Forest Ecology and Management 432 (2019) 558–567

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Biotic factors and increasing aridity shape the altitudinal shifts of marginal Pyrenean silver fir populations in Europe

Laura Hernández[a,*], J. Julio Camarero[b], Eustaquio Gil-Peregrín[c], Miguel Ángel Saz Sánchez[d], Isabel Cañellas[a], Fernando Montes[a]

[a] INIA-CIFOR, Silviculture and Forest Management Department, Madrid, Spain
[b] Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50059 Zaragoza, Spain
[c] Unidad de Recursos Forestales, Centro de Investigación y Tecnología Agroalimentaria de Aragón, Gobierno de Aragón, 50059 Zaragoza, Spain
[d] Departamento de Geografía y Ordenación del Territorio, Área de Análisis Geográfico Regional Instituto Universitario de Ciencias Ambientales, Universidad de Zaragoza, Pedro Cerbuna 12, 50009, Spain

ARTICLE INFO

Keywords:
Pyrenees
Abies alba
Rear edge
Demography
Climate change
Biotic interactions
Range shifts
Conservation planning

ABSTRACT

Rear-edge tree populations are currently at the forefront of habitat conservation. Understanding the dynamics of such marginal and peripheral populations is necessary to improve their preservation in the face of global change. Focusing on the south-western rear edge populations of silver fir (*Abies alba*) in Europe (Spanish Pyrenees) and using 763 resampled plots from the Spanish National Forest Inventory (1989–2000 and 2001–2010), we analyzed temporal changes in demographic parameters such as regeneration, growth and mortality as well as changes in diameter distribution and vitality of silver fir to identify shifts in the distribution. For this purpose, montane (900–1600 m a.s.l.) and subalpine (1600–2000 m a.s.l.) silver fir populations were considered separately. We then assessed the relative effects of various biotic and abiotic factors on the observed changes and specifically on each of the studied demographic parameters. In montane forests, early recruitment and the proportion of trees exhibiting high vitality decreased, while the amount of dead trees increased. In subalpine forests, silver fir has become more abundant and displays the highest growth and recruitment rates as well as the lowest mortality rate. The increase in radial growth and saplings were positively related to elevation but negatively associated with warmer and drier conditions, coinciding with the intensified aridification observed in the study area over recent decades. Our findings point to the contraction of montane silver fir forests but also to an upward expansion of subalpine forests. The results also indicate that the dynamics of marginal tree populations are driven not only by climate warming, but particularly, by biotic factors, suggesting a positive impact of interspecific interactions with tree species displaying differentiated ecophysiological traits. Given the singularity of marginal Pyrenean silver fir populations, their importance as regards the conservation of forest biodiversity at European scale, and the demographic changes revealed in this study, an integral conservation strategy to ensure their long-term preservation is necessary.

1. Introduction

Rear-edge tree populations, located at the current low-latitude margins of species distribution ranges (*sensu* Hampe and Petit, 2005), are extremely important for the long-term conservation of genetic diversity, phylogenetic history and evolutionary potential (Hampe and Petit, 2005). Since adaptation to climate change is currently at the forefront of habitat conservation and management strategies, the genetic resources of rear edge, marginal or peripheral tree populations are receiving renewed attention (Fady et al., 2016). However, appropriate strategies for conserving rear-edge tree populations require a sound understanding of their dynamics and an adequate characterization of their current conservation status (Hampe and Jump, 2011; ETC/BD 2008).

There is overwhelming evidence that climatic stressors including warming-induced aridification or climate extremes like droughts or frosts strongly influence the ability of tree species to establish, grow or adequately reproduce at the geographic margins of the species (e.g. Macias et al., 2006; Camarero et al., 2015a). However, factors other than climate, such as biotic interactions (e.g. facilitation, competition), dispersal constraints and genetic adaptation also influence the performance of species at the limits of their distribution range

* Corresponding author.
E-mail addresses: lauhmateo@gmail.com, hernandez.laura@inia.es (L. Hernández).

https://doi.org/10.1016/j.foreco.2018.09.037
Received 20 June 2018; Received in revised form 18 September 2018; Accepted 19 September 2018

Table 1
Summary of the ecological questions on the potential decline of marginal silver-fir populations addressed in this study based on the Spanish National Forest Inventory (SFI) cycles (1989–2000 and 2001–2010), parameters studied to address these questions and statistical methods used. GLM and *dbh* stands out for Generalized Linear Model and diameter at breast height, respectively.

Questions on potential silver fir decline	Parameters studied and units	Statistical methods used and related results (Tables and Figures)
Regeneration		
Early recruitment patterns	Recruitment density classes by altitudinal belt and SFI cycle	Pearson Chi-square test (Table2)
Changes for sapling density and dominance	Abundance (n°/ha) and dominance (%) by altitudinal belt and SFI cycle	Kruskal-Wallis test Nemenyi's post hoc test (Table 2)
Factors associated with saplings shifts between SFI cycles	Effect of biotic and abiotic factors in silver fir sapling abundance variation	GLM (Table 3)
Adult trees		
Size structure and dynamics		
Abundance and dominance patterns	Number of trees per ha and mean dominance of silver fir in the plot by SFI cycle and altitudinal belt	Pearson Chi-square test (Table2)
Changes in *Dbh* distribution of silver fir	Number of silver fir living trees by *dbh* class by cycle and by altitudinal belt	Bar plots (Fig. 3)
Vitality/tree health status		
Silver fir health status patterns	% of trees by health status class variation between cycles and by belts	Pearson Chi-square test (Table2)
Mortality		
Silver fir mortality rates patterns	Mean annual mortality rate (dead trees ha yr^{-1}) by altitudinal belt, cycles and variation between cycles	Kruskal-Wallis test Nemenyi's post hoc test (Table 2)
Factors associated to mortality rate shift between cycles	Variance of mortality rate explained by biotic and abiotic factors	GLMs (Table3)
Mean dbh growth		
Trends for silver fir mean dbh growth	Annual mean *dbh* growth (cm ha yr^{-1}) by altitudinal belt	Table2
Factors associated to mean dbh growth of silver fir between cycles	Variance of mean *dbh* growth explained by biotic and abiotic factors	GLMs (Table3)

(HilleRisLambers et al. 2013). As regards biotic interactions, increasing evidence exists of the positive role played by biotic tree-to-tree interactions as abiotic stress increases (Hooper et al., 2005). The benefits of these interactions are assumed to be greater when the coexisting species display differentiated ecophysiological traits and complementary niches (Hooper et al., 2005; Lebourgeois et al., 2013; Gazol and Camarero, 2016). Since climate warming is leading to shifts in the range of tree species in response to the variation in their climatic optimum, with major effects predicted at the edges of species' ranges (Davis et al., 2005; Lenoir et al., 2009), it is highly important to analyze the factors driving the demographic patterns of rear edge tree populations. However, the relative importance of the factors affecting range shifts dynamics at the distribution margins is a matter of ongoing research (Sexton et al., 2009; Hampe and Jump, 2011).

Theoretically, in the context of climate change, the "centre- periphery hypothesis" predicts that demographic performance will generally be lower at the edges of species' ranges than in the core area, and therefore marginal tree populations are more prone to decline and to local extinction (Lawton, 1993; Vucetich and Waite, 2003). However, recent empirical work has challenged these assumptions (Lenoir and Svenning, 2013). For instance, the rear edge of a species' range hosts low genetic diversity due to selection pressure over time (Hampe and Petit, 2005), although this selection is likely to provide a high potential for delaying range contractions under contemporary climate change by, for example, by selecting drought-resistant genotypes (Lenoir and Svenning, 2013). To elucidate current and future performance of rear-edge populations under current global change, Sexton et al., (2009) asked for more studies integrating demographic and community information.

Here we address these issues by focusing on silver fir (*Abies alba* Mill.), which is a late-successional coniferous tree species considered an important component of European forests (Tinner et al., 2013). The current distribution of silver fir is mostly associated to the mountainous regions of central Europe reaching its southernmost distribution limits in mountains subjected to Mediterranean influence such as the Pyrenees, the Apennines and the Balkans (Costa et al., 1997). However, paleoecological evidence, bioclimatic models and molecular markers point to a wider distribution range of silver fir in Europe during the Holocene, prior to the intensification of human activities, with interglacial refugia in these mountains (Svenning and Skov, 2004; Tinner et al., 2013; Cheddadi et al., 2014). After the widespread silver fir dieback which took place in Europe in the mid-1970s (Bert, 1993), the following decades witnessed an increase in silver fir productivity motivated by reduced air pollution and a warmer, though not drier climate, particularly in cool-humid regions such as Central Europe, the Carpathians and Italy (Elling et al., 2009; Büntgen et al., 2014). However, in some silver fir rear edge populations a dieback phenomenon at low-elevation and drought-prone areas, has been observed (Macias et al., 2006; Oliva and Colinas, 2007, Camarero et al., 2011; Sangüesa-Barreda et al., 2015). The future of European silver fir populations is currently subject to debate (Maiorano et al., 2013; Ruosch et al., 2016). In this regard, insights into the current conservation status and demographic trends of Pyrenean silver fir populations can shed new light on this debate.

The decline of tree species is usually characterized by a persistent decrease in the dominance and the abundance of the species due to rising mortality rates, poor vitality, and low growth and regeneration rates (Ficko et al., 2011). Consequently, in the case of long-lived organisms such as trees, demographic patterns cannot simply be inferred from their current recruitment or growth rates (Hampe and Jump, 2011). This data must be complemented by other long-term approaches such as studies of adult tree health and changes in adult mortality rates (e.g. Jump et al., 2006). Based on the information obtained from consecutive Spanish National Forest Inventory (SFI hereafter) cycles, here we investigate the recent (1989–2010) demographic changes of silver fir in the Spanish Pyrenees by analysing changes in: (i) silver fir regeneration (early recruitment and sapling abundance), (ii) dominance and abundance of silver fir, (iii) diameter structure, (iv) adult tree vitality, (v) mortality rates, and, (vi) radial growth (see Table 1 for a detailed description of the analyses). We aim to determine whether silver fir populations in the Spanish Pyrenees show distribution shifts. For this, we analysed changes in silver fir demographic rates by