Forest Ecology and Management 289 (2013) 123–132

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Landscape species pools and connectivity patterns influence tree species richness in both managed and unmanaged stands

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ARTICLE INFO

Article history:
Received 22 March 2012
Received in revised form 24 September 2012
Accepted 26 September 2012

Keywords:
Forest biodiversity
Graph theory
Long distance seed dispersal
Metacommunity
Partial harvesting

ABSTRACT

Disturbance intensity and metapopulation dynamics are among the theoretical mechanisms explaining species coexistence at the local and landscape scale. Both mechanisms might interact, so that the consequences of local disturbances might depend on long distance dispersal events. In this study we examined whether the richness of tree species potentially able to colonize a locality from the surroundings was associated with the tree species richness observed in that locality, and/or with the response of that richness to partial harvesting. The study was located in a Mediterranean region in central Spain where partially harvested forests had been found to have more tree species than unmanaged forests. We used a top-down hierarchical modeling structure to account for the effect of other factors such as climate, lithology and amount of forest cover at the landscape scale. Species richness of trees was strongly associated to annual precipitation, and was maximized at intermediate rainfall levels. Under homogeneous climate and lithological conditions, the composition and connectivity of seed sources in the landscape seemed to play a more relevant role explaining tree species richness than the amount of forest habitat in the surroundings. Particularly, higher species richness was observed in forest stands susceptible of receiving a higher diversity of seed fluxes. Patterns in the response of species richness to partial harvesting were less clearly explained by differences in the diversity of potential seed fluxes, but time lags in the responses, or differences in the proportion of shade-tolerant species in the landscape could mediate this interaction. Stronger importance of the amount of forest habitat and diversity of potential seed fluxes may be masked by their correlations with precipitation gradients in the study area. Our results emphasize the need of a wide scale approach to forest planning in order to be able to account for and to influence determinant processes of diversity patterns from the stand to the landscape levels.

1. Introduction

One of the fundamental objectives in ecology is the search for the general mechanisms that control the spatio-temporal patterns of species coexistence. For example, at large spatial (extent and/or grain) scales, patterns of plant species richness have been found to highly correlate with physical environmental gradients (e.g. Field et al., 2009). This can be explained by the fact that climate and lithology determine resources availability and influence plant physiology, thus directly shaping plant community composition according to the niche theory (Hutchinson, 1957). But apart from the equilibrium mechanisms based on the partitioning of spatio-temporal niche heterogeneity (MacArthur, 1972), many other dynamic-equilibrium mechanisms for species coexistence have been offered (reviewed in Palmer, 1994; and Wright, 2002). For instance, periodical disturbances when intermediate in intensity, frequency and/or extent are hypothesised to maximize plant species richness in local communities by preventing the competitive dominance of few species (Connell, 1978; Shea et al., 2004). Most likely, patterns of local plant species richness across extensive areas are driven by complex interactions of these factors operating at different spatial scales (Whittaker et al., 2001; Field et al., 2009). These interactions have been suggested to follow a top-down hierarchical structure (Levin, 1992) such that coarse-scale factors influencing local diversity (e.g. climate and lithology) are hardly affected by ecological processes taking place at smaller spatial scales (e.g. Sarr et al., 2005; Kallimanis et al., 2007); whereas ecological or human-induced local factors are strongly influenced by their regional environmental context.

To understand patterns of species coexistence in local communities, the necessity of incorporating processes occurring at intermediate, landscape scales is also increasingly accepted (Gardner and Engelhardt, 2008). For instance, it has been suggested that

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Abbreviation: LDD, long distance dispersal.

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http://dx.doi.org/10.1016/j.foreco.2012.09.036

inter-specific differences in competitive versus dispersal ability allow inferior competitors to persist by colonizing more rapidly or efficiently other localities (Horn and MacArthur, 1972). Species coexistence through such trade-offs in ecological traits may actually be linked to the occurrence of disturbance events at local scales. In other words, the impact of a particular disturbance on a community's species richness may depend on the composition of the surrounding communities and the degree of connection with them (Niemelä,1999; Bengtsson et al., 2000). Therefore, metacommunity dynamics, i.e., connections among local communities by dispersal of multiple potentially interacting species (Leibold et al., 2004), can have a crucial role in the maintenance of local species richness, either directly, or indirectly through interaction with local disturbances.

Connectivity among forest communities distributed within a landscape depends on long-distance dispersal events (LDD). LDD can be defined for each plant species in terms of a threshold distance, or as the tail from an empirically estimated dispersal density function or kernel (See Cain et al., 2000). Seed dispersal can be done by a variety of mechanisms, or dispersal syndromes, which are usually grouped in anemochory (wind), hidrochory (water), autochory (plant's means), ectozoochory and endozoochory (animals). Willson (1993), in a meta-analysis, found that wind-dispersed seeds had larger mean dispersal distances than animal-dispersed species. However, in a second part of the study, the dispersal syndrome was not related with the shape of the tail of the dispersal kernel (Portnoy and Willson, 1993); in other words, LDD events did not depend on the dispersal syndrome. Indeed, LDD events frequently rely on nonstandard dispersal vectors (or combinations of several of them) or result from exceptional behavior of the (standard) dispersal vector (Higgins et al., 2003). This particularity, along with their relatively low frequency, make LDD events difficult to sample, and empirical data is thus limited almost exclusively to short-distance dispersal events (Nathan and Muller-Landau, 2000). Even so, there is compelling evidence from many plant species that effective LDD do occur far beyond the otherwise normally observed dispersal distances (Nathan, 2006). Actually, studies have reported plausible dispersal distances for many plants up to 10–20 km (e.g. Clark et al., 1999; Cain et al., 2000; Jordano et al., 2007).

In this study, we attempt to assess the potential effects of metacommunity dynamics, and its interaction with local disturbances, on stand species richness, after controlling for other relevant factors operating at landscape and regional scales. In a previous study we found that silvicultural disturbances of intermediate intensity, i.e. partial harvesting, allowed the coexistence of more tree species than the absence of management in Mediterranean forests in central Spain (Martín-Queller et al., submitted for publication). Based on theoretical expectations, we hypothesize here that the increase in species richness after these disturbances may be more pronounced where more species from the surrounding landscape are potentially able to recolonize the opened gaps. Particularly, we addressed the following questions: (1) to what extent the number of tree species in a forest stand, managed or not, is associated with the richness and relative abundance of species potentially able to colonize it from the surroundings? and (2) to what extent the response of species richness to intermediate harvesting disturbances is affected by this propagule richness and availability in the landscape? In order to explore these questions, we focused on a Mediterranean region (ca. 88,000 km^2) in central Spain. We analyzed the relationship between the number of tree species in a stand, differentiating between unmanaged and partially harvested stands, and the richness of propagules potentially colonizing it through LDD (here $\geqslant 1$ km) from the surroundings. Potential seed flux was estimated through a graph theory approach for connectivity analysis. Additionally, we based the statistical analysis in a top-down hierarchical framework, assessing the pure effect of seed flux diversity on local species richness, after accounting for the direct and indirect effects of large-scale climate and lithology patterns. We also controlled for the amount of forest cover in the surrounding landscape, which may have influenced both patterns of seed flux diversity and local species richness (e.g. Fahrig, 2003; Montoya et al., 2010). To our knowledge, this is the first study adopting a graph-theoretical approach to evaluate the association between plant species richness in a local community and the diversity of potential seed sources from the surrounding landscape. Additionally, the evaluation of the effect on tree species richness of the interaction between silvicultural disturbances and potential seed flux diversity is also novel.

2. Methods

2.1. Study area and forest inventory data

The study area encompasses the forests located within the Mediterranean North Climatic Region (according to the European Environmental Stratification by Metzger et al. (2005)) of the Spanish regions of Castilla y León, Castilla-La Mancha and Madrid (Fig. 1A). We selected this region because under these climatic conditions partially harvested stands had been found to have more tree species than unmanaged stands (Martín-Queller et al., submitted for publication). Therefore, it is a particularly interesting area for further exploring and understanding the effects of harvesting on tree species richness in the Mediterranean. Further details about the study area can be found in Martín-Queller et al. (2011).

This study uses data from the third Spanish National Forest Inventory (3SNFI) (Ministerio de Medio Ambiente, 1997–2007). Plots in the 3SNFI were located systematically in the intersections of a 1 km × 1 km UTM grid that fall inside forests and other woodlands. Plots were circular and the inventory of tree stems depended on their diameter at breast height (DBH) and distance to the plot center, 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 total number of tree species, independently of the DBH, was inventoried within a 25-m radius in each plot. Silvicultural treatments were surveyed in the 3SFNI according to direct or indirect evidences assessed in the field, such as stumps or slash, normally not older than 10 years.

Species richness patterns were only assessed in a subset of 'forest' plots within the study area. 'Forests' were defined here as woodlands with a minimum Forest Canopy Cover (FCC) of 5%, excluding plantations, riparian or burnt forests and *dehesas* (extensive semi-forested areas with evergreen oaks scattered over grasslands or cereal crops). Selection of the study forest plots was made in order to ensure that a set of managed and unmanaged stands with similar environmental conditions, metacommunity dynamics, and ecological and evolutionary histories were represented. Firstly, all forest plots in the study area dominated by coniferous species and where partial harvesting had been applied were selected (696 plots). We focused on coniferous forests, for which sample size of managed plots was much bigger than for other functional groups. Secondly, all unmanaged, coniferous forest plots located within a 2.5-km radius around partial harvesting plots were also selected for the analysis (849 plots). We call this set of 1545 managed and unmanaged plots 'sink plots', since diversity and richness of potential seed flux to each of them was subsequently evaluated (see Fig. 1A and B). All 3SNFI plots surrounding each sink plot within a certain influence radius, independently of their functional group or type of management, were also included in the analysis to estimate the potential seed flux that could originate from them

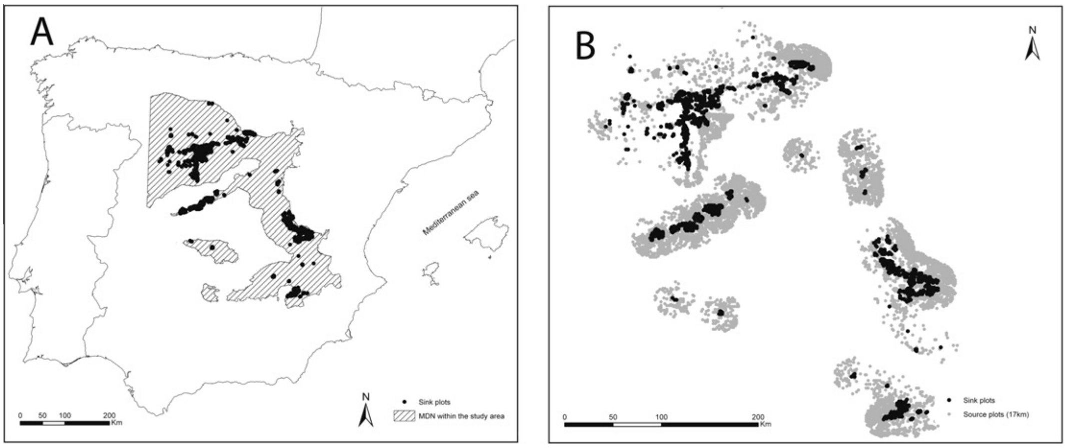

Fig. 1. Analysed sink plots in the Mediterranean North Region (MDN) in the study area (A) and detail of the neighbor source forest plots within a radius of 17 km around the analysed sink forest plots (B).

('source plots', Fig. 1B) and potentially reach the sink plots (see Section 2.2).

2.2. Estimation of potential seed flux

We used an approach based on graph theory to estimate the potential seed flux received by each sink plot (either partially harvested or unmanaged). Graph theory is an intuitive and very powerful approach to evaluate the functional connectivity between spatially structured ecological elements (individuals, populations, communities), as testifies the increasing number of ecological studies based on it (e.g. Pascual-Hortal and Saura, 2008; Urban et al., 2009; Pereira et al., 2011; Awade et al., 2012). A graph represents the landscape as a set of nodes functionally connected to some degree by links that join pairs of nodes (Urban and Keitt, 2001). A total of 49 graphs were built, one for each native tree species present in at least one of the sink plots according to the 3SNFI surveys (see Table 1). In each graph, nodes represent populations of the species throughout the landscape, and each link the probability of seed dispersal between two nodes. These graphs were composed of two different types of nodes: (1) the nodes represented by 'sink plots', i.e., forest stands where the effects of potential arriving seed flux on species richness were subsequently evaluated (1545 plots, see above); and (2) the nodes represented by 'source plots', i.e., forests and other woodlands susceptible to disperse seeds to the sink populations. Each graph, therefore, represented a set of populations (source plots) of a particular species distributed across the study area and susceptible to disperse seeds to the sink populations, where species richness was assessed. While sink plots included only 'forests' as defined here (see above), all 3SNFI woodland plots (including 'forests', plantations, riparian or burnt forests and *dehesas*) were potential source populations if at least one adult tree (potentially generating a significant seed output of the species) was present, according to the 3SNFI field plots. This implies that sink plots could also act as seed sources for other sink plots. Sexual maturity was evaluated in terms of a DBH threshold. However, the 3SNFI sampling design (see details above) implies a lower probability for individuals with $7.5\ \text{cm} \leqslant \text{DBH} \leqslant 12.5\ \text{cm}$ of being surveyed (radius = 5 m). Thus, in most cases, less frequent species, normally with smaller sizes and occurring in the dominated overstorey, had no stems with DBH $\geqslant$ 7.5 cm in 90% of the plots where they were surveyed. For these species, using a DBH threshold would be unrealistic and too restrictive. We applied a threshold of 7.5 cm only for those dominant species with a large number of tally trees in the study area (Table 1): these were defined as those species in which at least 30% of the plots (in most cases >50%) where they were present (according to the 3SNFI) had one or more individuals with this minimum DBH value. Sexual reproduction of many of the main, dominant tree species in Spain begins at the age of 15–25 years (Montero et al., 2003; Serrada et al., 2008), which corresponds to very variable DBH values, from 5 cm to 20 cm, depending on the species and on site quality. We considered that, given the scale of grain used, 1×1 km, the presence of an individual with 7.5 cm DBH indicates a very probable presence of a population in the neighborhood susceptible to disperse seeds at long distances. Also, high densities of young trees with low seed production may render a large crop size on a population basis.

Table 1
List of tree species present in at least one of the 1545 3SFNI plots included in the analysis, differentiating between dominant and non-dominant species for which a DBH threshold of 7.5 and 0 cm has been considered, respectively, to define source plots in each graph (see methods).

Dominant species	Non-dominant species
Alnus glutinosa	*Acer monspessulanum*
Castanea sativa	*Acer pseudoplatanus*
Fraxinus angustifolia	*Amelanchier ovalis*
Fraxinus excelsior	*Arbutus unedo*
Juglans regia	*Buxus sempervirens*
Juniperus thurifera	*Celtis australis*
Pinus halepensis	*Cornus sanguinea*
Pinus nigra	*Crataegus monogyna*
Pinus pinaster	*Crataegus* spp.
Pinus pinea	*Frangula alnus*
Pinus sylvestris	*Juniperus communis*
Populus alba	*Juniperus oxycedrus*
Populus nigra	*Juniperus phoenicia*
Quercus faginea	*Malus sylvestris*
Quercus ilex	*Myrtus communis*
Quercus pyrenaica	*Olea europaea*
Quercus suber	*Pistacia terebinthus*
Salix alba	*Prunus avium*
	Prunus spinosa
	Prunus spp.
	Pyrus spp.
	Rhamnus alaternus
	Salix atrocinerea
	Salix purpurea
	Salix spp.
	Sambucus nigra
	Sorbus aucuparia
	Sorbus spp.
	Sorbus torminalis
	Taxus baccata
	Ulmus minor

Internode seed dispersal probabilities (p_{ij}) were estimated as a negative exponential function of distance (Bunn et al., 2000):

$$p_{ij} = e^{-k \cdot d_{ij}}$$

where k is a constant that was specified by setting a probability $p = 0.01$ at the maximum dispersal distance of 17 km (see Jordano et al., 2007). Median dispersal distance ($p = 0.5$) according to this function corresponds to 2.6 km. Probabilities below 0.01 were not considered in the analysis. The potential seed flux of a given species to each sink plot j was equal to the sum of the probabilities of dispersal from the i nodes (source plots) within a 17 km-radius (i.e., $p \geqslant 0.01$). Finally, for each sink plot we estimated seed flux richness, as the number of species with a potential seed flux to the plot above zero; and seed flux diversity, as the Shannon diversity of potential seed fluxes of each tree species reaching the sink plot. We used the Conefor Sensinode software (CS) (Saura and Torné, 2009, http://www.conefor.org) to estimate this flux, by using the Flux (F) metric (Bunn et al., 2000; Urban and Keitt, 2001).

2.3. Estimation of habitat amount and connectivity

Patterns of seed flux diversity potentially reaching sink plots are expected to correlate with the amount of forest around these plots. This is explained by a generalized increase in species richness when habitat area is enlarged (see potential mechanisms in Gardner and Engelhardt (2008)). Additionally, the amount of habitat in the landscape is an indicator of habitat loss and fragmentation processes that have been shown to influence local species richness patterns (e.g. Fahrig, 2003; Montoya et al., 2010). For these reasons, we estimated an indicator of forest amount and connectivity, such that diversity of potential seed sources unambiguously reflects in the model the community composition in the surrounding landscape. Despite the term habitat is by definition species-specific, we used forest cover as a proxy of the amount of habitat for all tree species present in the study area, as in Montoya et al. (2010). An indicator of the amount of forest cover in the surrounding landscape could be obtained from the total number of plots located within a particular radius around each sink plot. However, in order to make this indicator comparable with seed flux diversity, connectivity patterns were also considered in its estimation, based on the graph theory. Thus, the contribution of each plot to the amount of forest in the landscape was weighted by its distance to the central, or sink, plot. In particular, we used the same Flux (F) index and negative exponential function, with the same decay rate (i.e. assigning a probability 0.001 at 17 km), but in this case, a unique graph included all the 3SNFI plots, except plantations, regardless of species composition. The variable was calculated for each of the 1545 target (‘sink’) plots as the sum of probabilities of direct connection with each plot in the neighborhood (radius of 17 km), therefore accounting for the amount of forest cover in the surroundings but with an exponentially decreasing weight as a function of the distance from the source plots. Hereafter we call this variable ‘forest cover’.

2.4. Statistical analysis

We used Bayesian regression models to explain patterns of tree species richness in the sink plots. Factors influencing local species richness are generally intercorrelated. In particular, factors operating at regional scales (climate and lithology) probably shape patterns of factors operating at landscape scales (forest cover and diversity of seed flux). Similarly, as discussed above, an association between local species richness and the diversity of seed flux could be mediated by an indirect effect of the amount of forest in the landscape. The pure effect of a specific factor on species richness is therefore difficult to be isolated from the indirect or mediated effects of other factors. Additionally, in a top-down hierarchical framework, larger-scale factors are expected to be seldom affected by ecological processes operating at smaller scales (e.g. climate by landscape forest cover, or the latter by the structure of a particular forest stand). In this context, it seems unrealistic to evaluate the association between species richness and all factors operating at different scales in a single multiple regression model. Doing so, the relative effect of each explanatory variable would be estimated once considered its covariation with each of all predictors in the model. To avoid this, we distinguished here three levels of potentially intercorrelated predictors: (1) regional factors: climate and lithology, (2) landscape factors: forest cover, and (3) local factors: silvicultural practices and forest structure. These predictors were thus evaluated hierarchically, introducing each group in a different step, such that the residuals of the previous step were used as dependent variable in the next one. Thereby, variables representing species richness in each step (i.e. residuals of previous step) were orthogonal (presented no correlation) to factors operating at the previous hierarchical level. Although indirect effects were thereby not quantified, this approach allowed isolating the pure effects of some of the analyzed factors. Diversity of seed flux, despite being a landscape factor, was not expected to influence the amount of forest cover in an ecological time scale. This variable was introduced in the third step in order to evaluate its potential interacting effect with local silvicultural disturbances. Spearman correlation values between all pair of variables were calculated to evaluate possible interactions between predictors of species richness and to discuss causality of the estimated relationships.

2.4.1. First step

In this step, the number of tree species was modeled with a Poisson distribution and log-link function against a set of climatic, topographic and lithological factors.

In order to reduce collinearity, and to represent environmental variability in a minimum number of variables, we performed a Principal Component Analysis (PCA) with these explanatory variables. The 13 environmental variables used in the PCA were: elevation, slope, annual and seasonal (spring, summer, autumn and winter) precipitation, maximum July temperature, minimum January temperature, mean annual radiation, Thornthwaite’s annual potential evapotranspiration (PET), drought length and Dry Season Water Deficit (DSWD). Climatic data were obtained from the Climatic Atlas of the Iberian Peninsula at a resolution of 200 m (Ninyerola et al., 2005), and topographic data from the official Spanish Digital Elevation Model at a resolution of 25 m (Ministerio de Fomento, 1999). Drought length was calculated as the number of dry months, that is, when the value of the monthly amount of precipitation (mm) was less than, or equal to, twice the value of the average temperature (°C) of the month considered (Allué-Andrade, 1990). Monthly water deficit was calculated as the difference between monthly precipitation and PET, and DSWD was the accumulated water deficit for all dry months (Dufour-Dror and Ertas, 2004). PCA was conducted using the *prcomp* function in R software.

Scores of the two first components of the PCA and an additional categorical variable, lithology, were used as explanatory variables in this step. Lithology had two categories: calcareous versus siliceous soils; this variable was obtained from the 3SNFI for each plot, where it was determined based on hydrochloric acid test. The shape of the relationship between each PC and tree species richness was previously explored and accordingly, linear or quadratic functions were included in the model.

2.4.2. Second step

Residuals from the previous step represented those patterns of tree species richness that were not explained by coarse environmental gradients. These residuals were now used as a response variable with a Normal distribution and with forest cover as explanatory variable. An intercept parameter was also included in this and the previous model. Since residuals were orthogonal to PCA scores, any joint effect of environmental variables and forest cover was not estimated in this step.

2.4.3. Third step

Residuals from the second step were included now used as response variable in this third model. We included in the model intercept parameters, α_r, for each category of management (partial harvesting or unmanaged) in order to evaluate the difference in species richness between these two types of stands. Different slope coefficient parameters for the diversity of potential seed flux, β_r, were also included for each category r of management. Both intercept and coefficient parameters, respectively, were estimated in a hierarchical fashion, and were assigned a common non-informative prior distribution:

$$\alpha_r \sim Normal(0, 10000)$$

$$\beta_r \sim Normal(0, 10000)$$

In order to evaluate the difference in species richness between partially harvested stands and unmanaged stands, we estimated within the model the difference, D, between intercepts corresponding to each category. Thus we obtained the posterior distribution of this difference, and the probability, p, that partial harvesting resulted in a different species richness than no treatment was then calculated as $p = \text{Maximum}(\text{pr}(D > 0), \text{pr}(D \leqslant 0))$, where $\text{pr}(D \leqslant 0)$ is the cumulative distribution of D up to zero and $\text{pr}(D > 0) = 1 - \text{pr}(D \leqslant 0)$. The same process was done for the two coefficients for the diversity of potential seed flux. This is a Bayesian form of a 'test statistic' from which the significance of differences due to silviculture was calculated.

If enrichment after partial harvesting with regard to unmanaged stands depends on the availability of large and diverse seed pools, then the slope coefficient of diversity of potential seed flux would be higher in partially harvested than in unmanaged stands (Fig. 2A). Conversely, if enrichment observed in species richness after partial harvesting is independent of the diversity of seed flux, then this coefficient will be similar for both managed and unmanaged stands (Fig. 2B). We also assessed the degree of shade-tolerance of the main analyzed tree species as reported by Montero et al. (2003) and Serrada et al. (2008), in order to evaluate if such species traits could have some role in the interaction between the gaps opened in the managed and unmanaged stands and the seed fluxes potentially received in the sink plots.

Local species richness also depends on the structural conditions of the forest stand, which determine microenvironmental conditions, influence species interactions and reflect ecological succession. To account for coarse differences in these aspects, we also included in this step another explanatory variable, Forest Canopy Cover (FCC).

Given that spatial autocorrelation in residuals violates the assumption of independence and invalidates inferences from a model (Legendre and Legendre, 1998), and that other factors not considered here could underlie the observed patterns of species richness, we included spatially explicit random effects in the model. We did not include them in previous steps because the processes object of study, metacommunity dynamics, are inherently spatially structured, and spatial effects could have accounted for this structure. For reasons of computational limitations, plots were grouped in 8×8 km cells. Spatial effects for each of these cells were assigned to a multivariate Gaussian distribution with covariances expressed as a negative exponential function of the distance between cell centroids (e.g. Diggle et al., 1998).

In order to quantify the explanatory power of the model at each step Bayesian measures of explained variance were calculated (Gelman and Pardoe, 2006). In the case of the model in the third step, we also estimated the explained variance when excluding the spatial term, in order to have an approximate idea of the explained variance attributable exclusively to the analyzed explanatory variables. We used the software OpenBUGs 3.1.2 for the statistical analyses (Thomas et al., 2006). All variables (including residuals) except tree species richness were standardized to zero means and unit variances to allow comparability among coefficients for variables measured at different scales. All parameters were given non-informative priors (*Normal*(0,10000)), allowing the data to drive their estimation. Models were run for 150,000 iterations, and convergence of the posterior means of the estimated parameters was assessed from two chains using the Gelman–Rubin statistic. Pre-convergence "burn-in" iterations (10,000 in steps 1 and 2; 40,000 in step 3) were discarded in the calculation of the parameters.

3. Results

The first two principal components extracted by the PCA accounted for 74% of the original variability in environmental (climate and topography) conditions (Fig. 3). PC1 represented a gradient of decreasing annual (spring, autumn and winter) water precipitation, independently of temperature conditions (Fig. 3). The second component, PC2, represented a decreasing summer water deficit, associated to diminishing temperatures and increasing precipitation levels in summer.

Fig. 4 shows the hypothesized top-down structure according to Spearman correlations of raw data. Correlations between factors included as potential drivers of species richness reflected a relatively important covariation between them. The environmental conditions, summarized by the first two components of the PCA, not only were correlated with tree species richness, but also, in the case of the PC1, showed correlations of $r = -0.34$ with forest cover (habitat amount and connectivity) and $r = -0.83$, with the diversity of seed flux. Forest cover was at the same time positively correlated with diversity of seed flux ($r = 0.23$), and had a slight negative correlation with tree species richness.

Model results in each step are described below:

- *Step* 1. Tree species richness in the first model was significantly higher ($p = 1.0$, using the approach to assess significance described in the methods) in calcareous soils than in siliceous soils (Table 2). Tree species richness had a quadratic relationship with the first axis (PC1) of the PCA (Table 2). Increased scores in PC1 were associated to higher number of species, but after a certain threshold (0.31 in the normal standard PC1 variable) the number of species tended to decrease. The posterior mean for the PC2 slope coefficient was not significantly different from zero (95% CI: -0.04 to 0.06; Table 2). This model explained 38.5% of the variance in tree species richness.
- *Step* 2. Forest cover was negatively associated (Table 2) with the residuals of step 1. This model explained 1.8% of the variance of residuals from the previous step, which corresponds to 1.1% of the total variance of tree species richness.
- *Step* 3. The Spearman correlation between diversity of potential seed flux and tree species richness was twice that of richness of potential seed flux ($r = 0.53$ and 0.25, respectively). For this reason, we selected diversity of potential seed flux as the indicator of metacommunity processes explaining species richness patterns. According to the posterior estimates for the intercepts, residuals from the model in step 2 were higher in partially harvested than in unmanaged forest plots ($p = 0.86$; Table 2). Given

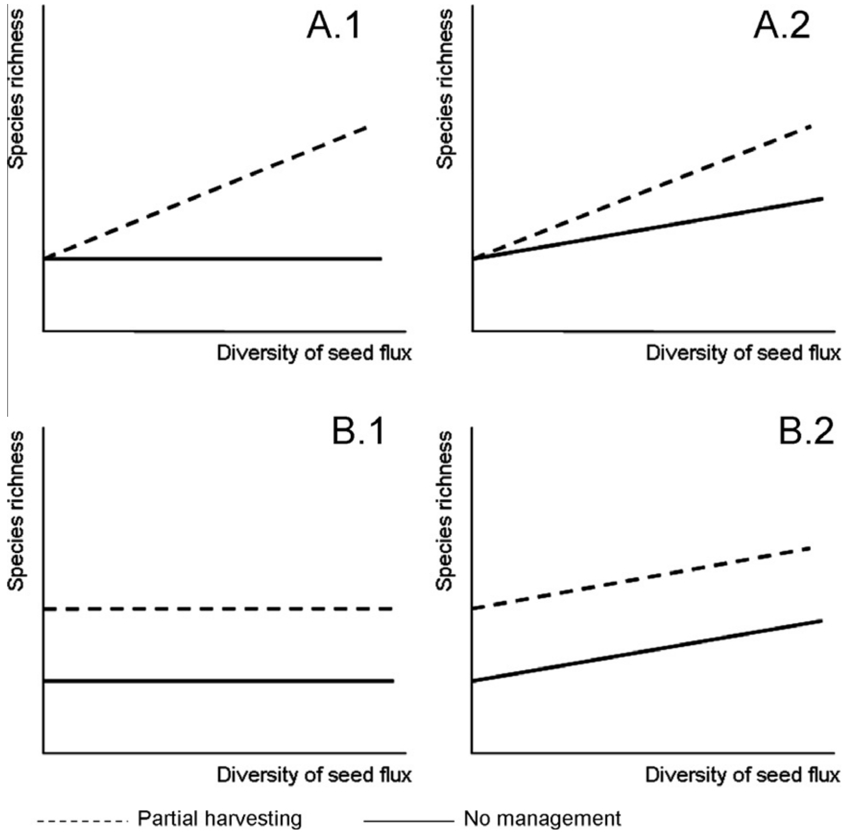

Fig. 2. Assuming a positive effect of partial harvesting on species richness with respect to unmanaged stands: A1. Increase in species richness due to higher diversity of potential seed flux only occurs when new niche opportunities are created after disturbance; A2. Positive effects of partial harvesting are more evident with enough diversity of potential seed flux, although the benefits of surrounding pool of species is also significant in unmanaged stands; B1. The diversity of potential seed flux does not influence local species richness; B2. Local species richness increases with increasing diversity of seed flux, but this increase occurs in the same amount no matter whether the stands are managed or not.

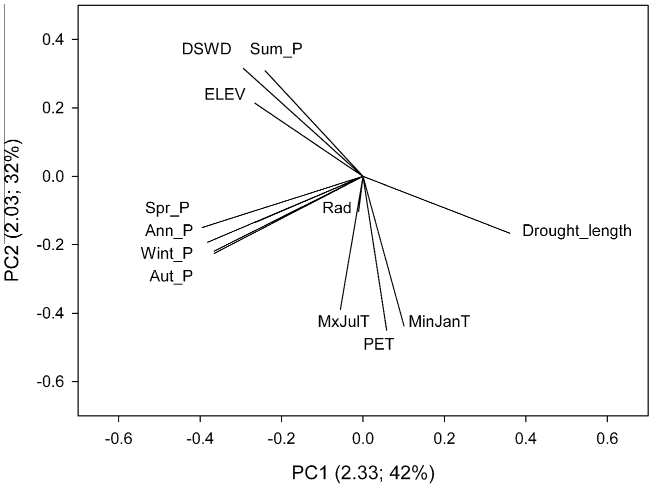

Fig. 3. Eigenvectors for the first two principal components extracted by the PCA. Standard deviation (i.e. squared root of the eigenvalues) and explained variance is shown in the parenthesis in the axis labels. **Ann_P, Spr_P, Sum_P, Aut_P and Wint_P**: Annual, Spring, Summer, Autumn and Winter precipitation; **MinJanT:** Minimum January Temperature; **MxJulT:** Maximum July Temperature; **DSWD:** Dry Season Water Deficit; **Elev:** Elevation; **Rad:** Radiation; **PET:** Potential Evapotranspiration.

that all variables were standardized to zero mean, this difference corresponds to intermediate conditions of FCC and potential flux diversity. As for the slope coefficient for diversity of seed flux, it was stronger in unmanaged forests than in those treated with partial harvesting ($p = 0.94$; Table 2). Fig. 5 shows the posterior mean and credible interval for the predicted species richness when FCC is 57% (mean FCC in the study area) according to model in step 3. The difference in species richness in managed versus unmanaged plots was higher at low levels of seed flux diversity, and became blurred at the highest levels of flux diversity. This model explained 28.1% of the variance in the response variable, that is, 16.9% of the total variance in species richness. However, when estimating the same model without the spatial effects the explained variance was 7.3% (4.4% of the variance in step 1). Finally, when the diversity of potential seed fluxes was low (first quartile), a 89% of the total amount of seed fluxes corresponded to shade-intolerant species, while this percentage decreased down to 45% when the seed fluxes were more diverse (forth quartile).

4. Discussion

4.1. Environmental gradients and tree species richness

Patterns of tree species richness in conifer forests of the Mediterranean North Region in Spain showed a strong association with the gradient of annual precipitation. The maximum levels of richness observed at intermediate precipitation levels concur with other analyses in a similar study area (Martín-Queller et al., 2011, submitted for publication). Given that in the Mediterranean region water availability is the main constraining factor of productivity, results agree with the frequently observed hump-shaped relationship between productivity and plant species richness

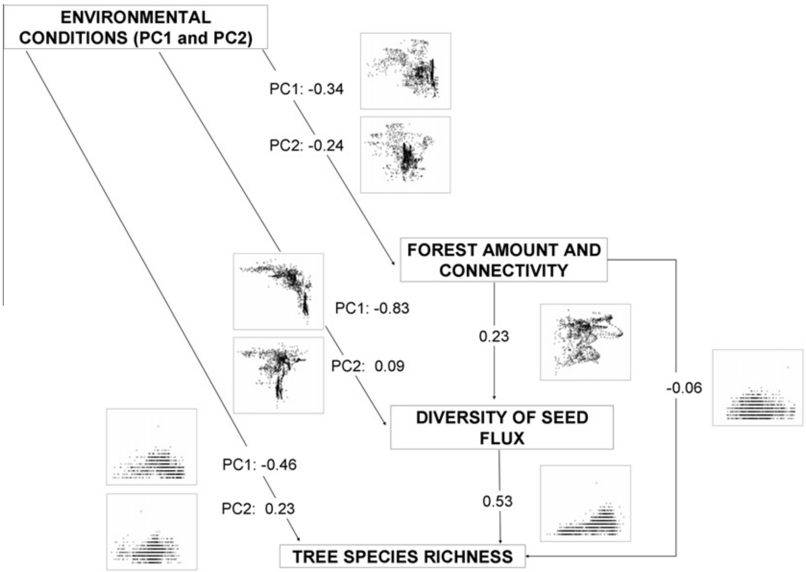

Fig. 4. Spearman correlation between variables considered in this study. The structure represents a top-down hierarchy in which coarse patterns of physical environmental conditions control other processes at smaller scales, which themselves influence local species richness. The arrows reflect the hypothesized sense of the causality. Note that all paths in this diagram were not specifically tested in our model.

Table 2
Posterior mean estimates and their standard deviation (SD) for the parameters used in the estimation of tree species richness, according to the models in each step. PH: Partially harvested stands; UN: unmanaged stands.

	Mean	SD
Step 1		
Calcareous	1.61	0.02
Siliceous	1.38	0.02
PC1	−0.77	0.04
PC1^2	−0.82	0.05
PC2	0.01	0.03
Step 2		
Forest cover	−0.14	0.03
Step 3		
FCC	0.14	0.02
Partial harvesting	−0.04	0.05
No management	−0.06	0.05
Diversity of flux (PH)	0.12	0.07
Diversity of flux (UN)	0.19	0.07

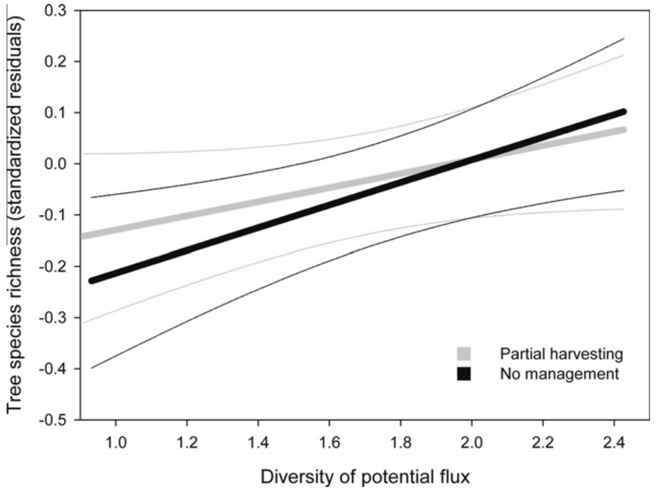

Fig. 5. Predicted tree species richness (standardized residuals from step 2) for the 95% central range of the diversity of potential seed flux in managed (partial harvesting) and unmanaged forests, while maintaining constant FCC (mean value of 57%). Parameters for the regression coefficients were estimated in step 3 with both dependent and explanatory variables standardized, although in order to facilitate interpretation, the original potential seed flux values are shown. Uncertainty on the parameter estimates is represented by the 95% central interval of their posterior distributions.

(Mittelbach et al., 2001). At the plot scale here analyzed, biotic competition in highly productive sites could explain richness reduction beyond a certain productivity threshold. It should be noted that precipitation patterns in the study area also showed some correlation with other considered factors. Indeed, areas with lower precipitation levels, independently of temperature conditions, tended to have a sparser forest cover, and less diverse and connected surrounding tree communities, with non-linear relationships according to raw data (Fig. 4). This might be explained by a higher ecosystem vulnerability to human disturbances under low productivity conditions (Kondoh, 2001), or by the tendency of the cultivated lands to be located in lowland areas within the Mediterranean North Region, which in our study area have lower precipitation (Fig. 3). Direct causality of the estimated association between annual precipitation and species richness might therefore not be straightforward. It is most likely that the PC1 regression coefficient in the first step reflexes a complex combination of all these factors, including a direct climatic effect on tree species richness and an indirect, or even spurious, effect through correlation with habitat loss, fragmentation or landscape diversity patterns. In any case, assuming there is a top-down hierarchical structure, i.e., that climate context shapes other small-scale processes influencing species richness patterns, direct and indirect effects of climate on tree species richness patterns were controlled in the first step of the analysis.

4.2. Does a higher amount of landscape forest cover explain by itself an increased diversity in local stands?

Contrarily to the commonly reported decrease in species richness with habitat loss (e.g. Fahrig, 2003; Montoya et al., 2008, 2010), an increase in surrounding forest cover was negatively related to those patterns of local species richness not explained by environmental gradients. In other words, under relatively homogenous climatic and lithological conditions, and once accounted for the effects of forest cover indirectly driven by climate, regions with more abundant and connected forest patches tended to have lower local tree species richness. The expected positive effect on species richness might somehow be captured in the estimated coefficients for PC1 in the first step, as supported by the initial Spearman correlations (Fig. 4), although this was not specifically tested in this study. Some stands located in productive regions with abundant forest have relatively high economic value. These stands could have lower richness than predicted by environmental conditions due to a higher intensity of human impact. By contrast, forests in more arid locations with a poor productivity, when not replaced by other land uses, might remain closer to their expected composition according to environmental conditions. In any case, it should be noted that this negative relationship accounted for a minor proportion of variance in tree species richness compared to the other analyzed factors.

4.3. Landscape diversity of well-connected seed sources as a determinant of local tree species richness

The present study adopted a conservative approach, as only the pure effect of diversity of potential seed flux was assessed, excluding its possible covariation with environmental or forest cover. Even so, we found that those localities where the potential flux of dispersed seeds was more diverse tended to have more tree species. This result suggests that the number of species in a local community is influenced by the degree of complexity of the community network to which it is connected through long distance dispersal, independently of its climatic and lithological context and the amount of surrounding forest.

Because of spatial autocorrelation of environmental conditions, the relative abundance of a particular species in a region can be, at least in part, an indicator of its competitive ability, that is, its degree of adaptation to the local environmental conditions in the 'sink' forest stand. Following this reasoning, low potential flux of a particular species is not necessarily always associated to low probabilities of recruitment, but might indicate the potential colonization by less frequent, inferior competitor species, that in some cases are more efficiently dispersed. In fact, in the study area, some species reached values of potential seed flux about 35–40 times higher than the maximum reached by many other species. The higher the number of species potentially colonizing a forest stand, the higher the probability that more species have suitable functional traits to exploit the ecological niches in that stand, and this was accounted by both richness and Shannon diversity metrics. However, Shannon diversity also penalized the excessive seed flux of superior competitors, whereas recognized the importance of the contribution of species with lower potential seed flux in the absence of an evident dominance of other species.

As in previous studies (Martín-Queller et al., 2011, submitted for publication), we found that tree species richness was higher in partially harvested, compared to unmanaged, conifer forests. This difference occurred under intermediate conditions of FCC and diversity of potential seed flux. We had hypothesized that the new niche opportunities created by disturbance would result in a greater enrichment of partially harvested stands with regard to unmanaged stands when the diversity of potentially colonizing species increased. We found that partially harvested stands presented more species when the diversity of potential seed fluxes from the surrounding communities was higher (Fig. 5). However, an increasing enrichment compared to unmanaged stands was not observed along an increasing landscape diversity of seed sources; that is, we did not observe any of the patterns illustrated in Fig. 2. Contrarily to our hypothesis, the difference in species richness between partially harvested and unmanaged stands was lower in more diverse and well-connected regions, and even became non-significant in those stands surrounded by the most diverse communities (Fig. 5). These results are difficultly explained by colonization dynamics since the establishment of additional tree species after disturbances is expected to be more probable when the sampling pool is enlarged (Grime, 1998). We observed that shade-tolerant species are present in the study area only in a sufficient amount as seed sources in the more diverse landscape metacommunities. This might explain the neutral effect of partial harvesting on species richness in these landscapes. Shade-tolerant species may better establish in unmanaged stands, where natural factors (wind, pests, etc.) might create smaller and fewer gaps and therefore sufficiently closed canopies. Partial harvesting is commonly regarded as less appropriate for the establishment of helophytes than complete harvesting. However, it should be noted that the initial stand conditions before harvesting may already correspond to relatively open stands in this Mediterranean area (average FCC in the analyzed stands is 57%), with partial harvesting further promoting light exposure for potential seedlings.

The processes addressed in this study, metacommunity dynamics and local disturbances, probably operate at different temporal scales. Metacommunity processes, that we showed are responsible, at least in part, for the number of species found in a local community, have probably operated at a historical or even evolutionary scale. At the spatial resolution used here (1 km^2), and the long distance dispersal analyzed, local disturbance events are probably linked to metacommunity dynamics in a much longer temporal scale than the one considered here. In such time scale, the historical disturbance regime rather than individual disturbances might have interacted with long distance dispersal events to shape current metacommunities structures or landscape pool of species. Thus, patterns of local richness would be mainly explained by evolutionary and historic extrinsic processes, which determine landscape or regional species richness, rather than by intrinsic local processes such as disturbances or biotic interactions (but see Akatov et al., 2005). This fits the statement by the species pool hypothesis (Eriksson, 1993; Pärtel and Zobel, 1999) in which the available pool of species in a region is the main determinant of local species richness. Moreover, given the initial correlations presented in Fig. 4, diversity of seed flux could be the main driver of local species richness, and the observed environmental effects in step 1 could be driven by common historical and evolutionary conditions of localities under similar current climate conditions (Ricklefs, 2004). Actually, the species pool hypothesis also predicts that the highest species richness can be generally found in habitats with somewhat less than intermediate productivity (Schamp et al., 2002). The reason argued is that this is the most common habitat productivity type over evolutionary time and therefore is linked to a higher past opportunity for origination of adapted species.

4.4. Managing forests for enhancing plant diversity

Our findings have important implications for foresters, since direct changes in species diversity derived from silvicultural practices might influence in the long term the diversity of other communities located some kilometres away. Lindborg and Eriksson (2004) observed that historical rather than current connectivity explained contemporary patterns of local plant diversity in grasslands in Sweden. Actually, a time lag in the response of sessile, long-lived tree communities surrounding the managed forest can be expected, and therefore these consequences are difficult to capture within the temporal scope of most management plans. The interactive effect on tree species richness of local disturbances and diversity of potential seed flux should be evaluated in longer time lags. This would provide a deeper understanding of the consequences of silviculture on plant species richness, and the underlying mechanisms. Additionally, the targets of enhancing local biodiversity by management plans should also recognize limitations emerging from the surrounding landscape. Indeed, our results showed that stand species richness does not just depend on the treatments that may (or not) be applied locally, but also on the diversity of forest communities in the landscape. Also, the response of species richness to canopy opening might depend on the amount of species adapted to the generated light conditions that are present in the landscape. This might result in landscape-dependent responses of species richness to the same harvest intensity. We contend that precautionary forest management for conserving and enhancing plant diversity requires a perspective much beyond the spatio-temporal scope of most of the traditional forest management plans (Lafortezza et al., 2008). In the case of Spain, this may be better addressed through the district-level forest plans PORFs (Planes de Ordenación de los Recursos Forestales) that have been established by the Spanish Forest law (passed in 2003) and are being increasingly recognized and applied as a basic planning instrument to broaden the traditional management scale focused on individual forest lands.

Acknowledgements

This research was financially supported by the Ministerio de Ciencia e Innovación (Spain) and European FEDER funds through DECOFOR (AGL2009-07140/FOR) and MONTES CONSOLIDER projects (CSD2008-00040).

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