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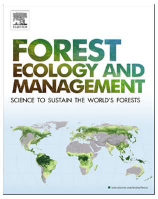

Determinants of functional connectivity of holm oak woodlands: Fragment size and mouse foraging behavior

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ABSTRACT

Demographic and genetic connectivity of fragmented plant populations will depend on effective propagule flow across the landscape. We analyze functional connectivity in a holm oak (*Quercus ilex*) fragmented landscape by considering three important stages driving recruitment: effective pollination, acorn production and acorn dispersal. We used a network approach to (1) determine if pollen-mediated gene exchange across the landscape was spatially structured; (2) estimate the effects of limited acorn dispersal on functional connectivity; (3) identify which landscape traits could drive source–sink dynamics of gene flow.

Although long distance dispersal was relatively frequent, most effective pollen flow occurred over short distances (<100 m). This resulted in a significantly modular structure of the mating network, yielding higher gene flow among nearby fragments. Limited mouse acorn hoarding activity had a strong impact on landscape connectivity, decreasing male gametic immigration rates into forest patches by one order of magnitude Besides, our results show that big forest fragments (>10 ha) are the main pollen sources, while small ones (<1 ha) are important pollen sinks. Thus, big fragments are critical to maintain functional connectivity, while small forest fragments may provide acorn crops better representing regional genetic diversity. In addition to area effects, less isolated and more central fragments showed higher migration rates and exchanged effective pollen with more fragments. Hence, we expected that landscapes with uniform or clumped distribution of big forest fragments would show optimal connectivity traits. However, despite that simulated gene flow was more evenly distributed across the landscape, connectance and migration rates decreased. Our results call for caution before translating patch-level management guidelines to the landscape scale. They also show that the level of functional connectivity may change throughout the recruitment process, suggesting that large-scale conservation strategies may fail if local effective seed establishment is disregarded.

1. Introduction

Land use changes have led to intense fragmentation of many temperate woodland ecosystems, replacing large continuous forests by a mosaic of isolated fragments, embedded in agricultural or urban matrices (Riitters et al., 2000). The demographic and genetic connectivity of fragmented plant populations depend on the effective dispersal of pollen and seeds across the landscape (Sork et al., 1999; Sork and Smouse, 2006). The intensity and scale of both seed and pollen dispersal across forest fragments are thus central to the decade-long debate about the extent to which tree populations are resilient to fragmentation (Kramer et al., 2008). High tree genetic diversity and outcrossing rates, and extensive long distance pollen dispersal may buffer the negative effects of forest fragmentation (Hamrick, 2004), while localized seed dispersal tends to increase spatial genetic structure and relatedness. Seed dispersal determines plant recruitment patterns, the successful establishment of both male and female migrant gametes and the final distribution of genotypes (Sork and Smouse, 2006; Sork et al., 2015). Pollen movement sets the template of male gametic gene flow, which depends on and is subsequently shaped by effective seed dispersal (Fig. 1). Integrating the joint effects of pollen and seed dispersal is thus necessary to gain realism in functional connectivity studies (Sork and Smouse, 2006; Jordano, 2010; Bacles and Jump, 2011).

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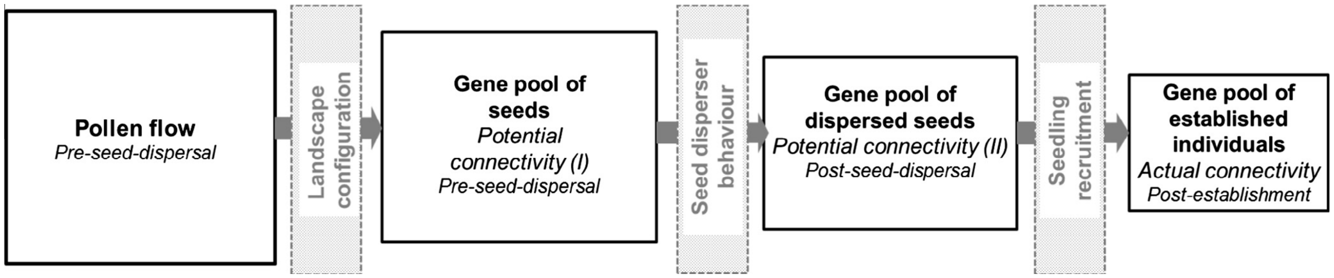

Fig. 1. Conceptual model of functional connectivity including changes along different recruitment stages (modified from Rico et al., 2012).

Analyzing fragmentation effects for trees using a metapopulation perspective is a daunting task, due to their typically long life span, delayed maturity, high recruit mortality, and long generation times (Bacles and Jump, 2011). Functional connectivity analyses provide a middle way between data-intensive (and costly to validate) metapopulation models and topological measures not underpinned by biological processes. Functional connectivity usually refers to demographic and genetic exchange among fragmented populations (Taylor et al., 1993; Rico et al., 2012). The application of graph theory methods to functional connectivity studies (Dyer and Nason, 2004, reviewed in Laita et al., 2011) has paved the way for evaluating which factors govern mating patterns and effective pollen- and seed-mediated gene flow at a landscape scale, and to detect genetic bottlenecks on fragmented populations (Dyer et al., 2010; Fortuna et al., 2008; Herrera-Arroyo et al., 2013). However, few landscape connectivity studies have integrated the effects of fragmentation on the functionally-related processes of pollen movement, effective mating, seed dispersal, and post-dispersal seed mortality, even if connectivity patterns may vary substantially throughout recruitment stages (Rico et al., 2012; Fig. 1).

Holm oak (*Quercus ilex*) forests are a suitable study system for addressing the effects of limited seed dispersal in functional connectivity. Like other wind-pollinated species, holm oaks typically exhibit leptokurtic distributions of pollen dispersal distances, combining a rapid decay at short distances with fat tails (Hampe et al., 2013; Ortego et al., 2014). As for acorns, forest management typically hampers their effective dispersal over long distances (Santos and Tellería, 1997; Pulido and Diaz, 2005; Morán-López et al., 2015, 2016). Eurasian jays (*Garrulus glandarius*), the main long-distance acorn disperser in Europe, are absent in small forest fragments (Andren, 1992; Brotons et al., 2004), where dispersal relies on wood mice (*Apodemus sylvaticus*), a moderately efficient local acorn disperser. Most acorns handled by mice remain within a close range of mother trees (<5 m), and many of them are finally predated (Gómez et al., 2008).

In fragmented holm oak woodlands, functional connectivity will thus depend on effective pollen flow among fragments, and subsequent mouse-mediated effective local acorn dispersal. The latter may in turn be strongly negatively affected by fragmentation (Santos and Tellería, 1997; Morán-López et al., 2015). The resulting recruitment failure within fragments may compromise the establishment of long-distance male gametic migrants, which may explain the low genetic diversity of holm oak saplings in small forest fragments (Ortego et al., 2010) in spite of extensive pollen flow (Ortego et al., 2014). If this were the case, any conservation strategy aimed at enhancing genetic cohesiveness at the landscape scale should explicitly include measures aimed at restoring local acorn dispersal.

The main goal of this study was to quantify functional connectivity of a holm oak fragmented landscape and to detect critical demographic factors potentially compromising gene exchange among fragments. For this purpose we built spatial networks of gene flow among forest patches considering effective pollination, acorn production and acorn dispersal. This allowed us to (1) gauge if pollen-mediated gene exchange within the landscape is spatially structured; (2) estimate the effect of mouse activity on functional connectivity; (3) determine which patch traits define source–sink dynamics within the network; and (4) evaluate if conclusions drawn from patch-level approaches can be directly scaled up to management guidelines at a landscape scale. We expected (a) a modular structure of the gene exchange network due to predominantly local pollen flow (Ortego et al., 2014), (b) a significant decrease of landscape connectivity with diminishing effective acorn dispersal (Rico et al., 2012), (c) an important effect of the spatial extent, centrality and isolation of fragments on pollen source–sink dynamics, and (d) a problematic extrapolation of these findings to the landscape scale, due to emergent properties in the connectivity network (Baguette et al., 2013).

2. Materials and methods

2.1. Study area

Field work was carried out in a Holm oak (*Q. ilex*) archipelago (14.4×10^3 ha; see Appendix B Fig. B1) located in the southern plateau of central Spain, near Quintanar de la Orden (39°35′N, 3°02′W, 870 m a.s.l.). Cereal cultivation has reduced forest cover to ~8% in the study area, with 401 patches ranging from 0.02 to 793 ha. The dominant tree is holm oak and the understory is composed of shrubby kermes oak (*Quercus coccifera*) and xeric Mesomediterranean shrubs (e.g. *Rhamnus lycioides*, *R. alaternus*, *Cistus ladanifer*, and *Asparagus acutifolius*). Annual precipitation and mean temperature are 421 mm and 14 °C, respectively. We chose this study site because it is representative of holm oak woodlands in central Spain (Santos and Tellería, 1998).

2.2. Sampling design

In autumn 2012, we simultaneously measured acorn production, acorn dispersal patterns by wood mice (*Apodemus sylvativus*) (Morán-López et al., 2015) and pollen flow. Eurasian jays are supposed to be absence in these patches (Tellería et al., 1999; Palomino et al., 2012), but we surveyed corvid presence during autumn–winter anyways. Two observers walked along 2–5 km transects, uniformly distributed throughout the study area (over 150 km in total), stopping every 100 m. Monitoring was performed at dawn and dusk (periods of peak bird activity). The openness of the study area, both among and within forest fragments, ensured easy acoustic or visual detection 200 m around observers, as ascertained by frequent contacts with magpies *Pica pica*, carrion crows *Corvus corone* and similar-sized birds. We did not detect any Eurasian jay, either during transects or while performing field work with mice and oak crops during 2012–2014 (Morán-López et al., 2015). Jay absence was further corroborated by interviews to local farmers and hunters.