + f + g$) and S ($c + e + f + g$). Finally, three new regressions were conducted to obtain the fractions of variation corresponding to tree

**Fig. 1** Geographic location of the study area showing the 278 UTM 10 × 10 km cells used in the analysis

species richness against each possible pair of groups, that is $L + E$ ($a + b + d + e + f + g$), $L + S$ ($a + c + d + e + f + g$) and $E + S$ ($b + c + d + e + f + g$), from which each of those seven fractions were determined.

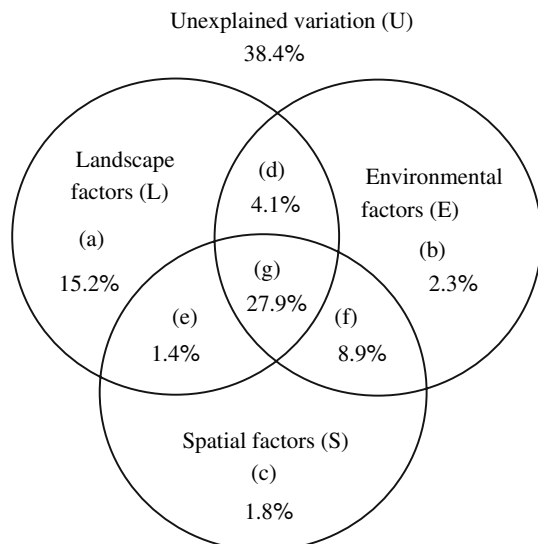
In order to evaluate the relative importance of the two aspects of forest landscape structure (composition and configuration) for tree species richness, we applied the same variation partitioning process considering only these two sets of variables. Additionally, we focused in the landscape variables to evaluate which were more significant and relevant to explain tree species richness at the scale of 10×10 km. This was performed through a multiple linear regression (forward-backward stepwise) for tree species richness against all the forest landscape variables. Finally, we took into account the problem of spatial autocorrelation, since it is an intrinsic property of forest and environmental variables (Legendre 1993, Legendre and Legendre 1998), and lattice datasets are almost always spatially autocorrelated (see Diniz-Filho et al. 2003). It is necessary to control for spatial autocorrelation (Legendre 1993) because it can cause non-independent errors than can invalidate regression assumptions. For this reason, after all the significant forest landscape variables were selected by the regression procedure, we performed a final regression step introducing the significant spatial terms of the third-degree polynomial. After including these significant spatial terms some of the landscape variables initially included in the models were no longer significant, and were dropped from the final landscape explanatory model.

Results and discussion

Variation partitioning

The whole set of variables explained nearly 60% of total tree species richness variation (Fig. 2). The largest fraction resulting from the variation partitioning corresponded to the joint effect of the three types of variables (27.9%, Fig. 2). This indicates that the

Fig. 2 Variation of tree species richness explained by the different fractions



environmental and forest landscape factors influencing species richness are spatially structured and present a considerable degree of covariation, which could be related to the remarkable topographic and climatic gradient in Catalonia, such as the transition of the dry Mediterranean conditions from the south to the Pyrenees in the north, and the east to west continental gradient. Among the pure fractions, forest landscape factors were those that most contributed to explain tree species richness (15.2%), compared to the pure effect of environmental (2.3%) and spatial factors (1.8%), as shown in Fig. 2. The unexplained variation may be due to noise and errors in the available data, to the effect of other variables not included in our analysis (e.g. soil data), or to non-linear relationships between tree species richness and the different variables.

This result highlights the importance of forest landscape variables at the scale of analysis (10×10 km). Although different factors explaining species richness can be found in the literature, altitude and climate are those more commonly highlighted. For example, altitude-related variables were found as the most significant explaining plant species richness by Lobo et al. (2001) at the scale of 50×50 km in the Iberian Peninsula and Balearic Islands. Topography was also found as the main determinant of species richness variation in other studies by Heikkinen (1996) and Bruun et al. (2003) studying vascular plants at scales of 1×1 km and 5×5 km respectively. In other studies like Kivinen et al. (2006) in Finland at 0.25 km^2 , variables related to climate were the major determinant factors of tree species richness variation. However, our results show the relevant role of forest landscape structure to explain forest tree species richness in a region like the Mediterranean where forest landscapes have been greatly managed and exploited for centuries. This suggests that as forest management and human influence modify the forest landscape, the patterns of species richness increasingly diverge from the potential tree species richness determined just by climatic and topographical factors. In these cases, a landscape ecology approach is needed to evaluate how biodiversity is distributed and affected in these human-modified Mediterranean forests, considering the high explanatory power of the landscape factors shown by our results. Certainly, general aspects of forest management according to sustainability rules and biodiversity conservation are well known (see Hunter 1999), especially at the stand level, but little emphasis has been put yet to provide guidelines for an adequate forest management at the landscape scale.

Regarding the other groups of variables, it is noteworthy the low importance of the pure spatial factors (1.8%), considerably lower than in other subject-related studies. Lobo et al. (2001) reported a pure spatial fraction of 6.5% at 50×50 km in the Iberian Peninsula, whereas Kivinen et al. (2006) found a higher value (17.1%) at the 0.5×0.5 km scale in Finland.

The scale at which the analysis is carried out is essential to explore relationships between patterns and ecological processes; the measurement of spatial pattern and heterogeneity is dependent upon the scale at which the measurements are made. We found that landscape factors have a considerable influence in Mediterranean tree species richness. However, our scale of study (10×10 km) may influence the variables that result important (Turner 1989), and multi-scale studies would provide useful additional information in order to evaluate the determinant factors operating at different scales.

Forest landscape analysis

Mean forest canopy cover (Mean-FCC) was the first variable to enter in the forest landscape model, influencing positively on tree species richness (Table 2), and indicating that a

high FCC in the forest landscape is more beneficial for tree species richness than the amount of forest area itself. Landscape composition has also resulted relevant in previous studies, but forest area has been the variable commonly regarded as the one most related to forest tree species richness variation (Pausas et al. 2003; Guirado et al. 2006), and FCC effects on tree species richness have been comparatively much less studied. Our result is in contrast with the negative effect of closed canopies on woody plant species richness found in Catalonia by Terradas et al. (2004), where closed forest tree canopies may be detrimental for other woody species with medium and high light requirements. However, here we only studied forest tree species, and the colonization of open areas with low FCC by forest trees in Catalonia comprises mostly a few pioneer species such as *Pinus halepensis* or some *Quercus* spp. These species quickly colonise the disturbed areas generating largely homogeneous stands. As the forest grows to more developed and closed canopies, it allows the establishment of other tree species in accordance with their ecological requirements (a certain degree of shade, soil moisture, microclimate effect, etc.). This is particularly relevant for management and conservation biodiversity in this region, due to the frequent and recurrent disturbances suffered by forests in Catalonia (forest fires, erosion, etc.), the climatic conditions governing the region (dry and hot summers, frost winters, etc.), and the long-lasting forest management, which results in that forests with a high FCC and an advanced development stage (and the tree species associated to them) are relatively less abundant in some areas. Nevertheless, forest area was the second most relevant variable in the model (after Mean-FCC), remarking the importance of forest area according to the well known species-area relationship (see Huston 1994; Begon et al. 1999).

Land cover diversity (Div-COVER) was positively related to tree species richness (Table 2). In general, it is expected that landscapes with higher spatial heterogeneity contain more species (Begon et al. 1999). In accordance with our results, species richness of vascular plants increased with both land cover diversity and forest area in the Iberian Peninsula and Balearic Islands (Lobo et al. 2001). This highlights the importance of landscape heterogeneity and landscape matrix effects for the conservation of forest biodiversity (Lindenmayer and Franklin 2002).

Several landscape shape irregularity metrics had a significant influence on forest tree species richness (Table 2), with a positive effect for two of the three shape irregularity indices included in the model (MCC and DSCP), which can be explained by two main reasons. On the one hand, narrow and irregular patches have more edge length and favour the number of edge species present in the forest (Forman 1995), as indicated by high values of MCC, which imply elongated and narrow patches (decreasing the compactness). On the other hand, more complex and irregular shapes (higher DSCP values) may indicate a lower

Table 2 Forest landscape regression model for tree species richness

	Non-standardized coefficients		R ²	Standardized coefficients (β)	t	Sig.
	B	Error				
Mean-FCC	2.247	0.350	0.304	0.318	6.416	0.000
Area	2.610	0.339	0.399	0.417	7.702	0.000
Div-COVER	1.620	0.275	0.448	0.256	5.891	0.000
MCC	1.104	0.317	0.454	0.180	3.488	0.001
AW-MSI	-0.697	0.272	0.467	-0.114	-2.561	0.011
DSCP	0.658	0.273	0.471	0.107	2.406	0.017

degree of human influence and more natural and potentially biodiverse landscapes (Moser et al. 2002, Saura and Carballal 2004). In Moser et al. (2002) the number of SCP was found to be a good indicator of plant species richness in rural areas. Saura and Carballal (2004) showed that MCC was the only index perfectly discriminating native and exotic forests patterns in Galicia (NW Spain), and that mixed forests presented more irregular shapes than monospecific ones. These two indices (DSCP and MCC) were also those most significant in our study. The negative effect of AW-MSI on tree species richness was the opposite of that obtained here for MCC and DSCP and as reported in previous studies (e.g. Moser et al. 2002). This may be due to the use of patch area as a weighting factor when computing the landscape mean for this index. Since larger patches tend to present more complex shapes as measured by the shape index (Saura 2002) those landscapes with bigger forest patches will present higher AW-MSI values. Therefore, AW-MSI would be more related to patch size distribution than to shape irregularity itself. In Honnay et al. (2003), the shape index quantified as a non-weighted average (MSI) has been found to be a predictor of total and native plant species diversity, showing again the association between shape irregularity and plant species richness.

In our study fragmentation metrics did not contribute significantly to explain variation in tree species richness. Although some studies suggested that the degree of fragmentation is a main factor explaining patterns in plant species (Hernandez-Stefanoni 2005), other studies with other taxons have concluded that fragmentation is hardly a significant factor at the landscape scale after considering the area effect (McGarigal and McComb 1995; Trzcinski et al. 1999). After applying partial linear regression to our data to decompose variation in tree species richness between forest composition and configuration landscape factors, pure composition effects explained a much greater amount of variation (22.6%), while the pure effect of landscape configuration only represented a 3.8%. The joint effect of both types of landscape variables explained 22.2% of tree species richness variation. This indicates that the configuration metrics are not really providing much new valuable information to explain tree species richness, and that the information they convey is largely correlated with landscape composition variables (forest area). This result is in accordance with Fahrig (2003), who noted that most studies about the effects of landscape structure on ecological processes did find large effects of landscape composition and not of configuration.

Conclusions

Our analysis in the Mediterranean region of Catalonia has shown that landscape structure provides an important contribution to explain tree species richness at the scale of 10×10 km, larger than other environmental (climate and topography) and spatial factors. While climate and altitude may control species richness distribution at broad scales, at finer scales other characteristics related to forest landscape structure may be much more relevant. This is especially true considering the strong and long-lasting human influence on forests in the Mediterranean region. The main factors determining tree species richness were FCC followed by forest area. Landscape configuration had a minor effect compared to landscape composition, and fragmentation metrics did not contribute significantly to explain variation in tree species richness. However, two shape irregularity metrics (minimum circumscribing circle index and density of SCP) were positively related to tree species richness, acting as indicators of the degree of human influence and the edge effects in the forest landscape. Our results highlight the importance of considering landscape

structure characteristics to understand and explain the distribution of forest vegetation diversity, as well as the need of an adequate landscape-level management of the forest ecosystems. Forest harvesting and other management practices should take into account the landscape structure of forests to benefit tree species diversity and its maintenance, for instance by avoiding opening too much the canopy cover. However and considering the spatial-scale dependence of ecological patterns, we recognise that additional research at other spatial scales is needed to provide further insights in this respect.

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