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Stand-level drivers of tree-species diversification in Mediterranean pine forests after abandonment of traditional practices

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ABSTRACT

The progressive abandonment of traditional forest management over the last few decades has led to significant densification processes in most Mediterranean pine stands. In parallel, some of these stands have also shown tree-species diversification processes, the occurrence of which is considered essential for future adaptability and resilience to change. Here we aim to gain further understanding of the main factors driving these diversification processes via a case-study approach using the long-term-managed black pine (*Pinus nigra* Arn. ssp. *salzmannii*) forests of the Catalan Pre-Pyrenees (NE Spain). For this purpose, we sampled 155 plots distributed in 8 different stands and analyzed the role played by a number of microsite factors and stand attributes (including canopy openness and heterogeneity) on the abundance of seedlings ($h < 1.3$ m) and saplings ($h > 1.3$ m; $dbh < 7.5$ cm) of the main tree-species in the area (i.e. black pine, evergreen oak and marcescent oaks). Results revealed ongoing black pine recruitment limitation processes mainly associated to the high canopy cover of the overstory and the increasing abundance of shrubs, which may compete with pines for light resources. In contrast, we found that current environmental and stand-level conditions favor the progressive advance of the recruitment of evergreen and marcescent oaks, which are able to establish successfully under the dominant pine canopy. However, in the absence of canopy openings, light levels may not allow the established oaks (in particular the evergreen *Quercus ilex*) to grow and progress to higher developmental stages. Our findings bring deeper insight into the role of stand-level factors regulating species diversification, and can be used by forest managers to adjust their practices (e.g. by modifying the spatial and temporal patterns of silvicultural treatments such as thinnings or selection cuttings) in order to favor this natural process and increase stand resilience.

1. Introduction

The distribution, structure and composition of Mediterranean forests have been shaped over millennia by human practices (Debussche et al., 1999; Vallejo, 2005; Nocentini and Coll, 2013). Over time, this long history of human use has resulted in a significant reduction of the extent and inherent structural and compositional diversity of Mediterranean forests (Ciancio and Nocentini, 2000; Blondel, 2006). In the context of the Iberian Peninsula, this long history of intense human-use reached its peak at the end of the 19th century (Garcia-Ruiz et al., 1996; Pausas et al., 2004; Linares et al., 2010). However, the 20th century brought major socioeconomic changes leading to generalized land abandonment processes in marginal areas -generally mountainous systems- and to land-use intensification in broad valleys and coastal regions (Garcia-Ruiz et al., 1996; Vicente-Serrano et al., 2004; Lasanta-Martinez et al., 2005; Chauchard et al., 2007). This, together with extensive reforestation programs initiated with the aim of restoring the most heavily-degraded areas -most of which with pine species-, have triggered extended encroachment and densification processes in forest stands (Ameztegui et al., 2010; Navarro and Pereira, 2012; Ruiz-Benito et al., 2012).

Black pine-dominated forests (*Pinus nigra* Arn. ssp. *salzmannii*) in the Pre-Pyrenean range (NE Spain) are clear examples of forests undergoing such processes. These forests were intensively managed for timber harvesting and pasture grazing until the mid-20th century (Ruiz de la Torre, 2006), but from that point onwards the intensity of human practices decreased significantly (Vicente-Serrano et al., 2004). During the past few decades, just a few individual-tree selection cuttings affecting only the most vigorous and well-shaped trees have been conducted on these forests (Trasobares and Pukkala, 2004; Aunós et al., 2009). Such lessening of human pressure (particularly the strong decrease of silvicultural

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interventions and livestock grazing) has allowed the establishment of new cohorts of the dominant pine species, causing a generalized densification of the stands (DGCN, 2005) and a progressive process of colonization by late-successional tree species, mainly *Quercus* species (e.g., Urbieta et al., 2011; Carnicer et al., 2014; Vayreda et al., 2013).

The promotion of diversified forests is gaining currency as an appropriate management strategy to improve stand adaptability to environmental variations, including changes in disturbance regimes (e.g. Campbell et al., 2009; Thompson et al., 2009; Puettmann, 2011). Advancing knowledge of the ecological factors driving tree-species diversification in Mediterranean forest stands is of major interest, due to the particular vulnerability of this bioclimatic region to the effects of global change (Lindner et al., 2010). In the particular case of black pine-dominated forests, for example, the occurrence of natural diversification processes allowing resprouting species such as oaks to establish in the pine understory is reportedly essential for rapid vegetation recovery after the occurrence of large wildfires (Puerta-Piñero et al., 2011).

The progressive diversification of a given stand by tree species others than the ones occupying the dominant canopy is a complex process, the success of which depends on a number of factors acting at different spatio-temporal levels (seed dispersion into the stands, establishment of the plants and growth to reproductive maturity) (Zavala et al., 2011; Sheffer et al., 2013). Seed arrival, for example, is influenced by the abundance and spatial distribution of seed sources in the surrounding landscape (Zamora et al., 2010; González-Moreno et al., 2011), but also depends on other factors such as the abundance and behavior of seed dispersers or predators (Pérez-Ramos and Marañón, 2008; Gonzalez-Rodriguez and Villar, 2012). Once the seeds are dispersed into the stands, and in the absence of significant human disturbances and/or intensive browsing events, plant establishment and future growth will be triggered by a combination of factors acting at micro-site level: the environmental conditions of the site (climate, soil, etc.), the characteristics of the stand (over- and understory structure and composition) and the attributes of the canopy layer (gap shape, size) (e.g. Lookingbill and Zavala, 2000; Smit et al., 2008; Garcia-Barreda and Reyna, 2013).

The occurrence of natural or anthropogenic small-scale disturbances leading to moderate openings of the stands is a key element of the above mentioned process of tree-species diversification. These openings generate heterogeneity in the understory and lead to micro-site-level changes in environmental conditions (humidity, temperature) and resource availabilities (e.g. light, soil water) allowing the seedlings of the dominant species and those coming from adjacent stands to prosper (Runkle, 1981; Runkle and Yetter, 1987; Yamamoto, 2000; Ligot et al., 2014).

This study aims to shed light on these processes which, contrary to other bioclimatic regions, have so far been little explored in the Mediterranean. More specifically, we aimed to answer the following questions: (*i*) have the sub-Mediterranean black pine forests undergone active regeneration and tree-species diversification processes during the last decades? (*ii*) Which are the main stand-level factors driving such processes? and (*iii*) Do the canopy openness and the gap attributes play a key role on them? For this purpose, we used the long-term-managed Sub-Mediterranean black pine forest of the Catalan Pre-Pyrenees (NE Spain) as case study. We selected a number of stands showing a large gradient of canopy openness and structural heterogeneity and analyzed the role played by different stand-level factors in the abundance of the different species at different life-history stages: seedlings and saplings. We expected stand structure and, particularly, canopy attributes to play a key role in driving stand-level species diversification allowing species other than pine to survive and prosper under the dominant pine canopy.

2. Materials and methods

2.1. Study area and stands selection

The study was conducted in the Catalan Pre-Pyrenees, Northeastern Iberian Peninsula, in a mountainous range limited at East and West by the basins of the rivers Segre and Cardener (between 1° 11′ 6″ and 1° 36′ 57″ E, and 41° 56′ 57″ and 42° 3′ 43″ N, DATUM WSG84) (Fig. 1). These mountains are formed by folded structures of sedimentary carbonate rocks (mainly lutite, marlstone, limestone and conglomerate), characterized by vertical elevation ranging from 400 to 1000 m.a.s.l. Climate in the area is sub-humid from Mediterranean-continental to Mediterranean-montane, characterized by mean annual precipitation of around 700 mm and mean annual temperature around 12 °C (Ninyerola et al., 2005). Rainfall is usually concentrated in autumn and spring, and winter is the season with least precipitation. In summer, short convective storms also provide significant precipitation input (around 100–130 mm in average during the hottest months, July and August). However, due to the high inter-annual variability in the occurrence of this type of rainfall events, the occurrence of summer dry periods is not unusual. Within this general geographic context, the study focused on the forests dominated by black pine (*P. nigra* Arn. ssp. *salzmannii*) which are the most abundant in the study area.

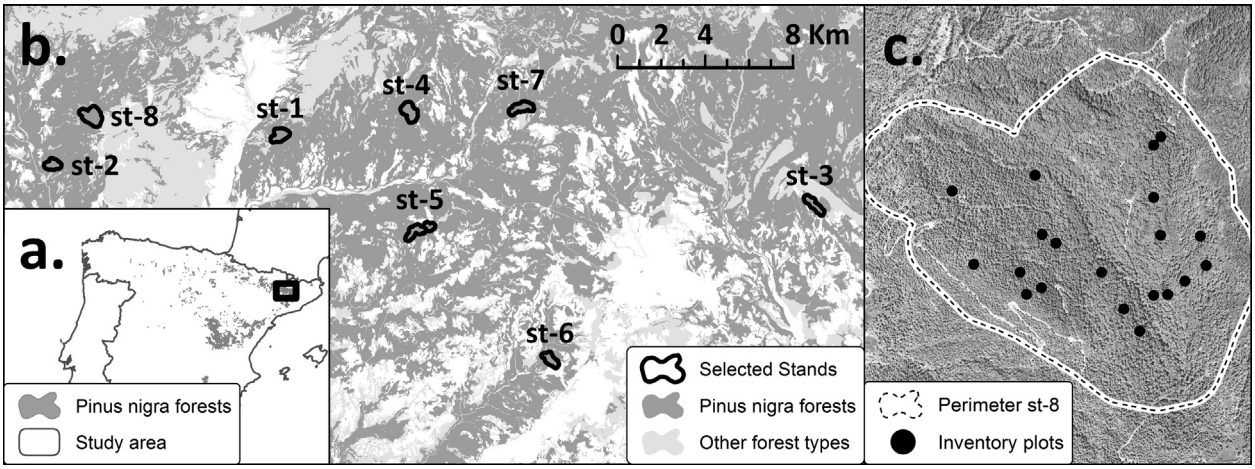

Fig. 1. Location of the study area (a), the sampled stands (b), and the inventory plots within one of the stands (c).