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Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes

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Abstract

While maximizing plant species richness continues to be central in the design, conservation and reforestation action plans, plant life histories are receiving increasing attention in assessments for the conservation of biodiversity in fragmented landscapes. We investigated the determinants of woody plant species (trees, shrubs and climbers) richness in the forest patches of the Guadalquivir river valley, a Mediterranean agricultural landscape with ~1% forest cover. We analyzed three species richness variables, total, and those corresponding to species with short-distance (ballistic, barochorous, myrmecochorous and short-distance anemochorous) and long-distance (anemochorous, endozochorous, exozoochorous, hydrochorous and dyszoochorous) dispersal systems, which significantly characterize earlier and late successional stages, respectively. We selected eleven predictor variables related to habitat structure (patch area, shape, distances to the nearest patch and reserve, and general isolation), physical environment (temperature, precipitation, elevation, and lithological heterogeneity), and anthropogenic influences (disturbance and proportion of old-growth forest). We used ordinary-least-squares multiple regression (OLS) and the Akaike's information criterion (corrected for spatial autocorrelation) and derived indices to generate parsimonious models including multiple predictors. These analyses indicated that plant species richness increase primarily along with increasing patch area and decreasing disturbance, but also detected secondary effects of other factors when dispersal was considered. While the number of species with potential long-distance dispersal tended to increase in more isolated patches of areas with greater precipitation and lithological heterogeneity (e.g. highlands at the valley edges), the number of species with short-distance dispersal increased towards drier and less lithologically complex zones with shorter between-patch distances (e.g. central lowlands). Beyond emphasizing the need to consider dispersal in fragmentation studies, our results show that woody plant species richness would be favoured by actions that increase patch area and reduce anthropogenic disturbances particularly in lowland forests.

Keywords: Biodiversity conservation; Habitat fragmentation; Mediterranean forest restoration; Seed dispersal; Woody plant species richness

1. Introduction

Deforestation begun in Europe ~6.0 ka BP when Neolithic agriculturalist settlements began to clear forests for cultivation, grazing, and obtaining fodder (Williams, 2000). This process of forest destruction and fragmentation has been particularly intense and severe in the Mediterranean region (Valladares et al., 2004), where forest fragments are frequently sparsely distributed across an agricultural matrix of extensive cultivations. Still, this region is considered a hot spot for biological diversity (Médail and Quézel, 1997), and although its relictual forested landscape (*sensu* McIntyre and Hobbs, 1999) is far from a pristine example of Mediterranean vegetation, it often contains unique populations of endemic plant species (Garrido et al., 2002; Aparicio, 2005).

It is important to understand the function of these landscapes as plant diversity reservoirs and how their diversity relates to characteristics of the remaining habitat fragments. Among these, forest cover is considered the pre-eminent determinant of forest species richness (Boutin and Hebert, 2002; Fahrig, 2003). However, for the case of relict landscapes, where the amount of forest cover drops to 10% or below (McIntyre and Hobbs, 1999), habitat structure-related attributes such as patch size, shape and spatial configuration may also have strong impacts

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on plant species richness (Saunders et al., 1991; Boutin and Hebert, 2002). The main goal of this study is to document relationships of woody species richness with habitat configuration in the forest patches of the Guadalquivir river depression, a relict landscape of southwestern Spain where natural or semi-natural forest retention is about 1% (Aparicio, 2008).

Because maximizing species richness has been central to set targets for conservation and to design conservation and reforestation action plans in general (Honnay et al., 1999; Godefroid and Koedam, 2003; Peintinger et al., 2003; Desmet and Cowling, 2004; Wilsey et al., 2005), species richness has often been explored within the species–area relationship as theoretical framework (Lomolino, 2000). However, the generally highly stochastic processes of extinction and recolonization determining within patch species richness do not only depend on patch area, but also on characteristics of the physical environment, disturbance regimes, and, notably, plant life histories (Honnay et al., 1999; Butaye et al., 2001). Consequently, the study of life history traits of plant species is receiving increasing attention in assessments for the conservation of biological diversity in fragmented landscapes (Graae and Sunde, 2000; Benítez-Malvido and Martínez-Ramos, 2003; Kolb and Diekmann, 2005; Purves and Dushoff, 2005; Wiegand et al., 2005; Chust et al., 2006; but see Yates and Ladd, 2005). In particular, seed dispersal is considered a functional core trait with relevance for both understanding and predicting ecological patterns and processes associated with population dynamics and evolution (Herrera, 1992; Weiher et al., 1999; Duminil et al., 2007), not only at the species level but also for species assemblages (Jacquemyn et al., 2001). In this regard, the spatial scale at which dispersal operates is fundamental in biological conservation since short-distance dispersal is primarily related to local population recruitment, whereas long-distance dispersal is much more influential on the potential of colonization of new habitats, the migration capacity of the species and the spatial genetic structuring of populations (Calviño-Cancela et al., 2006).

According to Ozinga et al. (2005), the critical question for conservation is not whether dispersal is an important process, but whether differences in dispersal translate into differences in local plant diversity. The response of each plant species to habitat fragmentation may depend largely on its potential for long-distance dispersal, relying on the type of diaspore (Butaye et al., 2001; Ozinga et al., 2005; Chust et al., 2006). In principle, from a functional perspective, morphological adaptations of diaspores for animal- and wind-mediated dispersal (fleshy pulps, wings, hooks, hair tufts) provide longer dispersal distances compared to diaspores lacking such morphological adaptations, or bearing food bodies for ant dispersal (Willson, 1993; Hughes et al., 1994). Thus, in theory, those species in which long-distance dispersal can be facilitated by the intervention of animals or wind should be less sensitive to habitat fragmentation than species lacking this possibility, or that are disseminated by animals with reduced home ranges such as ants.

Along with dispersal, responses of plant species richness to both environmental variation and anthropogenic modifications of habitat characteristics may be conditioned by a number of interrelated life history characteristics including flowering time, longevity, vegetative spread or life form (e.g. Tilman et al., 1994; Kolb and Diekmann, 2005), but reliable information to assign accurately these other traits to large plant species sets rarely exists (Herrera, 1984, 1992). Yet Herrera (1992) compiled up to ten of such morphological and functional characters for up to 66 of the woody plant genera that inhabit in the Mediterranean southwestern Spain. This allowed him to classify the woody vegetation of this region into two well-defined groups, each characterized by genera exhibiting a particular association of traits or character syndrome (Herrera, 1992; see also Verdú et al., 2003). Among other traits, the first syndrome corresponds to non-sclerophyllous, insect-pollinated, small-seeded dry-fruited lineages evolved during the Quaternary (e.g. *Cistus*, *Halimium*, *Thymus*, *Lavandula*, *Erica* or *Calluna*) and the second syndrome involves sclerophyllous, wind-pollinated, large-seeded fleshy-fruited lineages already evolved during the Tertiary (e.g. *Pistacia*, *Osyris*, *Juniperus*, *Rhamnus*, *Quercus* or *Myrtus*). On the other hand, Verdú (2000), Pausas and Verdú (2005) and Paula and Pausas (2006) have shown that post-disturbance resprouting capacity (as opposed to diaspore germination) is another common functional trait among the genera representative of the Tertiary set of species and that the Quaternary species are more drought-tolerant and fire-adapted. In all, while Tertiary species are characteristic of pre-forestal, more successionally mature communities, Quaternary species characterize earlier successional stages or woody pioneer plants (Herrera, 1992).

We asked three questions in this study. First, to what extent characteristics of habitat configuration, physical environment and anthropogenic influence determine total woody species richness variation across the studied forest patches? Second, do major plant dispersal potentials condition the response of species richness to these factors? Third, what are the implications of the observed relationships for the conservation of woody species richness in Mediterranean relict landscapes?

To address these questions we have used data from the 'Island-Forests of Western Andalusia' database BIANDOCC (property of the Andalusian Regional Government) generated from a complete sampling that involved all the woody species and all the forest patches currently occurring in the Guadalquivir river valley (Aparicio, 2008).

2. Methods

2.1. Study area

The study area in the project BIANDOCC extends from the Atlantic coast through the mean and lower stretches of the Guadalquivir river valley, a landscape of about 21,100 km^2 dominated by a fairly uniform agricultural matrix (Fig. 1). The climate is mild Mediterranean, with cool humid winters and warm, dry summers. Annual precipitation ranges from 460 to 1027 mm and mean annual temperature from 15.1 to 18.5 °C.