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Rangewide determinants of population performance in *Prunus lusitanica*: Lessons for the contemporary conservation of a Tertiary relict tree

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ABSTRACT

Relict species are an extremely important part of biodiversity and as such studies on the factors that allow their current persistence are required. The aim of this study was to assess the determinants of the distribution and range-wide population performance of the Tertiary relict tree *Prunus lusitanica* L. This threatened species is confined to Iberia, Northern Morocco and Macaronesia with a fragmented and scattered distribution. Using ecological niche modelling, we calculated the level of range filling across the range and tested its relationship with human impact. We then assessed the relative importance of climatic suitability as obtained through niche modelling, topographic factors and contemporary human impact on range-wide population performance. Results showed that the species occupies only 2.4% of the overall area predicted to be climatically suitable for its presence and the level of range filling varied across regions. A weak negative relationship among range filling and human impact was found. Overall climatic suitability was the strongest predictor of population performance. However, it showed high variability across regions: the effect was positive in Iberia whereas negative but not significant in Macaronesia and Morocco. Human impact showed a significant negative effect and finally topographic factors such as altitude had a minor negative effect. Our results highlight that both climate and human impact play a major role in the current limited range filling and performance of the species. Management plans to minimize anthropogenic disturbances together with reforestation measures are urgently needed in order to conserve this unique species.

1. Introduction

Understanding the factors that affect population persistence across the geographical range of species is of vital importance, although only few studies have addressed range-wide variation in population performance to date (Defeo and Cardoso, 2002; Jump and Woodward, 2003; Sanz et al., 2009). From a theoretical perspective, these studies can give us a better idea on the role played by different mechanisms in shaping species ranges. And on the applied side, they can improve the use and interpretation of ecological niche models, which generally predict large scale changes in the climatic suitability of species ranges in the face of climate change (Thuiller et al., 2005a, b). Understanding whether there is a link between suitability predicted by ecological niche models and population performance could inform us better about the likelihood of persistence of species under climate change. Population performance is defined here as population recruitment success, which can be particularly useful to evaluate population growth or decline in rare and endangered species (Schemske et al., 1994).

Contemporary population persistence and distribution across the geographical range of a species can be affected by climate, topography and human impact among other factors. Climate is recognized to be among the main determinants of species distributions at global and subcontinental scales (Chuine and Beaubien, 2001; Pither, 2003). However, it is not clear to what extent that role is a primary or secondary one with respect to other drivers (Gaston, 2003). Several studies have shown that many European tree species are not in equilibrium with climate –that is, they do not occur in all climatically suitable areas (Araújo and Pearson 2005)– occupying a small fraction of the potential range (low 'range filling') as a consequence of postglacial dispersal limitations on their potential distribution (Svenning and Skov, 2004; Svenning et al., 2008; Willner et al., 2009; Dullinger et al., 2012). Moreover, evidence is accumulating on how biotic interactions, including human impacts, and dispersal ability have shaped species distributions at broad spatial extents (Channell and Lomolino, 2000; Wisz et al., 2012). Thus, anthropogenic impacts on species' range filling limitation might play an important role and this effect could be coupled with dispersal limitation (Araújo and Peterson, 2012), given the greater difficulty to effectively disperse when there is less suitable habitat

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Additionally, geographical variation in population performance reflects both environmental suitability across the range and demographic processes in populations. Unfortunately, empirically-based analyses of the determinants of population performance at large scales have seldom been conducted, especially for large-sized organisms, due to the lack of integrated range-wide data. In this study, we explored these relationships focusing on the relict tree *Prunus lusitanica* L., which represents a good model given that relict species have been able to persist close to their environmental tolerance limits for long periods of time (Hampe and Jump, 2011). Hence, they represent a key for understanding the persistence of species and populations in response to global change. Due to their great antiquity, relicts are very important elements for the conservation of the genetic diversity, phylogenetic history and evolutionary potential of species (Hampe and Petit, 2005; Habel and Assmann, 2010; Hampe and Jump, 2011). They are therefore highly important components of local and regional biodiversity and appropriate strategies for their conservation require a sound understanding of their origins, current dynamics and future prospects. Range filling of relict species is generally limited and characterized by very uniform environmental conditions (climatic refuges) (Hampe and Jump, 2011). Moreover, it is assumed that relict species have not been able to recover from past climate-driven range contractions due to the influence of non climatic reasons, such as limited colonization ability or interspecific competition (Hampe and Jump, 2011). Finally, past and contemporary human impact is known to extensively affect population performance of relicts across their range (Calleja et al., 2009; Hampe and Jump, 2011). Habitat destruction by agriculture, livestock, forestry or infrastructures and the subsequent effects on demographic processes remains a major cause of disturbance on species performance (Lienert, 2004; Newman et al., 2013), and particularly for relicts (Calleja et al., 2009). Gaining a better understanding of the relevance of each driver is thus essential to design appropriate conservation measures for threatened relict species.

In this study we combine information on contemporary human impact with niche modelling in order to disentangle the relative importance of the factors that affect range delineation and population performance of the relict tree *P. lusitanica*. Specifically we addressed the following questions: 1) Does *P. lusitanica* exhibit a low level of range filling as theoretically expected from a relict species? 2) What is the importance of each driver (climatic suitability, human impact and topographic factors) in determining its current population performance? 3) Does the effect of these drivers change across regions? 4) Is there an association between human impact and contemporary population performance? Future conservation prospects for the species are discussed under the light of these results.

2. Material and methods

2.1. Study species

P. lusitanica is a wild cherry tree considered to be a survivor of the laurel forests that inhabited the Mediterranean basin during the Tertiary (Pignatti, 1978). It needs a high level of soil moisture to reproduce sexually (Pulido et al., 2008). It is also self-compatible and its fruits are mainly dispersed by birds (Calleja, 2006). *P. lusitanica* comprises three subspecies, *P. lusitanica* subsp. *lusitanica* L. represented by Iberian and North African populations, *P. lusitanica* subsp. *azorica* (Mouill.) Franco, found in the Azores and *P. lusitanica* subsp. *hixa* (Willd.) Franco, which inhabits the Canary Islands and Madeira (Franco, 1964). Both in the Iberian Peninsula and Morocco the species is distributed along streams and near springs, whereas in Macaronesian islands it is a component of the laurel forest. The current fragmented and scattered distribution of this relict subtropical tree in southern Europe (Fig. 1) is the result of known extinction and recolonization processes due to drastic climatic changes (Calleja et al., 2009). Moreover, anthropogenic impacts through habitat destruction by livestock, forestry or infrastructures have likely contributed to its current limited distribution, particularly in Macaronesia where laurel forests have been extensively destroyed and replaced by agricultural areas, intensive pastures and exotic forests (Fernández-Palacios et al., 2011). Due to its rarity and conservation concern, *P. lusitanica* has been listed as a vulnerable or endangered species by different protection bodies such as the Spanish Ministry for the Environment (IUCN red list categories for Spain) and the Canary Islands Regional Government (Cardoso et al., 2008; Bañares et al., 2009).

2.2. Population census, performance, human impact and topographic factors

This study has made use of exhaustive distributional data for *P. lusitanica*, collected throughout the whole native range of the species. The database comprises occurrence and demographic records from all known populations ($n = 267$) distributed throughout the Iberian Peninsula, the Canary Islands, the Azores, Madeira and Morocco. Population performance was measured as the index of sexual regeneration (recruitment rate), which was obtained by dividing the number of young individuals (less than 5 cm in stem diameter) by the number of adults for each population. This kind of index has been successfully used to examine large scale population performance constraints in other relict trees such as *Taxus baccata* L. (Sanz et al., 2009). Contemporary human impact was determined by recording all current anthropogenic disturbances on the populations (felling, forestry activities, fires, market gardening, different types of transport infrastructures and grazing by wild ungulates and domestic livestock). To obtain a quantitative measure of anthropogenic impact, an index which ranges from 0 to 100% was calculated for each population. First, the intensity of each type of disturbance was determined: low intensity (1) for cases when recorded disturbances do not cause a reduction in population size, medium (2) when disturbances could reduce population size in the near future, and high intensity (3) when the disturbances could hamper population survival. This intensity factor (1, 2 or 3) was multiplied by the percentage of area affected by each type of disturbance and, finally, the resulting numbers were summed in order to achieve the total human impact index for each population (Cáceres, 2014). Topographic factors including mean altitude, aspect and slope were obtained for each population from a global digital elevation model (Jarvis et al., 2008).

2.3. Ecological niche modelling and range filling

We were able to draw on an exhaustive database of *P. lusitanica* population records across its entire distribution range thanks to extensive previous work including reviews of the botanical literature and field surveys throughout the species range (Calleja, 2006; Cáceres, 2014). Our ecological niche modelling exercise was hence based on a precise occurrence data with a spatial resolution of population records of 1 km.

Five climatic variables were used as predictors in modelling exercises, which were selected as considered the most relevant in limiting the distribution of *P. lusitanica*: 1) annual mean temperature, 2) mean maximum temperature of the warmest month, 3) mean minimum temperature of the coldest month, 4) annual precipitation and 5) precipitation of the warmest quarter. Temperature data were obtained from WorldClim (http://www.worldclim.org/) averaging data for a period of 40 years (1950-1990). Precipitation data were instead obtained from the Spanish National Meteorological Agency (AEMET) for the Iberian Peninsula and Macaronesia as we observed it was more accurate than the WorldClim dataset. This was corroborated through in situ readings of a weather station in a mountainous part of the range and subsequent cross-checking with national meteorological and worldclim datasets. For Morocco, precipitation data were obtained from a precipitation model created from the interpolation of 68