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

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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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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