



# Lack of local adaptation to the establishment conditions limits assisted migration to adapt drought-prone *Pinus nigra* populations to climate change

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## ABSTRACT

The intentional movement of tree genotypes, or assisted migration, is an operational approach proposed to adapt forest management to climate change. Assisted migration assumes that tree populations are locally adapted to environmental conditions, but this fact should be tested specifically. In this study, both a reciprocal transplant and a common garden experiment were carried out to test local adaptation to variable environmental conditions of seedling emergence and survival of the tree species *Pinus nigra*. Reciprocal sowing experiments involved the cross-sowing of four seed origins among four destination habitats, located in high- and low-altitude sites within central and peripheral populations of *Pinus nigra*. Evidence of local adaptation was taken to be a significant destination x origin interaction. Then, the possibility of local adaptation was further evaluated under the “local versus foreign” and the “home versus away” criteria. Results showed negative evidence of local adaptation to the emergence and survival environment faced by *Pinus nigra* seedlings, which would reduce the utility of assisted migration as an effective tool to adapt forests to ongoing climate change.

## 1. Introduction

Climate envelope models predict the movement of tree geographical ranges toward higher elevations and latitudes as temperature and evapotranspiration increase due to ongoing climate change (Araújo and Rahbek, 2006; Ruiz-Labourdette et al., 2012; García-Valdés et al., 2013). Other climate changes have occurred in the past, forcing the migration of tree species to new areas as they tracked the climate to which they were adapted (Davis and Shaw, 2001; Hampe and Petit, 2005; Iverson and McKenzie, 2013). However, a similar natural migration in response to current climate change is unlikely to occur for at least two reasons: expected change will be more rapid than trees are able to disperse to spread their domains, and natural migration would be almost impossible because of forest fragmentation and existing barriers to seed dispersal (Aitken et al., 2008; Valladares et al., 2014). Consequently, it has been argued that the persistence of forests will need to rely on the presence of sufficient genetic variation within tree populations, the maintenance of habitat connectivity and the implementation of some management strategies such as ‘assisted migration’ (Loss et al., 2011; Schwartz et al., 2012).

Assisted migration (also referred to as assisted colonization, assisted

translocation and managed relocation in scientific literature) has been defined as the movement of species and populations to facilitate natural range expansion in direct management response to climate change (Vitt et al., 2010). Here, we will emphasize the intentional movement of tree populations (genotypes) so that propagates from the warmer range areas could be moved upward or northward in order to catch up with their expected future ranges (Millar et al., 2007; Pedlar et al., 2012; Williams and Dumroese, 2013).

Although the proposal derives from logical reasoning, it comes with various issues that have raised concerns among forest managers and ecologists (Loss et al., 2011; Williams and Dumroese, 2013; Schwartz et al., 2012). For instance, it has been highlighted that projections made by climate envelope models may be unsuitable to guide long-term forest planning under a climate change scenario, because the effect of climate on tree distribution is frequently mediated through topographic variation, soil properties and inter-specific interactions (Lo et al., 2010; Liancourt et al., 2013; Tíscar et al., 2017). There is also a risk of causing genetic introgression through the hybridization of the relocated and the native genotypes (Hufford and Mazer, 2003; Ricciardi and Simberloff, 2009).

Genotypes differences along species distribution ranges are mostly

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due to natural selection acting under the specific environmental conditions at each site. In this sense, assisted migration assumes that natural tree populations are adapted to their local environmental conditions and, particularly, to the climatic ones. However, local adaptation seems to be less common in plant populations than usually thought (Leimu and Fischer, 2008) and, when present, its scale and relative strength might vary (Galloway and Fenster, 2000; Garrido et al., 2012). For this reason, studies on local adaptation should be undertaken before considering assisted migration as a suitable management strategy to adapt forests to climate change.

Local adaptation can be seen as an outcome of the natural selection process whereby the frequency of the traits that enhance fitness increases within a population. It is typically assessed by means of reciprocal transplant experiments in which the average relative fitness of different demes is measured across a set of habitats, and the deme  $\times$  habitat interaction statistically tested (Kawecki and Ebert, 2004). Experiments of reciprocal transplant can be carried out in the field, in a common garden or combining both methodologies (Pahl et al., 2013).

In this study, both a reciprocal transplant and a common garden experiment were performed in order to test for local adaptation in Spanish black pine (*Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco, *Pinus nigra* hereafter). Although fecundity is more advisable for fitness evaluation (Kawecki and Ebert, 2004), its use was inadequate here because *Pinus nigra* takes several years to produce fruiting cones (Alía et al., 2009). Alternatively, we used seedling emergence and early seedling survival as estimates of fitness. These plant traits are typically important in the recruitment dynamic of tree species and are particularly relevant for Mediterranean forests, where summer drought imposes an extremely high seedling mortality during the first years after emergence (Tíscar and Linares, 2011; Matías et al., 2012; Vizcaíno-Palomar et al., 2014).

Opportunities for local adaptation may be enhanced at the latitudinal and altitudinal limits of species' geographical ranges, since populations on the distribution edges might become isolated from the central ones due to any barrier that limits gene flow (García-Ramos and Kirkpatrick, 1997; Herrera and Bazaga, 2008; Bastida et al., 2015). This would be the case of Spanish black pine, which distribution is fragmented over the eastern mountains of Spain with areas isolated from each other by unsuitable lowland habitat and, within each area, by altitudinal gradients that may involve the variation of biotic and abiotic factors. We thus selected low- and high-altitude demes originating from central and peripheral localities for the experimental design. Aridity increases north to south along the *Pinus nigra* natural range (Tíscar and Linares, 2014). Taking all this into account, the study hypothesis was that, if local adaptation to the establishment conditions, i.e. during the emergence and seedling life stages, was to exist in populations of *Pinus nigra*, seeds collected in the warmer, drier southern peripheral forests should exhibit higher recruitment in those sites than seeds from the less warm, dry central forests. The existence of this potentially adaptive character should be concealed under wet conditions. Therefore, we included an irrigation treatment in the experimental design in order to validate the hypothesis and to get more insights into the *Pinus nigra* regeneration process under a climate change scenario. The specific questions addressed by this study are: (a) Does *Pinus nigra* exhibit local adaptation to the emergence environment faced by its seedlings? (b) Does this result extend to the survival environment? (c) Which may be the determinants of the found local adaptation pattern?

## 2. Material and methods

### 2.1. Study species and sites

*Pinus nigra* is a tree species of economic and ecological interest. It thrives along the eastern mountain ranges of Spain on rich calcium and mainly shallow soils under a Mediterranean-type climate with cold, wet winters and hot, dry summers. Seeds of *Pinus nigra* mature at the

beginning of the second winter after pollination. Seed predation, herbivory by ungulates, the presence of unsuitable soil conditions, and the irregular production of seed crops are factors which negatively affect *Pinus nigra* regeneration in natural stands, but summer drought is considered the major cause of seedling mortality in this species (Tíscar and Linares, 2011).

The *Pinus nigra* distribution area is fragmented. We conducted the reciprocal transplant experiments between the mountains of Cuenca and the mountains of Cazorla, covering *Pinus nigra* populations in the core and the southernmost edge of the species' range (Fig. 1). The Cuenca and Cazorla mountains are located within two different *Pinus nigra* provenances: *Sistema Ibérico Meridional* and *Cordilleras Béticas*, respectively. Climate conditions differ between these two provenances (Alía et al., 2009), with summers being specifically longer, hotter and drier in the provenance of the Cazorla mountains (Table 1). Meteorological conditions during the study span were coincident with these general climatic differences (see Appendix A).

Two sites were selected in the Cazorla mountains, namely, "Navillas" and "Puertollano", and two sites were selected in the mountains of Cuenca: "El Cardozo" and "La Fuenseca". The Navillas site (37°56'N – 2°53'W, 1220 m a.s.l.; Peripheral-Low population hereafter) is a representative low-altitude stand of *Pinus nigra* from the species' southernmost populations. It consists of *Pinus nigra* trees intermixed with some individuals of *Quercus ilex* and *Pinus pinaster*. The site of Puertollano (37°48'N – 2°56'W, 1820 m a.s.l.; Peripheral-High population hereafter) is located near the forest limit in the area and consists of a pure stand of *Pinus nigra* with scattered individuals of *Acer opalus* and *Sorbus aria*. El Cardozo (39°54'N – 2°04'W, 1082 m a.s.l.; Central-Low population hereafter) is a mixed forest stand mostly composed of *Pinus nigra* with some *Pinus pinaster* individuals, while the site of La Fuenseca (40°20'N – 1°47'W, 1640 m a.s.l.; Central-High population hereafter) is almost a pure stand of *Pinus nigra*, although some individuals of *Pinus sylvestris* are present. Pairwise geographical distances between study populations ranged between 14 and 268 km (Fig. 1).

### 2.2. Plant and soil material

From each study population, we collected a minimum of 10 cones from at least 10 widely separated trees of *Pinus nigra* in December 2014. Cones were completely opened in an oven set at 40 °C during 48 h, and seeds from the same site were pooled together. As *Pinus nigra* seed mass varies depending on collection habitat (Tíscar, 2002) and seed mass might influence emergence and survival (Castro et al., 2006), we weighed seeds individually to the nearest 0.1 mg. Seeds of less than 14 mg were discarded as they probably would be empty (Tíscar and Lucas-Borja, 2010). A sub-set of the weighed seeds was used to check seed viability in a growth chamber in the laboratory. Seeds from the four study sites exhibited germination rates that exceeded 96%. Thus, we could obtain samples of sound seeds from every study site or origin population that were kept in the fridge until the sowing experiment began.

We also took a soil sample from each study site at the time of cone collection. Specifically, we removed the soil litter and took a big enough sample of soil from the upper layer in a representative place of the site. Soil samples were analyzed using standard analytical procedures, in order to determine texture (percentage of sand, silt and clay), pH, the total content of moisture, carbonates, nitrogen, phosphorous and potassium, percent organic matter, soil respiration and dehydrogenase activity (see Lucas-Borja et al., 2017 for details). We performed a principal components analysis (based on correlation matrix) to synthesize in independent factors the variation of these soil properties among destination habitats.

### 2.3. Reciprocal transplant

The reciprocal transplant was carried out sowing seeds in the field. *Pinus nigra* regeneration is better achieved in managed stands through

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