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Relating landscape structure, environment and management to biodiversity indicators estimated from forest inventory data in Catalonia (NE Spain)

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Abstract

There is an increasing need to develop efficient methods for characterising and monitoring forest biodiversity. A landscape scale approach and assessment can provide complementary and valuable information in this respect, by considering patterns and processes that operate at broad scales and influence different aspects of forest biodiversity. Here we analysed the relationships between six forest biodiversity indicators (related to the tree and shrub layers and estimated from a large set of field plots from the Third Spanish National Forest Inventory) and landscape structure, environmental and management variables at a 10 x 10 km scale in the region of Catalonia (NE Spain) through the variation partitioning method. The tree layer indicators were those most predictable from the set of explanatory variables considered, and up to 77.2 % of total variation was explained for tree species richness. Landscape variables were much more relevant to explain biodiversity patterns than environmental and spatial factors, and landscape composition outperformed the predictive capacity of configuration metrics. Management had a weak but positive effect on the tree layer indicators, while the amount of early successional forest was negatively associated to the tree layer indicators but positively to those of the shrub stratum. Our results highlight the need to (1) concentrate field sampling efforts in those indicators that are less predictable from the landscape scale, such as those related to rare species with a high conservation value, and to (2) incorporate landscape structure variables for forest biodiversity assessments in the Mediterranean, where a landscape management approach may be particularly suited to allow the adaptation of forest biodiversity to the ongoing landscape dynamics related to broad-scale processes such as rural land abandonment or climate change.

Key words: forest biodiversity indicators, landscape configuration metrics, silvicultural treatments, variation partitioning.

Resumen

Efectos de la estructura del paisaje, variables ambientales, y gestión forestal en indicadores de biodiversidad estimados a partir de parcelas de inventario forestal en Cataluña (NE España)

Dentro de la creciente necesidad de desarrollar métodos eficientes para caracterizar y monitorizar la biodiversidad forestal, una perspectiva de paisaje puede proporcionar información valiosa y complementaria al considerar patrones y procesos que operan en escalas amplias y que influyen en diferentes aspectos de la biodiversidad de nuestros bosques. Aquí se analizan las relaciones entre seis indicadores de biodiversidad forestal (relacionados con el estrato arbóreo y arbustivo y estimados a partir de un amplio conjunto de parcelas de campo del Tercer Inventario Forestal Nacional) y variables de estructura del paisaje, ambientales y de gestión a una escala de 10 x 10 km en Cataluña (NE España) mediante el método de partición de la variación. Los indicadores del estrato arbóreo resultaron ser los más predecibles mediante el conjunto de variables explicativas consideradas, con un máximo de un 77.2 % de la variación total explicada para la riqueza de especies arbóreas. Las variables del paisaje fueron más relevantes para explicar los patrones de biodiversidad que los factores ambientales y espaciales, y la composición del paisaje presentó mayor capacidad predictiva que los índices de configuración. La gestión

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tuvo un efecto débil aunque positivo sobre los indicadores del estrato arbóreo, mientras que la cantidad de bosque en los primeros estados de la sucesión estuvo negativamente asociada con los indicadores del estrato arbóreo y positivamente con los del arbustivo. Los resultados subrayan la necesidad de concentrar esfuerzos de muestreo en los indicadores menos predecibles a escala de paisaje, tales como los relacionados con las especies raras con un elevado valor de conservación, así como la necesidad de incorporar variables de la estructura del paisaje para la evaluación de la biodiversidad forestal en el contexto mediterráneo. Por último, se sugiere que una gestión forestal concebida a escala de paisaje puede resultar especialmente adecuada para favorecer la adaptación de la biodiversidad mediterránea a las actuales y futuras dinámicas que actúan a escalas amplias y que están relacionadas con procesos como el abandono rural o el cambio climático.

Palabras clave: indicadores de biodiversidad forestal, índices de configuración del paisaje, tratamientos selvícolas, partición de la variación.

Introduction

The increasing loss of biodiversity has made evident the need to develop efficient methods to characterise and monitor biodiversity through a set of relevant and cost effective indicators. In forest ecosystems, most of the biodiversity indicators used so far are based on field surveys (forest inventory plots), which despite being an essential component of any forest monitoring system are in general costly and can only be undertaken with low sampling intensities when intending to cover large areas. National and regional inventories such as the Third Spanish National Forest Inventory (3SNFI, Ministerio de Medio Ambiente (MMA), 1997-2007) or the Catalan Ecological and Forest Inventory (Gracia *et al*., 2000-2004) have included new methodologies and measurements related to different biodiversity components (e.g. Alberdi *et al.*, 2005). However, complementary information from approaches taking into account larger spatial scales can improve and optimize the characterization and monitoring of forest biodiversity. In this sense, Noss (1990) suggested that landscape pattern may be an important feature for inventorying, monitoring and assessing terrestrial biodiversity structure at the regional and landscape level of organisation, and the landscape ecology premises offer new perspectives in this context that still need to be further explored (Moser *et al*., 2002; Saura and Carballal, 2004; Torras *et al*., 2008; Lafortezza *et al*., 2008; Saura, 2009).

Besides, spatial heterogeneity has also been recognized as a key factor favouring biodiversity (Rescia *et al.,* 1994; Atauri and de Lucio, 2001). Different measures of heterogeneity such as altitudinal or topographical gradients have been demonstrated to be determinants of plant diversity (Pausas *et al*., 2003; Dufour *et al*., 2006), and other authors have further explored the weight of environmental, geographic or landscape structure as a source of heterogeneity controlling biodiversity patterns (e.g. Huston, 1994; Lobo *et al*., 2001; Nogués-Bravo and Martínez-Rica, 2004; Ortega *et al*., 2008). In this sense, a landscape ecology approach makes emphasis on the ecological effects of the spatial patterning of ecosystems considering the relevance of spatial heterogeneity dynamics and the interactions of patterns and processes in landscape mosaics (Turner, 1989). However, the effect of management on biodiversity patterns at the landscape scale has been comparatively less analysed as a factor also promoting heterogeneity. Shifley *et al*. (2006) simulated the effects of management on landscape structure in the Midwestern United States, concluding that management alternatives with similar levels of disturbances produced similar landscape composition but different landscape pattern, with potential relevant implications for the associated forest biodiversity. Gustafson *et al*. (2007) also remarked the important effect of management on landscape structure, as evaluated through certain landscape configuration metrics. This kind of analyses and approaches can benefit a more comprehensive forest planning by deepening the understanding of the effect of silvicultural alternatives on biodiversity at broader scales (Rescia *et al*., 1994; Shifley *et al*., 2006; Torras and Saura, 2008). Likewise, they could be useful as additional information to interpret the state and trends in biodiversity conservation in a certain forested region (Lindenmayer *et al*., 2000), considering these relationships between management and biodiversity indicators at large scales. Although a number of authors have explored these associations (see a review in Rowland *et al*., 2005), additional research efforts are necessary to understand the effects and interactions of different landscape factors and management alternatives in the status and changes in forest biodiversity, particularly in the Mediterranean region (Saura, 2009).

Here we explore the relationships between a set of forest biodiversity indicators (estimated from 7,430 field plots from the 3SNFI) and environmental, landscape, management and spatial variables at a 10 x 10 km scale in the region of Catalonia (NE Spain). This scale was considered appropriate for this study because numerous biodiversity monitoring systems in Catalonia and the rest of Spain use the same UTM 10 x 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). This allowed us further linking and relating our results with other ongoing researches and monitoring projects, as is the case of the studies by Torras *et al*. (2008) or Gil-Tena *et al*. (2008, 2009), which have used the same scale. We specifically focus on the role of landscape configuration and forest management as potential relevant drives of the current forest biodiversity patterns at the landscape scale. This study is linked to a previous analysis by Torras *et al*. (2008) where a single biodiversity indicator (tree species richness) was considered and estimated from a continuous data set (forest map) with relatively limited thematic detail. Here, we largely improve that previous study by (1) considering a broader set of forest biodiversity indicators, (2) explicitly incorporating the role of forest management and its intensity, because we hypothesised that management may play a significant role explaining biodiversity patterns through its influence in the landscape composition and configuration, and by (3) estimating the biodiversity indicators from the more detailed and accurate information gathered in the field inventory plots of the Spanish National Forest Inventory (SNFI). In this latter respect, linking and combining the large amount of information gathered every ten years in the SNFI with the landscape scale, perspective and indicators could contribute to a more comprehensive forest biodiversity assessment and to complement two approaches and scales that have been mostly running in parallel without sufficiently exploring their synergies.

Materials and methods

Study area

The study was conducted in Catalonia (NE Spain), with a total extension of 32,098 km^2 and located within 0º15'E and 3º15'E longitude and 40º30'N and 42º40'N latitude (Figure 1). Catalonia comprises a high variety of landscapes and environmental conditions that has favoured a great vegetation diversity and makes this region particularly interesting for the purposes of this analysis.

According to the climatic stratification of Europe by Metzger et al. (2005), four of the five main zones defined in the Iberian peninsula are represented in Catalonia: Alpine South, Mediterranean Mountains, Mediterranean North, and Mediterranean South (only Lusitanian zone is not represented). This variety of conditions is also reflected in the Spanish phytoclimatic classification by Allué (1990), according to which Mediterranean (subtypes IV(VI)2, IV3 and IV1), Nemoral (subtypes VI(IV)1, VI(VII) and VI(IV)4) and Oroborealoid types (subtypes X(VIII) and VII(VI)) are all present in Catalonia (only subtypes occupying at least 100,000 ha are listed). The climatic gradient is mainly determined by the presence of the west-east oriented Pyrenean Mountains (with an altitude up to 3,143 m) at the north, and the Mediterranean Sea at the east, with an increasing temperature and decreasing precipitation to the south (higher xericity), and an increasing continentality to the west. About 38 % of the territory is occupied by forests (Terradas *et al*., 2004) and, according to the 3SNFI (MMA, 1997-2007), the main forest tree species in Catalonia are *Pinus halepensis, Pinus sylvestris, Quercus ilex, Pinus nigra, Pinus uncinata* and *Quercus suber*, followed by *Quercus pubescens*, *Fagus sylvatica*, *Pinus pinea, Quercus faginea*, *Quercus petraea*, *Abies alba*, *Pinus pinaster* and *Castanea sativa*.

About 80 % of the forested area in Catalonia is privately owned, with a remarkably small ownership size of about 20 ha in average, in contrast to the public forests that in general cover larger mountainous areas and have an average size of about 350 ha. However, forests in Catalonia are not too frequently managed, as a consequence of the poor economic benefit that most owners expect to get from the management of Mediterranean forests (Terradas *et al*., 2004), mainly due to the low growth and timber yields that are characteristic in this region.

Biodiversity indicators

Six different biodiversity indicators were estimated in a set of 10 x 10 km UTM grid cells covering all Catalonia from the information in 7,430 plots of the 3SNFI

(MMA, 1997-2007), which was gathered in Catalonia from July 2000 to August 2001. We used 216 UTM cells with most of their area within the territory of Catalonia and with a minimum number of 10 inventory plots for the characterization of the landscape-level indicators and subsequent analyses (Figure 1). Plots in the 3SNFI are circular and with a variable size, which depends on the tree diameter at breast height (DBH), ranging from a plot radius of 5 m for trees with DBH lower than 125 mm up to a maximum radius of 25 m for trees with a DBH of at least 425 mm. Plots are placed on the intersection points (vertices) of a 1 x 1 km UTM grid that are located inside woodlands.

The following six biodiversity indicators related to the tree and shrub layer were considered in the analyses: (1) Tree species richness, as the number of different tree species in each UTM; (2) tree species diversity, calculated through the Shannon diversity index (Magurran, 1989) based on the proportion of basal area (m^2/ha) of each species with respect to the total basal area in the UTM; (3) tree species rarity, calculated for all the tree species in a grid cell as the sum of the inverse of the number of UTM grid cells in which the species was present all throughout Catalonia; (4) shrub species richness, as the number of different shrub species in each UTM; (5) shrub species diversity, calculated through the Shannon diversity index based on the shrub abundance of each species with respect to the total shrub abundance in the UTM, where the abundance was defined as the product of shrub coverage (%) by height (dm); and (6) shrub species rarity, calculated in the same way than for the tree species. It should be noted however that shrub species identification in the 3SNFI is limited to a predefined list of 169 taxons (125 species, 42 genera and 2 subfamilies), where individual species are differentiated if they are frequent or considered important enough and can be successfully identified by the field crews, while the rest of the species are grouped mostly at the genus level.

Explanatory variables

Four groups of variables were considered as potential explanatory factors for the distribution of the forest biodiversity indicators: landscape structure (including landscape composition and configuration), environmental (topography and climate), management (frequency and intensity of silvicultural treatments) and spatial variables, all of them calculated for the same set of UTM 10 x 10 km grid cells than the biodiversity indicators (Figure 1). Forest landscape structure variables for each UTM were obtained from the Spanish Forest Map (SFM) at a scale 1:50,000, exception made of the forest management variables, which were obtained from the information gathered in the 3SNFI plots (see below). The SFM has been developed within the 3SNFI, has a vector data structure and a minimum mapping unit of 6.25 ha in general, but lowering to 2.25 ha for forest patches embedded in a non-forest land use matrix. The

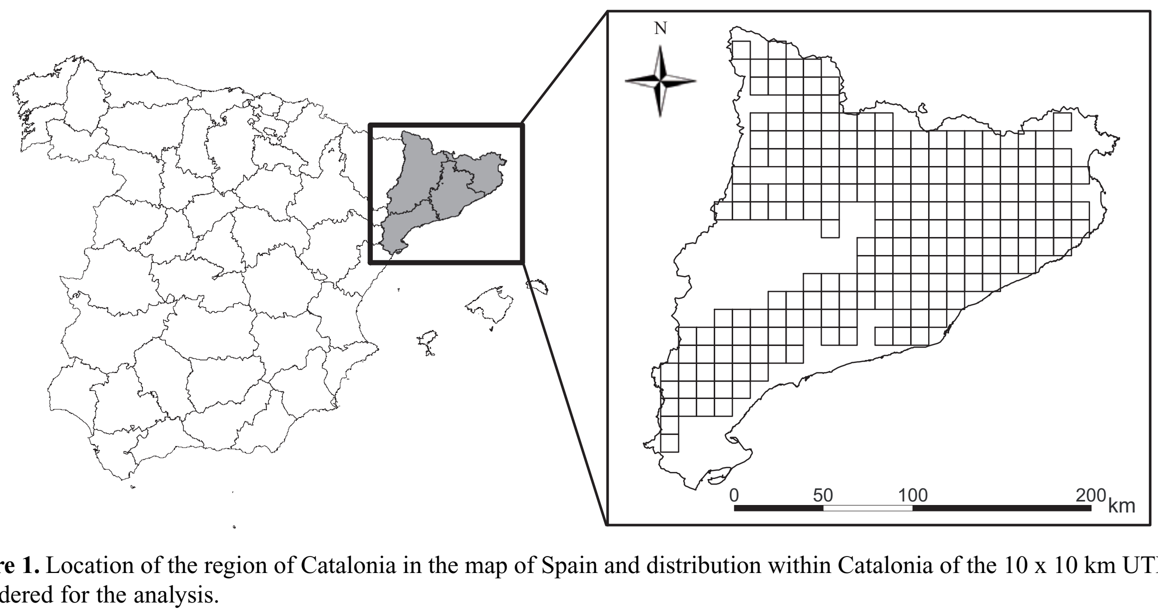

Figure 1. Location of the region of Catalonia in the map of Spain and distribution within Catalonia of the 10 x 10 km UTM cells considered for the analysis.

SFM has been obtained in Catalonia from the interpretation of aerial photographs combined with pre-existing maps and field inventory data. The following forest landscape composition variables were considered: total area covered by forests, computing nine different forest area variables as the area of land with a forest tree canopy cover above different thresholds ranging from 5 % to 90 %; mean forest canopy cover (FCC); mean forest development stage, obtained from the proportion of forest land area corresponding to the four development stages discriminated in the SFM, which are recently regenerated (up to canopy closure), thicket (up to natural pruning), trees with diameter at breast height (DBH) ≤ 20 cm, and trees with DBH > 20 cm; diversity of FCC; diversity of development stages; and diversity of land cover types (considering the 28 land cover types differentiated in the SFM for Catalonia). All the diversity variables within the 10 x 10 km cells were calculated through the Shannon diversity index (see Magurran, 1989): $H' = - \Sigma p_i \ln p_i$, where p_i is the area proportion of each of the categories corresponding for each variable.

Forest landscape configuration was quantified through a wide set of metrics related to fragmentation and shape irregularity, all of them computed in the original vector format of the SFM. The fragmentation metrics calculated 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 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); Saura *et al*., (2008)).

The forest management variables were obtained directly from the information in the 3SNFI plots. For each plot, the inventory reports the silvicultural treatments that have been performed as observed by the field crews, differentiating three regeneration (clearcutting, shelterwood and selection cutting) and four stand improvement treatments (cleaning, precommercial thinning, thinning and pruning). The explanatory variables obtained from this information were: the percentage of managed plots in each UTM cell, the percentage of plots with respectively regeneration and improvement treatments (two variables), and the percentage of basal area removed by management in the UTM cell. We calculated this latter variable as the amount of basal area of those tally trees that had been inventoried in the 2SNFI (MMA, 1986-1996) but were not present in the same permanent plots when inventoried ten years later in the 3SNFI (MMA, 1997-2007), divided by the total basal area of the stand.

Environmental variables included topographic and hydrologic 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 (Shannon index) in each cell. The hydrologic variables corresponded to the density of fluvial courses and the accumulated water flow (estimated from the digital elevation model) summarised as the mean, maximum, minimum, range, and standard deviation. 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.

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

Statistical analysis

The statistical analysis was based on the variation partitioning method (Borcard *et al*., 1992), which has been widely applied in previous studies (e.g. Lobo *et al*., 2001, 2002; Heikkinen *et al*., 2004; Nogués-Bravo and Martínez-Rica, 2004; Torras *et al.,* 2008), being particularly suited to explore the relative importance of different groups of variables for explaining the distribution of species or other biodiversity indicators. This method allows to detect redundancies between the explanatory power of different groups of variables and to isolate the actual and distinctive contribution of certain explanatory variables that is not covered by the rest of the variables considered in the partitioning. At the scale of study, the geographical structure of data is a major source of false correlations between explanatory and dependent autocorrelated variables (Legendre and Legendre, 1998). In addition, the spatial structure not shared by the factors included in the model can provide insights about ignored historical, biotic or environmental variables influencing the studied dependent variable (Legendre and Legendre, 1998). In order to take into account the possible existence of false correlations at the coarse-scale we considered the spatial factors as a separate group in all the analyses. We previously standardised all the explanatory variables and then performed several variation partitioning analyses to determine the percentage of variation of the biodiversity indicators explained by three different groups of variables in each partitioning (including spatial variables as one of them) through partial linear regression (Legendre and Legendre, 1998). Each partitioning resulted in seven non-overlapping fractions explaining the variation in biodiversity indicators, in addition to the unexplained variation (Bocard *et al.*, 1992). Three of the fractions corresponded to the pure effect (explanatory power) of each group of considered variables, and the rest to the joint effect of the different combinations of the groups of variables (three fractions for the joint effect of each pair of groups and one more for the joint effect of all the three groups together). The three groups considered in each of the four variation partitioning analyses were the following:

- Partitioning 1: (a) landscape (configuration and composition variables), (b) environmental and (c) spatial factors, in order to disentangle to which extent the distribution of biodiversity indicators was driven by landscape factors or by environmental variables (topography and climate) not directly modifiable (in the short term) by human action.
- Partitioning 2: (a) landscape configuration, (b) landscape composition and (c) spatial factors, in order to evaluate the relative importance of landscape composition and landscape configuration as indicators of forest biodiversity, which is a controversial issue that has been producing an active scientific debate (Dauber *et al.*, 2003; Fahrig, 2003; Saura *et al.*, 2008) and needs from further insights, particularly in the Mediterranean landscapes.
- Partitioning 3: (a) landscape shape, (b) landscape fragmentation and (c) spatial factors, in order to refine the previous analysis with a closer look and further insights on the contribution of these two major and distinct components of landscape configuration (fragmentation and shape) (Saura *et al.*, 2008).
- Partitioning 4: (a) landscape variables (composition and configuration), (b) management variables and (c) spatial factors, in order to specifically evaluate the potential impact of management on forest biodiversity indicators at the landscape scale and the additional information provided by variables related to silvicultural treatments that may not be covered by other landscape variables.

In order to explore the sign of the relationships between biodiversity indicators and the different groups of explanatory variables (considering in this case four groups corresponding to landscape configuration, landscape composition, environmental, and management variables), we performed a factor analysis with the principal component analysis as the extraction method. Factor analysis is often used in data reduction to identify a small number of factors that explain most of the variance observed in a much larger set of variables. We extracted the principal components that explained a minimum of about 75 % of the variance within each group of explanatory variables, and assigned each component to a major explanatory driver by examining which variables had a larger weight on each of them. We performed Pearson's correlations between the six biodiversity indicators and the different principal components of each group of variables. We discarded additional principal components explaining above the remaining 25 % of variance because they had a marginal explanatory power, with no significant correlations with the analysed biodiversity indicators.

Results

Environmental, landscape and spatial variables were jointly able to explain above 50 % of the variation for all the indicators except tree species rarity and shrub species rarity (Table 1). The percentage of explained variation was higher for the indicators related to the tree layer than for those related to the shrub stratum. The variation partitioning showed that the joint effect of the three groups of variables was the fraction that explained the highest percentage of variation for the tree layer indicators, while the dominant fractions for the shrub species diversity and rarity were respectively the pure spatial factors and the pure landscape factors (Table 1). The pure effect

Table 1. Percentage of the variation in the biodiversity indicators explained by the fractions resulting from the variation partitioning of landscape, environmental and spatial factors

Fractions	Biodiversity indicators					
	Tree species richness	Tree species diversity	Tree species rarity	Shrub species richness	Shrub species diversity	Shrub species rarity
Pure effect of landscape factors (L)	9.2	6.4	4.6	8.6	8.8	14.7
Pure effect of environmental factors (E)	5.5	2.6	0.9	6.3	6.4	9.6
Pure effect of spatial factors (S)	1.5	1.2	1.4	5.2	20.0	0.0
Joint effect of L + E factors	16.1	7.0	8.9	13.0	3.5	-11.7
Joint effect of L + S factors	2.1	5.1	-1.3	0.7	-2.1	0.0
Joint effect of E + S factors	2.1	4.2	7.4	23.9	-4.2	5.5
Joint effect of L + E + S factors	40.7	28.3	18.7	6.8	19.6	9.7
Unexplained variation	22.8	45.2	59.4	35.5	48.0	72.2

of landscape factors explained less than 10 % of the variation of all biodiversity indicators except for shrub species rarity, but it was always higher than the pure effect of environmental or spatial factors (with the only exception of the spatial factors for shrub species diversity). Variation is not a strict estimation of variance but is calculated by mathematic operations, and the negative values of the explained variation that resulted for some of the fractions indicated that some groups of variables, together, explained better the variance of the indicator than the sum of their individual effects.

The decomposition of variation among the landscape configuration, landscape composition and spatial factors showed that the pure effect of landscape composition was much higher than that of landscape configuration, and the latter was slightly higher than zero only for half of the biodiversity indicators (Table 2). The pure effect of landscape composition was particularly prominent for the indicators related to the tree layer. The largest fraction corresponded to the combined effect of the three groups of variables for tree species richness and diversity, while the spatial factors were comparatively more important to explain the distribution of the shrub layer indicators (Table 2). The partitioning between shape, fragmentation and spatial factors confirmed in general the weak effect of landscape configuration variables, with the spatial factors being by far those explaining a largest proportion of the indicators variation (Table 3). However, the pure effect of landscape fragmentation was considerable for tree species richness, while the pure effect of landscape shape was higher than that of fragmentation for other three indicators (Table 3). Landscape shape had no pure effect on tree species rarity and shrub species richness, while landscape fragmentation had no pure effect on tree species diversity and shrub species rarity.

Table 2. Percentage of the variation in the biodiversity indicators explained by the fractions resulting from the variation partitioning of landscape configuration, landscape composition and spatial factors

Fractions	Biodiversity indicators					
	Tree species richness	Tree species diversity	Tree species rarity	Shrub species richness	Shrub species diversity	Shrub species rarity
Pure effect of landscape configuration (CF)	0.0	1.4	0.7	2.9	0.0	-2.0
Pure effect of landscape composition (CP)	13.5	10.2	11.9	3.3	3.6	0.0
Pure effect of spatial factors (S)	3.6	5.4	8.8	29.1	15.8	5.5
Joint effect of CF + CP factors	11.8	1.8	0.9	15.4	8.7	5.0
Joint effect of CF + S factors	0.0	0.4	0.8	-4.2	1.5	9.6
Joint effect of CP + S factors	21.6	14.1	7.5	16.2	3.7	9.5
Joint effect of CF + CP + S factors	21.2	18.9	9.1	-4.5	12.3	-9.4
Unexplained variation	28.3	47.8	60.3	41.8	54.4	81.8

Table 3. Percentage of the variation in the biodiversity indicators explained by the fractions resulting from the variation partitioning of landscape shape, landscape fragmentation and spatial factors

Fractions	Biodiversity indicators					
	Tree species richness	Tree species diversity	Tree species rarity	Shrub species richness	Shrub species diversity	Shrub species rarity
Pure effect of landscape shape (SH)	2.9	4.4	0.0	0.0	1.9	0.4
Pure effect of landscape fragmentation (FR)	8.4	0.0	1.9	2.7	0.7	0.0
Pure effect of spatial factors (S)	25.2	19.5	16.3	45.3	19.5	15.0
Joint effect of SH + FR factors	0.5	-1.2	-0.3	15.6	6.1	2.6
Joint effect of SH + S factors	-1.0	2.2	1.0	0.0	20.6	-3.0
Joint effect of FR + S factors	1.0	4.1	4.9	-1.4	16.8	0.0
Joint effect of SH + FR + S factors	21.2	13.0	4.0	-7.3	-23.6	3.2
Unexplained variation	41.8	58.0	72.2	45.1	58.0	81.8

The partitioning between landscape, management and spatial variables showed that the landscape factors were those with a highest pure effect for the tree layer indicators, while the dominant pure fraction corresponded to the spatial variables for the shrub species indicators (Table 4). The direct and pure effect of management on the biodiversity indicators was rather weak at this scale (only had a slight contribution to explain tree species diversity) and in general did not provide additional explanatory power not already provided by the landscape or spatial factors (Table 4).

The effects of landscape configuration were summarized by three principal components corresponding to fragmentation, shape elongation and shape complexity (Table 5) and most of the variability in the environmental variables was captured by other three components related to altitude (and the correlated decreasing temperature), water flow accumulation and slope. Landscape composition and management effects were summarized by two and one principal components respectively, indicative of forest area and the amount and features characteristic of early successional forest and management intensity (Table 5). All the indicators but shrub species richness had a significant negative correlation with landscape fragmentation, while the effects of landscape shape were much weaker, especially for the case of shape elongation (Table 5). Only tree species richness and shrub species diversity were positively associated to more complex boundaries in the landscape. A larger forest area correlated significantly and positively with almost all the indicators, while the amount of young (early successional) forest was significantly associated to lower indicator values in the tree layer and higher in the shrub layer (Table 5). The management intensity had a significant positive effect in the tree layer indicators, but not in the rest. Tree species

Table 4. Percentage of the variation in the biodiversity indicators explained by the fractions resulting from the variation partitioning of landscape factors (both configuration and composition variables), forest management and spatial factors

Fractions	Biodiversity indicators					
	Tree species richness	Tree species diversity	Tree species rarity	Shrub species richness	Shrub species diversity	Shrub species rarity
Pure effect of landscape factors (L)	25.3	16.0	18.9	21.6	12.3	4.6
Pure effect of forest management (MG)	0.0	2.6	0.0	0.0	0.0	0.0
Pure effect of spatial factors (S)	1.5	5.1	7.9	29.1	15.8	5.5
Joint effect of L + MG factors	0.0	-2.6	-5.4	0.0	0.0	-1.6
Joint effect of L + S factors	26.0	19.8	1.2	7.5	15.7	8.1
Joint effect of MG + S factors	2.1	0.3	0.9	0.0	0.0	0.0
Joint effect of L + MG + S factors	16.8	13.6	16.2	0.0	1.8	1.6
Unexplained variation	28.3	45.2	60.3	41.8	54.4	81.8

Table 5. Pearson's correlations among biodiversity indicators and the principal components of each group of explanatory variables. The percentage of variance explained by each individual component and the variance explained by all the components within each group is indicated. Significant correlations at a probability level of 0.05 and 0.01 are indicated by * and ** respectively

Principal components	Variance explained (%)	Biodiversity indicators Tree species richness	Tree species diversity	Tree species rarity	Shrub species richness	Shrub species diversity	Shrub species rarity
- Landscape configuration	**80.72**						
Fragmentation	49.20	-0.53**	-0.38**	-0.30**	-0.15*	-0.03	-0.17*
Shape elongation	17.83	-0.60	-0.06	-0.03	0.01	-0.01	0.02
Shape complexity	13.69	0.14*	-0.07	-0.05	0.11	0.15*	-0.05
- Landscape composition	**83.36**						
Forest area	60.32	0.70**	0.43**	0.41**	0.20**	0.05	0.14*
Early successional forest	15.80	-0.21**	-0.22**	-0.19**	0.27**	0.37**	0.09
- Management	**73.95**						
Management intensity	73.95	0.30**	0.24**	0.23**	0.03	-0.04	0.02
- Environmental	**84.22**						
Altitude	56.45	0.24**	0.22**	0.05	-0.47**	-0.15*	-0.19**
Water flow accumulation	14.97	-0.13	-0.02	-0.16*	0.06	0.13*	0.01
Slope	6.66	-0.05	-0.12	-0.09	0.41**	0.40**	0.22**

richness and diversity tended to increase with altitude, while the opposite occurred for the shrub indicators, which in turn were positively associated with steeper slopes. The effects of water flow accumulation were in general much weaker.

Discussion

Predictability of forest biodiversity indicators estimated from national forest inventory data

Tree and shrub species richness were the most predictable indicators, with 77.2 % and 64.5 % of explained variation respectively (Table 1), which can be considered quite high given the wide scale and range of environmental conditions considered in this analysis. A previous study by Torras *et al*. (2008) at the same scale could explain 61.6% of the variation in tree species richness estimated from the spatially continuous information provided by the SFM in the study area, unlike the forest inventory plots used in this research. The SFM is limited to report up to three different tree species in each forest patch, and is therefore likely to underestimate and perhaps provide some bias in the richness estimates. The more detailed information from the plots in the SNFI here allowed characterizing diversity patterns with a stronger link to the environmental and landscape variables, indicating the adequacy and improvement provided by the field inventory data also for this kind of broad scale assessments.

When the indicators considered the relative abundance or dominance of each species and not just the number of species present (species diversity vs. richness), the percentage of explained variation was considerably lower both for trees and shrubs. This may be due to the fact that the Shannon index used to characterise diversity is biased towards species dominance, being more affected by the abundance of the most common species (Magurran, 1989), which could be less sensitive to landscape and environmental factors.

The tree layer indicators were more predictable from the set of explanatory variables here considered than those of the shrub layer, which may be explained by different reasons. First, this may be in part a consequence of the limitations on the taxonomic identification for shrub species in the 3SNFI, where not all individual species are differentiated. Second, the distribution of shrubs is probably determined by local patterns that may have not been fully reflected at the 10 x 10 km scale. In this sense, Hernandez-Stefanoni (2005) related landscape-pattern metrics and species richness at much finer scales than the one here considered and found a similar behaviour and predictability both for tree and shrub species, and Gracia *et al*. (2007) reported an important effect of topography on shrub species abundance at local scale in the Pyrenees.

The least predictable variables were those related to species rarity. This result can be explained because rare plant species do not necessarily follow general coarse-scale tendencies in a given region, either because they are at the edge of their distribution range, because they depend on local conditions, such as soil moisture patterns and microclimatic variables (as occurred also for extrazonal tree species as reported by Thuiller *et al.* (2003)), or because they are primarily determined by local disturbances or fine scale historical factors that are difficult to capture at the landscape level and scale here considered. In this sense, and in relation to the taxonomic identification for shrub species in the 3SNFI described above, we suggest that rare species should receive more attention in field sampling in forest inventories, given their low predictability from a landscape scale approach but great importance and conservation value, and considering that they add a qualitative perspective on the characterization of biodiversity to the quantitative one provided by species richness. This situation is already being improved in the recently started 4SNFI, where the occurrence of some threatened plant species will be inventoried.

In general, the unexplained variation for the different indicators may be related to variables not included in the analyses, such as soil conditions and other types of human influence different from forest management, as well as to artifacts, errors or noise in the available data or non-linear relationships between the biodiversity indicators and the analysed explanatory variables.

The relative importance of landscape and environmental factors for explaining the distribution of forest biodiversity indicators

According to our results, landscape variables were the prominent pure fraction explaining variation in all the biodiversity indicators except shrub species diversity, when compared to the pure effect of environmental and spatial factors. This means that the relationships between landscape factors and biodiversity indicators were less affected by potential coarse-scale false correlations generated by spatial autocorrelation. The determinant and environmentally independent role of landscape factors, also found in previous studies such as Torras *et al.* (2008), suggests that in human-modified regions like the Mediterranean the biodiversity patterns largely diverge from the potential ones that may be determined just by climatic and topographic factors, which partially agrees with Lobo *et al.* (2001). In these conditions the landscape characteristics gain importance compared to other geographical regions. These results are in accordance with the potential use of landscape structure (including both landscape composition and configuration) as an effective biodiversity indicator at broad scales (Lindenmayer *et al.*, 2000; Dauber *et al.*, 2003).

However, for the indicators related to the tree layer, the joint effect of the three groups of variables (landscape, environmental and spatial) was responsible of about half of the total explained variation, indicating that some environmental and forest landscape factors are spatially structured and present a considerable degree of covariation. Disentangling the processes that underlie biodiversity patterns is constrained by the complex relationships existing between the cited groups of explanatory variables. Landscape patterns are accepted to be originally modelled by environmental conditions and subsequently by human action, which at the same time can be governed by the environment (e.g. field crops location) (Forman and Godron, 1986). In the indicators related to the shrub layer, the explanatory dominance of these jointly spatially structured factors was less clear. In the case of the diversity of shrub species, there was an important fraction of the variation explained uniquely by the geographical patterns, which may be due to the existence of other spatially structured explanatory factors not included in the analysis but that have a direct influence on the distribution of this indicator. However, and more interestingly, the relevance of the pure spatial fraction could indicate an autocorrelation in the shrub diversity caused by internal ecological spatial processes, such as competition, dispersal or succession; or by historical variables that might not be easily documented, and therefore, included in the model (Legendre and Legendre, 1998).

The relatively low percentage of variation explained by environmental factors suggests that in this Mediterranean study area the energy variables related to climatic factors are not a limiting or decisive factor for woody plant species richness at the landscape scale. At wider scales, however, it is recognised the determinant role of climatic factors in the distribution of biodiversity (e.g. Field *et al.*, 2005). The role of the scale may be in this respect relevant to explain discordances among different studies, as shown by Nogués-Bravo and Araújo (2006) when analysing correlations between species richness and both the size of the sampled area and climatic factors.

The greater part of the variation in shrub species richness was explained by the spatially structured environmental fraction and this could be related to the remarkable topographic and climatic gradient in Catalonia, which was probably detected by the spatial polynomial model. The results of the variation partitioning without the set of environmental variables highlight the relevance of the geographical patterns, not shared by composition or configuration variables, in the explanation of coarse-scale variation in shrub species richness.

Among the landscape factors, the minor effect of landscape configuration compared to landscape composition (except for shrub species rarity) agrees with the results obtained in a previous study in Catalonia by Torras *et al*. (2008) and with others analysing these associations in other taxonomic groups such as Gil-Tena *et al*. (2008) or McGarigal and McComb (1995) for avian species richness. In this respect, Fahrig (2003) noted that most studies about the effects of landscape structure on ecological processes found larger effects of landscape composition. This indicates that the primary requirement of species is a significant amount of habitat (that is measured through composition variables) apart from other needs regarding forest landscape pattern characteristics (Gil-Tena *et al*., 2008). The part of the variation of biodiversity indicators explained by configuration variables was due either to fragmentation or shape depending on the indicator, although in general a higher influence of fragmentation variables was found.

The weak but positive effect of forest management at the scale 10 x 10 km

Management variables had a minor role explaining the variation of the biodiversity indicators at the 10 x 10 km scale compared to other groups of explanatory variables. This result is in contrast with the prominent effect of silvicultural treatments on biodiversity indicators found at the stand scale, both in the Mediterranean (Fabbio *et al*., 2003; Torras and Saura, 2008) and in other study areas (e.g. Hansen *et al*., 1991; Green and Peterken, 1997; Marage and Lemperiere, 2005; Deal, 2007). It is widely accepted that management affects key forest characteristics and biodiversity at multiple scales, including spatial pattern and relevant ecological processes (Franklin and Forman, 1987; Turner, 1989; Rescia *et al*., 2004; Gustafson, 2007), but the direct impacts on Mediterranean biodiversity at the landscape scale have been much less analysed. A recent study by Gil-Tena *et al*. (in press) focused on forest birds and also found that the forest structure changes in managed localities did not seem to have a noticeable influence in the distribution of expanding specialist forest birds at 10 x 10 km. This weak effect here reported can be explained by the fact that most of the Catalan forests are unmanaged (about 73 % according to the NFI data as reported by Torras and Saura (2008)) and, even when managed, a landscape perspective is largely lacking from the planning process, making difficult that the potential benefits of those treatments may arise with sufficient prominence at broader scales. In addition, when coarsening the scale of analyses (up to 10 x 10 km) increased correlations between the relevant variables are found, and those areas with more frequent management tend to be also those with a larger amount of forest, canopy cover and more developed structures, diminishing the potential pure statistical effect of the silvicultural treatments apart from that already covered by other landscape composition and configuration variables.

However, despite these difficulties, we still found a positive effect of forest management on the tree layer biodiversity indicators, which agrees with Torras and Saura (2008), who concluded that moderate-intensity silvicultural practices (those most common in the region) may improve in some cases Mediterranean forest understory and canopy biodiversity indicators at the stand scale. This is consistent with the intermediate disturbance hypothesis applied also at the landscape scale, which postulates that maximum diversity is provided by intermediate disturbance size, frequency and intensity (Roberts and Gilliam, 1995). Indeed, the rural land abandonment processes and the reduction in forestry activities due to the low profitability of traditional forest products and the introduction of new fuel sources have favoured forest maturation, increased biomass (Poyatos *et al*., 2003; Roura-Pascual *et al*., 2005; Gil-Tena *et al*., 2009) and a potentially excessive landscape homogenization and densification that may induce the dominance of a few adapted species and may have a negative effect on some forest generalists or open habitat species (Vallecillo *et al*., 2008). For example, many forest bird species in the Mediterranean seem to be adapted to landscape heterogeneity derived from anthropogenic practices (Tellería and Santos, 1999), and Lasanta-Martínez *et al*. (2005) also observed a negative impact of abandoned rural landscapes and homogenization on biodiversity. In this context, an active landscape management may be a keystone in order to counteract the potentially negative effects of current global change on forest biodiversity in the Mediterranean by favouring landscape diversity and heterogeneity and promoting landscape patterns and connectivity that enhance the ability of the species to adapt to the ongoing landscape dynamics (Gil-Tena *et al*., in press; Saura 2009).

Relationships among explanatory variables and forest biodiversity indicators

Forest area showed the highest positive correlations with all the biodiversity indicators, especially for the tree layer, agreeing with previous studies focusing on forest tree species richness variation (Pausas *et al*., 2003; Guirado *et al*., 2006) and with the premises of the island biogeography theory. At the same time, forest habitats tend to be located in the mountains, which may lead to a certain degree of covariation of the forest area variable with the altitude, and consequently also with spatial factors, for the reasons exposed above. On the contrary, Torras *et al*. (2008) found that a high FCC in the forest landscape was more beneficial for tree species richness than the amount of forest area itself. However, the fact that the amount of early succession forest (initial development stages and with more open canopies) is here negatively correlated to the tree layer indicators tends to capture the same effect and is consistent with the previous results by Torras *et al.* (2008) on the relationships between forest landscape composition and biodiversity. Indeed, mature forests are in general characterised by a higher diversity than early successional forests, mainly due to the complex vegetation structure (Brokaw and Lent, 1999) and to the presence of dead wood and cavities that provide environmental conditions that are beneficial for many taxonomic groups (McComb and Lindenmayer, 1999). Besides, many of these young forests correspond to reforestations or natural colonisations of open areas by communities of edge and pioneer species that are dominated by a few *Pinus* spp. or *Quercus* spp. tree species. On the contrary, early successional forest stages were positively associated to the shrub species indicators, probably as a consequence of higher light availability in the understorey and other competence-related processes.

Two different aspects can be distinguished in the process of fragmentation: the loss of habitat amount and the fragmentation per se (Fahrig, 2003), which in turn is a complex combination and result of different spatial processes (Forman, 1995). Some fragmentation metrics, like mean patch size or the percentage of interior area, are not independent from habitat area, as regions where there is more amount of forest habitat often have larger patches (Fernández-Juricic, 2000). Results on the correlations between these metrics and the biodiversity indicators therefore do not allow a straightforward interpretation of the effects of each fragmentation aspect on biodiversity and at least a part of the negative correlations found between the fragmentation metrics and the biodiversity indicators may be due to the underlying effect of forest habitat abundance. The consequences of habitat loss on species richness have been demonstrated to be much stronger than those of fragmentation per se, and most studies concur in its negative effect (Fahrig, 2003). On the contrary, shape complexity metrics tend to be much less correlated with habitat area than those related to fragmentation (Saura *et al.* 2008), and the positive effect of shape complexity on some indicators here reported highlights the need of including this type of metrics in the analysis of biodiversity patterns, even when the effects of landscape shape on biodiversity have been much less studied than those of habitat fragmentation (Noss, 1990). In some studies, shape complexity has been shown to be relevant for explaining biodiversity and a good predictor of species richness (Moser *et al*., 2002; Saura *et al.* 2008; Torras *et al.* 2008). Indeed, the shape of landscape patterns may be linked to the imprint of the factors that have configured the boundaries and influenced the diversity of forest patches. An increased human influence and land use intensity yields simpler and more rectilinear landscape shapes, which may be associated to a lower species richness for different taxonomic groups (Moser *et al*., 2002; Saura and Carballal, 2004; Saura *et al*., 2008).

The altitude was significantly correlated with all biodiversity indicators (except rarity), and the strength of the correlation was especially relevant in the case of shrub species richness. The relevance of the altitudinal factors has been widely recognised in literature, and a number of authors have found negative relationships between altitude and plant species richness (e.g. Rey-Benayas, 1995; Heikkinen and Neuvonen, 1997; Lobo *et al*., 2001; Bruun *et al*., 2003). The primary cause underlying this relationship is accepted to be the decrease in the length of the growing season and in vegetation productivity with altitude, which determines a lower number of plant species being able to colonise the highest altitudinal ranges. However, several authors found the contrary phenomenon in the Iberian Peninsula (Castro-Parga *et al*., 1996; Lobo *et al*., 2001; Moreno-Saiz and Lobo, 2008), arguing that, under a Mediterranean climate, the climatic conditions in the upper mountain areas are not constraining biodiversity, but on the contrary, are the extreme temperatures and low precipitations occurring at lower altitude which, through hydric stress, might limit plant productivity and diversity. The presence of mountains has also been suggested to be a potential surrogate of many factors that might influence positively plant species richness (see Vetaas and Ferrer-Castán, 2008), like the increase in surface area, the higher geological heterogeneity, or its role as refuge during the last glacial periods. In our results, the increase in tree species richness and diversity with altitude is consistent with the cited analyses in the Iberian Peninsula, and might also be related to the increase in forest area in the Spanish mountains. However, shrub species indicators, which seemed to be more affected by the altitudinal gradient, showed the inverse tendency, which may be a result of the longer growing seasons, the resource availability and competence with the tree strata and the higher disturbance intensity and more open canopies of those forests located at lower altitudes. On the other hand, only shrub species indicators were significantly correlated to slope variables, which may be explained by the fact that many shrub communities are present in areas unsuitable for forest development, due to insufficient soil depth or adverse climate conditions.

Concluding remarks

A high percentage of variation of tree and shrub species richness and diversity has been explained by the set of variables considered in the analysis. However, this type of research should be further extended to other study areas and spatial scales, since the underlying patterns and ecological processes are certainly scale-dependent. Although the different biodiversity indicators showed distinct associations and responses to landscape, environmental and spatial variables, the information gathered in the national forest inventories has revealed useful to analyse biodiversity patterns at the landscape scale. Our results highlight the need to concentrate more efforts in the field sampling related to the least predictable indicators, which cannot be easily estimated from other surrogate variables at the landscape scale, such as those related to rare species with a high conservation value. In this sense, the recently started 4SNFI has already incorporated new measurements, such as the occurrence of some threatened plant species, or indicators related to the herb layer and to different deadwood types and decay stages. On the other hand, it is also necessary to incorporate landscape structure variables in the assessment and monitoring of forest biodiversity, as they have shown to have a prominent importance for these purposes in the Mediterranean areas compared to other environmental variables.

Finally, although management variables have here presented a minor but positive effect on some of the biodiversity indicators, there is still a lack of knowledge on how management may affect forest biodiversity at the landscape scale. Further studies in this respect are particularly needed in the Mediterranean region, where great changes are occurring on our forest landscapes due to different broad-scale processes such as the rural abandonment, climate change or the increasing fire frequency, and where certain management practices and intensities could be crucial to promote biodiversity and allow the adaptation of our forest ecosystems to the ongoing dynamics.

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