



Species coexistence in a mixed Mediterranean pine forest: Spatio-temporal variability in trade-offs between facilitation and competition



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ABSTRACT

Studying species coexistence is key to understanding the way in which forests will respond to climate change. We studied the patterns of mixed stands including two main Mediterranean pine species: *Pinus pinaster* Ait. and *Pinus pinea* L. The spatial distribution of adult trees and saplings was studied via a point pattern approach. The effect of competition on growth of adult trees was investigated by comparing the performance of several competition indexes for each pine species through generalized linear models. Adult trees formed mixed clumps in which individuals of both species appeared together. Part of the tree growth variation was explained by tree size along with tree competition. However, the effect of conspecific vs heterospecific competition on tree growth differed and reflected species-specific neighbor-asymmetric competition. Facilitation was fundamental in the early stages for tree species development. The spatial distribution of saplings was strongly related to the spatial distribution of adult trees, also being asymmetrically clustered and neighbor-species-dependent. However, the required facilitation in early life-stage trees shifted to competition among trees in the adult stage. Species mixture may be desirable in terms of increasing and diversifying productivity, although the conditions currently present in the stand are likely to lead to future dominance of *P. pinea* over *P. pinaster* due not only to the greater competition tolerance of the former but also to a greater ability to successfully recruit in the plots, forming clusters that may be in turn be impenetrable to *P. pinaster*. Therefore, in order to maintain mixed stands, it would be necessary to enforce adequate silvicultural management strategies which avoid future stand dominance by *P. pinea*.

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1. Introduction

The spatial patterns observed in plant communities have been explained in terms of ecosystem self-organization, resulting from different mechanisms and factors (both direct and indirect as well as their interactions) acting on trees (Law et al., 2001). These mechanisms generate the observed spatial structure in ecological communities (Callaway and Walker, 1997; Koppel et al., 2006). However, the link between processes and patterns is not clear because many processes can create the same pattern (McIntire and Fajardo, 2009; Perry et al., 2006). Although examining a

pattern does not allow the specific mechanism that determines that pattern to be identified, some ecological information can, nonetheless, be discerned (Brown et al., 2011; Law et al., 2009). A clumped distribution is an indication of species having similar ecological requirements (Rüger et al., 2009), facilitation among individuals (Barker et al., 1997; Bever, 2002), or dispersal limitations at larger scales (Burslem et al., 2001). Segregation of species reflects different ecological requirements of species, niche partitioning or the existence of a mechanism that prevents the development of a particular species in the proximity of another species (Callaway and Walker, 1997). A regular distribution pattern arises when net competition dominates, causing repulsion between individuals (Stoll and Newbery, 2005).

In addition, the factors which affect the pattern of a species in plant communities could change over the life of the individual,

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given that many species appear to exhibit different ecological habitat preferences over the various life stages (Comita et al., 2007). Moreover, the sign of the interactions may not be constant throughout the life of the individual (Cavard et al., 2011). Furthermore, plant–plant interactions can shift from competition to facilitation when high levels of stress are present in herb and shrub communities (García-Cervigón et al., 2013; Gea-Izquierdo and Cañellas, 2009; Brooker et al., 2008). These notions tie in with the postulated stress gradient hypothesis (Bertness and Callaway, 1994; Maestre et al., 2009), which states that facilitative plant–plant interactions are more important and more intense in high-stress environments, such as arid ecosystems (Bertness and Callaway, 1994). This hypothesis has been tested in Mediterranean arid ecosystems, although with differing conclusions (Lortie and Callaway, 2006; Maestre et al., 2009), hence the question has yet to be resolved.

There is, nevertheless, some evidence of the existence of shifts in intraspecific facilitation/competition in Mediterranean shrub communities (García-Cervigón et al., 2013; Verdú et al., 2010) and mixed Mediterranean tree stands (Peñuelas and Boada, 2003; Zavala et al., 2000). Some species may also be better adapted than others to new environmental conditions, such as intense dry periods (Jump and Penuelas, 2005; Peñuelas et al., 2001). Differences in competition or facilitation responses in relation to climatic variability, along with differences in the spatial organization of the species in a mixed stand may lead to a reduction in coexistence; certain species benefitting more than others, increasing their dominance and thereby modifying the previously mixed stands.

Research and management efforts in Mediterranean forests have often focused on pure stands, despite the fact that mixed Mediterranean forest are complex ecosystems which exhibit greater potential than pure stands in terms of specific and structural diversity (Barbeito et al., 2009) as well as landscaping, resistance and resilience to biotic and abiotic hazards, economic income, optimal biomass production and stand stocking as well as landscaping and recreational use (Landeau and Landmann, 2008). In the Northern Plateau of central Spain, mixed stands of *Pinus pinea* L. and *Pinus pinaster* Ait have traditionally been favoured (Gordo et al., 2012). The economic importance of these multiple use species lies in the production of edible pine nuts in the case of *P. pinea* and good quality resin in the case of *P. pinaster*. These two species coexist in mixed stands, partially due to the fact that *P. pinea* and *P. pinaster* are quite similar in terms of ecological requirements, although they differ in certain aspects such as the primary dispersal method (Del Peso et al., 2012; Manso et al., 2012). These species coexist in the area in natural or seminatural formations (Gordo et al., 2012).

Recent research undertaken in mixed stands of these species has revealed that both *P. pinea* and *P. pinaster* have severe problems for natural regeneration (Gordo et al., 2012). In the case of *P. pinaster* the main limiting factor is seed survival during the summer of the first year, reducing recruitment almost to zero in these sandy soils, except in the area under the crown where higher moisture levels are present (Del Peso et al., 2012; Rodríguez-García et al., 2010, 2011). The main problems for natural regeneration in *P. pinea* are: mast-year occurrence (Calama et al., 2011), seed dispersal limitations and seed predation (Manso et al., 2012). However, under favorable conditions, seedlings can establish and successfully develop under the crowns (Barbeito et al., 2008). Mediterranean ecosystems are threatened due to their sensitivity to new climatic conditions caused by climate change (Benito-Garzón et al., 2008; Gea-Izquierdo et al., 2013; Lindner and Calama, 2012; Ruiz-Labourdette et al., 2012). Hence, it is crucial to determine the main factors allowing tree coexistence in Mediterranean ecosystems.

The aim of the present study is to investigate the arrangement of tree species in mixed *P. pinaster* and *P. pinea* stands in order to gain an insight into the mechanisms which determine tree species coexistence. Through the following analyses, an attempt is made to clarify the spatial strategies of trees that allowed coexistence and competition among them: (1) analysis of the spatial distribution of adult pine trees and whether or not DBH, tree height, crown size and slenderness are spatially structured; (2) tree growth modeling, comparing different competition indices which express different ecological assumptions, analyzing competition involving each species separately and (3) spatial distribution modeling of saplings in relation to adult trees, including alternative spatial covariates.

2. Materials and methods

2.1. Study area and field sampling

Two plots of 1 ha (100 m × 100 m) were installed in late fall 2009 in two mixed *P. pinea*–*P. pinaster* stands located in the Spanish Northern Plateau. Plots were selected in which the proportion of stems/ha and basal area of the least represented species was at least 30%. In each plot, all the adult trees of both species (DBH > 7.5 cm) were positioned (coordinates x , y) and breast height diameter measured as the average of two perpendicular diameters (DBH) was recorded along with total height (h), crown diameter (cw) and height to crown base measured as the average of two perpendicular diameters (hcb). Increment cores at 1.30 m were extracted from all adult trees using a Pressler increment borer. All juvenile trees ($h > 1.30$ m; DBH < 7.5 cm) within the plot were positioned and marked (Fig. 1). Core samples for 5 dominant trees of each species in each plot were taken. This information was used to calculate the site-quality for both species in the plots. The tree-ring measurement of these trees indicated that they were all aged between 79 and 92 years. The mature trees were naturally regenerated in the area, so the current spatial pattern reflects natural conditions. Some clear cutting may have been carried out, but there is no detailed information available in this regard. In the Íscar area, the management method employed is the floating periodic block method. However, in the plots included in this analysis, no regenerative cuttings have been undertaken, and the current regeneration is due to the natural dynamic of the stand.

2.2. Characterization of the spatial pattern of adult trees

The spatial organization of adult trees was studied through a point pattern analysis approach. To test the null hypothesis of spatial independence among the individuals, the Ripley's univariate K cumulative function (Ripley, 1977) was employed, with the complete spatial randomness null model, along with its non-cumulative o -ring function (Ripley, 1981). The rejection of this hypothesis would imply the existence of either a cluster or a regular pattern, as reflected in Ripley's K function. This function was calculated including (i) all adult trees pooled together; (ii) only *P. pinea* trees; (iii) only *P. pinaster* trees. To assess the spatial dependence between pairs of species, the bivariate K_{rs} function with the toroidal shift null model (Dale, 1999; Van Lieshout and Baddeley, 1999) was employed. The toroidal shift null model simulates independent distribution conditioned on the observed point pattern of both classes, keeping the position of the points of one class unchanged and shifting all the points of the other class by the same random vector, assuming that there is continuity between the upper and lower and between the right and left boundaries of the plot. The toroidal shift null model was chosen because we assumed that the spatial distribution of both species

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