Large-scale determinants of diversity across Spanish forest habitats: accounting for model uncertainty in compositional and structural indicators

E. Martin-Queller[1,2]*, O. Torras[2], I. Alberdi[3], J. Solana[4] and S. Saura[4]

[1] Centre Tecnològic Forestal de Catalunya. Ctra. Sant Llorenç de Morunys, km 2. 25280 Solsona. Spain
[2] Departament d'Enginyeria Agroforestal. ETSEA. University of Lleida.
Avda. Alalce Rovira Roure, 191. 25198 Lleida. Spain
[3] Departamento de Sistemas y Recursos Forestales. CIFOR.INIA. Ctra. A Coruña, km 7,5. 28040 Madrid. Spain
[4] Departamento de Economía y Gestión Forestal. ETSI Montes. Polytechnic University of Madrid.
Ciudad Universitaria, s/n. 28040 Madrid. Spain

Abstract

An integral understanding of forest biodiversity requires the exploration of the many aspects it comprises and of the numerous potential determinants of their distribution. The landscape ecological approach provides a necessary complement to conventional local studies that focus on individual plots or forest ownerships. However, most previous landscape studies used equally-sized cells as units of analysis to identify the factors affecting forest biodiversity distribution. Stratification of the analysis by habitats with a relatively homogeneous forest composition might be more adequate to capture the underlying patterns associated to the formation and development of a particular ensemble of interacting forest species. Here we used a landscape perspective in order to improve our understanding on the influence of large-scale explanatory factors on forest biodiversity indicators in Spanish habitats, covering a wide latitudinal and altitudinal range. We considered six forest biodiversity indicators estimated from more than 30,000 field plots in the Spanish national forest inventory, distributed in 213 forest habitats over 16 Spanish provinces. We explored biodiversity response to various environmental (climate and topography) and landscape configuration (fragmentation and shape complexity) variables through multiple linear regression models (built and assessed through the Akaike Information Criterion). In particular, we took into account the inherent model uncertainty when dealing with a complex and large set of variables, and considered different plausible models and their probability of being the best candidate for the observed data. Our results showed that compositional indicators (species richness and diversity) were mostly explained by environmental factors. Models for structural indicators (standing deadwood and stand complexity) had the worst fits and selection uncertainties, but did show significant associations with some configuration metrics. In general, biodiversity increased in habitats covering wider topographic ranges and comprising forest patches with more complex shapes. Patterns in other relationships varied between indicators (*e.g.* species richness *vs.* diversity), or even were opposed (trees *vs.* shrubs). Our study (1) allowed deepening the understanding of biodiversity patterns in a large set of Spanish forest habitats and (2) highlighted the increasing complexity of identifying common landscape conditions favouring forest biodiversity as the range of analysed biodiversity aspects is widened beyond the more commonly assessed species richness indicators.

Key words: Akaike Information Criterion; landscape ecology; Margalef and Shannon diversity; national forest inventory; snags; habitat spatial configuration.

Resumen

Factores que explican la diversidad de los hábitats forestales españoles a escala de paisaje: incertidumbre en la selección del modelo en indicadores posicionales y estructurales

El estudio integral de la biodiversidad requiere la exploración de sus numerosos componentes y de los diversos factores potencialmente determinantes de su distribución. El enfoque de la ecología y escala de paisaje representa un complemento necesario a los estudios locales centrados en parcelas de inventario o montes individuales. No obstante, la mayoría de los estudios a escala de paisaje han utilizado cuadrículas como unidad de análisis para la identificación de los factores responsables de la distribución de la biodiversidad. La estratificación del territorio por hábitats forestales

con una composición relativamente más homogénea podría ser más adecuada de cara a la identificación de los patrones subyacentes asociados a la formación y desarrollo de un determinado conjunto de especies forestales relacionadas funcionalmente. En este estudio adoptamos una perspectiva de paisaje para profundizar en el conocimiento de la influencia de factores a grandes escalas espaciales sobre la biodiversidad forestal de los hábitats forestales españoles, cubriendo un amplio rango latitudinal y altitudinal. Consideramos seis indicadores de biodiversidad forestal estimados a partir de más de 30.000 parcelas del inventario forestal nacional de España, distribuidas en 213 hábitats forestales y 16 provincias diferentes. Exploramos la respuesta de la biodiversidad frente a diversas variables ambientales (clima y topografía) y de configuración del paisaje (fragmentación y complejidad de formas), a través de modelos de regresión lineal múltiple (creados y evaluados con el Criterio de Información de Akaike). En concreto, tenemos en cuenta la incertidumbre inherente a la selección del mejor modelo al analizar conjuntos de datos complejos, y consideramos diferentes modelos posibles y su probabilidad de ser considerados como el mejor candidato para explicar la variabilidad observada. Nuestros resultados mostraron que los indicadores de composición (riqueza y diversidad de especies) fueron principalmente explicados por los factores ambientales. Los modelos para los indicadores estructurales (madera muerta en pie y complejidad del rodal) tuvieron los peores ajustes e incertidumbres de selección, pero mostraron una asociación significativa con algunos de los índices de configuración. En general, la biodiversidad aumentó en los hábitats que abarcan un mayor rango altitudinal y con teselas de formas más complejas. El resto de patrones en las relaciones variaron entre indicadores (e.g. riqueza *vs.* diversidad de especies), o incluso presentaron tendencias opuestas (árboles *vs.* arbustos). Nuestro estudio permite profundizar en la comprensión de los patrones de biodiversidad a través de un amplio conjunto de hábitats forestales españoles y pone de manifiesto la creciente complejidad y dificultad de identificar un conjunto común de condiciones del paisaje que favorezcan la biodiversidad forestal a medida que se amplía el número de aspectos analizados más allá de los más habitualmente considerados indicadores de riqueza de especies.

Palabras clave: árboles muertos en pie; configuración espacial del hábitat; Criterio de Información de Akaike; diversidad de Margalef y Shannon; ecología del paisaje; inventario forestal nacional.

Introduction

The effects of biodiversity on key ecological processes, such as productivity, stability or nutrient cycling (Loreau *et al.*, 2001; Hooper *et al.*, 2005), have stimulated an increasing effort to comprehend and characterize it (Huston, 1994; Begon *et al.*, 2006). However, given the difficulty of thoroughly measuring and quantifying biodiversity even in a small area, suitable indicators have to be found (Duelli and Obrist, 2003). In the last years, multiple international agreements such as the Ministerial Conference on Protection of Forests in Europe (MCPFE, 2003), or the COST Action E43 (2004-2008) have resulted in a general consensus of the scientific community about some common indicators of forest biodiversity. Biodiversity indicators are frequently classified into three categories (Noss, 1990): compositional, those related to the identity and variety of elements; structural, those related to the physical organization of the elements; and functional, those related to ecological and evolutional processes. The more aspects are considered through these types of indicators, the better the characterisation and monitoring of biodiversity. Species richness and diversity are the most common compositional indicators. Examples of structural indicators, less frequently used, are age evenness, which may indicate the degree of naturalness and complexity in a forest; or the amount of deadwood, which provides nesting, refugia and foraging sites for a variety of species.

Landscape ecology approaches provide a necessary complement to the conventional local approaches in the study of forest biodiversity distribution. Indeed, metrics related to landscape structure can be used as effective, indirect biodiversity indicators (Lindenmayer *et al.,* 2000; Dauber *et al.*, 2003; MCPFE, 2003; Lafortezza *et al.*, 2010). Aspects such as configuration are necessary for a comprehensive assessment of temporal changes in the forest landscape (Ortega *et al.*, 2008). Several studies have evaluated the contribution of configuration indices to explain the distribution of landscape biodiversity. Fragmentation is considered in some cases a major determinant of biodiversity loss (see Fahrig, 2003, for a review). According to Fahrig (2003) the process of fragmentation has to be evaluated separately from habitat loss and is related to several aspects: increase in the number of habitat patches, decrease in the size of the habitat patches, and increase in the isolation of patches. However, the current understanding on the separate explanatory power of each of these aspects in explaining biodiversity patterns is limited (Smith *et al.*, 2009). Some authors have found a significant correlation between shape irregularity indices and plant species richness in various study areas

and scales of analysis (Honnay *et al.*, 1999; Moser *et al.*, 2002; Honnay *et al.*, 2003; Saura and Carballal, 2004; Baessler and Klotz, 2006; Saura *et al.*, 2008; Torras *et al.*, 2008). This association was attributed to the level of human energy input or to patterns derived from ecological edge processes.

Landscape biodiversity patterns are strongly influenced by multiple factors, both biotic and abiotic (see Huston, 1994; Begon *et al.*, 2006). Climatic factors have been shown to be the main explanatory variables of species richness at large scales (see the meta-analysis by Field *et al.*, 2009). Large climatic trends of species richness are mainly explained by the influence of the interaction between energy and water on plant development (O'Brien, 1993). Besides, many studies found that altitude correlates with plant species richness (*e.g.* Rey-Benayas, 1995; Heikkinen and Neuvonen, 1997; Lobo *et al.*, 2001; Bruun *et al.*, 2003). The altitudinal range, as a measure of heterogeneity, has also been demonstrated to be a major determinant of plant diversity (Wohlgemuth, 1998; O'Brien *et al.*, 2000; Rey-Benayas and Scheiner, 2002; Pausas *et al.*, 2003; Vetaas and Ferrer-Castán, 2008). Therefore, underlying environmental drivers need to be considered when analysing forest landscape biodiversity patterns.

Large datasets accurately representing large study areas are not easily obtained. National Forest Inventories (NFIs) are very useful tools for the analysis of large scale biodiversity patterns in this context (Newton and Kapos, 2002). Recently there has been an increased number of studies that benefited from NFI data for these purposes (Lloret *et al.*, 2007; Vilà *et al.*, 2007; García López and Allué Camacho, 2008; Juutinen *et al.*, 2008; Montoya *et al.*, 2008; Gil-Tena *et al.*, 2009; Torras *et al.*, 2009). However, a complex issue is how to scale up the biodiversity data from the plot level (at which the NFI data are gathered) to wider spatial scales where many of the drivers of forest biodiversity operate. Many landscape studies use squared UTM cells as the unit of analysis (*e.g.* Lobo *et al.*, 2001; Torras *et al.*, 2008; Vetas and Ferrer-Castan, 2008). UTM cells are expected to represent relatively homogeneous values of factors with spatial trends at intermediate to large scales or extents, such as climate. However, these units may comprise a variety of forest types (with considerably different biota, management intensity, disturbance history, etc.) and correspond to artificial boundaries that do not match with the physical and ecological boundaries actually influencing the composition of forest communities and that artificially introduce a higher spatial variability in some of the analyzed variables (such as topography, spatial configuration, etc.).

For these reasons, here, instead of focusing of equally-sized cells, we used the less frequently explored habitat level to characterize and analyse the distribution of six forest biodiversity indicators over a large study area of about 150,000 km^2 comprising different Spanish provinces and forest types. We analysed large scale patterns of biodiversity once removed the variability due to those forest types. The average of some of the explanatory factors would be, in that case, more representative of actual causal factors at the habitat level than at the cell level. Specifically, our objectives were (1) to explore which environmental (climatic and topographic) and landscape variables (fragmentation and shape irregularity) better explained their distribution patterns, and (2) to compare the responses of five different biodiversity indicators (compositional and structural) derived from national forest inventory data. We aimed at an improved understanding of the relationships between a large set of biodiversity indicators (larger than those typically considered in previous studies, which have mainly focused on species richness) and the abovementioned explanatory factors, which have less been explored in Mediterranean or Spanish landscapes compared to other regions of the world. Finally, we improved the assessment of these relationships using the information-theoretic approach by Burnham and Anderson (2002). Most studies evaluate the strength and significance of the relationships with biodiversity according to the full model, *i.e.* that single best model including all the explanatory variables eventually selected according to statistical criteria. However, regression coefficient estimates based on a single best model do not take into account model selection uncertainty and therefore ignore the fact that the «best» model is often highly variable depending on the sample data set. The misestimation of the true explanatory power of a particular variable that may result from the widespread use of a single statistical model is thus avoided in this study (Stephens *et al.*, 2005).

Methods

Study area and forest habitats

Sixteen Spanish provinces —belonging to the regions of Galicia, Asturias, Cantabria, Navarra, Catalonia, La Rioja, Madrid, Extremadura and Murcia— were selec-
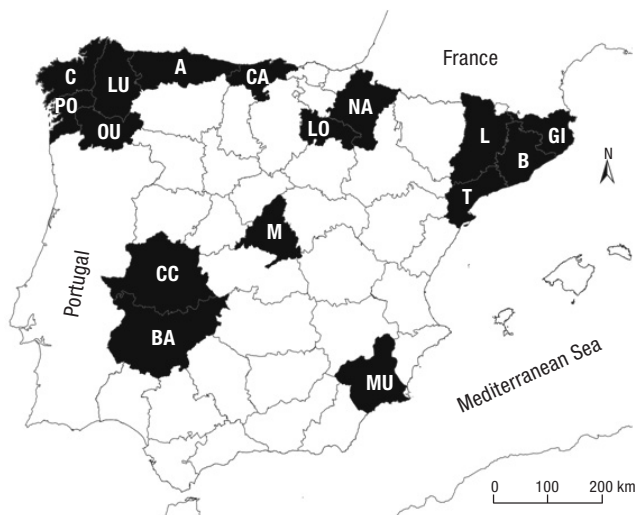
Figure 1. Spanish provinces considered in the analysis (shown in black). See Table 1 for the full province names.

ted as the study area (Fig. 1). These were the provinces where the 3SNFI was already fully completed when the study was started. The study area covered a large part of the Spanish latitudinal and altitudinal range. While most of the study area falls mainly within the Mediterranean region, approximately a third of the region belongs to the Atlantic bioclimatic region (North-West), and the higher mountains correspond to the Alpine region.

In order to avoid the potentially confounding factor of habitat heterogeneity, we stratified data by forest habitats. A total of 238 different forest habitat types were initially differentiated in the study area from the information in the Spanish Forest Map at a 1:50,000 scale (SFM). The SFM was developed within the Third Spanish National Forest Inventory (3SNFI) (Ministerio de Medio Ambiente, 1997-2007). The SFM has a vector data structure and a minimum mapping unit of 2.25 ha. It has been developed from the interpretation of aerial photographs combined with pre-existing maps and field inventory data. Forest habitats were defined attending to the dominant tree species and its abundance, the stand development stage and the forest canopy cover. Thereby, variability within these units of analysis was reduced for these variables. Other environmental factors, such as climate or topography, can still show a wide range of variation depending on the ecological requirements of the dominant tree species, but still will correspond to those conditions that are suitable for the development of a particular forest habitat. In addition, the division of habitats according to the province in which they were present, as required by the design of the

SNFI and SFM, allowed a decrease of environmental variability within habitats (*i.e. Quercus ilex* forests in the province of Cantabria and *Q. ilex* forests in the province of Murcia were considered as two different habitat types). The definition of forest here includes all areas with forest tree canopy cover ranging from 5 to 100%, as defined in the SFM.

Riparian forests were excluded from this analysis, as their configuration characteristics are strongly governed by hydrogeomorphic processes not considered in this study (Rex and Malanson, 1990). We also excluded *dehesas*, which are scattered tree open woodlands typical of Spanish extensive farmlands. The spatial and biodiversity patterns of these are agroforestry systems are determined by a particularly high degree of human influence. Processes occurring in *dehesas* are outside the scope and the set of variables considered in this study. Thus, a final set of 213 forest habitat types was considered for subsequent analyses (Table 1). Forest habitats with dominance of *Quercus ilex*, *Pinus halepensis*, *P. pinaster*, *P. sylvestris*, *Eucaliptus globulus* or *Fagus sylvatica* are the most abundant in the study area (Table 1). The range of environmental conditions represented by the analysed forest habitats is considerably wide, with mean altitude ranging from 122 to 1,951 m, mean annual precipitation from 353 to 1,936 mm, and mean annual temperature from 5.7 to 15.9°C.

Forest biodiversity indicators

Forest biodiversity indicators for each of the analysed habitats were obtained from a total of 30,929 inventory plots in the 3SNFI (Ministerio de Medio Ambiente, 1997-2007). Plots in the 3SNFI are located systematically in the intersections of the 1 km × 1 km UTM grid that fall inside forests and other woodlands. The average sampling intensity is of one plot per 1 km² of land. The plots are circular and their size depends on the tree diameter at breast height (DBH), ranging from a plot radius of 5 m for trees with DBH between 75 and 125 mm up to a maximum radius of 25 m for trees with DBH of at least 425 mm.

We considered four compositional and two structural biodiversity indicators from the information gathered in the 3SNFI: tree species richness, tree species diversity (quantified through both Margalef and Shannon indices), shrub species richness, percentage of uneven-aged stands and snag abundance (Table 2). Plant or tree

Table 1. Dominant tree species in the most abundant forest habitats in each province (corresponding to those occupying nearly half of the forest area in the province)

Province	Dominant forest tree species
Asturias (A)	*Castanea sativa, Fagus sylvatica, Eucalyptus globulus*
Cantabria (CA)	*Eucalyptus globulus, Fagus sylvatica, Quercus petraea, Quercus robur*
Barcelona (B)	*Pinus halepensis, Pinus sylvestris, Quercus ilex*
Girona (GI)	*Quercus ilex, Quercus suber, Pinus sylvestris, Pinus halepensis*
Lleida (L)	*Pinus sylvestris, Quercus ilex, Pinus nigra, Pinus uncinata*
Tarragona (T)	*Pinus halepensis*
Badajoz (BA)	*Quercus ilex, Quecus suber*
Cáceres (CC)	*Quercus ilex, Quercus suber, Quercus pyrenaica*
A Coruña (C)	*Eucalyptus globulus, Pinus pinaster*
Lugo (LU)	*Eucalyptus globulus, Pinus radiata, Quercus robur, Pinus pinaster*
Ourense (OU)	*Pinus pinaster, Quercus pyrenaica*
Pontevedra (PO)	*Eucalyptus globulus, Pinus pinaster*
La Rioja (LO)	*Quercus pyrenaica, Fagus sylvatica, Pinus sylvestris*
Madrid (M)	*Quercus ilex, Pinus sylvestris, Quercus pyrenaica*
Murcia (MU)	*Pinus halepensis*
Navarra (NA)	*Fagus sylvatica, Pinus sylvestris, Pinus halepensis*

species composition, forest (age) structure and deadwood are accepted indicators of forest biodiversity (MCPFE, 2003; COST E43, 2004-2008). Other important indicators, such as additional deadwood types (apart from standing dead stems) and decay classes, were not inventoried in the 3SNFI. Although for simplicity we will refer to shrub species richness throughout the manuscript, it should be noted that this indicator, as measured in the 3SNFI, is not a strict estimator of the total number of shrub species because it is based on a predefined list of 169 taxons. The inclusion of a certain plant in the list at the level of species or genus depends on its abundance in the Iberian Peninsula: most frequent species that can be easily identified are determined at the species level, whereas the rest of shrubs are grouped at the genus level.

Landscape and environmental variables

Initially we considered 22 explanatory variables as potential candidates to explain the distribution of the forest biodiversity indicators at the habitat level. The following fourteen (computed through the SFM) were landscape structure variables: total forest area, number of forest patches, mean size of the forest patches, maximum size of the forest patches, percentage of core area at 100 and 300 m from forest edge, patch cohesion index, mean distance to the nearest neighbour habitat patch, edge length of the forest patches, mean shape index, area weighted mean shape index, density of shape

characteristic points, elongation index, and minimum circumscribing circle index. The remaining eight independent variables were related to climate or topography: mean, maximum, minimum, range and standard deviation of elevation, mean annual precipitation, mean annual radiation and mean annual temperature.

To avoid multicollinearity problems, when the Pearson correlation coefficient between two of the above variables was higher or equal than 0.6 one of them was discarded for subsequent analyses. The selection of the final explanatory variables took into account that each of the following categories of landscape or environmental factors should be represented by at least one variable: fragmentation, shape irregularity, water-energy availability (productivity), altitudinal gradient, and heterogeneity resulting from topography. Each of these categories has, according to literature, a distinctive contribution to relevant processes that affect biodiversity (see Introduction). In addition, in the case that two highly correlated metrics fell in the same category, selection was based on metric simplicity and therefore easier interpretation of the results. The eight independent variables finally selected for subsequent analyses are described in Table 2.

The four landscape configuration metrics were computed for all forest habitat types using the SFM. We considered that the spatial resolution of this map was enough for the goals of our study (Díaz-Varela *et al.*, 2009). The information source for the topographic variables was the official Spanish Digital Elevation Model (DEM) at a resolution of 25 m (Ministerio de

Table 2. Description of the analysed forest biodiversity indicators and the explanatory variables finally considered in the analysis. Categories represented by each explanatory variable are shown in italics

Category	Abbreviation	Description
		Biodiversity indicators
Forest composition	Tree species richness	Total number of different tree species found in all the plots in the habitat, included the regeneration strata.
Forest composition	Tree species diversity	Calculated through the Margalef and Shannon diversity indices, based on the proportion of basal area (m^2/ha) of each species with respect to the total basal area in the plot, and averaged at the habitat level.
Forest structure	% uneven-aged stands	Percentage of plots with uneven-aged stands (as a measure of stand structure complexity). Uneven-aged stands are defined in the SNFI as those in which stems are distributed in at least three different age classes (with at least 10% of the stems in each of them).
Forest structure	Snag abundance	Amount of standing dead wood (number of stems per ha).
Forest composition	Shrub species richness	Total number of different shrub species found in all the habitat plots (based on a taxon list, see methods).
		Explanatory variables
	Configuration	
Fragmentation	Mean-SIZE	Mean size (area) of the forest patches in the habitat.
Fragmentation	MNND	Mean nearest neighbour distance (arithmetic mean of the distance between each habitat patch and the nearest patch belonging to the same forest habitat).
Shape irregularity	DSCP	Density of shape characteristic points. The total number of shape characteristic points is 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). The density results from dividing the sum of NSCP in the habitat by the total perimeter of the forest patches (Saura and Carballal, 2004).
Shape irregularity	MCCI	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).
	Environmental	
Altitudinal gradient	Mean-ELEV	Mean elevation of the forest habitat.
Heterogeneity	Sd-ELEV	Standard deviation of elevation of the forest habitat.
Water availability	Mean-PREC	Mean total annual precipitation in the forest habitat.
Energy availability	Mean-RAD	Mean annual solar radiation in the forest habitat.

Fomento, 1999). Climatic data were obtained from the Climatic Atlas of the Iberian Peninsula at a resolution of 200 m (Ninyerola *et al.*, 2005).

Data analysis

We performed multiple linear regression analyses, taking biodiversity indicators as dependent variables and configuration and environmental data as explanatory variables. Different sampling efforts are expected to influence the value of the indicators in each forest habitat. To control this, simple linear regressions of each biodiversity indicator against the total number of plots per habitat were performed. The residuals resulting from these regressions were used as the final dependent variables in the models. By controlling the sampling effort, the effect of the amount of habitat on

each biodiversity indicator can be assumed to be removed, given the intensive and systematic sampling design of the SNFI. Dependent variables were previously transformed ($\sqrt{x}$, *ln*x and x^2) to meet parametric assumptions.

The selection of the best regression model (or set of models) for each biodiversity indicator was based on the Akaike Information Criterion, correcting for sample size (AICc) (Burnham and Anderson, 2002). We estimated the AICc for all the possible combinations of the eight explanatory variables: 255 possible models for each indicator (2^8 minus the model with an intercept only). The best model had the lowest AICc score, and each model was compared to it in terms of the difference in the AICc value (Δi). Models for which $\Delta i < 2$ were selected, as they were considered to have substantial support and to be reasonable models for the data (Burnham and Anderson, 2002). Akaike weights (w_i) provide a relative importance of evidence for each model, and can be interpreted as the probability that a particular model is the best for the observed data, given the candidate set of models (Burnham and Anderson, 2002).

The same analysis, based on the AICc values and Akaike weights, was performed considering only the four landscape explanatory variables (landscape models), and considering only the four environmental explanatory variables (environmental models). Thus, two sets of 15 (2^4-1) candidate landscape and environmental models, respectively, were evaluated for each biodiversity indicator.

The relative importance of each explanatory variable was assessed using all the set of models considered, instead of a single model, as proposed by Burnham and Anderson (2002). For each biodiversity indicator, the sum of Akaike weights across all the models where the considered explanatory variable occurred was calculated; the larger this sum is, the more important that variable is, compared to the other variables. Regression parameters were obtained from the average of their values on the subset of best models (those models with $\Delta_i < 2$ for each indicator) weighted by the Akaike weights (w_i).

Results

Models performance

Global models

The ranking of the resulting best global models (comprising both environmental and landscape explanatory variables) for the six biodiversity indicators was almost similar according to R^2 and Akaike weights criteria (Table 4). The highest amount of variance was explained for the shrub species richness, with only two models with substantial empirical support to be the best ones ($\Delta i < 2$) (Table 3). Tree species richness and diversity quantified through the Margalef index had also relatively little uncertainty in model selection, with w_i of the best model above 0.2 and 40% and 33% of total explained variance, respectively (Table 3). The uncertainty of the models increased in the case of Shannon diversity of tree species, existing seven to nine models with substantial empirical support to be the best ones, the best one explaining about 30% of the variance (Table 3). Finally, the worst fits and greatest model uncertainties were found for the percentage of uneven-aged stands and snag abundance models (Table 3).

Table 3. Corrected coefficient of determination (R^2) and Akaike weight (w_i) of the best global model (considering both environmental and landscape explanatory variables), environmental model and landscape model for the six biodiversity indicators studied. The number of models with $\Delta_i < 2$ is also indicated

	Global model			Environmental model			Landscape model		
	R^2	w_i	Models $\Delta_i < 2$	R^2	w_i	Models $\Delta_i < 2$	R^2	w_i	Models $\Delta_i < 2$
Tree species richness	0.32	0.20	3	0.19	0.24	6	0.09	0.28	4
Tree species diversity (Margalef index)	0.40	0.32	3	0.33	0.57	2	0.008	0.20	4
Tree species diversity (Shannon index)	0.32	0.11	9	0.30	0.47	2	0.04	0.25	4
% uneven-aged stands	0.19	0.04	24	0.006	0.15	8	0.16	0.48	2
Snag abundance	0.08	0.05	13	0.021	0.19	5	0.06	0.25	4
Shrub species richness	0.50	0.45	2	0.46	0.87	1	0.17	0.38	2

Table 4. Ranking of the explanatory variables according to their relative importance as predictors for the six biodiversity indicators considered. The relative importance was estimated considering the weight evidence (w_i) of the models where the considered explanatory variable appeared

Tree species richness		Tree species diversity (Margalef index)		Tree species diversity (Shannon index)	
DSCP	(1.00)	Sd-ELEV	(1.00)	Sd-ELEV	(1.00)
Sd-ELEV	(1.00)	Mean-PREC	(1.00)	Mean-ELEV	(0.98)
Mean-PREC	(1.00)	DSCP	(1.00)	MNND	(0.90)
MPS	(0.87)	MNND	(0.97)	Mean-PREC	(0.86)
Mean-ELEV	(0.77)	Mean-RAD	(0.93)	Mean-RAD	(0.74)
MNND	(0.74)	MPS	(0.77)	MPS	(0.40)
MCCI	(0.64)	MCCI	(0.68)	DSCP	(0.39)
Mean-RAD	(0.39)	Mean-ELEV	(0.61)	MCCI	(0.38)

% uneven-aged stands		Snag abundance		Shrub species richness	
MCCI	(1.00)	MNND	(0.95)	Mean-PREC	(1.00)
MPS	(1.00)	DSCP	(0.94)	Mean-ELEV	(1.00)
Sd-ELEV	(0.65)	Sd-ELEV	(0.70)	Sd-ELEV	(1.00)
Mean-RAD	(0.53)	MCCI	(0.56)	MPS	(0.99)
Mean-PREC	(0.53)	MPS	(0.44)	DSCP	(0.97)
Mean-ELEV	(0.44)	Mean-RAD	(0.44)	Mean-RAD	(0.92)
MNND	(0.41)	Mean-PREC	(0.36)	MCCI	(0.32)
DSCP	(0.39)	Mean-ELEV	(0.36)	MNND	(0.26)

Environmental and landscape models

In general, environmental models performed better than those using only landscape variables, both in terms of explained variance and model uncertainty (Table 3). Even so, the contrary occurred for the uneven-aged stands and snag abundance. It is noteworthy the case of shrub species richness, where a single environmental model had a very high probability of being the best ($w_i = 0.87$), with a $R^2 = 0.46$ (Table 3).

The role of the explanatory variables

The density of shape characteristic points (DSCP) was highly associated to all the compositional indicators except the Shannon index, and to the snag abundance (Table 4). According to these indicators, higher biodiversity can be found in forest habitats with more complex patches' boundaries (Table 5). The minimum circumscribing circle index (MCCI) and mean patch size (Mean-SIZE) were also positively associated to the percentage of uneven-aged stands (Tables 4 and 5).

The standard deviation of elevation (Sd-ELEV) was one of the most remarkable explanatory variables

for all the indicators related to species richness and diversity (Table 4), with positive relationships (Table 5). Mean total annual precipitation (Mean-PREC) was an important factor for the same indicators, except for the case of tree species diversity as quantified through the Shannon index (Table 4). However, the effect of Mean-PREC on tree species indicators was opposite in sign to that for the shrub species indicator (Table 5). Forest habitats in more humid regions tended to have higher levels of tree species richness and Margalef diversity but lower shrub species richness.

Mean elevation (Mean-ELEV) was a relevant factor for the shrub species richness, and the tree species Shannon diversity (Table 4). Both biodiversity indicators tended to increase in habitat forests distributed mainly in lowlands (Table 5). Mean radiation had a minor role in the models compared to other explanatory variables (Table 4).

Mean-SIZE was especially relevant in the shrub model, where a greater size of forest patches favoured shrub species richness (Tables 4 and 5). As for the mean distance to the nearest habitat patch, it was a relative important correlate for tree species diversity (Margalef) and snag abundance (Table 4), in all the cases showing a positive relationship (Table 5).

Table 5. Average partial regression coefficients based on the subsets of models with $\Delta_i < 2$ for each indicator and on the Akaike weights. R^2 of the best model and average R^2 for the subset of models with $\Delta_i < 2$ are reported. K is the number of independent variables appearing in the best model for each biodiversity indicator

	Tree species richness	Tree species diversity (Margalef index)	Tree species diversity (Shannon index)	Uneven-aged stands (%)	Snag abundance	Shrub species richness
MPS	0.16	0.13	–0.07	0.31	0.09	0.18
MNND	0.12	0.17	0.16	0.08	0.19	—
DSCP	0.44	0.28	0.09	0.09	0.21	0.18
MCCI	0.12	0.12	0.07	0.36	–0.13	0.04
Mean-ELEV	–0.15	–0.13	–0.25	–0.12	0.06	–0.42
Sd-ELEV	0.37	0.38	0.50	–0.13	0.15	0.30
Mean-PREC	0.36	0.47	0.18	0.13	0.08	–0.45
Mean-RAD	–0.08	–0.18	–0.14	–0.13	–0.09	0.16
R^2	0.328	0.403	0.316	0.187	0.077	0.495
Average R^2	0.326	0.398	0.316	0.178	0.076	0.495
K	7	8	5	6	4	6

Discussion

Can environmental and landscape variables explain the distribution of the biodiversity indicators in the Spanish forest habitats?

The amount of variation of the biodiversity indicators explained by the global models was moderate, with a maximum of 49.5% for shrub species richness (Table 3). These percentages of explained variance can be considered, however, relatively high for some indicators given the wide scale and range of environmental conditions considered in this analysis. For example, in similar studies the maximum percentages of explained variation in species richness estimated was 65% (Lobo *et al.*, 2001), 62% (Torras *et al.*, 2008), or 24% (Rey-Benayas and Scheiner, 2002), although caution in the comparison of these percentages is needed given the different scales of study and data stratification.

The two groups of indicators, compositional and structural, presented clearly different tendencies. In the case of the compositional indicators, despite the stratification of the data by forest habitats rather than cells, environmental models still explained higher variance and had more acceptable selection uncertainty. The global models for the forest structure variables (snag abundance and percentage of uneven-aged stands) were unsatisfactory. These indicators are probably affected by factors acting at more local scales that vary within the habitat (*e.g.* forestry practices applied at the

stand level). Interestingly, our results at the habitat level emphasize the role of configuration indices for structural indicators (especially for the percentage of uneven-aged stands), rather than the environmental variables.

The two diversity indices used in this study for the tree stratum (Margalef and Shannon indices) performed quite differently. Global and environmental models performed better for the Margalef index than for the Shannon index. Actually, Margalef index followed the tendency of the rest of indicators related to vegetation composition, both tree and shrub species richness. By contrast, important factors found for these biodiversity indicators, such as the Mean-PREC or the shape complexity (DSCP), were not relevant in Shannon diversity models. The reason may be the higher bias of the Margalef index towards species richness (*i.e.* it is more affected by rare species), while the Shannon index is biased towards species dominance (*i.e.* it is more affected by changes in the abundance of the most common species) (Magurran, 1989). This is supported by the Pearson correlation coefficients (r) between biodiversity indicators, as the Margalef index was more closely related to tree species richness (with $r = 0.870$) than to the Shannon index ($r = 0.640$). The results of this study suggest that evenness on tree species abundance is more difficultly modelled, and is barely affected by landscape configuration metrics related to shape complexity or fragmentation, or by environmental variables such as Mean-PREC that did have a prominent effect on tree species richness.

Responses of forest biodiversity indicators to environmental variables

Since forest habitats were defined here by the realised ecological niche of a particular dominant tree species, higher ecological plasticity (*e.g.* tree species adapted to wide altitudinal ranges) resulted in an increased heterogeneity within the habitat. According to results, in general those habitats with higher topographic complexity were remarkably associated to higher woody plant diversity. This factor has been reported to remarkably influence diversity in other studies carried out in the Iberian Peninsula (Lobo *et al.*, 2001; Rey-Benayas and Scheiner, 2002; Pausas *et al.*, 2003; Moreno-Saiz and Lobo, 2008; Vetaas and Ferrer-Castán, 2008). In our study, high standard deviations of the elevation in a particular type of forest habitat indicate two characteristics on its distribution (1) it can be found in mountainous, and thus topographically complex, regions; and/or (2) it extends in a wide altitudinal range, including elevations from the see level up to 2000 m. In both cases, the inclusion in the models of heterogeneity induced by topography corrected for the unrealistic assumption that average climate values were uniform in the large grid cells or habitat types (O'Brien *et al.*, 2000). In the first case, mountains would also favour diversity through a higher surface area, bedrocks heterogeneity and availability of refugia during the last glacial period (Vetaas and Ferrer-Castán, 2008). The second characteristic would influence indirectly biodiversity through heterogeneity of other environmental, biologic or human variables not considered here. It should be noted that especially shrub species richness, but also tree Shannon diversity, were found to decrease with mean habitat elevation. This suggests that habitats covering a larger variety of environmental conditions but not restricted to the upper mountainous regions had more shrub species and diversity of trees. These results contrast with previous research in the Iberian Peninsula where the higher number of vascular plant or fern species was found in mountainous areas (Castro-Parga *et al.*, 1996; Lobo *et al.*, 2001; Moreno-Saiz and Lobo, 2008); this can probably be attributed to several reasons. One could be the focus on different groups of plant species. Most species in upper mountain areas are non woody phanerogams species, which are not considered in this study. Pausas (1994) also showed a negative relationship of understorey woody species richness with altitude in Pyrenean coniferous forests. To add to such discussion,

more than a third of the study area is located within the Atlantic and Alpine bioclimatic regions, whereas in the studies cited above the Mediterranean region is comparatively more represented. This implies that productivity limitation induced by hydric stress at lower altitudes, one of the arguments given in previous studies for the increased species richness at higher elevations (Lobo *et al.*, 2001), might not be so applicable here. Lobo *et al.* (2001) found that coastal cells with lower mean altitude presented an increase, although less pronounced, in plant species richness; ocean influence might determine the presence of species not found in other areas of the habitat range.

Water and energy variables have been shown to play a determinant role explaining biogeographical patterns of plant species richness (O'Brien, 1993, 1998; Field *et al.*, 2005), agreeing with our results. However, weak correlations were found between water-related variables and plant species richness in previous analysis in the Iberian Peninsula (Lobo *et al.*, 2001; Vetaas and Ferrer-Castán, 2008). Again, it should be noted that rigorous comparisons between studies in the literature are difficult, given the wide variety of variables used as surrogates of water availability (*e.g.* summer precipitation, annual evapotranspiration, soil moisture). For example, Pausas (1994) found no significant relationship between plant species richness and Mean-PREC in Catalonia (cells of 10×10 km), whereas the Thornthwaite moisture index and aspect, also characterising water availability, showed a positive relationship. Here we found that Mean-PREC was a remarkable explanatory variable of almost all biodiversity indicators characterising vegetation composition (except Shannon diversity index), while radiation had a negligible role in most of the models. This fits with Whittaker *et al.* (2007), who concluded that plant richness approximately south of 46° N (which covers all the study area here analysed) should be more related to water variables than to energy. Higher tree species richness and diversity (Margalef index) is expected in forest habitats within the Atlantic bioclimatic region of the study area, where Mean-PREC is greater than in other Mediterranean regions. This phenomenon has also been found for tree species in other regions (Currie and Paquin, 1987; Leathwick *et al.*, 1998). Interestingly, the contrary occurred in the shrub layer. Indeed, the number of shrub species had a strong negative correlation with water availability, assessed by Mean-PREC in the forest habitat. This may be interpreted as a consequence of tree biomass accumulation in humid forest habitats. The increase in

Mean-PREC determines greater productivity leading to canopy closure. As a consequence of the decline in light penetration in the forest understorey, the lower availability of resources may limit the number of shrub species that can tolerate these conditions.

Responses of forest biodiversity indicators to landscape configuration variables

Although environmental variables had a more relevant role in the models, some configuration metrics had a remarkable association with the analysed biodiversity indicators. The shape irregularity metrics resulted much more relevant than the fragmentation ones for explaining the distribution of the indicators of forest biodiversity, agreeing with Saura *et al.* (2008). Among these shape metrics, the DSCP clearly stood out as a good correlate of almost all the indicators considered in the analysis. In some cases the DSCP was even more relevant for explaining forest biodiversity than other environmental variables. More complex shapes of forest patches at the landscape scale harboured greater biodiversity in all cases. Similar results were observed in other studies for different groups of plants, and in a moderate variety of scales, regions and analytical units (Moser *et al.*, 2002; Saura and Carballal, 2004; Baessler and Klotz, 2006; Saura *et al.*, 2008; Torras *et al.*, 2008). It has been suggested that simpler shapes of forest patches indicate higher degree of land use intensity and hence potentially less biodiverse habitats (Moser *et al.*, 2002; Saura and Carballal, 2004).

The other shape metric considered in the analysis, MCCI, differentiates another characteristic of patch shape: elongation (Saura and Carballal, 2004; Saura *et al.*, 2008). Forest habitats with more elongated patches tended to have more structurally complex stands (as measured by the percentage of uneven-aged stands). This agrees with the results of Saura and Carballal (2004) who found that in Galicia the MCCI was the index that better discriminated between native and exotic forest patterns (typically even-aged plantation forests). This shape elongation metric was significantly correlated with tree species richness in a landscape analysis in Catalonia (NE Spain) by Torras *et al.* (2008), but this was not verified here. Stand structure complexity was also positively associated with patch size in the habitat; more homogeneous and simpler forest structures resulting from forest management and other human-induced disturbances are actually characterised

by a higher fragmentation, accessibility and spatial mixture with other agricultural cover types.

The Mean-SIZE is not generally independent from habitat amount, as habitats that cover larger areas tend to present patches of bigger sizes (*e.g.* Fernández-Juricic, 2000). If this was not statistically controlled, the role of fragmentation in the models might have been overestimated, given that the habitat loss is the primary driver of the loss of biodiversity and should be evaluated independently from fragmentation (Fahrig, 2003). According to our results, the relative importance of habitat fragmentation per se, despite a few exceptions, was lower in most cases than shape complexity, precipitation or the standard deviation of slopes.

Finally, Honnay *et al.* (1999) found that many small forest patches contain more plant species than one large patch of the same total area. The authors concluded that this finding could be the result of the probability of higher inter-patch diversity in more dispersed habitat patterns, which would enhance biodiversity. Our analysis also suggests that the potential negative effects of isolation (higher distances to the nearest patch) in terms of tree species diversity are less important than the benefits of covering as much as possible different physical environments. In the case of the snags, the processes that explain their positive association with MNND are less evident and further studies are needed.

Limitations and final remarks

The present paper deepens the understanding of the patterns of forest biodiversity in a wide range of Spanish habitats and provides useful considerations about the indicators included in the 3SNFI. The stratification of the analysis by forest habitat types still highlighted the importance of climatic and topographic factors as determinants of forest biodiversity distribution. Nonetheless, this approach conveys a different perspective, focused on functional aspects and community composition rather than on space, which complements and provides additional insights compared to other studies using a cell grid approach. Finally, when widening the range of aspects of biodiversity considered (from the more widely explored species richness indicators), identification of the landscape conditions favouring forest biodiversity becomes increasingly complex. In our study, some habitat conditions improved some particular aspects of biodiversity but not others (*e.g.*

species richness *vs.* diversity), or even produced different responses according to the indicator considered (*e.g.* trees *vs.* shrubs, or compositional vs. structural). In the recently started forth SNFI the number and quality of the assessed biodiversity indicators has already been increased compared to the 3NFI; for example, indicators related to the herb layer and other deadwood types (apart from standing dead stems) and decay classes are now considered. This will allow improving and widening these analyses to a broader set of indicators within a few years, as well as evaluating if more consistent trends on the determinants of biodiversity in Spanish forest landscapes emerge as a result of the improved detail and quality of the related data gathering in the filed plots.

We also showed that deriving conclusions on biodiversity determinants from a single best model might produce misleading conclusions particularly when large and complex data sets are explored. By basing our results in a set of plausible models, we were able to take into account uncertainty in the selection of the best combination of explanatory variables and provide a potentially less biased picture of the analysed relationships. We are however aware that even the information-theoretic approach here applied assumes a priori selection of suitable predictor variables to build a set of candidate models. Other variables not included in this study might also be significant predictors of forest biodiversity patterns in the Iberian Peninsula (*e.g.* forest management, continentality) and further studies considering them may provide a more comprehensive assessment at a variety of spatial scales and forestry contexts.

Acknowledgements

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