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Tracking the leading edge of *Fagus sylvatica* in North-Western Iberia: Holocene migration inertia, forest succession and recent global change

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ABSTRACT

The Iberian Peninsula constitutes the south-western limit of the European distribution of *Fagus sylvatica* L. However, although the Iberian North-West extreme would appear to be climatically suitable for the species, *F. sylvatica* is not present there. This fact has led to the suggestion that the species is not yet in equilibrium with the climate and that there is a migration lag in the post-glacial expansion of the species. The objective of this work is to understand the main biotic and abiotic factors driving *F. sylvatica* distribution and population dynamics in the Iberian Atlantic biogeographical region over recent decades. Furthermore, in the light of other studies which suggest that the expansion of *F. sylvatica* in North-Western Iberia might be related to the retraction of *Q. petraea* (Matt.) Leibl. forests, we also study the demographic trends of both *F. sylvatica* and *Q. petraea* along with oak-beech interaction processes to infer forest succession dynamics.

Using data from the last two cycles of the Spanish National Forest Inventory (1986–2012) for the study area (the Iberian Atlantic biogeographical region); dominance, population structure, recruitment and basal area increment were analyzed in different forest types for the two target species. General linear models and Bayesian structural equation modelling techniques were also applied to study the direct and indirect drivers of recruitment and forest succession.

Contrary to what might be expected under the current conditions of climatic change, the population of *F. sylvatica* in North-Western Iberia is expanding, the basal area increment of *F. sylvatica* increasing westwards and new recruitment occurring in the lowlands. Accordingly, the Iberian Atlantic biogeographical region may be considered one of the leading edges of *F. sylvatica*. Our results also identify an inter-specific relationship between *Q. petraea* and *F. sylvatica* which negatively affects *Q. petraea*. The findings demonstrate that *Q. petraea* forests are being replaced by *F. sylvatica* forests in North-Western Iberia. These results not only confirm a previous biogeographical hypothesis but also provide new leads for forest management and conservation strategies under current and future climatic conditions.

1. Introduction

European beech (*Fagus sylvatica* L.) is a widespread late-successional deciduous tree species in Europe. Its latitudinal distribution extends from Sweden and Norway to Sicily. From west to east it is present from the Cantabrian Mountains in North-Western Spain to the Carpathians and Balkan Mountains (Ellenberg, 1966) (Fig. 1). However its modern distribution in Europe dates from very recent times. Both palaeobotanical and phylogenetic studies reveal that the expansion of *F. sylvatica* from its glacial refugia started during the Late-Glacial (aprox. 13,000–11,000 cal. yr bp) and that the increase in the area occupied by beech populations was exponential from the Late-Glacial until about 3,500 cal yr bp in central-northern Europe, then slowed down towards an equilibrium value (Magri, 2008). Due to its late post-glacial expansion in Europe, at the time *F. sylvatica* started to spread most of Europe was already covered by forests within which it was difficult for new species to establish (Green, 1987; Giesecke et al., 2007; Brewer et al., 2002). Thus, around 5,000 cal. yr bp, European beech occupied no more than approximately 50% of the area potentially occu-

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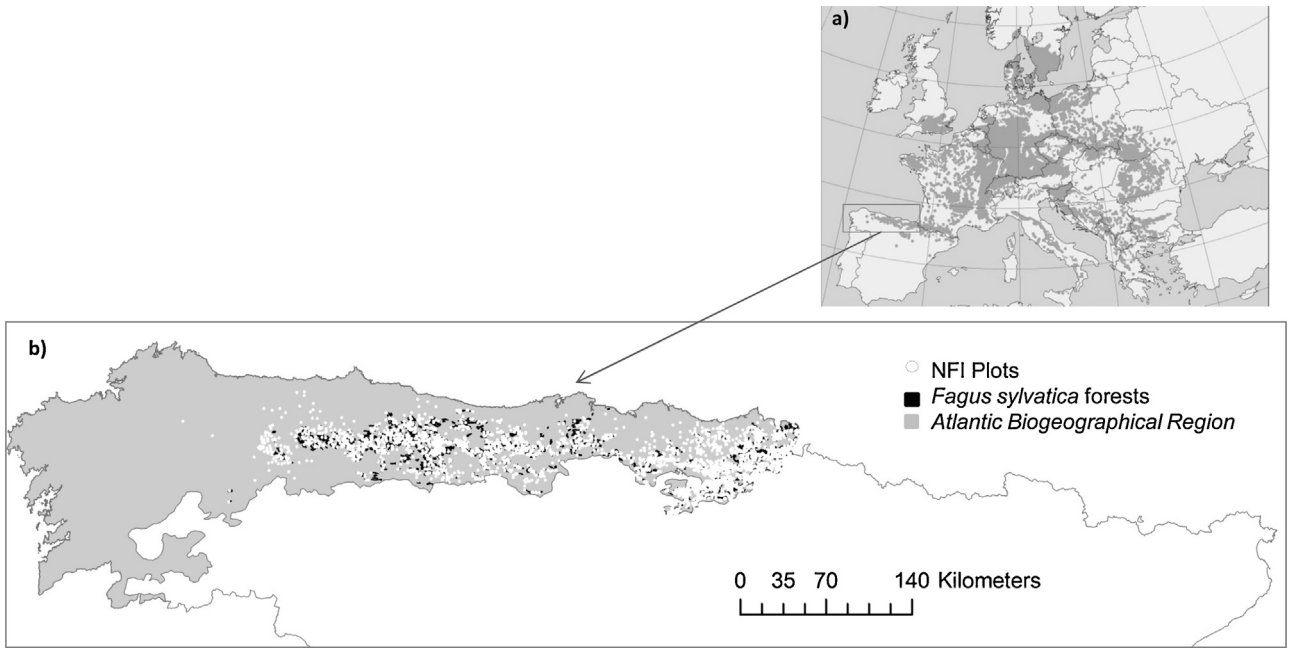

Fig. 1. Study area: (a) Study area located at the southwestern limit of *Fagus sylvatica* European distribution (EUFORGEN, 2009). (b) Location of the selected NFI plots and *Fagus sylvatica* forests (Ruiz de la Torre 1986–2002) in the study area. The Atlantic Biogeographical region (European Environment Agency boundaries, 2011) is highlighted.

pied today (Pretzsch et al., 2013). In addition to favorable climatic conditions, other intrinsic biotic and anthropic factors such as competitive interactions, dispersion capacities, genetic adaptations and habitat disturbance induced by human activities have been identified as factors underlying the rapid expansion of *F. sylvatica* in the late Holocene (Tinner and Lotter, 2006; Giesecke et al., 2007; Saltre et al., 2013).

As regards the Iberian Peninsula, although *F. sylvatica* was present in the Iberian Atlantic mixed forests before the Late Glacial (Ramil-Rego et al., 2000; López-Merino et al., 2008), the dominance of the European beech over other Atlantic species as well as over *Pinus sylvestris* L. and the establishment of monospecific beech forests is recent (Rubiales et al., 2008; Muñoz-Sobrino et al., 2009). Traditionally, the current distribution of *F. sylvatica* in the Iberian Peninsula has been explained by an east-west postglacial migration of beech forests from East and Central Europe via the Pyrenees during the late Holocene (Huntley and Birks 1983; Peñalba, 1994). However recently, macrofossils, palaeopalynologic and genetic data point to a late expansion from local glacial refugia in Northern Iberia since the Late Glacial (Magri et al., 2006; Magri 2008; Muñoz-Sobrino et al., 2009). Some authors, however, propose an intermediate model where Iberian *F. sylvatica* populations would be the result of both East-West migrations and expansion from glacial refugia (Martínez Atienza and Morla Juaristi, 1992; Rodriguez-Guitán, 2004; López-Merino et al., 2008). This last hypothesis is still to be tested.

Today, *F. sylvatica* is the most widespread broadleaved tree species in northern Spanish forests (388,000 ha as dominant species and 80,000 ha in mixed and other forests) (MFE50, 2001). The Iberian Peninsula constitutes the south-western edge of the distribution of the species, where it is mostly present in the montane bioclimatic belt in north-central Iberia (Costa et al., 1997) (Fig. 1). In the Spanish Atlantic biogeographical region, the species is found in the Cantabrian range. In these mountains, the abundance of *F. sylvatica* decreases from east to west and it is absent in the westernmost part, where sessile oak (*Quercus petraea* (Matt.) Liebl.) forests are more abundant.

However, North-Western Iberia would seem to be climatically suitable for *F. sylvatica* when modelling the species distribution (Benito-Garzón et al., 2008; Meier et al., 2011; Saltre et al., 2013). These findings support recent hypotheses suggesting that the postglacial expansion of beech has been and still is strongly dispersal-limited with multimillenial migration lags and therefore it is not yet in equilibrium with the climate (Svenning and Skov, 2004; Fang and Lechowicz, 2006; Svenning et al., 2008; Svenning and Sandel, 2013). In this regard, Saltre et al. (2013) found that *F. sylvatica* was only in equilibrium with climate in some parts of its range. The fact that North-Western Iberia was not one of those regions has led some authors to suggest that the expansion of European beech forests in the northern Iberian Peninsula may be still in progress (Rodriguez-Guitán, 2004). Others have associated the expansion of *F. sylvatica* in North-Western Iberia with the retreat of *Q. petraea* forests (Costa et al., 1997). However, to date there have been no published studies of the recent spatio-temporal dynamics of *F. sylvatica* populations on a broad-scale in the region to support these hypotheses.

In the present study we analyse the dynamics of *F. sylvatica* over recent decades in the Spanish Atlantic region, which makes up 85% of the distribution area of the species in Spain (MFE50, 2001). Our hypothesis is that *F. sylvatica* is still expanding, following the Holocene migration inertia at its leading edge (according to the "centre-periphery hypothesis", Hampe and Petit, 2005). The leading edge model of colonization states that range expansions involve increases in species abundance and/or distribution area as a result of recruitment success concomitant with a high level of demographic stochasticity, low mortality rates and an increase in dominance and growth. Moreover, it is thought that we are still witnessing the substitution of Atlantic sessile oak forests by *F. sylvatica* forests.

The main objectives of this study are to: (1) analyse the population dynamics of *F. sylvatica* to assess the existence of colonization shifts; (2) study both *F. sylvatica* and *Q. petraea* demographic trends and oak-beech interaction processes to infer forest succession dynamics; (3) examine the structure of the causal relationships (direct and indirect) among the explanatory factors that modulate recruitment in both species and (4) identify the main driving factors (climate, topography, forest succession) that determine the observed patterns of basal area increment in *F. sylvatica*. We used