



# Impact of tree decline on spatial patterns of seedling-mycorrhiza interactions: Implications for regeneration dynamics in Mediterranean forests



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## ABSTRACT

In the last decades, an increasing number of forest decline events and widespread tree mortality have been reported worldwide as a consequence of different global change drivers. Such a general decrease in tree health and cover has a large potential to impact mycorrhizal communities, but this issue remains largely unexplored.

We used a Bayesian framework to analyze the impact of *Quercus suber* decline on spatial patterns of seedling-mycorrhiza interactions in mixed Mediterranean forests in Southern Spain, and evaluate the relative importance of this symbiosis as a driver of oak seedling establishment.

Our models showed that the spatial variability found in the patterns of oak seedling colonization by both arbuscular mycorrhizas and ectomycorrhizas was partially linked to the process of *Q. suber* decline. Moreover, seedling survival and growth was influenced by the intensity of mycorrhizal colonization, but in quite unexpected ways. Arbuscular mycorrhizas had a larger effect on seedling performance than ectomycorrhizas, and the effects of both groups were negative or neutral but never positive.

We conclude that because the spatial distribution of the seedling-mycorrhiza association responded to the identity and health status of individual trees, and mycorrhizal infection did in turn affect seedling performance, tree decline might affect forest dynamics through changes in plant–soil biota feedbacks.

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## 1. Introduction

The plant–mycorrhiza association is one of the most common symbioses among organisms in forest ecosystems (Smith and Read, 2008). Mycorrhizal fungi help plant roots uptake water and nutrients in exchange for C, which may improve plant growth or their resistance to biotic and abiotic stresses (van der Heijden et al., 2008; Smith and Read, 2008). By altering plant performance, plant–mycorrhiza association plays an important role in community development and ecosystem processes (see van der Heijden et al., 2008 and cites therein). For example, it has been shown that the success of seedling establishment, one of the most critical processes determining ecosystem structure (Grubb, 1977), can be greatly improved by seedling-mycorrhiza associations (Amaranthus and Perry, 1987; Perry et al., 1989; Horton et al., 1999; Dickie et al., 2002). The likelihood of this interaction, and consequently its implications for forest stand dynamics, will be

strongly dependent on the spatial relationship between the mycorrhiza and the tree seedling community at fine spatial scales (Wolfe et al., 2009). However, so far relatively few spatially-explicit studies have attempted to disentangle the main factors determining the probability and functional significance of seedling mycorrhizal infection in forest communities (Dickie et al., 2002; Dickie and Reich, 2005).

The spatial distribution of mycorrhizas in forest soils can be shaped by several biotic and abiotic variables (Smith and Read, 2008). Specifically, the density and composition of the plant canopy are major factors that influence the assemblage of mycorrhizal communities both directly and indirectly. Tree species act as direct sources of fungal inoculum and determine the dominant mycorrhizal type (e.g. ecto [ECM], arbuscular [AM] or ericoid) or species due to the strong host-specificity of some fungi (Molina et al., 1992; Dickie et al., 2001, 2002). Canopy trees also indirectly influence mycorrhizal presence or abundance acting as modulators of key abiotic conditions such as soil moisture (Worley and Hacskeylo, 1959; Allen and Kitajima, 2013) or nutrient availability (Dickie et al., 2006; Aponte et al., 2010). The strong response of

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mycorrhizas to canopy composition implies that any disturbance occurring aboveground at the overstory level could translate into important changes in belowground mycorrhizal communities, which in turn could affect the probability of seedling establishment in the forest understory in a feedback process (Bever et al., 2010).

In the last decades, an increasing number of forest decline events and widespread tree mortality have been reported worldwide as a consequence of one or more global change drivers (Allen et al., 2010; Carnicer et al., 2011). Such a general decrease in tree health and cover has a large potential to impact mycorrhizal communities, but this issue remains largely unexplored. The few studies that have assessed the effect of tree dieback on mycorrhizas have shown that mycorrhizal communities in the roots of declining trees can differ in type, abundance and/or composition compared with those found in healthy trees (Perrin and Estivalet, 1989; Causin et al., 1996; Montecchio et al., 2004; Ishaq et al., 2013; Lancellotti and Franceschini, 2013). Defoliation might negatively affect mycorrhizal fungi through C allocation to roots, since the progressive loss of photosynthetic area in declining trees could translate into a reduction of the amount of soluble carbohydrates delivered to the symbiotic fungal partners (Gehring and Whitham, 2003; Druebert et al., 2009). Additionally, mycorrhizal communities could be indirectly affected by changes in abiotic conditions associated with the process of decline and gap opening after tree death, such as higher light availability (Royer et al., 2011) or changes in soil fertility (Orwig et al., 2008; Cobb et al., 2013). However, because most studies analyzing the consequences of tree dieback on mycorrhiza have been conducted in monospecific stands, comparing affected vs. not affected trees, we still lack a clear picture of the implications of species-specific tree decline for the spatial distribution of mycorrhizas in mixed forests. Moreover, it is unknown how these decline-induced changes in the mycorrhizal community could impact tree regeneration dynamics.

In this study we aim to analyze the impact of tree decline on spatial patterns of seedling-mycorrhiza interactions in Mediterranean oak forests, and evaluate the relative importance of this symbiosis as a driver of seedling establishment in the forest understory. We focused our work on mixed forests in southwest Spain undergoing severe problems of adult mortality and recruitment limitation of one of their dominant species, *Quercus suber* (Brasier, 1992, 1996). Using a Bayesian framework, we combined spatially-explicit data on mycorrhizal colonization in planted seedlings, the distribution of the woody plant community, and the abiotic environment to answer the following questions: (1) Does canopy composition and health status directly influence mycorrhizal colonization of seedling roots? (2) Does the abiotic environment (i.e. soil nutrients, soil moisture, soil texture, light) influence mycorrhizal colonization of seedlings? (3) What is the relative importance of mycorrhizal associations and abiotic factors as determinants of seedling survival and growth in the forest understory?

## 2. Materials and methods

### 2.1. Study sites and species

The experiment was carried out in Los Alcornocales Natural Park, a region considered as a *hot spot* of biodiversity in the Mediterranean Basin (Médail and Quézel, 1997). The climate is Mediterranean type with warm, dry summers and cool, humid winters. Mean annual rainfall is 970 mm (mean for 1951–1999). Mean annual temperature ranges from 14.6 to 18.4 °C, with a mean monthly maximum of 36 °C (July) and a mean monthly minimum of 2.8 °C (January). Vegetation in the overstory is dominated by the

evergreen, shade semi-tolerant *Q. suber* (cork oak). In the drier lowlands of the park, characterized by clayish soils, *Q. suber* coexists with the evergreen, shade-intolerant *Olea europaea* var. *sylvestris* (wild olive) forming open woodlands. The understory in these woodlands is usually very dense and dominated by shrub species such as *Pistacia lentiscus* L. (Supplementary material Table A.1). In wetter areas and sandier soils *Q. suber* coexists with the winter-deciduous, shade-tolerant *Quercus canariensis* Willd. (Algerian oak), forming closed forests. These closed forests are characterized by a species-rich understory dominated by tall shrub species, such as *Arbutus unedo* L., *Phillyrea latifolia* L., *Erica arborea* L., and *Erica scoparia* L. (Table A.1). Both *Quercus* species typically associate with ectomycorrhizas, while the other coexistent tree and shrub species (e.g. *O. europaea*, *P. lentiscus* or *Erica* spp.) mainly interact with arbuscular or ericoid mycorrhizal fungi (Molina et al., 1992).

In the study area, a severe decline affecting *Q. suber* has been reported since the early 1990s (Brasier, 1992, 1996). Several biotic (e.g. pathogens and insects) and abiotic (e.g. drought) factors are potentially involved in this decline (Tuset and Sánchez, 2004). However, the isolation of the aggressive soil-borne pathogens *Phytophthora cinnamomi* and *Phytium spiculum* from symptomatic *Q. suber* trees has addressed these exotic pathogens as the primary drivers of the species decline (Brasier, 1996; Romero et al., 2007). No other tree or shrub species in the study area showed evident symptoms of decline.

We selected six sites within the park to conduct our experiment, three located in open woodlands of *Q. suber* and *O. europaea* var. *sylvestris* (hereafter woodland sites) and three in closed forests dominated by *Q. suber* and *Q. canariensis* (hereafter closed forest sites) (Fig. A.1). At each of the six sites, we established a 70 × 70 m permanent plot in a topographically uniform area. Topography was kept constant in order to avoid confounding effects of this variable on mycorrhizal communities. Each plot was subdivided in 49 10 × 10 m subplots ( $n = 294$  subplots).

### 2.2. Seed sowing experiment

Seeds of *Q. suber*, *O. europaea* and *Q. canariensis* were collected from different trees within the park and sowed in winter (January 2010). At each site, sterilized and weighed seeds were sown in two adjacent 30 × 30 cm quadrats at the center of each of the 49 subplots. Each quadrat contained three lines of seeds separated 7.5 cm from each other and from the border of the quadrat. Each line was randomly assigned for sowing either three *Quercus* or six *Olea* seeds (*Q. suber* in both forest types, *Olea* at the woodland sites and *Q. canariensis* at the closed forest sites). The larger number of *Olea* seeds was chosen based on their lower probability of germination (Voyiatzis and Porlingis, 1987). Sowing quadrats were protected with 1-cm mesh hardware to exclude seed predators. As a whole, we sowed 2646 seeds of *Q. suber*, 2646 seeds of *O. europaea*, and 1323 seeds of *Q. canariensis*. Seedlings that emerged during the spring were measured in early June (initial height) and revisited in early autumn (October 2010) to record survival after the first summer, the main period of seedling mortality in Mediterranean systems (Gómez-Aparicio et al., 2008; Pérez-Ramos et al., 2012). Surviving seedlings were measured again at the beginning of the second spring (final height) to quantify seedling growth during the first year.

At the end of the spring 2010, we collected one healthy seedling per subplot and species when available (a total of 27 seedlings per site and species on average). Unfortunately, emergence of *O. europaea* was virtually nil in all sites (data not shown), which precluded us from including this species in the analyses. The harvested seedlings were kept moist and in cold temperatures in sealed plastic bags until taken to the laboratory, and stored at 4 °C for one or

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