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Recruitment patterns of four tree species along elevation gradients in Mediterranean mountains: Not only climate matters

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ABSTRACT

Evidence of tree regeneration failure of some species in the Iberian Peninsula forests warns us about the impact that the global change may exert on the preservation of Mediterranean forests, such as we know them. Predictions agree about an exacerbation of the summer drought there, acknowledged as the main limiting factor for the recruits' survival. On the other hand, many studies have also proved the relevant role that local heterogeneity has over the spatial distribution of forest species recruitment by providing safe sites. Therefore, to unravel how climate interacts with local factors over juveniles' performance seems crucial for the design of successful management strategies that allow facing the global warming. Here, we surveyed the natural recruitment of four dominant tree species in seven mountainous regions in the Iberian Peninsula, along entire elevational ranges as surrogates of their climatic ranges. Two of them have alpine and temperate distributions with populations at their rear edge in the Spanish mountains: *Fagus sylvatica* and *Pinus uncinata*; and the other two have a genuine Mediterranean distribution: *Quercus ilex* and *Pinus nigra*. Our main goal was to analyze for each species the effect of climate, local factors (*i.e.* light availability, stand structure and ground cover) and the interactions among them to identify the main drivers leading the regeneration process, assessed in terms of presence, abundance and mean annual growth of juveniles. The results showed different environmental factors determining the recruitment patterns of each species. Nevertheless, they highlighted the pervasive role exerted by both climate and fine scale factors, particularly the co-occurring vegetation on recruits' abundance, and the light availability on their growth. Moreover, we found some interactions among annual mean temperature and local factors, suggesting that climate and local heterogeneity act hierarchically, *i.e.* the local conditions may mitigate or exacerbate the impact of climate on juveniles. These results advocate for further research to increase our knowledge on the complex net of interactions among factors involved in recruitment at different scales, which in turn should be taken into account and incorporated in forthcoming management strategies.

1. Introduction

The Mediterranean Basin is one of the most vulnerable areas for biodiversity loss due to climate warming (Bakkenes et al., 2002; Thuiller et al., 2005). Predictions agree that increasing aridity and temperature, and more frequent extreme climatic events will occur there (Giorgi and Lionello, 2008; Nogués-Bravo et al., 2008). Therefore, since summer drought is acknowledged as the main limiting

Abbreviations: S1, seedlings, from one to five years; S2, saplings, over five years; ZIP, Zero-Inflated Poisson distribution.

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factor for the performance of Mediterranean species, its exacerbation would be critical, especially for those species that have there their southernmost distribution limit (Castro et al., 2004; Hampe and Petit, 2005; Benavides et al., 2013).

Emergence and survival during the earliest life stages are critical for population dynamics (Harper, 1977). In fact, juveniles of woody species are considered to be more susceptible to climate and particularly to extreme events (Castro et al., 2005), responding quicker than adults to environmental changes (Lloret et al., 2009). Thus, viability and persistence of these populations rely heavily on the success of the current recruitment under the ongoing changing conditions. In Mediterranean areas, the coincidence of drought with high temperatures makes the summer season a critical bottleneck for life. Hence, recruitment in Mediterranean climate-type forests is episodic and depends on the appearance of favorable windows, *i.e.* rare wet summers entail the opportunity for establishment (Matías et al., 2012); whereas episodic events of severe drought occasionally cause massive seedlings' mortality (Herrero, 2012). In this line, recent studies carried out at large spatial scale using the data from the Spanish National Forest Inventory, revealed a relatively widespread regeneration failure in many forest stands, mainly in those dominated by pines like *Pinus sylvestris*, *P. uncinata*, *P. nigra*, species that naturally occur at the Iberian mountains (Vayreda et al., 2013; Carnicer et al., 2014; Tíscar and Linares, 2014). Additionally, other studies have shown a lack of regeneration of these and other species at their rear edge of their distributions (Peñuelas and Boada, 2003; Peñuelas et al., 2007; Benavides et al., 2013), sometimes accompanied by a gradual replacement with more heat-, drought- and shade-tolerant species, like *Quercus ilex*, that becomes a great competitor under the current climate and management changes (Galiano et al., 2010; Coll et al., 2013; Carnicer et al., 2014).

In parallel, encouraging studies have reported demographic responses that provide stabilizing processes (either by compensation or mitigation) and advocate resilience and stability in populations against the global warming (Doak and Morris, 2010; Lloret et al., 2012, 2013). For instance, Benavides et al. (2015) found higher growth rates at low elevations of different tree species along altitudinal gradients, despite a lower survival rate of recruits there. They suggested that these higher individual growths during seedling life stage bestow more chances to survive because they may overcome quicker this critical life stage, in terms of climate sensitivity and damage from browsers (Zamora et al., 2001), counterbalancing at population level the negative effect of global warming at the trailing edges. Moreover, they found a diminishing sensitivity to climatic conditions of the successive cohorts of juveniles (*i.e.* seedlings more sensitive than saplings), becoming relevant other fine scale factors that attenuate the effects of climate on saplings

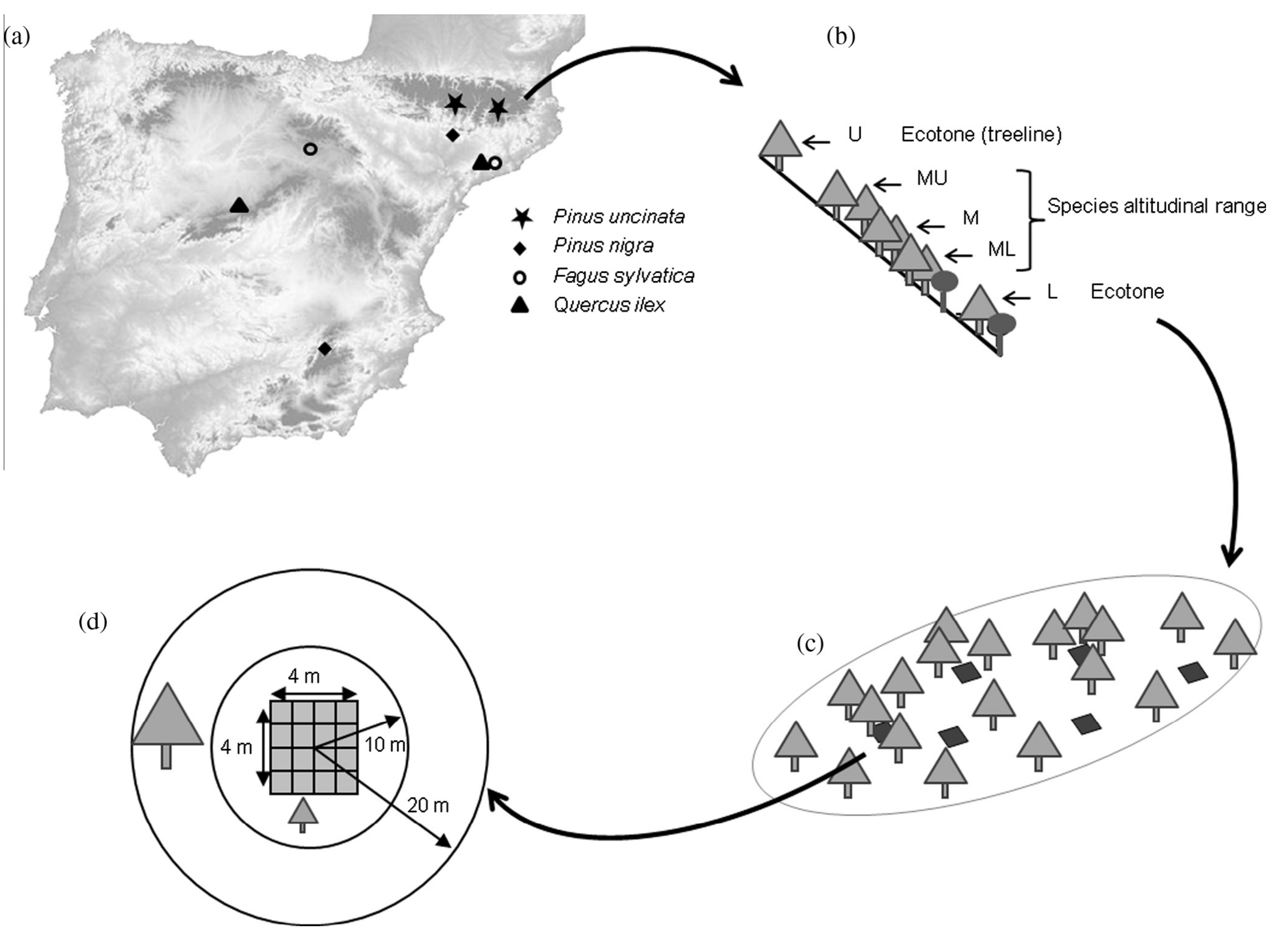

Fig. 1. Sampling design: (a) site locations, (b) diagram of transects layout within a site, (c) display of plots layout (gray squares) within a transect, and (d) plot design. Two sites for every species were sampled. Within each location, five transects were established at five elevations (three in sites with *Quercus ilex*) coded as: upper (U), mid-up (MU), middle (M), mid-low (ML) and lower (L) transects. Within each transect, six plots were established, three of them under closed canopy and the other three in gaps. Each plot encompasses a 4 × 4 m central squared regeneration plot – with 16 subplots of 1 m^2 size, and round plots where adult trees were mapped and measured: a 10-m radius area for every adult tree (>7.5 cm dbh), and 20-m radius circle for bigger trees (>20 cm dbh).