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Recruitment into the seedling bank of an undisturbed Mediterranean pinewood: Increasing forest resistance to changing climates

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ABSTRACT

Although typically considered shade-intolerant, Mediterranean pine species may form seedling banks due to the existence of facilitative interactions between seedlings and canopy trees. Consequently, seedling banks could be considered as part of the seedling pool that should restock managed Mediterranean pinewoods, thus increasing the resistance of these forests to climate change. The study investigated the characteristics of the seedling bank in a silviculturally undisturbed forest of *Pinus nigra* subsp. *salzmanii* exposed to increasingly arid conditions. The study site was located in the southernmost range limit of the species. The dynamics of the seedling bank was studied by comparing current seedling (height $<$ 1.30 m, age $<$ 2 yr) and pole tree (height $\geq$ 1.30 m and diameter at breast height $<$ 12.5 cm) altitudinal distributions, using altitude as a proxy of aridity. Aridity was proved to have increased in the study area along the last four decades. These climatic trends were identified by means of Mann-Kendall tests for trend. Additionally, the effects of summer drought, light availability, soil compaction, litter layer and micro-slope as explanatory variables of the recruitment outcome were analysed by means of Generalized Linear Mixed Models and survival analysis. Altitude affected positively seedling establishment, but had no effect on the current abundance of pole trees, indicating a recent upwards displacement of the regeneration niche due to increasingly arid conditions. Water and light availability, the latter at intermediate levels of irradiance, affected tree recruitment positively, whereas the effects of soil compaction, litter layer depth and micro-slope were negative. Implementing extended rotation periods and maintaining intermediate values of tree cover are proposed as important management recommendations to achieve successful natural regeneration in Mediterranean pinewoods.

1. Introduction

In the northern Hemisphere, the low-altitude and southern limits of tree ranges are expected to move upwards and northwards as conditions become more arid due to ongoing climate change (Dyderski et al., 2018). This shift in species distribution should be the product of two processes: increased adult tree mortality and reduced self-recruitment, insufficient to compensate for adult decline. In this regard, some studies have documented recent episodes of adult mortality due to increased climatic dryness in the Mediterranean region (Candel-Pérez et al., 2012; Vilà-Cabrera et al., 2013). However, the long-term impact of climate change on tree recruitment may be difficult to assess for at least two reasons: (i) trees are long-lived, iteroparous plants that may fail many times before achieving successful regeneration, and (ii) desiccation is already the main cause of seedling mortality among Mediterranean tree species (Castro et al., 2005; Ruano et al., 2009; Matías et al., 2012; Tíscar et al., 2017). These limitations can be overcome by combining observational and experimental data as in the present study.

Despite the major importance of water availability for the successful regeneration of Mediterranean tree species, irradiance plays a general key role as well (Puerta-Piñero et al. 2007). The response of tree seedlings to the amount of light reaching the forest floor is specific. Therefore, foresters commonly rank tree species on a continuum of shade tolerance and apply regeneration methods accordingly, removing most trees from the stand in order to regenerate shade intolerant species, or maintaining a canopy of mature trees to allow the establishment of shade tolerant ones (O'Hara, 2014). This general rule can however vary under the stressful conditions of Mediterranean forests. Shade buffers against high temperatures and excessive evapotranspiration, and consequently improves water balance (Gómez-Aparicio et al., 2004). Thus, several studies have reported increased seedling survival of both shade tolerant and intolerant pine species under the canopy of taller plants in Mediterranean forests (Castro et al., 2005; Ruano et al., 2009; Tíscar and Linares, 2014; Andivia et al., 2018). The beneficial effects of shade are still present even when water is artificially added to simulate the stormy summers that sporadically occur in Mediterranean

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mountains (Gómez-Aparicio et al., 2008). As a result, shade by itself, or combined with increased water availability during atypically wet summers, may facilitate pine recruitment under the canopy of undisturbed stands. This generates an opportunity to consider tree regeneration in managed Mediterranean pinewoods not only in relation to silvicultural disturbances, but also in relation to the probable presence of seedling banks. Seedling banks are formed by those seedlings that develop beneath an intact canopy and the establishment of which is not consequently related to the entries of planned cutting cycles in managed forests (O'Hara, 2014). Mediterranean pinewoods currently tend to remain silviculturally undisturbed for decades, due to poor conditions of the timber market and/or the implementation of extended rotations for biodiversity conservation and carbon sequestration (Bravo et al., 2008). Consequently, whilst expanded drought due to climate change might prevent seedling establishment at the time planned by management cutting cycles, the seedling bank could be crucial for increasing forest resistance. Resistance was considered to be the ability to recruit new seedlings even though increasingly arid conditions will make this more difficult.

An increasing trend in temperatures and a decreasing trend in precipitation are already being observed in southern parts of the Iberian Peninsula (Linares and Tíscar, 2010; Ruiz-Sinoga et al., 2011). Considering this, I used both observational and experimental data to evaluate the impacts of the resulting more arid conditions on the recent recruitment dynamics of *Pinus nigra* subsp. *salzmannii* (*P. nigra* hereafter) in an undisturbed forest. By working with silviculturally undisturbed stands, I could quantify recruitment into the seedling bank. Forests of *P. nigra* occupy 405,983 ha in the eastern calcareous mountains of the Iberian Peninsula. Summer drought is considered to be the major limiting factor for the recruitment of *P. nigra* (Tíscar and Linares, 2011). However irradiance is equally important, as seedling establishment occurs more frequently under intermediate levels of canopy cover (Tíscar and Linares, 2014).

Models fitted to simulate forest occupancy under a climate change scenario project an important future decline of *P. nigra* forests (Benito-Garzón et al., 2008). Thus, some signs of range contraction could be already evident at the southernmost distribution limit of this species (Matías and Jump, 2014). In this regard, I used observational data obtained from 198 forest inventory plots to test whether the regeneration niche of *P. nigra* has moved upwards during recent decades by comparing current seedling and pole tree distributions along an altitudinal gradient that would reproduce projected climate changes in temperature (Rabasa et al., 2013). Specifically, I understood that a higher positive effect of altitude should be expected on the establishment of seedlings rather than on pole trees, because seedlings would have established under warmer, drier climatic conditions. Since water availability is decreasing for seedling establishment due to contemporary climate change, I also used experimental data from an irrigation experiment to analyse the influence of water availability on the establishment of *P. nigra* seedling banks (Matías et al., 2012). I additionally accounted for the effects of several variables acting at the microhabitat scale that could affect water infiltration and soil desiccation under closed canopies, namely micro-slope, soil compaction, depth and cover of the litter layer, and light availability. Hereafter, I will refer to all these variables including water availability as abiotic factors. Finally, I also used temperature and precipitation data to confirm climate trends towards more arid conditions in the study forest.

The following questions are specifically addressed: (1) is summer aridity progressively increasing in the study area? (2) is the range of *P. nigra* moving upwards in the southernmost forest of the species distribution? (3) what are the effects of abiotic factors on the recruitment of undisturbed *P. nigra* forests? (4) what is the potential role of seedling banks in the natural regeneration of managed *P. nigra* forests?

2. Materials and methods

2.1. Study site

The study was carried out in the Cazorla, Segura and Las Villas Natural Park (southeast Spain) (37°54′N–2°53′W) in a managed forest named 'Navahondona'. The site is part of the most extensive *P. nigra* forest at the southernmost limit of the species distribution area (Fig. A.1.). Climate is Mediterranean. Snowfalls and frost are common during the winter, but summers are dry and hot. The Navahondona forest covers 16456 ha along an altitudinal gradient from 780 to 2108 m above sea level (a.s.l.). Previous research has found that mean annual temperature decreases linearly in the study area by 0.64 °C for every 100 m of elevation, whereas annual precipitation increases by ~84 mm for every 100 m of elevation (Linares and Tíscar, 2010). Therefore, altitude is a good proxy of climatic aridity in the study site. *P. nigra* dominates forest stands located between 1000 and 2000 m a.s.l., co-occurring with *Rosa* sp., *Thymus* sp., *Helleborus foetidus* and other shrubs, although the understory is generally weakly developed (Tíscar, 2015a). Other pine (*Pinus halepensis* and *Pinus pinaster*) and oak species (*Quercus ilex* and *Quercus faginea*) are also present. Management prescriptions for Navahondona have varied during the 20th century. As a result, the forest was initially regenerated by applying the shelterwood silvicultural method with a rotation period of 120 years, followed by the selection method with a period of 150 years. While applying the selection method, a BDq system was used, where B is for basal area (20.5 $m^2 ha^{-1}$ in this case), D for maximum diameter (50 cm in this case) and q is for the q-factor (1.7 in this case) (O'Hara, 2014).

2.2. Climatic data

Climatic data were obtained from two meteorological stations: Vadillo-Castril (37°55′20″N–2°55′37″W, 970 m a.s.l.) and Cazorla (37°54′35″N–3°00′07″W, 885 m a.s.l.). Vadillo-Castril occupies a centered position within the Navahondona forest. It has a precipitation record that goes from 1951 to present, but it does not record temperature. For this reason, I obtained temperature records (for the period 1972 to present) from the nearby meteorological station of Cazorla, which were then corrected according to an adiabatic lapse rate of −0.64 °C for every 100 m of elevation to translate them into the altitudinal level of Vadillo-Castril (Linares and Tíscar, 2010). From these data of precipitation and temperature, a monthly water balance was calculated as the monthly difference between precipitation and potential evapotranspiration estimated by the Thornthwaite's method (see Vicente-Serrano et al., 2010). Values of water balance were assumed to reflect aridity.

In order to address question (1), I then estimated temporal trends of monthly mean temperature, monthly total precipitation and monthly water balance using the Mann–Kendall test (Mann, 1945; Kendall, 1975). Mann–Kendall tests (hereafter MK) are non-parametric tests for the detection of trends in a time series. These tests are widely used in environmental science because they are simple and robust and can cope with missing values and values below the detection limit. When significant trends were obtained from MK tests, computed from the year 1972 onwards, the rates of change of the climatic variables were estimated by obtaining their slope from linear least squares regression (Linares and Tíscar, 2010). MK tests were performed with the 'MannKendall' function in the 'Kendall' package of R (R Development Core Team 2014).

2.3. Forest inventory data

The observational part of the study was carried out with data that came from the last Navahondona Forest Inventory carried out in 2010 (2010NFI hereafter). The 2010NFI consisted of 15 m radius circular plots systematically distributed on a square grid of 200 m throughout