



ORIGINAL ARTICLE

Coexistence in the Mediterranean-Temperate transitional border: Multi-century dynamics of a mixed old-growth forest under global change



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ABSTRACT

Old-growth forests, particularly those located at the interface between different bioregions, are unevaluable sources of long-term vegetation dynamics and historical stand response to natural and anthropogenic disturbances. Although old-growth forests are scarce, the information gathered studying them may assist forest ecosystem restoration and management under forthcoming climate and land-use changes.

We analysed how complementary dynamics of a mixed old-growth forest composed by temperate (*Fagus sylvatica*, *Quercus petraea*) and submediterranean (*Quercus pyrenaica*) tree species were driven in response to global changes in the last two centuries. The old-growth forest, named El Hayedo de Montejo, is located at the interface between the Mediterranean and temperate bioregions in the centre of the Iberian Peninsula. The populations of temperate species growing in El Hayedo de Montejo (*F. sylvatica* and *Q. petraea*) are at the dry and warm edges of their natural distribution area in Europe, whereas the submediterranean species *Q. pyrenaica* is at the core of the distribution range. In order to analyse the long-term dynamics, we developed basal area increment and disturbance chronologies for each of the tree species under study. Furthermore, we assessed the climate influence on tree growth during the most recent decades.

Our results reveal historical shifts in forest dominance (as reflected by growth) induced by changes in climate and forest management between temperate and sub-Mediterranean species. This was particularly noticeable for *F. sylvatica* and *Q. pyrenaica* the least and most drought-tolerant species, respectively. A reduction in growth of *F. sylvatica* unprecedented in the context of the last two hundred years was observed during the last decades concurrent with forest densification and marked changes in climate. Conversely, both oak species seem to be better suited to current environmental conditions as expressed by increasing growth rates.

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1. Introduction

Old-growth forests are scarce but still a relevant global carbon sink (Luyssaert et al., 2008) and a source of genetic diversity (Mosseler et al., 2003). They are also essential benchmarks for studying and understanding ecosystem processes in long-time

scales (e.g., D'Amato and Orwig, 2008) and in the face of environmental change (Rackham, 2008; Messier et al., 2009). The value of old-growth forests is multiplied with increasing marginality since populations at the limits of the species distribution conform the edge for adaptation and evolution of plant species under forthcoming climate change (Hampe and Petit, 2005).

Given the rate of global and regional warming, climate conditions during the growing season may challenge the tolerance and ability of marginal populations to locally adapt and persist (Midgley et al., 2007; Moritz and Agudo, 2013). Concretely, future enhancement of dry conditions may induce changes in species dynamics of marginal mixed forests, reduce the distribution area of species

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with lower drought-tolerance and/or force their retreat to higher altitudes/latitudes, especially at the rear-edge of the distribution range (Thuiller et al., 2005; Lenoir et al., 2008; Zimmermann et al., 2009; Czúcz et al., 2011; Gómez-Aparicio et al., 2011; Vacchiano and Motta, 2015; Hanewinkel et al., 2013). Persistence of populations at the rear edge is particularly important as specific genetic variables conferring local adaptation to strong abiotic stresses may foster the evolution and maintenance of species as a whole (Lesica and Allendorf, 1995; Aitken et al., 2008; Hampe and Jump, 2011). Currently and due to climate change, the conditions needed for regeneration and establishment may be taking place more sparsely and scarcely than before (Castro et al., 2004; Hampe and Petit, 2005; Hampe and Jump, 2011; Gea-Izquierdo et al., 2015). Therefore, marginal populations of temperate species at the rear edge, particularly old-growth, encode valuable long-term information not only on stand dynamics, but also on species acclimation and tolerance to periods of dryness (Holt and Keitt 2005; Piovesan et al., 2005; Di Filippo et al., 2015). Studies on species tolerance limits are critical to forecast shifts in plant communities, which may result in tree species persistence or, conversely, extirpation (Aitken et al., 2008).

Forest persistence largely depends on the ability of individual species to adapt their structure and dominance during regimen shifts and mixed forests show evolutionary advantages on climate change adaptation and persistence compared to monospecific (e.g. Thompson et al., 2009; Ruiz-Benito et al., 2014). The biodiversity and associated climate response heterogeneity contained in multispecies forests might provide an alternative against ecosystem regimen shifts whilst monospecific systems may shift to a less desired state (Elmqvist et al., 2003). Furthermore, some evidences point to a stress release by inter-specific facilitation as well as enhanced species productivity in mixed compared to monospecific forests under suboptimal site conditions (e.g. Pretzsch et al., 2013a,b).

The Iberian Peninsula conforms the rear edge of the natural distribution of many temperate and boreal tree species such as *Fagus sylvatica* L., *Quercus petraea* (Mattuschka) Liebl., *Quercus robur* L., *Abies alba* Mill., *Pinus uncinata* Ram. and *Pinus sylvestris* L. coexisting with more drought tolerant taxa (i.e., typical mediterranean *Quercus* and *Pinus* spp.). Population growth rate is a sensitive and useful indicator on incipient changes in dynamics (Dobbertin, 2005) and significant changes in rear-edge forests growth have been detected and linked to environmental dryness at the Iberian Peninsula (e.g. Gutierrez, 1988; Peñuelas et al., 2008; Jump et al., 2006; Gea-Izquierdo et al., 2014; Chen et al., 2015; Heres et al., 2014). However, recent changes in climate inducing variations in forest growth have often been concurrent with changes in forest management and distinguishing those effects is challenging (Peñuelas and Boada, 2003; Peñuelas et al., 2008; Gea-Izquierdo et al., 2015).

In this context, the analysis of chronologies derived from old-growth forests provides a unique opportunity to reconstruct forest history in response to climate and non-climatic disturbances, including management (e.g., Piovesan et al., 2005). In an effort to understand the dynamics of co-occurring tree species at the transitional border between two bioregions coupled with the changes in climate, we investigate the historical dynamics of an old-growth forest dominated by a combination of temperate species (*F. sylvatica* and *Q. petraea*) and a sub-Mediterranean tree species (*Quercus pyrenaica* Willd.). We focus on analysing the factors inducing changes in species growth and performance, to detect potential shifts in species dominance at the stand level and, particularly, how complementary dynamics of these three species was driven in response to environmental changes in the last two centuries. We hypothesise that the species with the lowest drought-tolerance (*F.*

sylvatica) will show higher vulnerability to recent enhancement in dry conditions, as expressed by reduced growth rates.

2. Material and methods

2.1. Site description

The study site, El Hayedo de Montejo (Montejo hereafter), is a natural old-growth beech-oak forest of 125 ha located at the rear-edge distribution range of the two temperate species at the Sistema Central of the Iberian Peninsula (41° 7' N; 3° 30' W) between 1250–1500 m a.s.l. (Fig. 1). Montejo is a forest located at the interface between the Mediterranean and the Temperate bioregions (Hernández Bermejo et al., 1983) where typical temperate species such as *Fagus sylvatica* (FaSy hereafter) and *Quercus petraea* (QuPe hereafter) coexist with typical sub-Mediterranean species such as *Quercus pyrenaica* (QuPy). Documents dating back to the 13th century made already reference to the existence and management of the mixed beech-oak Montejo forest (Ubieto Arteta, 1959). The forest has historically been exploited for firewood and used as a resting place for livestock. However this traditional management almost disappeared during the 20th century along with a marked decrease in the number of inhabitants (Pardo and Gil, 2005). Since the 1960's decade, cattle management is forbidden in the forest, although the protection of the area was effective only since 1974 (Pardo, 2000). Because of its great ecological importance, in 2005 the forest was declared a biosphere reserve where human intervention and access is very limited (Gil et al., 2010).

The climate is Mediterranean continental (Oromediterranean humid according to Rivas-Martínez, 1983) with two precipitation maxima in spring (May) and autumn (November) (Fig. 1). The mean annual temperature is around 9.5 °C and the annual sum of precipitation is 900 mm with a summer dry period spanning 1.8 months approximately (Gil et al., 2010). The soil has been classified as humic cambisol (Pardo et al., 1997) and the horizon A reaches 50 cm of depth on average which allows to store water during dry periods so that temperate species such as QuPe and FaSy can thrive. QuPy is the most drought-tolerant species among the three, hence more adapted to sub-Mediterranean climatic conditions, whereas the two temperate species, particularly FaSy, require higher moisture levels during the summer period (Lendzion and Leuschner, 2008). QuPe is considered more-drought tolerant than FaSy (Raftoyannis and Radoglou, 2002; Aranda et al., 2005; Lendzion and Leuschner, 2008) and FaSy more shade tolerant than QuPe (von Lüpke, 1998).

2.2. Growth and climate data

Sampling took place during spring of 2013. At least, 20 dominant or co/dominant trees including different size classes were sampled per species. Diameter at breast height (DBH) and total height were measured in every tree and two cores of 5 mm of diameter were taken. Cores were air-dried and sanded until ring boundaries were clearly visible under a stereo-microscope. Samples of each species were visually crossdated following Stokes and Smiley (1968) and uncrossdatable samples were discarded from further analysis. The ring-width of each sample was measured with a precision of 0.01 mm using a Linntab 6 (RINNTech) measuring device. The correct dating of every sample was re-checked using COFECHA (Holmes, 1983). Individual tree-ring series were converted to Basal Area Increments (BAI) to avoid age-related trends in non-juvenile ring-width measurements (Biondi and Quedan, 2008). The conversion of the individual ring-width measurements to individual-BAI series follows the equation:

$$BAI_t = \pi(wt^2 + 2w_t R_t)$$

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