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Regeneration of three pine species in a Mediterranean forest: A study to test predictions from species distribution models under changing climates

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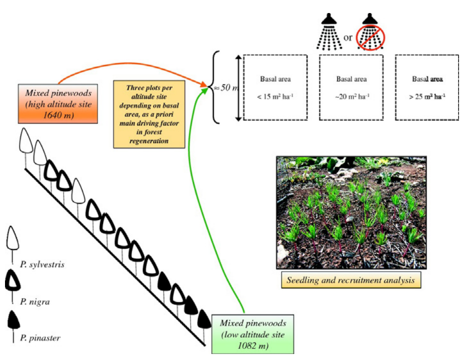
HIGHLIGHTS

- Water availability during the summer season was the major factor driving recruitment.
- Stand basal area was a factor influencing positively seedling abundance for the three study species
- *P. nigra* could retreat and eventually disappear from its rear-edge area and extend in its expanding-edge area.
- *P. sylvestris* presented higher seed emergence percentages at high and medium stand basal area
- *P. pinaster* recruitment was favored by low stand basal area.

GRAPHICAL ABSTRACT



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ABSTRACT

The study tested the hypothesis that future changes in the composition of tree communities, as predicted by species distribution models, could already be apparent in the current regeneration patterns of three pine species (*Pinus pinaster*, *P. nigra* and *P. sylvestris*)inhabiting the central-eastern mountains of Spain. We carried out both an observational study and a seed-sowing experiment to analyze, along an altitudinal and latitudinal gradient, whether recent recruitment patterns indicate an expansion of *P. pinaster* forests to the detriment of *P. nigra* ones in the low-altitude southern sites of these mountains; or whether *P. sylvestris* is being replaced by *P. nigra* in the high-altitude sites from the same area. The observational study gathered data from 561 plots of the Spanish National Forest Inventory. The seed-sowing experiment tested the effects of irrigation and stand basal area on seedling emergence and survival. Data were analyzed by means of Generalized Linear Models and Generalized Linear Mixed Models. Regeneration of the three pine species responded similarly to the explicative factors studied, but the density of tree seedlings and saplings exhibited a wide spatial heterogeneity. This result suggested that a mosaic of site- and species-specific responses to climate change might mislead model projections on the future forest occupancy of tree species. Yet, we found no indications of neither an expansion nor a contraction of the near future forest occupancy of the tree species studied.

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1. Introduction

The current diversity and distribution of tree species across the Iberian mountains is the result of both historical and ecological factors. Historically, temperate and boreo-alpine species have found refuge in these Mediterranean mountains as they migrated northwards and upwards after the last glacial period (Schmitt and Varga, 2012). Ecologically, soil and microclimatic conditions vary over relative short distances in Mediterranean mountainous areas, generating a patchwork of habitats occupied by different plant communities at the landscape scale (Blondel et al., 2010). Consequently, Iberian Mountains contain assemblages of tree species with disparate biogeographical origins and ecological factors, distributed in a mosaic-like fashion that follows altitudinal and/or latitudinal gradients (Blanco et al., 1998). These forests may thus constitute an adequate natural laboratory to observe how changing climates shift tree distributions.

The distribution areas of *Pinus pinaster* Aiton, *Pinus sylvestris* L. and *Pinus nigra* Arn. subsp. *salzmannii* Dunal (Franco) (*P. pinaster*, *P. sylvestris* and *P. nigra*, respectively, hereafter) coincide in the central-eastern mountain ranges of Spain. Here, the three pine species show clear altitudinal and latitudinal distribution patterns. *P. pinaster* is present in the low-altitude and southern-most forests of the mountains, whereas *P. nigra* occupies the central and mid-altitude forest zone, and *P. sylvestris* inhabits the northern and upper altitude areas. This geographical distribution pattern reflects the biogeographical origins and the ecological characteristics of each species. *P. pinaster* is a genuine Mediterranean species that is mainly found in the Iberian Peninsula. *P. sylvestris* is a Euro-Siberian species which range has undergone continuous latitudinal and altitudinal changes during glacial-interglacial cycles of the Quaternary (Blanco et al., 1998). Currently, the Spanish populations of *P. sylvestris* represent the low-latitude margin of the species' distribution area (Matías and Jump, 2012). In its turn, *P. nigra* is a sub-Mediterranean species, i.e. it inhabits the transition zones between the Mediterranean and the Euro-Siberian regions, with its core distribution area in central-eastern Spain (Blanco et al., 1998).

In this particular area, local climatic data spanning the 20th century have yielded a trend of warming, increased aridity and increasing drought events since the onset of the 1980s (Candel-Pérez et al., 2012). Under this ongoing climate change, the three aforementioned pine species are expected to respond in accordance with their biogeographical and ecological characteristics (Mendoza et al., 2009). Specifically, models fitted to simulate forest occupancy under a climate change scenario project a rapid reduction in the *P. sylvestris* Spanish range, due to the lack of areas of sufficient altitude to which this species could migrate, and a decline in *P. nigra* forests. On the contrary, *P. pinaster* would maintain or increase the area it occupies, because it could colonize new suitable habitats created by climate change (Benito Garzón et al., 2008; Ruiz-Labourdette et al., 2012). These predictions in forest occupancy could be interpreted as a dynamic that would produce the retreat of *P. nigra*'s rear-edge populations and its northward and upward displacement within the mountains of central-eastern Spain, supporting the idea that species responses to changing environments are determined by population responses at range margins (Hampe and Petit, 2005).

Some authors have already reported recent growth declines and increased mortality related to climatic dryness in Iberian populations of *P. nigra* (Candel-Pérez et al., 2012; Linares and Tíscar, 2010) and *P. sylvestris* (Vilà-Cabrera et al., 2013). However, juvenile individuals may respond quicker than adult trees to environmental changes (Lloret et al., 2004) and, particularly, to extreme climatic events (Castro et al., 2005). Thus, recent regeneration patterns could be interpreted as a first evidence of coming shifts in forest composition as result of ongoing climate change.

Considering the latter and the aforementioned projections of forests occupancy under the observed climate change scenario, with conditions being progressively warmer and drier in the central-eastern mountains of Spain since 1980s onwards, we made two confluent hypotheses. First, that *P. nigra* recruitment should have been poorer during recent decades than the recruitment of *P. pinaster* in the low-altitude southern mixed-forests of these mountains (the rear-edge of *P. nigra* populations here). Second, that, conversely, recruitment of *P. nigra* should have been higher than *P. sylvestris* recruitment in the high-altitude northern mixed-forests (the expanding edge of *P. nigra* populations) during the same period of time.

In order to test these hypotheses, we performed both an experimental and an observational study to analyze recruitment patterns of *P. pinaster*, *P. nigra* and *P. sylvestris* in forest stands from central-eastern Spain. Experimental data resulted from a seed-sowing experiment conducted to recreate two potential climatic scenarios (wet summers vs. dry summers) in forest stands that differed in stand basal area. We distinguished between wet and dry summers, because Mediterranean ecosystems are typically characterized by hot-dry summers, yet some scattered summers are rainier than normal allowing for regeneration pulses (Castro et al., 2005; Mendoza et al., 2009). Stand basal area was introduced as a driven factor, because it affects directly and indirectly regeneration outcomes. For instance, drought effects might be ameliorated under the shade of canopy trees (e.g. Castro et al., 2005 on *P. sylvestris*; Ruano et al., 2009 on *P. pinaster*; Tíscar and Linares, 2014 on *P. nigra*).

Observational data were obtained from 561 plots of the Third Spanish National Forest Inventory. Given that increased aridity is one of the predictions of climate change for the Mediterranean Basin (Giorgi and Lionello, 2008), we used the observational study to assess recent forest regeneration along a gradient of aridity (a proxy of water availability) in an area that is changing to warmer and drier conditions (Peñuelas et al., 2007; Vilà-Cabrera et al., 2013).

2. Methods

2.1. Study site

The study was conducted in the Cuenca Mountain Range (ca. 73,000 ha) located in the region of Castilla-La Mancha, central-eastern Spain (Fig. 1). This mountainous area belongs to the Iberian System Mountains, which are composed of numerous haphazard and motley series of mountain ranges, massifs, plateaus and depressions. The main soil types in the region overlie calcium-rich and mainly shallow calcareous bedrock. The climate is mountain Mediterranean characterized by wet and cold winters, and dry and hot summers. Data of meteorological stations from the Cuenca Mountain Range have proved the existence of topographical gradients, with both mean annual temperature decreasing linearly by 0.64 °C and mean precipitation increasing by ~97 mm for every 100 m of elevation. Altitudes of the Cuenca Mountain range from 610 to 1866 m a.s.l. *P. nigra* is naturally distributed in the area between 1000 and 1700 m a.s.l. and dominates the forest composition, as nearly pure stands, along this altitudinal range. However, mixed-stands of *P. nigra* and *P. pinaster* occur at low elevations (c. 1000–1100 m), and *P. nigra* and *P. sylvestris* arrange as mixed-stands at the upper elevation limit of the study area (ca. 1400–1700 m) (Candel-Pérez et al., 2012). These same authors showed that temperature has significantly increased in the Cuenca Mountain range from 1980 onwards, causing increased evaporative demands and reduced water availability.

2.2. Observational study

We used data from the Third Spanish National Forest Inventory (3SNFI hereafter) to perform the observational part of the study. Even though the 3SNFI was carried out during 2003, it is still the most recent National Forest Inventory for the study area. The SNFI consists of permanent inventory plots systematically distributed on a one-square kilometer grid. Each plot is divided in four concentric subplots of 5, 10, 15, and