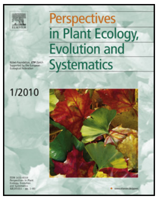
Perspectives in Plant Ecology, Evolution and Systematics 17 (2015) 369–378

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Research article

# Survival *vs.* growth trade-off in early recruitment challenges global warming impacts on Mediterranean mountain trees

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## ARTICLE INFO

*Article history:*
Received 23 January 2015
Received in revised form 21 April 2015
Accepted 10 June 2015
Available online 27 June 2015

*Keywords:*
Climate change
Climatic gradient
Demographic stabilising processes
Elevational shift
Forest regeneration
Mediterranean forests
Species distribution

## ABSTRACT

Climate change is expected to alter the geographic distribution of many plant species worldwide. However, there is still no clear evidence showing a generalised direction and magnitude of these distribution shifts. Here, we have surveyed, in nine mountainous regions in Spain, an array of tree species along entire elevational ranges, as surrogates of their global climatic ranges, to test for elevational shifts towards cooler locations. We analysed the distribution recruitment patterns of five dominant tree species, recording the abundance and measuring the primary growth of juveniles in 306 plots. Three of the species have a temperate-boreal distribution with populations at their southern edge in the Mediterranean mountain ranges: *Pinus sylvestris*, *Pinus uncinata* and *Fagus sylvatica*; and the other two species have a Mediterranean distribution: *Quercus ilex* and *Pinus nigra*. Despite the contrasting phylogenies and biogeographies, we identified a similar pattern in recruitment abundance across species, with an asymmetric distribution of juveniles (more recruits in the middle-upper elevation of their range), but higher annual growths at lower elevations. This survival-growth trade-off at the early recruitment stage may potentially counterbalance at population level the negative effect of global warming on recruit survival at the lower edge of species ranges. These findings suggest a demographic stabilisation process at the early recruitment stage of these tree species, and highlight the importance of considering the different demographic stages across the whole climatic range to understand the effects that climate change may exert on species distributions and population dynamics.

Abbreviations: Sampled transects' position along elevational gradients: U, upper; MU, mid-up; M, middle; ML, mid-low; L, lower transects; Se, seedlings emerged during the current growing season; S1, saplings from one to five years; S2, saplings over five years

## 1. Introduction

An increasing number of studies are showing latitudinal and elevational shifts of many species in response to climate change (Parmesan and Yohe, 2003; Rabasa et al., 2013). Although changes in traditional land uses contribute to some of these species distribution shifts (Peñuelas and Boada, 2003; Batllori and Gutiérrez, 2008; Ameztegui et al., 2010), most of the studies have suggested that global warming and the increased frequency of extreme climatic events are the main causes of gradual upward and poleward

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http://dx.doi.org/10.1016/j.ppees.2015.06.004
1433-8319/

movements and consequent changes in the species composition of ecosystems (Wardle and Coleman, 1992; Peñuelas and Boada, 2003; Thuiller et al., 2005; Beckage et al., 2008; Bertrand et al., 2011b; Benavides et al., 2013; Matías and Jump, 2014). However, this evidence runs in parallel with other studies showing a lack of species distribution changes (Lenoir et al., 2009, 2010), species that have increased their cover and/or abundance with rising temperature or aridity (Wang et al., 2006; Gimeno et al., 2012) or even that have experienced a downslope range displacement (Lenoir et al., 2010; Crimmins et al., 2011; Rabasa et al., 2013).

Lloret et al. (2012) shed some light on these apparent contradictions suggesting that some stabilising demographic processes may mitigate or compensate the negative effects in plant communities induced by extreme climate events (Table 1). Within the mitigation category, local factors (both biotic, like facilitation, and abiotic, like physiography or site quality) may provide microrefugia and attenuate the direct negative effects of a changing climate on individuals (Pearson and Dawson, 2003; Araújo and Luoto, 2007; Dobrowski, 2011; McLaughlin and Zavaleta, 2012). Moreover, species-specific characteristics related to their adaptation or acclimation ability may also buffer the expected climatic impacts on populations (Aitken et al., 2008; Nicotra et al., 2010; Richter et al., 2012). Accordingly, recent studies have suggested that the direct impacts of global warming may be smaller than predicted, and have shown a high degree of homeostasis in different processes of some species in response to increasing temperatures (Gunderson et al., 2010; Baldi et al., 2012). Within a second category of compensatory processes, Lloret et al. (2012) included the beneficial effect that warmer temperatures may have over some life cycle stages and ecological processes. For instance, an increase in growth with temperature may compensate a lower seedling survival (Doak and Morris, 2010); or reduce current competitive or antagonistic interactions (McDowell et al., 2006; Carnicer et al., 2011), and increase mutualistic relationships (Le Conte and Navajas, 2008; Giménez-Benavides et al., 2011).

The mismatch between both types of observational outcomes (shift *vs.* no-shift) may not only reflect the species-specific characteristics, but also differences in the spatial and temporal study scales. Undoubtedly, some species are more vulnerable to environmental changes and will respond earlier than others. Nevertheless, the studies showing shifts have been frequently conducted considering a single species or population, or have been focused on changes occurring at the edge of species ranges, being then unable to reveal the whole picture by neglecting the overall distribution of the species (but see these studies with waterbird species—Lehikoinen et al., 2013 and stream fish species—Comte and Grenouillet, 2013). Thus, it is a priority to conduct more comprehensive studies in which a set of species are simultaneously surveyed at several spatial scales, covering their whole distribution range (Lenoir and Svenning, 2015), and including different life stages (*i.e.* including the regeneration niche, see Grubb, 1977). This will shed light on the demographic mechanisms and trade-offs involved in the shift *vs.* no-shift responses, and will help to identify global responses to current warming and design strategies to mitigate its impact over plant communities.

In this study, we contribute to this goal and we analyse the distribution of the recruitment (seedlings and saplings), in terms of abundance and primary growth, of four dominant tree species, surveying their entire elevational range in Mediterranean mountains, as a surrogate of the climatic range that each species experiences along their latitudinal distributions. Using elevation as a surrogate for climate range is a useful tool to study responses under different climatic scenarios within a single population and, therefore, minimising differences due to genetic variability, compared to surveys carried out in large areas, and therefore, including different populations (Ruíz-Benito et al., 2012; Vayreda et al., 2013; Carnicer et al., 2014). Three of the target species have a temperate-boreal distribution with populations at their global southernmost limit in the Iberian mountain ranges: Scots pine (*Pinus sylvestris* L.), mountain pine (*Pinus uncinata* Ramond ex DC.) and European beech (*Fagus sylvatica* L.); and the other one has a Mediterranean distribution: Iberian black pine (*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco). Another Mediterranean dominant tree species was included in the target species pool of this study due to its great relevance in the Iberian Peninsula: holm oak (*Quercus ilex* L.). However, this species was not surveyed along its entire elevational range and its trailing edge was left out, because this species has no low elevational limit in the Mediterranean mountains. Our main aim is to test in the study populations whether there is an overall, pervasive elevational shift of the young cohorts towards cooler locations within the entire elevational range of the adult, which would be transferable to poleward shifts in response to the ongoing climate change, or if the altitudinal patterns are species-specific (Lenoir et al., 2009; Woodall et al., 2009). We expect that the recruits of the Mediterranean species, better adapted to summer drought, would be less affected by the ongoing climate change and be more abundant near their central part of the elevational range, where the density of conspecific adults and, therefore, seed rain are greater than at the edges of their range. By contrast, we expect that the species with populations at their trailing edge of their distribution, therefore marginal populations, would show shifts of their optimum juvenile abundance towards higher elevations (Matías and Jump, 2014). This outcome would show the different climatic conditions imposed by the global warming between the conditions when the current adult stand established, and the present situation. Hence, we hypothesise an idiosyncratic response of the different species with no general upward trend, and where a potential compensatory process enhancing the performance of the juveniles under warmer conditions may be relevant, especially for those species whose populations are at their southern limit.

## 2. Material and methods

### 2.1. Study sites

The study was conducted in nine mountain ranges across Spain during the early summer in 2010 and 2011 (Fig. 1). The entire

**Table 1**
Summary of the stabilising processes proposed by Lloret et al. (2012).

| Stabilising processes | Basis | Underlying predisposing factors/processes |
|---|---|---|
| Mortality mitigation | Existence of microrefugia<br>Adaptation, acclimation ability | Site quality<br>Facilitation<br>Tolerance<br>Plasticity<br>Phenotypic variability |
| Mortality compensation | Enhanced future survival or recruitment[a] | Beneficial effects of climate change<br>Release competition<br>Release antagonism<br>Increase mutualism |

[a] By improvement of the conditions for recruits or adult reproductive performance.