



Research article

Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species



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ABSTRACT

Despite growing evidence of changes in plant functional traits (FT) along environmental gradients, the way they shape species niches (i.e. how they alternatively influence the limits, width and environmental optimums of species niche) remains only partially understood. Thus, Species Distribution Models were developed and evaluated using distribution data from the Spanish Forest Inventory for 21 of the most common Mediterranean woody species, and used to derive different environmental characteristics of species niche, which were then correlated against species-specific values of 14 FT and combinations of relatively orthogonal FT. Species leaf traits, and in particular Specific Leaf Area (SLA), were highly correlated with species niche characteristics regarding aridity (especially with the more arid limit). Hydraulic traits, i.e. the water potential at which a species loses 50% of xylem hydraulic conductivity due to cavitation (PLC₅₀), and species hydraulic safety margins (SM), were better correlated with species aridity niche optimums. Overall, the best model fits, particularly regarding species' optimum and maximum aridity limit, were obtained when SLA and hydraulic traits (either PLC₅₀ or SM) were used in combination. The study shows how in the Mediterranean region a single trait may be able to explain broad differences in species distributions, but also that the coordination of relatively independent traits achieves a more accurate representation of their environmental limits, particularly at the dry end of the species' range. The approach used in this study relies on the physiological limits of a species and, to a certain extent, on the mechanisms behind them, adding robustness and accuracy to predict species distribution and mortality under climate change scenarios.

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1. Introduction

Functional Traits (FT) may be defined as the “morpho-physio-phenological” plant attributes that drive species success on the environment (Violle et al., 2007). Despite the great interest on the role of plant FT in plant strategies, community ecology, and ecosystem functioning (Keddy, 1992; Lavorel et al., 2007; Westoby et al.,

2002), the mechanism with which they shape species environmental niches (i.e. how they alternatively influence their limits but also the optimum and the width of their niches) is complex and has been addressed directly by relatively few articles (but see Dvorský et al., 2015; Pollock et al., 2012; Stahl et al., 2014; Thuiller et al., 2004; Violle and Jiang, 2009). The fundamental niche of a species is determined by its physiological responses to abiotic factors (Austin et al., 1984; McGill et al., 2006) which as consequence partially determine their distribution (Woodward and Williams, 1987). It is thus reasonable to hypothesise the existence of a relationship between specific FT and species environmental niche, which would provide insights on the mechanisms governing plant communities assemblage and species distribution (McGill et al., 2006; Westoby and Wright, 2006).

The role of FT in determining species establishment in a given environment can be framed in the context of Keddy (1992)

Abbreviations: SDM, species distribution models; FT, functional traits; SLA, specific leaf area; PLC₅₀, the water potential at which a species loses 50% of xylem hydraulic conductivity due to cavitation; SM, hydraulic safety margin.

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assembly rules, which imply that environmental filtering eliminates species with unsuitable traits. Several studies have indeed shown that species living in different environments are characterized by different trait values. For instance, Specific Leaf Area (SLA) usually decreases with site aridity and nutrient scarcity (Fonseca et al., 2000; Wright et al., 2001; Niinemets, 2001) because a low SLA is associated with drought resistance and also increases nutrient residence time (Poorter et al., 2009). Similarly, the water potential at which a species loses 50% of xylem hydraulic conductivity due to cavitation (PLC₅₀) tends to be lower in species from arid areas (Maherali et al., 2004; Choat et al., 2012). Variability in trait values also occurs within species (i.e. intraspecific trait variability), with substantial variation among populations along environmental gradients (Albert et al., 2010; Jung et al., 2010; Laforest-Lapointe et al., 2014). For instance, SLA and wood density (WD) vary in *Nothofagus pumilio* according to temperature and moisture gradients, respectively (Fajardo and Piper, 2011).

Functional traits are not independent of each other, and their relationships have been used to define global spectra of trait covariation (Chave et al., 2009; Díaz et al., 2015; Reich, 2014; Reich et al., 2003; Wright et al., 2004). FT reflect patterns of resource allocation, potentially affecting growth and survival, but also representing trade-offs among plant strategies (Wright et al., 2004; Reich, 2014). Correlations among FT may reflect causality or coordination between FT (Reich et al., 2003). An example of causal link is the dependence of species photosynthetic rate on photosynthetic enzymes concentration in leaves, i.e. their leaf nitrogen content. Instead, coordination reflects an improvement of species response when two or more specific traits that appear to be mechanistically independent co-vary (Reich et al., 2003). For instance, in tropical dry forests, the resistance to xylem cavitation in evergreen species coordinates with leaf turgor loss point and modulus of elasticity (Markesteijn et al., 2011). Coordination among FT may imply that different combinations of traits may be adopted by species to maximize their performance in a given environment (Maire et al., 2013; Manzoni, 2014).

Since FT determine the success of a species in a given environment it is also expected that they should also shape the species' environmental niche. However, it is not clear what specific characteristics of the niche will be better reflected by species traits and, in particular, whether FT will reflect mostly the optimal conditions or the environmental limits over which a species can strive. Indeed, several studies suggested that along an environmental gradient, competition mostly affect species performance on the high-resource end of the gradient, whereas their low-resource boundary would be mostly influenced by species physiological tolerance (Brown et al., 1996; Normand et al., 2009). Cornwell and Ackerly (2010) observed that SLA scaled with species abundance across different plant communities in coastal California, suggesting that SLA accurately represented species optimal conditions in those environments. However, species are not always abundant at their physiological optimal because biotic interactions affect species realized niche (McGill et al., 2006). For instance, *Pinus sylvestris* is commonly displaced from its optimal temperature location due to competition processes (Rehfeldt et al., 2002). Thus, the accuracy and reliability of studies in land-plant ecology (Westoby and Wright, 2006), community ecology (McGill et al., 2006), or climate change impacts (Guisan and Thuiller, 2005) would benefit from a deeper understanding of how FT, or combinations of FT, relate with species' niche characteristics e.g. the optimal value or the upper and lower limits.

Species Distribution Models (SDM) are well-established methods to characterize and study species niches (Higgins et al., 2012). SDM use species presence/absence data and the environmental values at those locations to predict species distribution across the territory (Guisan and Zimmerman, 2000). Thus, SDM integrate the

combined dependencies of different significant variables and the embedded information provided by species absences, in addition to species presences, to provide an accurate representation of species environmental niche. Interpreting SDM results requires knowledge of underlying ecological processes that may set differences among the physiological and the realized niche (e.g. assumptions on species pseudo equilibrium with the environment, sink source process, or extreme events; Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Zimmermann et al., 2009). Nevertheless many of these confounding effects can be reduced with appropriate model use (e.g. application at biologically and biogeographically suitable scales, Araujo and Peterson, 2012), and thus SDM have been proved useful to address a number of hypotheses including e.g. niche stability and evolution (Pearman et al., 2010).

The objective of this study was to determine the relationship between several FT and the environmental niche for 21 of the most common Mediterranean woody species in Spain, where water availability is the main limiting factor for plants. We hypothesise that: i) the environmental niche of Mediterranean species is better predicted by traits related to drought resistance rather than by traits related to other functions; ii) since trait effects on performance may be interactive or largely independent between traits, we expect that predictions of species environmental niches will improve when a combination of traits is used rather than a single trait; iii) finally, since niche characteristics are not equally set by competition and species physiological tolerance, we also expect that drought resistance traits would be better correlated with the arid limit of species rather than with other niche characteristics such as the optimum or the high-resource limits (i.e. the humid limit).

2. Methods

2.1. Study area and datasets

The study area comprises the Spanish continental territory, located between 36° N and 44° N of latitude, and between 10° W and 3 E longitudes. The main Köppen climatic domains are Dry and Temperate, with annual mean temperatures ranging from ~3 to ~17 °C and precipitations from ~300 to ~2200 mm/year (Chazarra, 2011). More than three quarters of the territory belong to the Mediterranean biogeographic region, being conifers, sclerophyllous shrubs, and evergreen forests the main vegetation types (Rivas-Martínez, 1987).

The Third Spanish National Forest Inventory (IFN3) (<http://www.magrama.gob.es/>; Dirección General de Conservación de la Naturaleza, 2006) was used to retrieve species distribution data (i.e. presence and absence). The Spanish National Forest Inventory involves periodical surveys (every ~10 years) of the whole forested area of Spain and includes exhaustive information on stand composition, structure, and productivity. It has a regular sampling design with one sample plot every ~1 km² accounting for more than 90 000 plots in total. IFN3 was conducted between 1997 and 2007. We selected 21 of the most common Mediterranean woody species from ten different families and six functional groups (Table 1, see Appendix A). We only included species for which their overall environmental (climatic) range was well represented in Spain (central and northern European species such as *Quercus robur* L. and *Fagus sylvatica* L. were excluded).

A dataset including 19 bioclimatic variables at a resolution of 30 arc-seconds (Hijmans et al., 2005) was downloaded for the area of interest from the WorldClim webpage (<http://www.worldclim.org/>). A soil pH dataset at a resolution of 5 km² was downloaded from the European Soil Portal (<http://eusoils.jrc.ec.europa.eu/>, Panagos et al., 2012). The number of

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