

Effects of silviculture on native tree species richness: interactions between management, landscape context and regional climate

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Summary

1. Patterns of forest biodiversity are shaped by a complex set of processes operating over different spatial scales. Climate may largely determine species richness at regional scales, but biotic interactions and disturbance events are known to be important at local scales. The interactions between these local and regional processes are poorly understood, complicating efforts to manage for biodiversity.

2. In this study, we used Spanish forest inventory data, together with hierarchical Bayesian models, to analyse how different harvest intensities affect patterns of species richness in a 152 000 km² area in central Spain. Particularly, we quantified the interacting effects of locally applied silvicultural disturbances, of those applied in the surrounding landscape, and of the regional climate on native tree species richness.

3. Our study supports the overall hypothesis that a hierarchical set of processes influence species richness, with regional climate contributing to shape the impacts of local harvesting practices and other environmental variables (topography and productivity).

4. In particular, we found that partial harvesting in both coniferous and broad-leaved Mediterranean forests may support greater tree species richness than complete harvesting and no management. However, this effect depended on the ecosystem and the surrounding landscape, being much less likely in semi-arid regions under water stress conditions and in landscapes dominated by managed forests (and particularly by completely harvested stands).

5. In general, forest stands exhibited increased tree species richness when surrounded by species-rich riparian forests, probably due to metacommunity dynamics and/or ecological history (land uses) of the area.

6. *Synthesis and applications.* The effects of forest management on local species richness were shaped by coarse climate conditions and by the type and extent of other management practices in the surrounding landscapes. Therefore, to develop effective forestry management plans that optimize local diversity, we need to (i) apply regionally tailored practices with lower harvest intensities in areas of greater hydric stress; (ii) avoid the extensive application of a single silvicultural system over large areas and (iii) preserve a mosaic of species-rich forests that can act as sources of colonizers to enrich the regenerating stands nearby.

Key-words: biodiversity, disturbance ecology, hierarchical Bayes, intermediate disturbance hypothesis, landscape ecology, Mediterranean forests, metacommunity dynamics, partial harvesting, spatial scale

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Introduction

It is widely accepted that the drivers of species diversity and their relative importance vary with spatial scale (Whittaker, Willis & Field 2001; Field *et al.* 2009). For instance, climate has been found to be the main driver of regional scale (grain and/or extent) patterns of plant species richness, while processes affecting biotic interactions, such as disturbances, have been suggested to explain patterns at finer scales (Sarr, Hibbs & Huston 2005; Kallimanis *et al.* 2007). Thus, considering scale and the hierarchical structure of ecosystems – in space, time and/or ecological organization – are fundamental to understand ecological processes influencing species diversity (Levin 1992; McMahon & Diez 2007). In particular, species-richness patterns likely derive from the interaction of factors taking place at varying scales (e.g. Sarr, Hibbs & Huston 2005). Still, most studies analysing biodiversity patterns do not account for the different scales of the driving factors and their potential interactions (although with few exceptions, that is, classification and regression trees (De'ath & Fabricius 2000)), nor consider the hierarchical organization of natural ecosystems.

The importance of interacting variables across scales is particularly relevant for determining the influence of large-scale environmental constraints on the response of ecological communities to local disturbances. For example, the effects of resource release following disturbance on species interactions will depend on the overall levels of resources in a system. Similarly, the stress resulting from disturbances will be greater where growth is already constrained by abiotic stresses from climatic extremes (Kondoh 2001). Furthermore, species perception of stress (e.g. shade, drought and late-frost sensitivity) is usually associated with evolutionary forces related to coarse climatic conditions and to the historical disturbance regime (e.g. Lloret *et al.* 2007). Therefore, climatic conditions may affect not only large-scale patterns of species richness through their effects on productivity (Currie & Paquin 1987; Field *et al.* 2009), but also local patterns through their effects on plant community responses to disturbances.

In addition to natural disturbances, human-caused disturbances such as harvesting can also modify species diversity in local communities (e.g. Roberts & Gilliam 1995). Through its varying levels of canopy removal, silviculture helps determine the competitive environment for tree seedlings, the most sensitive life history stage of trees (Grubb 1977), thereby shaping understorey dynamics and influencing tree species diversity for decades (e.g. Halpern & Spies 1995; Onaindia *et al.* 2004; Torras & Saura 2008). The effect of silvicultural regeneration treatments on local forest biodiversity has been the focus of substantial research in the last few decades. These studies are common in North America and Scandinavia where intensive forest management occurs over large areas (e.g. Kuuluvainen 2009). However, few such studies exist for

the Mediterranean region (but see Torras & Saura 2008; González-Alday, Martínez-Ruiz & Bravo 2009; Navarro *et al.* 2010). Additionally, much of this research has been short-term experiments, best suited for evaluating changes in the herbaceous community during the first successional stages (e.g. Hannerz & Hanell 1997; Götmark *et al.* 2005). Thus, there is a knowledge gap on the potential medium- to long-term effects of silvicultural practices on forest diversity.

The recovery process after a disturbance event will depend on propagule availability and connectivity with populations in the surrounding landscape (Damschen & Brudvig 2012). Therefore, the number of species in a community may also be influenced by metacommunity dynamics occurring at intermediate spatial scales (Jamoneau *et al.* 2011). In the Mediterranean basin, hundreds of years of human management have shaped modern forest landscapes (Blondel & Aronson 1999) and still do today. In Spain, *dehesas* are traditional systems characterized by extensive semi-forested areas with evergreen oaks (*Quercus ilex* and/or *Quercus suber*) scattered over grasslands or cereal crops (e.g. Díaz, Pulido & Marañón 2003). Pine plantations are another common type of managed woodland in Spanish landscapes due to a policy of reforestation prevailing since the beginning of the 20th century that have promoted millions of hectares of planted forests, mainly conifers (Valbuena-Carabaña *et al.* 2010).

In this study, we use a hierarchical framework to test how several interacting factors – regional climate, harvesting practices and the surrounding landscape – affect the native tree species richness of forests in central Spain (152 000 km²). In particular, we evaluated whether the effects of different harvest intensities on tree species richness are contingent on regional climate and the neighbouring landscape. Our main questions are the following: (i) after accounting for processes operating at larger scales, that is, regional climate, how do different harvest intensities affect native tree species richness of forest stands? (ii) how do the effects of harvesting on tree species richness depend on forestry practices in the surrounding landscape? and (iii) does the composition of the surrounding landscape affect local tree species richness?

Materials and methods

STUDY AREA

The study area covers the Spanish regions of Castilla-La Mancha, Madrid and most of Castilla y León (Fig. 1). According to the European environmental stratification by Metzger *et al.* (2005), each of the main environmental zones (EnZ) in the European Mediterranean basin is represented in our study area (Fig. 1a): Mediterranean Mountain (MDM), Mediterranean North (MDN) and Mediterranean South (MDS). There is a gradient MDM–MDN–MDS of increasing temperature and decreasing precipitation (Fig. 1b), being the southern region characterized by a particularly marked water deficit in summer.

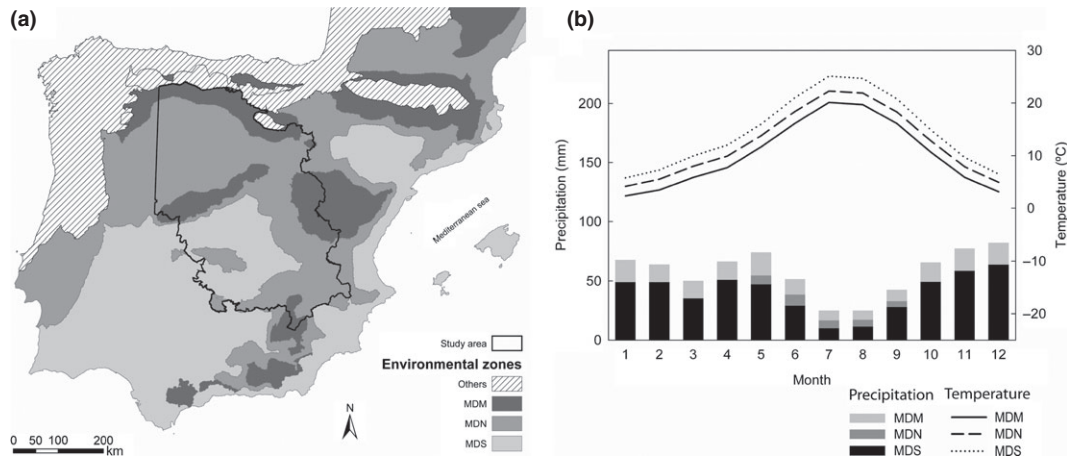


Fig. 1. Location of the study area. (a) Environmental zones according to the European stratification by Metzger *et al.* (2005): MDM, Mediterranean Mountain; MDN, Mediterranean North; MDS, Mediterranean South. (b) Climate diagrams for each environmental zone in the study area (data source: Ninyerola, Pons & Roure 2005).

DATA

The Third Spanish National Forest Inventory (3SNFI, Ministerio de Medio Ambiente 1997–2007) was used as the data source for native tree species richness, type of forest or functional group, harvest intensity, successional stage, basal area and forest canopy cover. The 3SNFI had a systematic sampling design, with plots located at the intersections of a 1 × 1 km UTM grid that fall within forests with a minimum canopy cover of 5%. A total of 24 498 inventory plots were surveyed in the study area from 2000 to 2004. For each plot, the total number of tree species, including saplings, was recorded within a 25-m radius circle using a predefined list of 177 tree species. For this study, we excluded exotic species and plots corresponding to plantations, *dehesas*, riparian and burnt forests, leaving a total of 78 native species in 14 306 inventory plots (referred to hereafter as ‘forest plots’). However, all 24 498 plots were used to assess land use/cover composition in the landscape surrounding these forest plots (see below).

A functional group, or forest type, variable (FUNC) was defined based on the functional identity of the dominant tree species of each plot. The following categories were distinguished: broad-leaved deciduous (BD), sclerophyllous evergreen (SE) and coniferous forests (CO). Mixed-forest plots, those with two co-dominant species of different functional groups (<1%), were not considered in the analysis of tree species richness.

The 3SNFI surveys also characterized the type of harvesting – clear-cutting, shelterwood cutting or selection cutting – applied in each forest stand, based on either direct knowledge or indirect evidence such as stumps or slash indicating management activity within approximately 10 years since the previous SNFI survey. Because a one-time field assessment only gives evidence of the degree of canopy removal, rather than the whole set of forestry practices during the rotation period, we renamed harvesting categories as the following: complete harvesting (clearcutting), partial harvesting (selection cutting) and no treatment. Species richness was not assessed in forest plots with shelterwood cutting due to the small sample size (only 79 plots). The numbers of plots and dominant tree species for each combination of environmental zone (EnZ), functional group (FUNC) and harvesting intensity category are presented in Table 1.

We also obtained data for each plot from the 3SNFI on four additional variables that may affect species richness: basal area,

forest canopy cover (FCC), slope and successional stage. Basal area and FCC accounted for coarse differences in forest types across the study area. Basal area ($\text{m}^2 \text{ha}^{-1}$) was estimated in the 3SNFI from a sample of trees selected depending on the stem diameter at breast height (DBH), and its distance to the plot centre, ranging from 5-m radius 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. Slope and FCC were measured in the field in the 3SNFI. The number and composition of tree species naturally varies across successional stages. Successional stage was therefore considered and estimated as an ordinal variable based on the average development stage of the three dominant tree species inventoried in each plot: (i) recently regenerated (up to canopy closure); (ii) thicket (up to natural pruning); (iii) trees with $\text{DBH} \leq 20$ cm and (iv) trees with $\text{DBH} > 20$ cm.

Three climatic variables important for tree species richness in this region were also considered: total precipitation from September to May (representing the Mediterranean growing season), maximum temperature in July (as a proxy for maximum annual temperature) and minimum temperature in January (representing the lowest annual temperature). Climate variables were obtained at a resolution of 200 m from the Climatic Atlas of the Iberian Peninsula (Ninyerola, Pons & Roure 2005) and matched to each of our plots. We also considered plot elevation, which was calculated from the official Spanish Digital Elevation Model at a resolution of 25 m (Ministerio de Fomento 1999). The selection of these variables was based on exploratory analyses and on the literature about factors affecting plant species diversity. Temperature and precipitation are critical determinants of productivity and stress (e.g. Currie & Paquin 1987; Mittelbach *et al.* 2001). Elevation was intended as a proxy for altitudinal gradients in additional factors difficult to quantify, such as total altitudinal bands area, net primary productivity or those derived from evolutionary geometric constraints or historical human land-use intensity (see Nogués-Bravo *et al.* 2008).

The landscape context surrounding each forest plot was characterized using all 3SNFI plots, including those outside the boundary of the study area to avoid edge effects. For this landscape context analysis, plots from the 3SNFI were classified into the following categories: forests, plantations, *dehesas*, riparian forests and ‘others’. *Dehesas* were defined in the 3SNFI as woodlands of scattered trees with a minimum FCC of 5% (and

Table 1. Sample size (number of plots, n) and proportion of dominant tree species within the stands for each combination of environmental zone (EnZ), functional group (FUNC) and harvesting intensity

EnZ	FUNC	Complete harvesting		Partial harvesting		No treatment	
		n	Composition	n	Composition	n	Composition
MDM	BD	21	90% <i>Quercus pyrenaica</i>	49	71% <i>Quercus pyrenaica</i> 18% <i>Quercus faginea</i>	1321	78% <i>Quercus pyrenaica</i> 15% <i>Quercus faginea</i>
	SE	0	–	26	100% <i>Quercus ilex</i>	793	96% <i>Quercus ilex</i>
	CO	179	90% <i>Pinus sylvestris</i>	523	44% <i>Pinus pinaster</i> 28% <i>Pinus nigra</i> 22% <i>Pinus sylvestris</i>	2649	30% <i>Pinus nigra</i> 30% <i>Pinus sylvestris</i> 17% <i>Juniperus thurifera</i> 14% <i>Pinus pinaster</i>
MDN	BD	0	–	37	43% <i>Quercus pyrenaica</i> 43% <i>Quercus faginea</i>	846	59% <i>Quercus faginea</i> 29% <i>Quercus pyrenaica</i>
	SE	0	–	64	97% <i>Quercus ilex</i>	2260	
	CO	427	90% <i>Pinus pinaster</i>	772	44% <i>Pinus pinaster</i> 33% <i>Pinus pinea</i> 10% <i>Pinus halepensis</i> 8% <i>Pinus nigra</i>	2974	39% <i>Pinus pinaster</i> 21% <i>Pinus halepensis</i> 14% <i>Juniperus thurifera</i> 11% <i>Pinus pinea</i>
MDS	BD	0	–	0	–	69	30% <i>Quercus faginea</i> 28% <i>Quercus pyrenaica</i>
	SE	0	–	42	98% <i>Quercus ilex</i>	939	96% <i>Quercus ilex</i>
	CO	0	–	74	73% <i>Pinus pinea</i> 20% <i>Pinus pinaster</i>	214	51% <i>Pinus pinea</i> 22% <i>Pinus pinaster</i> 13% <i>Juniperus oxycedrus</i>
Total		627		1587		12065	

MDM, Mediterranean Mountain; MDN, Mediterranean North; MDS, Mediterranean South. BD, broad-leaved deciduous; SE, sclerophyllous evergreen; CO, coniferous.

normally with a FCC lower than 20%) and croplands or pastures in the understorey. Additionally, plots within the forest category were subclassified into three harvesting categories according to the observed harvesting intensity: completely harvested forest (including both clear-cut and shelterwood plots), partially harvested forest and unmanaged forest. All missing plots (i.e. the intersections of the 1 × 1 km grid falling outside of forest cover) were assigned to an 'others' category, which encompassed agricultural, urban and other nonforest land uses. The percentage cover of each of these seven land-use categories [forests (partially or completely harvested or unmanaged), plantations, *dehesas*, riparian forests and others] was calculated within two radii of each forest plot, 3.5 and 5.5 km. Selection of these radii was based on a trade-off between exploratory analyses of spatial residuals, ecological criteria on long distance dispersal (e.g. Jordano *et al.* 2007) and assuring a minimum number of plots to represent landscapes.

MODEL DEVELOPMENT

Tree species richness was defined as the number of native species of trees surveyed in a particular 3SNFI forest plot. We constructed a hierarchical, or multilevel, model to account for the different scales, and potential interactions, represented in the data (see Fig. 2 for a conceptual diagram of the hierarchical structure). We followed a Bayesian approach to estimate the model parameters, as is suitable for multilevel models (Gelman & Hill 2007). For our final model (see Table S1 for models considered), tree species richness in plot i , S_i , was estimated as a function of the climatic, topographic, forest structure and management variables presented in the previous section using a Poisson likelihood:

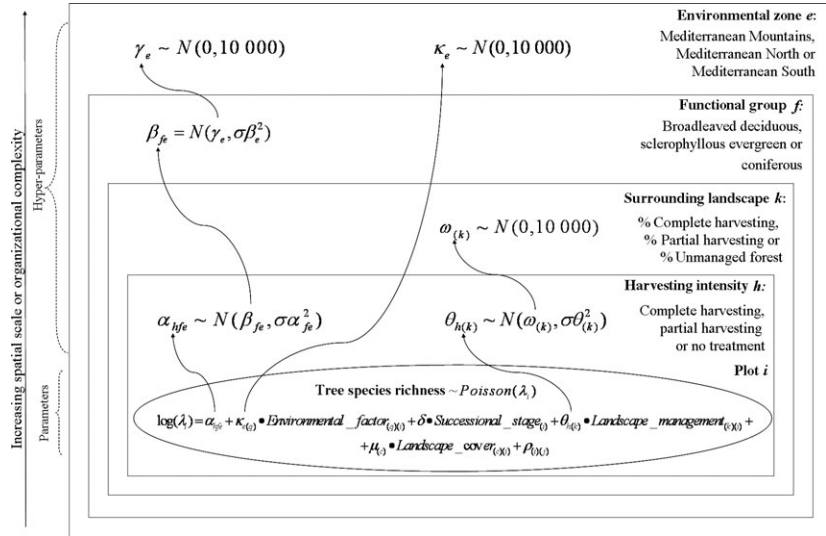
$$S_i \sim \text{Poisson}(\lambda_i)$$

with the plot level mean richness modelled as:

$$\ln(\lambda_i) = \alpha_{hfe} + \delta \bullet \text{Successional_Stage}_{(i)} + \kappa_{e(q)} \bullet \text{Environmental_Factor}_{(q)(i)} + \mu_{(c)} \bullet \text{Landscape_Cover}_{(c)(i)} + \theta_{h(k)} \bullet \text{Landscape_Management}_{(k)(i)} + \rho_{(j)(i)}$$

where α_{hfe} is a nested effect of harvest intensity, h , for each functional group, f , and environmental zone, e (nested structure discussed further below). The parameter δ describes the effect of successional stage on species richness, and $\kappa_{e(q)}$ is a vector of coefficients describing the nested effects of q Environmental Factors (precipitation, temperature, elevation, slope, basal area and FCC) in each environmental region, e (for each q variable, $\kappa_e \sim \text{Normal}(0, 10\ 000)$). We also included quadratic terms for some of the environmental variables, according to exploratory analyses. The vector of parameters $\mu_{(c)}$ represents the regression coefficients associated to each Landscape Cover variable (c = percentage of plantation, *dehesa* and riparian forest). The vector $\theta_{h(k)}$ represents effects of each Landscape Management variable (k = percentage in the landscape of complete harvesting, partial harvesting or no management), depending on each plot's harvesting practice, $\theta_{h(k)} \sim \text{Normal}(\omega_{(k)}, \sigma_{\theta_{(k)}}^2)$. Finally, spatially explicit random effects, $\rho_{(j)(i)}$, were included to reduce autocorrelation in the residuals (Legendre & Legendre 1998). For reasons of computational limitation, plots, i , were grouped in $j = 192$ cells of 30 × 30 km to estimate these spatial random effects. Spatial effects were assigned to a multivariate Gaussian distribution with covariance expressed as a negative exponential function of the distance between cell centroids (e.g. Diggle, Tawn & Moyeed

Fig. 2. Conceptual diagram of the hierarchical structure of the model. Boxes represent levels of ecological organization and arrows represent parameter organization (i.e. prior probability distributions for model parameters and hyperparameters, defined by other hyperparameters).



1998). Further detail can be found in Fig. S1 in the online Supporting Information.

As mentioned above, the effects of local harvest intensities, *h*, were nested within functional groups, *f*, and environmental zones, *e*, as follows:

$$\alpha_{hfe} \sim \text{Normal}(\beta_{fe}, \sigma\alpha_{fe}^2)$$

$$\beta_{fe} \sim \text{Normal}(\gamma_e, \sigma\beta_e^2)$$

$$\gamma_e \sim \text{Normal}(0, 10\,000)$$

Note that γ_e represents an estimate of the mean species richness in plots within each environmental zone, controlling for differences in functional groups and management among stands and is therefore a stand level, rather than regional level, indicator of biodiversity.

To assess whether managed plots had higher or lower species richness with regard to unmanaged plots, for each combination of environmental zone, *e*, and forest functional type, *f*, differences between intercepts for complete harvesting, or partial harvesting, and unmanaged plots were calculated within the model:

$$D_{e,f,\text{complete harvesting}} = \alpha_{e,f,\text{complete harvesting}} - \alpha_{e,f,\text{no treatment}};$$

$$D_{e,f,\text{partial harvesting}} = \alpha_{e,f,\text{partial harvesting}} - \alpha_{e,f,\text{no treatment}}$$

The resulting posterior distributions of these differences were used to calculate whether treatments had significant effects on species richness. The probability, *Pr*, that a particular harvest intensity resulted in the same species richness than no treatment was then calculated as $Pr = \text{Maximum}(Pr(D > 0), Pr(D \leq 0))$, where $Pr(D \leq 0)$ is the cumulative distribution of *D* up to zero and $Pr(D > 0) = 1 - Pr(D \leq 0)$. The maximum of these values yields a probability that two treatments are different, a Bayesian 'test statistic' from which the significance of a treatment may be assessed. A value greater than 0.95 could be interpreted as analogous to a frequentist *P*-value of 0.05, but these probabilities can be interpreted as more continuous probability measures than frequentist *P*-values. Because the hierarchical modelling approach used in this study represents the data complexity and inherent variability better than more conventional multivariate analyses,

we have considered here as statistically significant those values of $Pr \geq 0.90$.

We assigned noninformative priors to all parameters. All variance terms were assigned noninformative Gamma priors, $1/\sigma^2 \sim \text{Gamma}(0.01, 0.01)$. Similarly, regression coefficients and hyperparameters were assigned noninformative Normal distributions:

$$\delta \sim \text{Normal}(0, 10\,000)$$

$$\mu_{(c)} \sim \text{Normal}(0, 10\,000)$$

$$\omega_{(k)} \sim \text{Normal}(0, 10\,000)$$

Models were fit using OpenBUGS 3.1.0 (Thomas *et al.* 2006). The final model was run for 405 000 iterations on three independent chains, and convergence was assessed, after discarding pre-convergence burn-in interactions, via visual inspection and using the Gelman–Rubin statistic (Gelman & Rubin 1992). Although we structured these models to reflect our understanding of these ecological processes and to answer the main questions of the study, we also used model selection to help determine the best model. We calculated the Deviance Information Criteria (DIC) for models of increasing complexity (see Table S1), to evaluate their fit to the data while penalizing for increased numbers of parameters (Spiegelhalter & Best 2000). Also, to quantify the explanatory power of the model, explained variance was calculated. Finally, as a tool to explore the results, we generated predictions of species richness at the environmental zone level using the γ_e parameters, as a function of each explanatory variable (conditional on mean values of the others).

Results

The final model explained 53% of the variance of tree species richness. We report posterior mean parameter estimates, and their 90% credible interval, for the effect of the environmental and forest structure variables on tree species richness (Fig. 3). Predicted richness as a function of each of these variables is shown in Fig. 4 to better interpret quadratic relationships. Higher species richness was associated

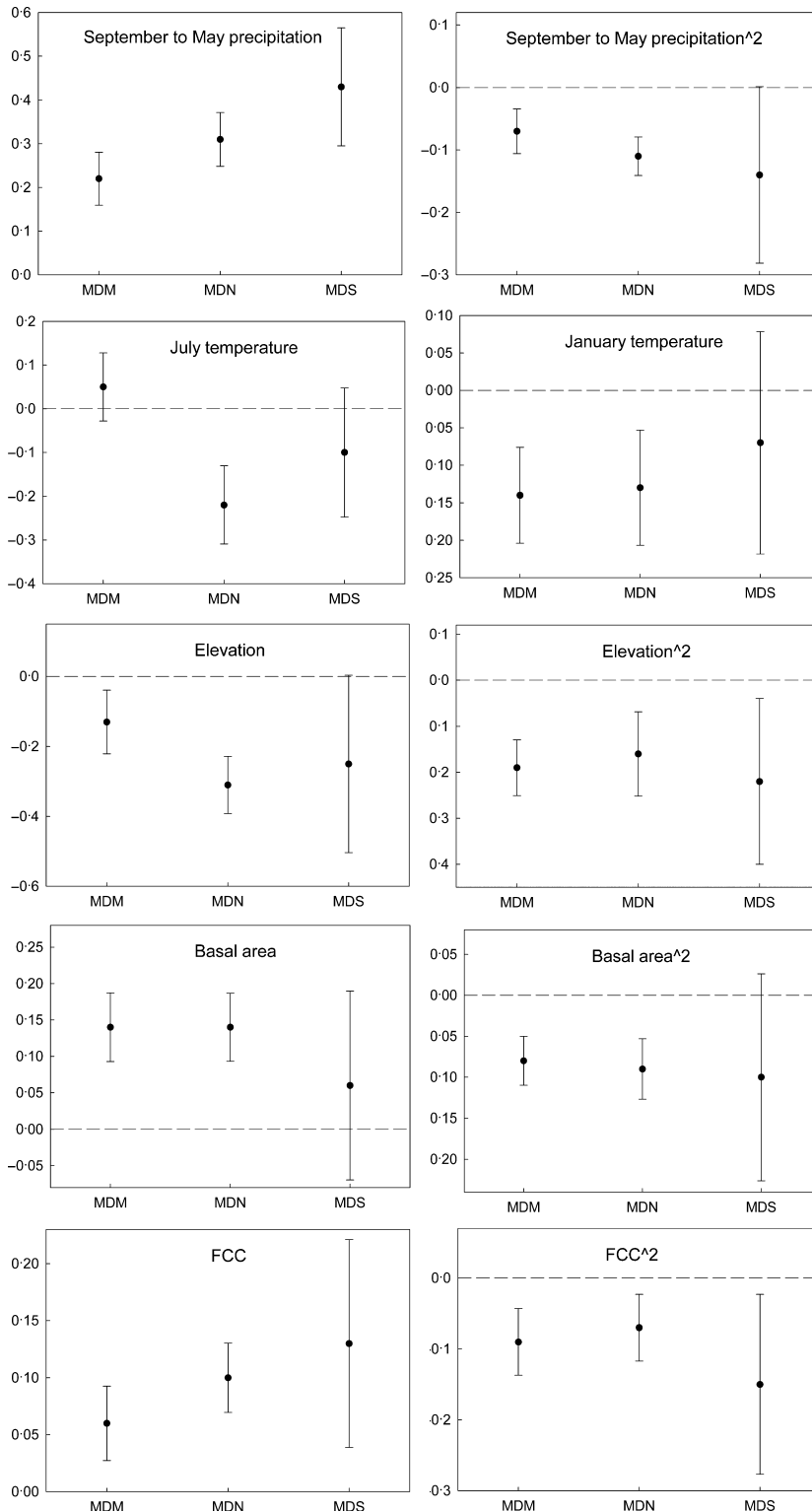


Fig. 3. Posterior mean parameter estimates, $\kappa_{e(q)}$, and their 90% credible intervals, for the effect on tree species richness of the environmental and forest structure variables, in each environmental zone (MDM, Mediterranean Mountain; MDN, Mediterranean North; MDS, Mediterranean South) and their quadratic term (see also Fig. 4). Those variables with intervals that do not overlap the horizontal zero line may be considered significantly different from zero at the 90% level.

with increased precipitation, slope, basal area and forest canopy cover (FCC) in all three regions (Figs 3 and 4). Negative second-order terms for these variables (with the exception of slope) suggested attenuating gains in species richness at more extreme values of each variable (Fig. 4). The strength of some relationships also varied among regions, with the strongest response to precipitation in the southern region (MDS) and weakest in the mountain region

(MDM) (Figs 3 and 4). The slope of the terrain also had the most positive relationship with species richness in the southern region, but the weakest relationship in the northern region. In contrast to the consistent effects of precipitation, the relationship with July temperature varied among regions, with positive associations in the mountains (MDM) and negative in the southern (MDS) and northern regions (MDN) (Figs 3 and 4). Species richness also

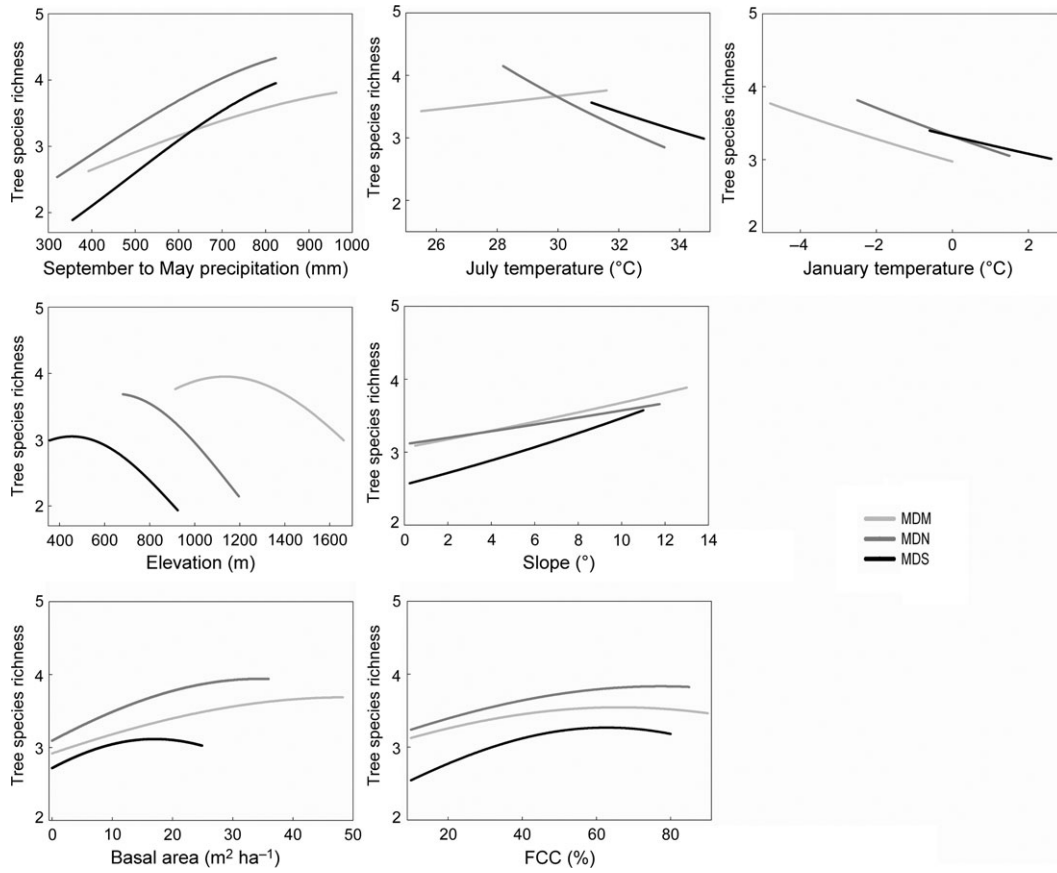


Fig. 4. Predicted tree species richness for the 95% central range of each explanatory variable in each environmental region, conditional on the mean values of the remaining variables. The overall intercept for each EnZ (γ_e) was used. Results are shown for the three environmental zones: MDM, Mediterranean Mountain; MDN, Mediterranean North; MDS, Mediterranean South.

declined at higher elevations in most of the study area (Fig. 4), although the strength differed between the mountainous (MDM) and northern regions (Fig. 3). Finally, successional stage also had significant effects on species richness, which increased ($\delta = 0.012$, $SD = 0.009$) as stands moved from recently regenerated stands (ordinal category 1) to stands with $DBH > 20$ cm (category 4).

The effects of harvesting intensity (parameter $\alpha_{h/c}$ comparisons) on species richness also varied among regions and functional groups. Overall, partial harvesting had positive effects on species richness relative to unmanaged forests (seven of eight of these comparisons were positive, Table 2), while complete harvesting had negative effects on species richness (three of three comparisons were negative, Table 2). The effects of complete harvesting were not significantly different from those of no management ($Pr < 0.90$ in Table 2). In contrast, the effects of partial harvesting were stronger, with high probabilities of there being differences from unmanaged forests (Table 2). In the Mediterranean Mountain zone (MDM), partially harvested coniferous forests had significantly lower tree species richness than unmanaged coniferous forests and higher species richness in broad-leaved forests (Table 2). In the Mediterranean Northern region (MDN), partial harvesting was associated with higher species richness in

all functional types, but was only significant in coniferous and sclerophyllous forests ($Pr = 0.92$ and $Pr = 0.99$, respectively, Table 2). In contrast, there were low probabilities that partial harvesting affected species richness in the southern region (all $Pr < 0.65$, Table 2).

Landscape variables within a radius of 5.5 km around each forest plot yielded lower DIC values than those within 3.5 km (see Fig. S1 and Table S1); results are then given for the 5.5 km radius. Tree species richness was higher in forest plots with more riparian forests in the surrounding landscape ($Pr > 0.99$; Fig. 5a). By contrast, results suggest a trend of species impoverishment in forest plots with greater proportions of plantations and *dehesas* in its surroundings (Fig. 5a), although this effect was not statistically significant ($Pr = 0.88$ and 0.89 , respectively). Independently of the harvesting intensity, plots had fewer species when located in a landscape with greater proportion of completely harvested forests (Fig. 5b). Species richness was also significantly lower, although to a lesser extent, in partially harvested forests with increasing partial harvesting in neighbouring landscape. Finally, species richness of unmanaged forest plots was greater when higher proportions of unmanaged forest were found in the surrounding landscape, whereas this association was not observed in completely and partially harvested plots (Fig. 5b).

Table 2. Effects of harvesting practices on tree species richness when compared with unmanaged forests of the same functional type and in the same environmental region (EnZ). For each combination of EnZ (*e*) and FUNC (*f*), the difference, *D*, between intercepts (α_{hfe}) for unmanaged and harvested (complete or partial) plots was calculated, and the probability that the difference is different from zero, *Pr*, is provided (higher *Pr* indicating a greater probability that species richness is different in the harvested and nonharvested forests)

EnZ	Functional type	Complete harvesting		Partial harvesting	
		Effect	<i>Pr</i>	Effect	<i>Pr</i>
MDM	Broad-leaved deciduous	–	0.64	+	0.91
	Sclerophyllous evergreen	no data	no data	+	0.88
	Coniferous	–	0.79	–	0.93
MDN	Broad-leaved deciduous	no data	no data	+	0.83
	Sclerophyllous evergreen	no data	no data	+	0.99
	Coniferous	–	0.77	+	0.92
MDS	Broad-leaved deciduous	no data	no data	no data	no data
	Sclerophyllous evergreen	no data	no data	+	0.53
	Coniferous	no data	no data	+	0.63

MDM, Mediterranean Mountain; MDN, Mediterranean North; MDS, Mediterranean South.

Discussion

In this study, we found that the effects of local silvicultural practices on tree species richness in Spain depend on both large-scale environmental gradients and on the management of surrounding landscapes. This overall result is supported by basic research suggesting that species richness is determined by drivers acting at different scales, including regional climate, local disturbances, effects of neighbouring landscapes and historical legacies (Bunnell & Huggard 1999; Sarr & Hibbs 2007). These complex, scale-dependent effects on species diversity are increasingly acknowledged in management scenarios, but their interactions have been difficult to quantify (Ohmann, Gregory & Spies 2007). In addition to the general lesson that management effects can vary depending on landscape and regional contexts, these findings also have practical implications for the region's forestry practices which we discuss below.

ENVIRONMENTAL AND FOREST STRUCTURE VARIABLES

Our results illustrate how the effect of particular environmental variables on tree species richness may vary among regions. This may be caused by nonlinearities in how that variable affects richness or interactions with other environmental variables at coarser spatial scales. For instance, the influence of water availability (precipitation) is more prominent in regions marked by hydric stress conditions (low precipitation and high temperatures), such as the southern Mediterranean region. Likewise, the negative effect of increasing summer temperature observed in the northern and southern Mediterranean regions was not evident in the more humid mountainous region. Even topography-related changes in species richness, such as those associated with slope and elevation variability, have been shown here to be inconsistent across regional scales. Most modelling of large-scale species richness patterns in the

literature does not account for regional differences in the response to particular climatic variables. However, as shown here, the response of plant species richness to factors such as precipitation might be context dependent, and therefore, global trends in extensive areas should be interpreted carefully (Martín-Queller, Gil-Tena & Saura 2011).

HARVESTING INTENSITY AND NATIVE TREE SPECIES RICHNESS

We identified a number of management practices that can influence native tree species richness. First, with some exceptions, partially harvested forests tended to have greater species richness than those unmanaged, after controlling for regional environmental conditions, forest functional group, successional stage and forest structure (i.e. basal area and FCC). The canopy removal associated with complete harvesting results in drastic environmental changes favouring disturbance-tolerant species that out-compete shade-tolerant species (e.g. Halpern & Spies 1995). By contrast, the canopy gaps originated by partial harvesting create a more heterogeneous environment that allows shade-tolerant species to persist, while also promoting additional species in the high nutrient and light canopy gaps (e.g. Rousset & Lepart 2000; Rodríguez-Calcerrada *et al.* 2010). Moderate harvest intensity can thereby maximize tree species richness (see also Torras & Saura (2008), allowing a balance between a potential environmental stress derived from more intensive harvesting (our results did not clearly support this, but see Martín-Queller, Gil-Tena & Saura 2011), and a potential competitive exclusion and environmental homogenization in unmanaged stands, as predicted by the intermediate disturbance hypothesis (Connell 1978; Shea, Roxburgh & Rauschert 2004).

However, these environmental changes may have contrasting effects depending on the biotic and abiotic context. For example, the gaps formed by partial harvest-

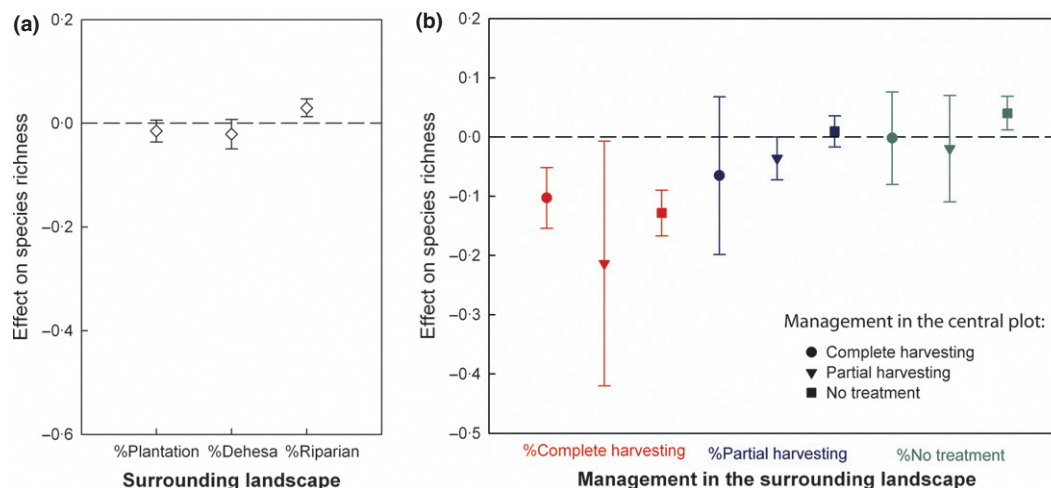


Fig. 5. Posterior mean parameter estimates and the 90% credible intervals for (a) the regression coefficients describing the effects of landscape cover (μ parameter) and (b) landscape management (θ parameter) variables on local tree species richness. Different coefficients for the effect of harvesting practices across the landscape were distinguished depending on the harvesting practices applied in the central forest plot, where species richness was assessed. Those variables with intervals that do not overlap the horizontal zero line may be considered significantly different from zero at the 90% level.

ing also favour herbaceous plants, which can increase competition with tree seedlings (Aussenac 2000). This competition, together with photodamage, may compromise seedling viability under strong radiation and water stress conditions, as in southern Mediterranean summers. Indeed, numerous studies suggest that canopy facilitation, rather than competition, prevails in semi-arid regions (e.g. Castro *et al.* 2004; Gómez-Aparicio *et al.* 2008). These mechanisms can explain the lack of effect of moderate canopy removal on tree species richness observed in the southern Mediterranean region compared with the results obtained in the rest of the study area. These results support the hypothesis that disturbance intensities maximizing species richness may be lower under more stressful environmental conditions than in more mesic environments (Odion & Sarr 2007).

We also found that in Mediterranean mountains, unmanaged coniferous forests had greater tree species richness than those managed through partial harvesting. These partially harvested forests have high percentages of *Pinus nigra* and *Pinus sylvestris* (Table 1), which are species of high commercial value. This fact may promote more intense application of other forestry practices, such as elimination of competitor species, thereby counteracting the positive effect of canopy opening on tree species richness. Additionally, conifer stands currently managed through partial harvesting are mainly located in eastern mountains in the study area. Forests in these mountains have historically been harvested through complete harvesting (shelterwood) treatments until late 20th century (Del Campo Sanchís & Solís Camba 1993), which may have influenced composition of current plant communities (Hermy & Verheyen 2007), that is, historical legacies.

Although we selected two contrasting levels of harvest intensity, additional forestry practices throughout the entire rotation period (e.g. mechanical site preparation,

shrub removal, disturbance frequency, etc.) could not be controlled here. The exact time since disturbance was also unknown, although successional stage can be a proxy in completely harvested stands. This time period is probably lower than one decade for many plots (see Materials and Methods), but may nonetheless affect species richness (Roberts & Gilliam 1995).

EFFECTS OF THE SURROUNDING LANDSCAPE ON TREE SPECIES RICHNESS

Results from this study also support the hypothesis that high species richness in the surrounding landscape is a key factor allowing recolonization and enrichment of local sites. Despite low representation in these landscapes (maximum 5%), riparian forests had a positive impact on tree species richness of surrounding forests. These forests probably increase the regional pool of species by harbouring temperate deciduous species poorly adapted to drier Mediterranean habitats. The proportion of *dehesas* and plantations in the landscape did not have a significant impact on forest species richness; however, the slight negative relationships observed were not surprising. Unlike their remarkable high levels of herbaceous and animal diversity (Díaz, Pulido & Marañón 2003; Ramírez & Díaz 2008), *dehesas* have low tree species richness (they are managed for one or two species) and therefore may not contribute to the propagule pool regenerating in forest stands. Also, forests located in landscapes dominated by *dehesas* may have been used as pastures and agricultural fields some decades ago. Thus, the ecological history of these potentially abandoned *dehesas* may result in low tree species richness (Ramírez & Díaz 2008). Finally, pine woodlands reforested within the second half of the 20th century in Spain have scarcely been colonized by late-successional broad-leaved species because of their high

stand density (Gómez-Aparicio *et al.* 2009) associated to a frequent lack of silvicultural post-plantation operations (Valbuena-Carabaña *et al.* 2010). This lack of tree diversity also makes these stands a poor source of propagules at the landscape level.

MANAGEMENT IN THE NEIGHBOURING LANDSCAPE

Our results showed that management disturbances not only affected the forest stand where they were applied, but also influenced the number of tree species in forests in the neighbouring landscape. Forest stands embedded in landscapes with an increasing proportion of completely harvested forests tended to have fewer tree species. Similarly, species richness in partially harvested stands diminished when this treatment was extensively applied in the landscape. This suggests that a landscape perspective on forest management is critical, as the impacts of disturbances depend on the proportion of managed forests in the landscape. Even moderate intensity disturbances, which in some cases maximize local richness, may result in an impoverishment of the species pool in the landscape when applied extensively (Martín-Queller, Gil-Tena & Saura 2011). For example, the elimination of some shade-tolerant tree species from landscapes may hinder recolonization of small canopy gaps by this functional group, due to limitations in seed dispersal (Bengtsson *et al.* 2000). More research is needed, however, to determine whether these patterns derive from recent post-disturbance extinction – colonization dynamics, from correlation of current management with historical disturbance regimes or both.

BROADER MANAGEMENT IMPLICATIONS

Overall, our study provides novel quantitative results that suggest that the consequences of forest management on species richness depend on the broader landscape and regional context. These multi-scale effects on biodiversity are likely to be common across ecosystems, study organisms and types of management-driven disturbance. For example, the responses of benthic macro-invertebrates and algae to urbanization at the basin scale were also influenced by regional environmental factors (Cuffney *et al.* 2011). And in agricultural systems, the effectiveness of agro-environmental management to increase species richness was found to depend on the composition of the surrounding landscape (e.g. Batáry *et al.* 2011; Fischer, Thies & Tschardtke 2011).

The findings in this study have important implications for forest management, highlighting the potential benefits of intermediate harvesting intensities for native tree species richness in the Mediterranean region. This is especially relevant in the context of the current decline in silvicultural practices in the northern Mediterranean basin (Fabbio, Merlo & Tosi 2003). However, caution is needed in the most xeric regions, where our results suggest that the average degree of canopy opening applied in

Mediterranean forests may not necessarily benefit tree species richness. Additionally, this study supports the idea that an extensive application of the same harvest intensity throughout the landscape may be associated with a decline in tree species richness in managed stands. Thus, natural resource managers should favour a landscape-level mosaic of species rich forests to ensure the colonization and enrichment of regenerating stands nearby. This potential role of metacommunity dynamics in shaping stand responses to harvesting practices also highlights the importance of enhancing landscape connectivity in management plans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Patterns of the spatial random effects for each 30 × 30 km cell.

Table S1. Detailed description of the models with increasing complexity and their DIC values.