



Species richness of woody plants in the landscapes of Central Spain: the role of management disturbances, environment and non-stationarity

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Keywords:

Climatic gradients; *Dehesas*; *Gamma* species richness; Geographically weighted regression; Intermediate disturbance hypothesis; Mediterranean; Rural abandonment; Silvicultural treatments; Spatial scale.

Abbreviations:

3SNFI = Third Spanish National Forest Inventory; OLS = Ordinary Least Squares; GWR = Geographically Weighted Regression.

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Abstract

Questions: How important is management disturbance on *gamma* species richness of woody plants at intermediate landscape scales? How is species richness related to other climatic and biotic factors in the study area? How does the assumption of spatial stationarity affect assessment of relationships among species richness and explanatory variables (e.g. management, biotic and climatic factors) across extensive study areas?

Location: Central Spain (regions of Castilla y León, Madrid and Castilla-La Mancha).

Scale: Extent: 150 000 km². Grain: 25 km² (5 × 5-km cells).

Methods: Information from 21 064 plots from the 3SNFI was used to evaluate richness of tree and shrub species at intermediate landscape scales. In addition to variables well known to explain biodiversity, e.g. environmental and biotic factors, effect of management treatments was evaluated by assessing clearcutting, selection cutting, stand improvement treatments and agrosilvopastoral systems (*dehesas*). Results from GWR techniques were compared with those from OLS regression.

Results: Patterns of *gamma* species richness, although strongly affected by both environmental and biotic variables, were also significantly modified by management factors. Species richness increased with percentage of selection cutting stands and improvement treatments but decreased with percentage of clearcutting stands. Reduced species richness of woody plants was associated with agrosilvopastoral practices. Species richness for trees was closely related to basal area, annual precipitation and topographic complexity; species richness for shrubs was closely related to topographic complexity and agrosilvopastoral systems. Most relationships between species richness and environmental or biotic factors were non-stationary. Relationships between species richness and management effects tended to be stationary, with a few exceptions.

Conclusions: Landscape models of biodiversity in Central Spain were more informative when they accounted for effects of management practices, at least at intermediate scales. In the context of current rural abandonment, silvicultural disturbances of intermediate intensity increased *gamma* species richness of woody plants. Exclusion of factors such as agrosilvopastoral systems from models could have led to spurious relationships with other spatially co-varying factors (e.g. summer precipitation). Patterns of spatial variation in relationships, provided by GWR models, allowed formulating hypotheses about potential ecological processes underlying them, beyond generalizations resulting from global (OLS) models.

Introduction

Biodiversity is commonly used to assess ecosystem health because it affects key ecological processes (Loreau et al. 2001; Hooper et al. 2005). Woody plant species are a key component of forest ecosystems; woody plants are responsible for forest architecture (Stapanian et al. 1997) and influence the overall composition of forest communities.

According to the ecological equilibrium paradigm, the internal regulation and stability of ecosystems has traditionally been emphasized, but the importance of disturbances for the maintenance of vegetation diversity is now increasingly accepted (see Odion & Sarr 2007). Some types of anthropogenic disturbance could be regarded as part of normal forest functioning rather than an external disturbance (Christensen et al. 1996; Decocq et al. 2004), although this issue is controversial (Hall 2000; Fabbio et al. 2003). In European forests, the current flora might be adapted to regimes of secularly imposed disturbance (Niemelä 1999), such as forest management, particularly in the Mediterranean basin (Blondel & Aronson 1999). An extreme example of the close co-evolution of species composition and human activities are the *dehesas*. These agrosilvopastoral systems are typical of southwestern regions of the Iberian Peninsula. *Alpha* (local) biodiversity tends to be higher in *dehesas* than in other natural habitats (including Mediterranean forests from which they were created) for many functional groups (Díaz et al. 2003). This biodiversity depends on the maintenance of traditional low-intensity farming.

Effects of forest management on biodiversity have been assessed in most studies at the stand scale (e.g. Peltzer et al. 2000; Fabbio et al. 2003; Atauri et al. 2004; Torras & Saura 2008). These studies reveal that effects of forest management depend on the study region and type of management practices. Because forestry practices are mainly designed and applied at the stand or forest level, the most prominent impact of forest management may be found at these local scales. At broader scales (i.e. wider extents and coarser grain sizes), silvicultural factors (treatment type and intensity) might vary within the base unit of analysis and large effects on indicators of biodiversity might not be easily observed (e.g. Torras et al. 2009; Gil-Tena et al. 2010). In Spain, a focus on a broader scale for forest management planning (from the classical stand and forest level to the landscape and regional scales) has begun to be implemented only recently (Saura 2009). Few empirical studies have addressed the direct effect of forest management on biodiversity at a landscape scale, particularly for vegetation indicators. More insights into the effects of silvicultural disturbances and associated

ecological processes on *gamma* (landscape) diversity are necessary to provide guidelines for sustainable forest landscape management.

In assessment of the broad-scale effect of forest management on biodiversity, underlying environmental drivers should also be considered because their relationship to global patterns of biodiversity are widely recognized, as in the case of climate (O'Brien 1998; Field et al. 2005). Climatic factors have been shown to be the main determinants of plant species richness at large scales (see the meta-analysis of Field et al. 2009), mainly due to the influence of the interaction between energy and water on plant development (O'Brien 1998). In many studies, altitude and plant species richness are correlated (e.g. Rey-Benayas 1995; Lobo et al. 2001; Field et al. 2005), although this correlation is primarily a consequence of the associated climatic gradient (Nogués-Bravo et al. 2008). Topographic relief, as a measure of heterogeneity, has also been demonstrated to be a major determinant of plant diversity (e.g. O'Brien et al. 2000; Rey Benayas & Scheiner 2002; Pausas et al. 2003; Vetaas & Ferrer-Castán 2008). This variable is associated with the intensity of human-induced disturbances, microclimatic and geologic heterogeneity, increased area and geometric constraints (Nogués-Bravo et al. 2008). The inclusion of topographic heterogeneity in the models corrects for the unrealistic assumption that mean climate values are uniform in the large grid cells (O'Brien et al. 2000). Comparatively few studies have examined the effect of biotic interactions at the landscape level, and their role at intermediate scales might have been underestimated (Field et al. 2009).

In most of studies, the relationships between indicators of biodiversity and explanatory factors are assumed not to vary spatially, even in study areas of thousands of square kilometres; i.e. the spatial stationarity of the underlying processes in landscape forest biodiversity are assumed. However, spatial variation in the relationships can be expected due to (1) random sampling variations, (2) intrinsic differences across space, (3) relevant factors omitted from the model, or (4) an incorrect functional form of the relationships –linear, unimodal, etc. (Fotheringham et al. 2002). If the relationships are non-stationary in a given study area (i.e. they vary from one location to another), descriptive and predictive utility of global models (considering the entire area) may be compromised.

The main objectives of this study are (1) to characterize effects of forest management practices (agrosilvopastoral practices, forest regeneration and improvement treatments) on *gamma* species richness of woody plants at an intermediate grain scale (5 × 5 km); (2) to evaluate relationships among species richness and other

environmental and biotic variables and to compare them with those obtained in previous literature; and (3) to interpret the observed spatial patterns of the relationships and possible underlying ecological processes. The study was carried out in a region in Central Spain that covers about 150 000 km², using data from the Third Spanish National Forest Inventory (3SNFI) and other thematic sources. Local regression techniques were applied to evaluate the potential spatial non-stationarity of the analysed relationships, particularly, geographically weighted regression (GWR) techniques, which are being increasingly used in ecological models (e.g. Osborne et al. 2007; Guo et al. 2008).

Methods

Study area and the Spanish National Forest Inventory

The present study was carried out in the Spanish regions of Castilla y León, Castilla-La Mancha and Madrid (Fig. 1). A total of 3996 Universal Transverse Mercator (UTM) cells (5 × 5 km) were analysed. Cells in Zone 29N (European Datum 1950) were excluded to avoid effects of differences in cell size derived from the use of a common projection during data processing. We considered only cells that included some forest area according to the Third Spanish National Forest Inventory (3SNFI, Ministerio de Medio Ambiente 1997–2007). The scale of 5 × 5 km allowed (1) a

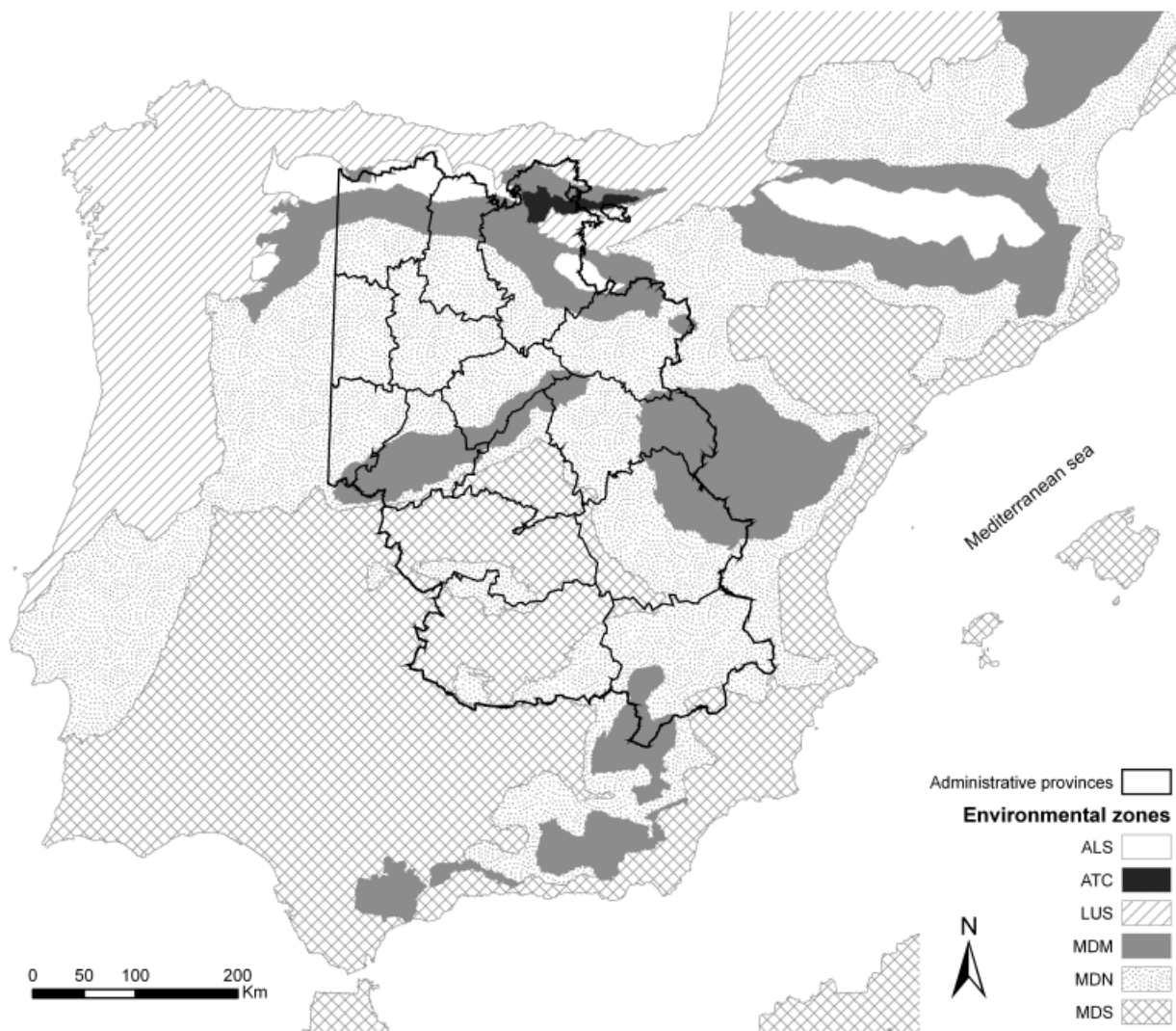


Fig. 1. Map of the study area and corresponding administrative provinces. Environmental zones according to the European stratification by Metzger et al. (2005) are represented. ALS, Alpine South; ATC, Atlantic Central; LUS, Lusitanian; MDM, Mediterranean Mountains; MDN, Mediterranean North; MDS, Mediterranean South.

sufficient number of 3SNFI plots to be captured to characterize the forests within each cell (see details below for sampling intensity) and (2) detection of potential spatial variability by yielding a sufficiently large number of cells throughout the study area.

According to the stratification of Europe performed by Metzger et al. (2005), each of the main environmental zones into which the European Mediterranean basin can be divided were represented in our study area (Fig. 1). South Alpine and Central Atlantic Zones also appeared in some of the northern sectors of the study area, contrasting with the dominant Mediterranean Zones. Mean elevation ranges from 300 m to 1900 m, mean annual precipitation from 300 mm to 1500 mm, and mean annual temperature from 5.5 °C to 16.5 °C. The most frequent tree and shrub species (taxa) in the study area are presented in Table 1.

In the 3SNFI, a systematic sampling design was used; plots were located at the intersections of a 1 × 1-km UTM grid that falls inside forests and other woodlands (defined as lands with tree canopy cover above 5%). Plots were circular and the inventory of tree stems depended on their diameter at breast height (DBH) and distance to the plot centre, which ranged from 5 m for trees with DBH from 7.5 cm to 12.5 cm up to a maximum radius of 25 m for trees with DBH of at least 42.5 cm. The number of inventory plots in the study area was 21 064. Plots were sampled from 2000 to 2004.

Biodiversity indicators and explanatory variables

For each 5 × 5-km UTM cell, two indicators of biodiversity were computed: *gamma* tree and shrub species richness. *Gamma* species richness was estimated as the sum of the

number of species of tally trees (DBH ≥ 7.5 cm) or shrubs surveyed in the 3SNFI plots belonging to one cell. For shrubs, the total number of species was measured only indirectly by species richness because richness was based on a predefined list of 169 taxa (125 species, 42 genera and two subfamilies). Only the most frequent of these taxa were identified at the species level.

To control variation in species richness of woody plants that was explained by differences in the sampling effort (number of observations) between cells, simple linear regressions of each indicator were computed against the number of 3SNFI plots per cell (indicating the real sampled area). We used the residuals resulting from these regressions as the final dependent variables in subsequent analyses.

Eight explanatory variables were included in the analysis (Table 2). Four variables were related to forest management. We distinguished two different methods of silvicultural regeneration treatment: percentage of plots per cell treated with clearcutting (CLEARCUT) or with selection cutting (SELECT). The variable CLEARCUT included plots with shelterwood treatments, although the shelterwood practices represented less than 15% of the total number of plots managed through these two silvicultural systems that are typical of even-aged stands. Stand improvement treatments were also considered (IMPR). These three variables were estimated from the specific information available in the 3SNFI plots. Silvicultural practices were applied to 30% of the plots in the study area. Regeneration treatments were applied to 15% of plots (selective cutting: 9%, clearcutting: 4%, and shelterwood: 1%). Improvement treatments were applied to 20% of plots. The fourth management variable, agrosilvopastoral practices (SILVOPAST), covered 6% of the

Table 1. Frequencies of the three most common species (or taxa) of woody plants in each of the six environmental zones in the sampling area according to Metzger et al. (2005).

Environmental Zone	Tree species	Frequency (%)	Shrub taxon	Frequency (%)
ALS (36 tree species, 44 shrub taxa)	<i>Quercus pyrenaica</i>	36	<i>Cytisus</i> spp.	32
	<i>Fagus sylvatica</i>	31	<i>Erica arborea</i>	30
	<i>Pinus sylvestris</i>	31	<i>Rosa</i> spp.	29
ATC (24 tree species, 49 shrub taxa)	<i>Quercus ilex</i>	44	<i>Genista</i> spp.	44
	<i>Pinus pinaster</i>	41	<i>Arctostaphylos uva-ursi</i>	42
	<i>Quercus faginea</i>	34	<i>Rosa</i> spp.	37
MDM (68 tree species, 108 shrub taxa)	<i>Pinus sylvestris</i>	30	<i>Thymus</i> spp.	42
	<i>Quercus pyrenaica</i>	27	<i>Rosa</i> spp.	33
	<i>Pinus nigra</i>	24	<i>Lavandula latifolia</i>	16
MDN (66 tree species, 116 shrub taxa)	<i>Quercus ilex</i>	43	<i>Thymus</i> spp.	60
	<i>Pinus pinaster</i>	30	<i>Rosmarinus officinalis</i>	21
	<i>Quercus faginea</i>	14	<i>Lavandula stoechas</i>	18
MDS (57 tree species, 86 shrub taxa)	<i>Quercus ilex</i>	75	<i>Cistus ladanifer</i>	30
	<i>Pinus pinea</i>	13	<i>Thymus</i> spp.	21
	<i>Pinus pinaster</i>	11	<i>Rosmarinus officinalis</i>	19

Table 2. Explanatory variables computed in each sampling unit (a 5 × 5-km cell) and considered in the final analysis.

CLEARCUT	Percentage of the 3SNFI plots managed with clearcutting or shelterwood treatments
SELECT	Percentage of the 3SNFI plots managed with selection-cutting treatments
IMPR	Percentage of the 3SNFI plots presenting stand improvement treatments (cleaning, precommercial thinning, thinning or pruning)
SILVOPAST	Land area occupied by agrosilvopastoral practices (m ²)
Ann-PREC	Average total annual precipitation (mm)
Jul-TEM	Average temperature in July (°C)
sd-SLOPE	Standard deviation of slopes (°)
BA	Average of the basal area in the 3SNFI plots (m ² ha ⁻¹)

total forest area and was concentrated in the southwest region (Fig. 2). The area occupied by these agrosilvopastoral systems was estimated using the Spanish Forest Map (SFM). The SFM, developed within the 3SNFI, has a vector data structure, a scale of 1:50 000 and a minimum mapping unit of 2.25 ha. It has been developed from the interpretation of aerial photographs (dated 1997–1998 in the study area) combined with pre-existing maps and field surveys.

Environmental and biotic variables were selected according to the major relationships identified in previous research (see Introduction). Accordingly, we included variables representing climate (water and energy), spatial heterogeneity and biotic interactions. However, the final set of variables was constrained by multicollinearity. The selected variables should not have Spearman correlation coefficients (r) higher than 0.5 between them. Thus, final climatic variables were mean annual precipitation (Ann-PREC) and mean July temperature (Jul-TEM). Climatic data were obtained from the Climatic Atlas of the Iberian Peninsula at a resolution of 200 m (Ninyerola et al. 2005). Topographic complexity was represented by the standard deviation of slopes in each cell (sd-SLOPE), quantified from the official Spanish Digital Elevation Model at a resolution of 25 m (Ministerio de Fomento 1999). Mean basal area (BA) was estimated from the tally trees of the 3SNFI plots to account for the effects of stand stocking and maturation on species richness of woody plants not covered by processes related to productivity (climate) and management. Additionally, BA could be reflecting biotic interactions between the tree stratum and other vegetation layers, such as shrubs. Spatial patterns of the explanatory variables are represented in Fig. 2. Each variable was standardized to zero mean and unit standard deviation to eliminate the effect of differences in the measurement scale and to allow a comparison of the regression coefficients between models (particularly in the case of GWR).

Statistical analyses

The relationships between the explanatory variables and each biodiversity indicator were evaluated using both global Ordinary Least-Squares (OLS) regression and local Geographically Weighted Regression (GWR) models; GWR models were computed using GWR 3.0 software (Charlton et al. 2003). OLS models, but not GWR models, were based on the assumption of spatial stationarity of the relationships.

A step-wise OLS model selection was performed based on the Akaike Information Criterion (AIC) to select the final OLS models. Each of the eight explanatory variables (Table 2) was included in the GWR model, in which variable selection was not possible, and in the initial OLS model for the step-wise selection. The most complex potential OLS model included each quadratic term and the interaction between energy (Jul-TEM) and water (Ann-PREC). The simplest model included only the intercept. We used the *step* function in R statistical software (<http://www.r-project.org>).

GWR provides local estimates of the parameters at each regression point – here the centroids of the 3996 UTM cells – using a weighted calibration in which the influence of the other observations decreases inversely to their distance to the location under consideration through a spatial kernel function (Fotheringham et al. 2002). The bandwidth determines the rate at which the weighting of an observation declines and reflects an approximation of the extent of the zone considered around each local regression model.

We applied a fixed-kernel Gaussian function. Bandwidth selection was based on analysis of the spatial autocorrelation of the residuals of the global (OLS) model. Autocorrelation of residuals can invalidate inferences from a model (Legendre & Legendre 1998); but allowing geographically varying relationships can reduce this problem (Fotheringham et al. 2002). We built correlograms with a lag distance of 5 km for each biodiversity indicator using the Rookcase Excel add-in (Sawada 1999). We calculated the distance at which the value of Moran's I crossed the expected value for the absence of spatial autocorrelation, indicating the spatial range of the pattern (Fortin & Dale 2005). In order to use the same extent and allow for the comparability of shrub and tree GWR models, the maximum spatial range of both correlograms was used as a common bandwidth. Remaining spatial dependence in OLS and GWR residuals was evaluated with global Moran's I coefficients using the corresponding bandwidth as the lag distance. The significance of the autocorrelation coefficient was assessed through a Monte Carlo randomization test with 999 runs, with the software Rookcase. In order to assess the improvement in GWR

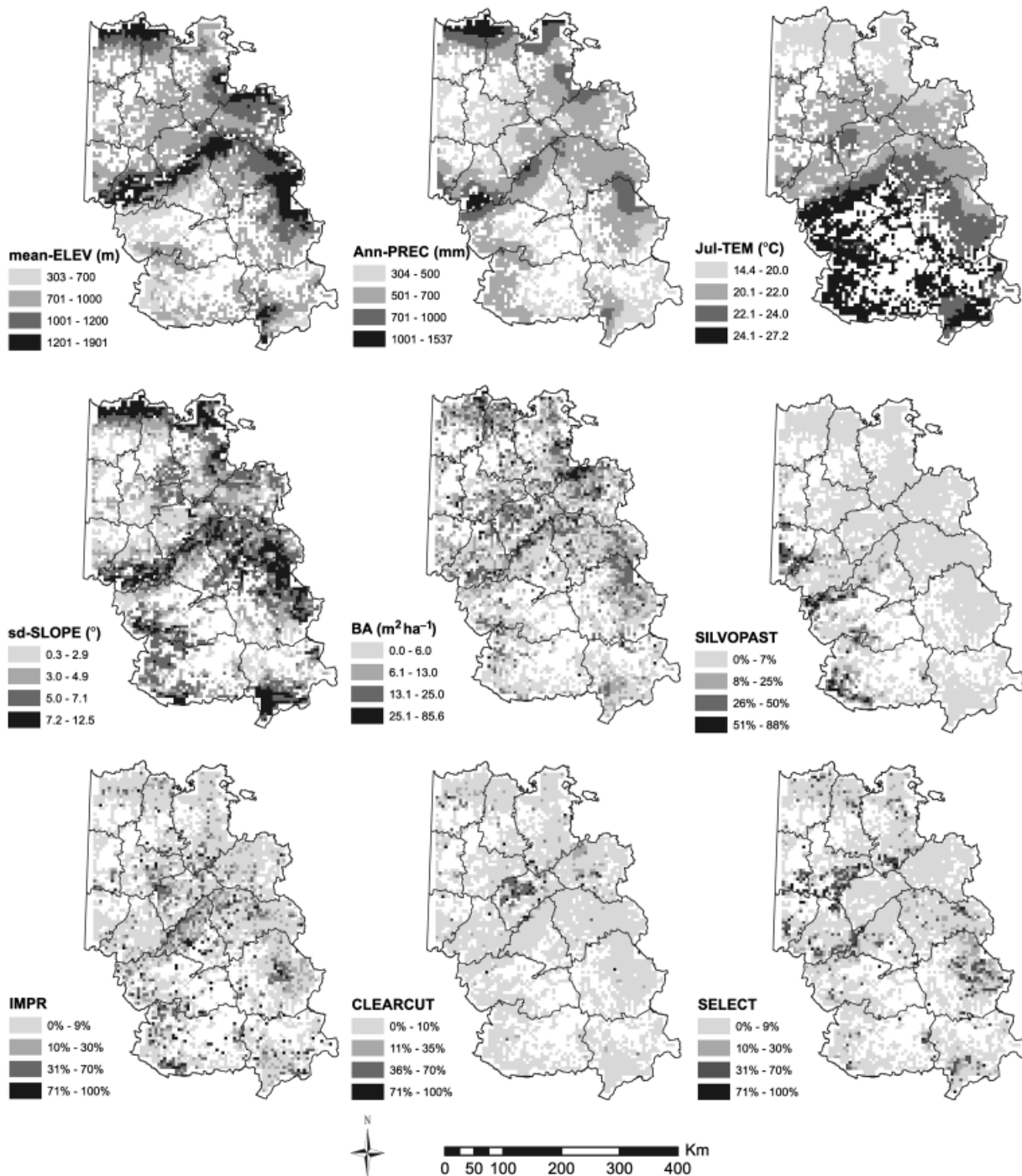


Fig. 2. Geographical patterns of the explanatory variables in the study area. Mean elevation (mean-ELEV) of the 5×5 -km UTM cells is also represented in order to show the distribution of the main mountain chains across the study area, although this was not included as an explanatory variable in the final models (see Methods).

models with respect to OLS models, differences in AIC values were estimated.

Simultaneously testing statistical significance of all the local parameters in the study area implies an increased

Type I error (Fotheringham et al. 2002). The choice of applying Bonferroni corrections is a conservative approach when considerably large sample sizes are analysed, as is the case in this study; alternative approaches

have been suggested (e.g. Benjamini & Yekutieli 2001). Here, we adjusted the family-wise error rate (i.e. 0.05), dividing it by the effective number of parameters (ENP), which in initial experiments suggested similar results as in the cited approach (Dr. Martin Charlton, personal communication). A Monte Carlo significance testing procedure was applied to examine if variability in local coefficients was due to random variation or reflected a true geographical trend (Fotheringham et al. 2002).

Results

OLS models had higher AIC values than GWR models (Table 3), indicating a better performance for the latter. Correlograms from OLS model residuals revealed spatial ranges of 60 km and 135 km for tree and shrub species richness, respectively, and consequently the selected bandwidth for both GWR models was set to 135 km. For the tree species, Moran's *I* values at distances above 60 km oscillated around the expected value (i.e. there was an absence of significant spatial autocorrelation in the error term). GWR analyses accounted for most of the spatial variation of the indicators. Residual autocorrelation, as measured by global Moran's *I* (Table 3), was much smaller for a GWR model than for the comparable OLS model.

Relationships between explanatory variables and species richness of woody plants in global (OLS) models

Each of the two indicators of biodiversity was highly correlated with environmental, biotic and/or agrosilvopastoral factors. Comparatively lower coefficients were found for silvicultural treatments (Fig. 3). The main explanatory variables for tree species richness were basal area and mean annual precipitation, and for shrub species richness were standard deviation of slopes and agrosilvopastoral practices. Each management variable was significantly related to each of the two biodiversity indicators (Fig. 3). Most relationships were curvilinear, except for mean July temperature, standard deviation of slopes and agrosilvopastoral practices in both models (Fig. 3). Linear regression coefficients for agrosilvopastoral practices were negative for each biodiversity indicator. The coefficient

was especially large for shrub species richness ($\beta = -0.18$ versus -0.06 for trees). Improvement and selection treatments had a weak positive coefficient for models of both trees and shrubs when less than approximately 40–60% of the plots in the cells received the treatment. The association became negative beyond these thresholds (Fig. 3). Only about 2% and 10% of the cells in the study area were beyond these thresholds. Clearcutting association with both indicators was significantly negative in cells with percentages below 60–70%, but became positive above these thresholds, only occurring in 1% of the cells.

The increase in annual precipitation was in general associated with an increase in tree species richness but a decline of shrub species richness (Figs 3 and 4). For shrub species richness, the effect of the interaction between the two climatic variables was significant (Fig. 4). Annual precipitation levels above 820 mm, which occurred mainly in the Alpine South and Atlantic Central Zones, were negatively associated with tree species richness (Fig. 3). The highest and lowest levels of mean annual precipitation and July temperature, respectively, occurred in these zones, which coincided with the lowest number of shrub species estimated by our model in those climatic conditions (Fig. 4). Values of standard deviation of slopes increased linearly with richness of tree and shrub species, particularly for the latter. Basal area had a strong positive regression coefficient with the number of tree species for the most common values of basal area ($0\text{--}30\text{ m}^2\text{ ha}^{-1}$), and negative for higher values. The quadratic term of basal area was significant in both models, but within the positive range of basal area values, its relationship with shrub species was always negative (Fig. 3).

Relationships between explanatory variables and species richness of woody plants in local (GWR) models

The test-wise error rate (i.e. $0.05/\text{ENP}$) used to assess the significance of the GWR regression coefficients was 0.0024. Almost all environmental and biotic factors had a spatially non-stationary relationship with the analysed biodiversity indicators (Fig. 5). Monte Carlo tests did not

Table 3. Results of the analysis of spatial autocorrelation in residuals from ordinary least squares (OLS) and geographically weighted regression (GWR) models. The bandwidth (135 km) was used as the lag distance in the estimation of Moran's *I* coefficients. AIC values for both types of model are also shown.

	OLS			GWR		
	AIC	Moran's <i>I</i>	<i>P</i> -value	AIC	Moran's <i>I</i>	<i>P</i> -value
Tree species richness	10 758	0.0034	0.001	10 664	0.0007	0.059
Shrub species richness	10 116	0.0493	0.001	9 859	0.0192	0.001

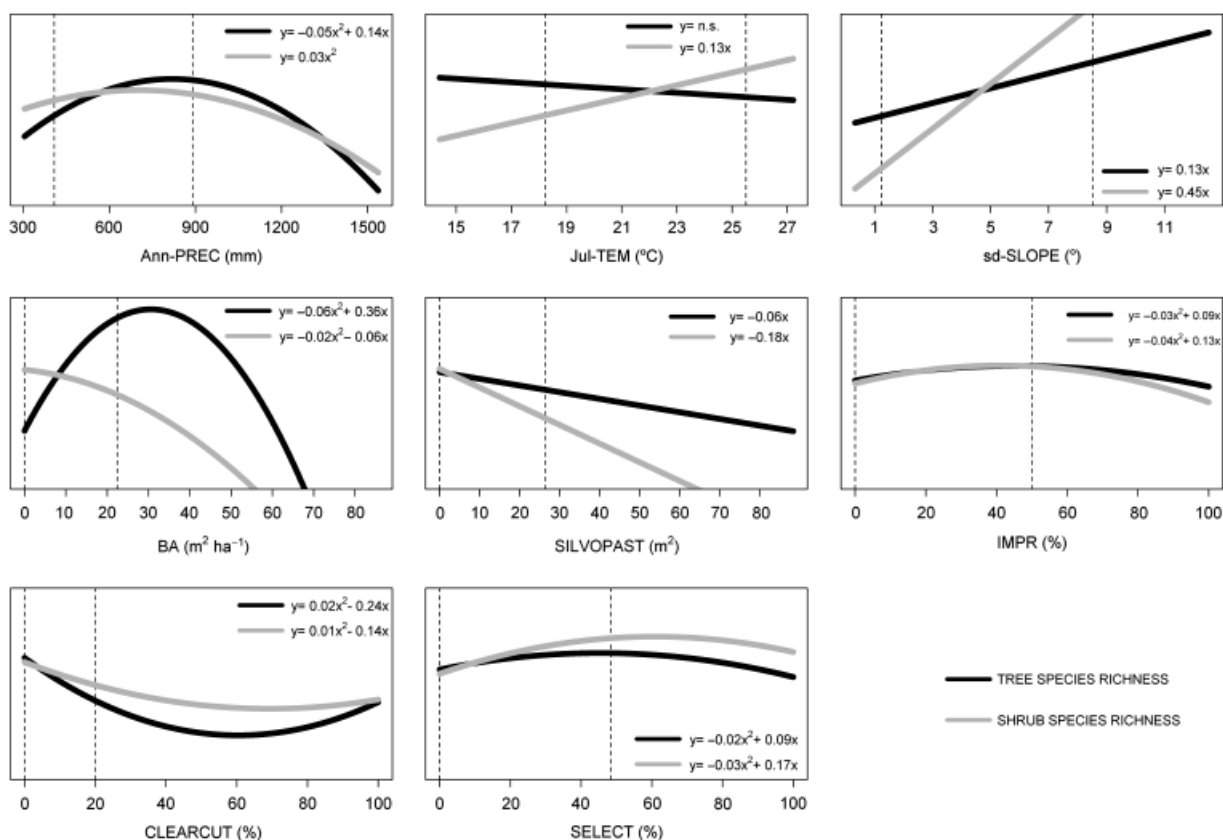


Fig. 3. Relationships, according to OLS results, among species richness for trees and shrubs and each of the explanatory variables, while maintaining constant the remaining variables (mean value). The X-axis represents the entire range of variation of the explanatory variable in the study area. The vertical dashed lines delimit the 90% X central distribution. The Y-axis range is constant in each plot and represents the 60% Y (trees or shrubs) central distribution. Partial regression coefficients in the formula are estimated with both dependent and explanatory variables standardized. In order to facilitate plot interpretation, the original X values are shown. ns: non significant.

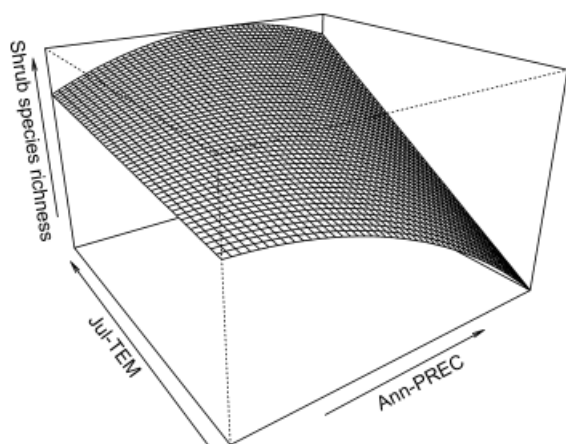


Fig. 4. Response surface of shrub species richness to the interaction Jul-TEM \times Ann-PREC ($\beta = 0.05$, $P < 0.001$). The rest of explanatory variables were kept constant (mean value). The displayed ranges of both explanatory variables correspond to those found in the study area.

show significant non-stationarity for most management variables. For the stationary factors (mainly management factors), the relationships found in the OLS models are assumed to be applicable to the whole study area and they were not mapped in Fig. 5. As shown in Fig. 5, only the intensity of the non-stationary relationships varied geographically (including an absence of a significant relationship in some localized areas), whereas spatial changes on sign were not observed. The spatial patterns of the intensity of the relationships between environmental or biotic factors and tree species richness were opposite to those for shrub species.

Discussion

Forest management factors

Patterns of biodiversity at biogeographical scales may not be affected by disturbances such as those due to forest

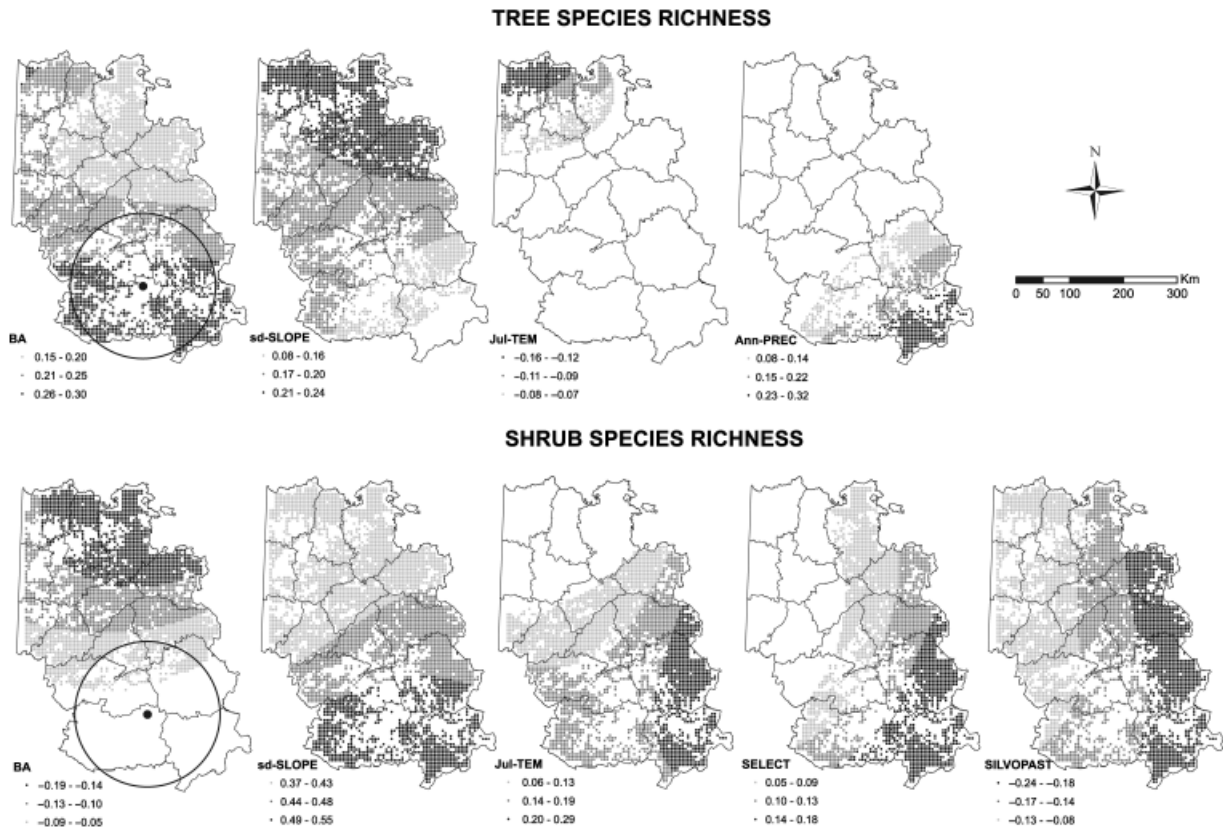


Fig. 5. Spatial variation of the local regression coefficients of GWR models for species richness of trees (top) and shrubs (bottom). Only significant coefficients after multiple testing corrections (see Methods) are drawn. Note that other explanatory variables may also be significant according to OLS results, but are not shown here when their relationships with the biodiversity indicators did not significantly vary spatially; significance level in Monte Carlo tests for the variables shown was always less than 0.001. The approximate extent of the area encompassed by each local model according to the size of the bandwidth (135 km) is shown with a circle.

management, which might be a consequence of an observed equilibrium linked to enlargement of the scale (de Angelis & Waterhouse 1987). However, although at the meso-scale here analysed (i.e. at a grain size of 25 km²), patterns of species richness of woody plants were strongly determined by environmental and biotic variables, these patterns were also modified by ecological processes induced by silvicultural treatments. This concurred with a recent study in Catalonia (NE Spain) by Torras et al. (2009), who found that management intensity had a small, positive effect on tree species richness and diversity at a grain size of 100 km², but not on shrub species richness.

Notably, we found that impacts on woody plant species varied among silvicultural treatments. Intense disturbances resulting from clearcuts were associated with lower species richness. In contrast, less intensive treatments such as selection cutting and improvement treatments were associated with higher species richness, at least below a proportion of managed forest area. This proportion is not frequently exceeded in central Spain. Indeed,

as stated above, most plots in the study area are currently unmanaged (70%). Agricultural land abandonment together with forest non-intervention has been occurring in the last decades in some areas of the Mediterranean Basin (e.g. Gil-Tena et al. 2010). The decline in forest management derives from the replacement of traditional forest products – with a current low profitability – with new fuel sources and building materials. In this context, some types of management practice could be a source of structural heterogeneity within forest patches that ultimately increases *gamma* biodiversity. In the framework of the non-equilibrium paradigm, the increase in biodiversity with moderate disturbance fits with the intermediate disturbance hypothesis. According to this hypothesis, the number of species is maximized if the intensity of ecological disturbances is moderate. At moderate levels, competitive exclusion is controlled, heterogeneity is favoured, and a balance with the consequent environmental stress is achieved (Connell 1978). Both selection cutting and improvement treatments, as currently applied in the study area at the grain size of 25 km², seemed to match

with the intermediate disturbance intensity, frequency and gap sizes found to be most favourable for species diversity. Our results are consistent with previous findings at the stand scale (e.g. Roberts & Gilliam 1995; Auri et al. 2004; Torras & Saura 2008). However, some authors have suggested that at a coarser grain size, the heterogeneity that results from the spatial age mosaic of even-aged clearcut stands (plots) might favour *gamma* diversity rather than a continuous uneven-aged forest with a uniform application of selection cuttings throughout the landscape (Decocq et al. 2004). The latter treatment may increase woody plant diversity locally (*alpha* diversity, at the plot level), while impoverishing the variety of species at wider spatial scales. The loss of *gamma* species richness of woody plants that may result from homogenization by selection cuttings was found in our study at intermediate scales only when more than 60–70% of the forest landscape was managed, which is rarely the case in Central Spain. For the same reasons, the positive response of species richness to clearcutting of more than 60–70% of the total forested landscape should be interpreted cautiously because such a response corresponded only to a few outlier cells that are not representative of the typical current practices in the study area (Fig. 3).

Although silvicultural impacts on species richness of woody plants were, in general, stationary across the study area, the relationship between selection cutting and shrub species richness varied spatially. The dynamic equilibrium model (Huston 1979) states that diversity depends not only on the intensity, periodicity and extent of the disturbance, but also on the growth rate. According to the model, the characteristics of the disturbances that maintain maximum diversity will vary depending on site productivity because different processes (competitive exclusion or environmental stress) will prevail (Odion & Sarr 2007). Competitive control between shrub species might dominate those areas in which selection cutting was found to favour species richness of shrubs (Fig. 5). In these areas, lower water availability reduces tree density or even favours shrubby land formations under poorer soil conditions.

Species richness of both trees and shrubs declined with an increase in the extent of traditional grazing systems (*dehesas*). The decline was particularly prominent in the western part of the study region (Fig. 5). The decline could have been anticipated: management practices that are typical of traditional grazing systems (tree clearing and pruning and periodical ploughing) encourage scattered formations of *Quercus ilex* or *Quercus suber* with < 5–10% of shrub cover (Plieninger 2006; Ramírez & Díaz 2008). This type of management, combined with the grazing pressure, inhibits the regeneration and establishment of other woody species and facilitates livestock grazing and

crop cultivation. *Dehesas* are highly diverse because of the herbaceous understorey and the variety of animals that benefit from the co-existence of microhabitats typical of grassland and forest formations (Díaz et al. 2003; Ramírez & Díaz 2008). For instance, in the study of Peco et al. (2006) more than 90% of the understorey plant species in these systems were annuals. Therefore, despite their low species richness of woody plants, *dehesas* have a remarkable intrinsic value and the need to conserve them is acknowledged (see Plieninger 2006).

Environmental and biotic factors

In the Mediterranean Zones, higher annual rainfall was associated with higher tree and shrub species richness in those regions with most extreme temperatures in summer (Figs 3 and 4) (such as the Mediterranean South Zone; Fig. 1), but with lower species richness of shrubs under milder conditions (Fig. 4). The positive association of woody species richness with precipitation might be due to a decline in productivity associated with hydric stress, as pointed out by Lobo et al. (2001). Hydric stress would be caused by scarce water and high energy inputs in the Mediterranean. Our results suggested that this stress has a greater limiting effect on tree species than on shrub species under moderate summer temperatures. These results could also be explained by a higher tree basal area expected in the most productive areas related to climate patterns.

Because temperature decreases with increasing altitude, effects of altitude could be mediated by climate at the local scale (i.e. as captured by GWR models). Especially in mountain regions in the edge of the study area, correlation coefficients above |0.9| were estimated in some local models in the Alpine Zone. This was not necessarily the same for the whole study area (OLS models), where r for annual precipitation and July temperature was, respectively, 0.55 and -0.65 . This means that, on the one hand, the different extent considered by GWR and OLS techniques could determine a focus on different processes underlying the observed relationships; on the other hand, local multicollinearity in the explanatory variables on GWR results (Wheeler & Tiefelsdorf 2005) might have influenced the observed patterns in the relationships (but see Smith et al. 2009). According to this, the global pattern of annual precipitation might reflect a reduced richness in tree species in the Alpine Zone when compared to other Mediterranean areas (OLS results; Fig. 3). Within the more reduced pool of species in the smaller extent of the Alpine Zone (GWR results; Fig. 5), a positive altitudinal gradient of tree species richness might exist, which is linked to the decrease in July temperature with elevation. However, this did not agree

with Nogués-Bravo et al. (2008), who found that, at the same grain and extent (0–2000 m), species richness for vascular plants, lichens and bryophytes decreased with increasing altitude in the Pyrenees. Therefore, it seems that along the Iberian Peninsula, the patterns of *gamma* species richness of woody plants with altitude at a landscape scale could vary because of different underlying processes related to resource availability and productivity, ultimately determined by larger scale climate patterns.

Species richness of woody plants increased with topographic complexity in our study. It was a particularly important factor in the shrub species model. This factor would favour species richness through an increase in surface area and a greater variety of microclimate conditions and bedrocks (see Vetaas & Ferrer-Castán 2008 and references therein), especially in the most xeric areas for shrubs, as shown by the GWR models. Additionally, these results could reflect shrub encroachment and colonization processes in those less productive and less accessible areas that are more likely to be abandoned.

Landscape patterns of forest basal area not explained by silviculture or climate patterns were a key factor positively associated with tree species richness. More mature forests with greater tree biomass were associated with an increase in the number of tree species at the landscape scale. This could be explained through the association between site productivity and higher basal areas and the significant relationship between productivity and tree species richness. Causality could exist in the opposite sense: higher tree species richness might allow more productivity and thus higher basal area (Vilà et al. 2007). Moreover, forests with currently higher basal area might have suffered from lower anthropogenic degradation in the past. However, cells with a mean basal area greater than $30\text{ m}^2\text{ ha}^{-1}$ had fewer tree species. Although this occurred in less than 2% of the studied cells, it might have been due to a homogeneous forest structure and age within the 25-km^2 area of the cell, which probably led to impoverishment of *gamma* diversity at this grain size. The increase in landscape basal area was, however, associated with a poorer shrub stratum independent of the range of BA. This was particularly true in the Atlantic Zone according to GWR results, probably because the density of the tree canopy was greater, penetration of light was reduced, and the growth of understorey plants was limited.

Conclusions

Management factors are not frequently evaluated in biodiversity models at the landscape scale. However, the impact of management on *gamma* species richness might be significant at an intermediate grain size, as shown in

our results. Furthermore, higher levels of species richness of woody plants were found in landscapes with moderate intensity management disturbances in Central Spain. The exclusion of factors such as agrosilvopastoral systems from the models in a study of this kind, given their characteristic geographical distribution, could have led to spurious relationships with other spatially co-varying factors (e.g. summer precipitation) and to potentially misleading conclusions about the biodiversity drivers in the study area.

Many relationships showed non-stationarity across the study area. Thus, global trends that were observed in vast study areas should be interpreted carefully (Fortin & Dale 2005). These trends could result from a counteraction of different strengths of the relationships across the study area. Spatial variation can be discerned via GWR, and hypotheses can then be formulated to explain spatial variation, complementing OLS results. However, the observed patterns of the relationships in OLS and GWR might not be comparable because differences in the extent could also determine a focus on different ecological processes in each analysis.

We acknowledge that species richness of woody plants should not be viewed as a surrogate for biodiversity. To have a more holistic view of the interactions between environment, management and forest ecosystem functioning, the impact of forestry practices on other functional groups and components of biodiversity (such as ecosystem and genetic diversity) should be considered in further studies. Many studies have reported the negative effects of some types of forest management on other taxa (e.g. birds, invertebrates, fungi) due to a decline in the amount of deadwood and old trees, among other factors (e.g. Loyn & Kennedy 2009; Vandekerckhove et al. 2009). However, other studies have suggested that moderate-intensity forest practices favour forest biodiversity or have a very minor effect compared to other large-scale processes, such as widespread maturation after large-scale rural abandonment (see Gil-Tena et al. 2010 and references therein). Population isolation and artificial regeneration should also be avoided in order to prevent the potential negative effects of harvesting treatments on genetic diversity (Finkeldey & Ziehe 2004). While we here took into account different extents and related ecological processes (as captured by GWR and OLS), the grain size was kept constant in all our analyses. We recognize the importance of extending the study to other grain sizes different from the 25 km^2 here considered, since this scale component largely determines the relative influence of large climate trends versus more local management factors on biodiversity patterns. This is part of our ongoing research. Finally, the variation of species diversity with scale and disturbance regime here reported

might differ from that existing in other regions with different forestry practices and productivity contexts.

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