



Limited validation of forecasted northward range shift in ten European tree species from a common garden experiment

Morgane Merlin^{a,*}, Anne Duputié^b, Isabelle Chuine^a

^a Centre d'Ecologie Fonctionnelle et Evolutive, UMR5175 CNRS-UM-UPVM3-EPHE-IRD, 1919 route de Mende, 34293 Montpellier cedex 05, France

^b Unité Évolution, Écologie, Paléontologie, UMR CNRS 8198, Université de Lille 1, Sciences et Technologies, 59655 Villeneuve d'Ascq cedex, France



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ABSTRACT

As climate change leads to global warming and modified precipitation patterns, the distribution of forest biomes and tree species is expected to shift towards higher latitudes and altitudes. Such shifts are currently projected by species distribution models fitted to different climate change scenarios. Field validation of these models for several life stages of different tree species is a necessity to adapt forest management and understand the future of forest ecosystems. The study presented here aims to assess whether signs of the projected near-future range shift, contraction or expansion of ten European forest tree species are already observable in survival and growth of their seedlings at the core, leading and trailing edges of their distribution.

The results show limited validation of the projected near-future changes in spatial distribution: seedling survival and growth paralleled modelled near-future habitat suitability for the three Mediterranean/Southern species, whereas cold-adapted species showed limited validation of model projections with lower growth and survival at their trailing edge; and widespread species showed inconsistent performance with model projections. Individuals of contrasting provenances did not show strong differences in survival; however they did show substantial differences in growth. The role of extreme events and biotic interactions might prove to be more important factors into shaping the future realized niche and the distribution of these species and thus should be investigated to complete the current studies on latitudinal and altitudinal shifts in relation to climate change.

1. Introduction

The distribution of many organisms is strongly controlled by climate factors (Woodward and Williams, 1987), and ongoing and future climate changes are projected to cause geographic range shift, contraction or expansion of a vast majority of species (IPCC, 2013; Parmesan and Yohe, 2003; Root et al., 2003). A number of studies have already detected such changes for mobile organisms such as insects, fishes, and birds (e.g. Parmesan and Yohe, 2003; Burrows et al., 2011; Sunday et al., 2012). Clear evidence of present-day range changes are harder to find and document in sedentary organisms such as plants, and even more in trees with long generation times (but see Crimmins et al., 2011; Delzon et al., 2013; Rabasa et al., 2013; Mathisen et al., 2014; Matías and Jump, 2015) as pressures such as herbivory, insect outbreaks and past land-use changes confound the direct effects of climate change.

Species distribution models (SDMs) offer a way to forecast potential changes in tree species distribution range under different climate change scenarios. SDMs have projected upward and poleward range shifts of different magnitude for many tree species across regional and

continental scales in Europe and North America ranging from a couple hundred meters for altitude shifts to hundreds of kilometers for latitudinal shifts (e.g. Iverson et al., 2008; Cheaib et al., 2012; García-Valdés et al., 2013). The equatorward/lowland trailing edge of tree species distribution is expected to experience severe reductions of tree growth and survival with the projected increase in temperature and in the frequency of extreme events such as droughts (Allen and Breshears, 1998; Fisichelli et al., 2014; Gworek et al., 2007; Matías et al., 2014; Ogaya and Peñuelas, 2004). The poleward/high altitude leading edge of the distributions is conversely expected to experience enhanced tree growth, survival and recruitment in the short to mid-term, as winter conditions will become milder with increased temperatures (Lenoir et al., 2008; Peñuelas et al., 2007; Reinhardt et al., 2011; Saltré et al., 2015; Vitasse et al., 2012).

However, in a large number of studies which have investigated tree range shifts during the last decades, detected changes do not appear to be always consistent with climate change (for example downslope and/or southward range shifts; Crimmins et al., 2011; Zhu et al., 2012; Monleon et al., 2015) and can point out the effects of past forest

* Corresponding author at: Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2E3, Canada.

E-mail addresses: morgane@ualberta.ca (M. Merlin), anne.duputie@univ-lille1.fr (A. Duputié), isabelle.chuine@cefe.cnrs.fr (I. Chuine).

practices, land-use related habitat modification or species interactions in response to global warming (Bodin et al., 2013). It is thus unclear how climate change alone may be the driver of species range shift, and how to quantify this effect in addition to the other biotic and historic effects. A growing body of studies focus on altitudinal range shifts in tree species, as altitudinal gradients in temperature and other climatic factors provide wide climatic gradients on a small-scale where species range shifts should be detected more easily and rapidly (Herrero and Zamora, 2014; Peñuelas et al., 2007; Reinhardt et al., 2011; Zurbriggen et al., 2013). Latitudinal shifts of tree species distribution edges are much less reported. Most of these studies compared either the presence and distribution of adult mature trees and their seedlings synchronously (Vitasse et al., 2012; Zhu et al., 2014) or the presence of adult mature trees through time (Lenoir et al., 2010, 2008).

Current adult mature trees have established 20–50 years ago for most of the managed forest ecosystems, hundreds of years ago for less managed ecosystems, and survived the climatic variations and extremes since then (Zhu et al., 2014). Adult mature trees thus established in climatic conditions up to $\sim 1^\circ\text{C}$ colder than their current seedlings in Europe (IPCC, 2013). Moreover, the climatic niche of seedlings is thought to be slightly different from that of adults (Grubb, 1977; Quero et al., 2008), especially regarding drought resistance (Cavender-Bares and Bazzaz, 2000). In particular, seedlings are expected to be more sensitive to climate change effects on temperature and water supply than adult mature trees (see for review Walck et al., 2011). Moreover, SDMs generally use the combined distributions of adults and seedlings to estimate a species' niche, hence may overestimate its ecological niche (Ashcroft et al., 2017) or fail to identify it. To understand the observed tree dynamics at the range limits and understand how climate mediates these dynamics, we need to delve into the climatic controls of a much less studied stage, regeneration. This step is crucial to understand how future climatic conditions will control seedlings performance at both the leading and trailing edges, but only a few studies have tackled this issue so far (Carón et al., 2015; Matías and Jump, 2014; Putnam and Reich, 2017; Reinhardt et al., 2011).

To form a better view on future seedlings performance at the edges of their distribution, we tested in this study the SDM-projected range shift in a very near future of ten of the most economically important and widespread European forest tree species. For each species, seeds from three to four provenances were sown at three common gardens in France showing contrasted climatic conditions, which would become part either of the leading edge, or the trailing edge, or would remain within the range of the species within France. Survival and growth of the seedlings were monitored for three years. More specifically, we aimed to answer the three following questions:

- (i) Do seedling's growth and survival correlate with current and/or future SDM-derived habitat suitability, and especially, are survival and growth higher at a species' leading edge than at its trailing edge?
- (ii) Does genetic differentiation lead to differential recruitment success when transferred at trailing and leading edges?
- (iii) How much is seedling performance dependent on climatic conditions during recruitment?

2. Material and methods

2.1. Study species

The study focused on the main forest tree species encountered in Europe: silver fir *Abies alba* Mill., sweet chestnut *Castanea sativa* Mill., European beech *Fagus sylvatica* L., European ash *Fraxinus excelsior* L., European larch *Larix decidua* Mill., Norway spruce *Picea abies* L., Aleppo pine *Pinus halepensis* Miller, Scots pine *Pinus sylvestris* L., holm oak *Quercus ilex* L., and pedunculate oak *Quercus robur* L. For each species, we used three to four provenances from geographically distinct

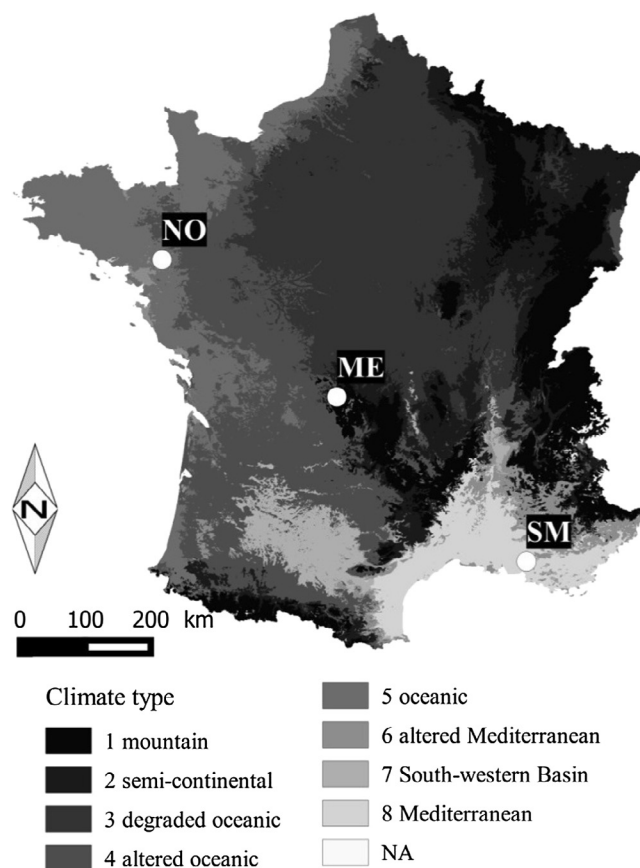


Fig. 1. Climate type and geographic location of the three common gardens in France (adapted from Joly et al., 2010).

locations in France to account for a potential genetic effect linked with local adaptation to climate in the species responses (see [Supplementary Material Fig. SA.1](#) for the location of each provenance within the species distribution). Note that the provenances used for *P. halepensis*, *L. decidua* and *Q. ilex*, species with more limited distribution in France, were from closer geographic locations than for the other species, thus interpretations of the provenance effects in subsequent analyses should be taken with caution.

2.2. Study sites

Three common gardens were installed in 2006 to conduct two experiments running from 2007 to 2010. These gardens show very different climatic conditions (Fig. 1): (1) a Northern-Oceanic (NO) site located in Guéméné-Penfao ($47^\circ37'51''\text{N}$, $1^\circ49'53''\text{W}$, 20 m a.s.l.) with oceanic climate (de La Broise, 1987); (2) a Medium Elevation (ME) site located in Peyrat-le-Château ($45^\circ48'49''\text{N}$, $1^\circ46'25''\text{E}$, 570 m a.s.l.) with a continental climate with some oceanic influence (Poly, 1987); (3) a Southern Mediterranean (SM) site located in Les Milles ($43^\circ30'13''\text{N}$, $5^\circ23'08''\text{E}$, 120 m a.s.l.) with Mediterranean climate (see Table 1). The three gardens show slightly different sandy soils typical of forest soils in France: sandstone heavy acidic soils at NO, sandy acidic soils with high humus content at ME and silty sand soils at SM.

2.3. Hypotheses building

Habitat suitability of the study sites was modelled at the European scale as in Duputié et al. (2013). To calibrate the models, we used occurrence data from the Atlas Flora Europaea, EuroVegMap, EU-FORGEN, JRC and ICP datasets, downloaded or upscaled to the resolution of $10'$ (Duputié et al., 2013). Five climatic variables were used

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