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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 21of 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 corre- lated 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 cavita- tion (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

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 ecosys- tem functioning (Keddy, 1992; Lavorel et al., 2007; Westoby et al., 2002), the mechanism with which they shape species environmen- tal 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 Dvorsky´ 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 deter- mined by its physiological responses to abiotic factors (Austin et al., 1984; McGill et al., 2006) which as consequence partially deter- mine 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 assem- blage 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) assembly rules, which imply that environmental filtering elimi- nates species with unsuitable traits. Several studies have indeed shown that species living in different environments are character- ized 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 (PLC_{50}) 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 gra- dients (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, respec- tively (Fajardo and Piper, 2011).

Functional traits are not independent of each other, and their relationships have been used to define global spectra of trait co- variation (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 rep- resenting trade-offs among plant strategies (Wright et al., 2004; Reich 2014). Correlations among FT may reflect causality or coor- dination 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 max- imize 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 char- acteristics of the niche will be better reflected by species traits and, in particular, whether FT will reflect mostly the optimal con- ditions 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 tol- erance (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 accu- racy 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 val- ues 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 knowl- edge 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 sta- bility 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 bet- ter predicted by traits related to drought resistance rather than by traits related to other functions; ii) since trait effects on perfor- mance 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 sin- gle 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 Koppen climatic domains are Dry and Tem-perate, 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/; Direccion General de Conservacion 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 km^2 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 envi-ronmental (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 resolu- tion of 30 arc-seconds (Hijmans et al., 2005) was down- loaded for the area of interest from the WorldClim webpage (http://www.worldclim.org/). A soil pH dataset at a resolution of 5 km^2 was downloaded from the European Soil Portal (http:// eusoils.jrc.ec.europa.eu/, Panagos et al., 2012). The number of potential explanatory variables was reduced to limit collinearity and obtain more parsimonious models (Bolker, 2008). Variables were selected based on their known ecological relevance and pairwise correlations (Dormann et al., 2013). At the end of the pro- cess, the variables selected were: Annual Precipitation (AP), Mean Annual Temperature (MAT), Precipitation of the Driest Quarter(PDQ), and soil pH.

2.2. Niche models

SDM were generated for each species using the presence and absence dataset and the selected environmental variables. Absences were randomly selected to equal three times the num- ber of presences, since some methods to evaluate SDM (e.g. Kappa coefficient) usually outperforms at low prevalence (i.e. the ratio between presences and absences) (Valverde-Jimenez and Lobo, 2007). The algorithm used to build SDM was Generalized Additive Models (GAM) to avoid constraining the species response curves to a predetermined shape (Austin, 2007) and because its performance is generally as good as that of more complex “black-box” methods like Neuronal Networks (Segurado and Araujo, 2004). Indeed, GAM are commonly used in ecological studies of species distributions (e.g. Araújo and Luoto, 2007; Guisan et al., 2002; Zimmermann et al., 2009).

Goodness of fit of the models was evaluated by the deviance explained (D2), while their accuracy was assessed after a 5 k-fold cross validation by the Area Under the Curve (AUC) and Kappa coefficient. To convert predicted probabilities into presences and absences the threshold selected was that which minimized the difference between specificity and sensibility. This criterion performs better than other methods (i.e. yields the most accurate predictions, Liu et al., 2005) because it is linearly related with prevalence, which is a necessary property for this type of models (Valverde-Jimenez and Lobo, 2007).

2.3. Niche characteristics

Niche characteristics were calculated after projecting SDM over continental Spain and associating each predicted location with its occurrence probability and its environmental value (see Fig. 1 for details). Note that predictions were preferred to response curves for extracting niche characteristics, as predictions do not constrain the value of the other explanatory variables included in the model. For each species and environmental variable a set of niche characteristics were obtained: a) the value at which the probability to find the species was highest (i.e. the optimum), b) the lowest and highest values at which the species can be found (i.e. the minimum and maximum, respectively), c) and the range over which the species can be found (see Appendix B for the matrix with species niche values). In addition, in order to integrate in the analysis the joint effect of the variables used in the SDM, niche characteristics were also calculated for a latent variable (hereafter called aridity) obtained from the first axis of a Principal Component Analysis of the four selected environmental variables (see Appendix C). The first axis of this PCA explained 60% of variance, and loadings for each variable were 0.49, −0.56, −0.59, 0.32 for AMT, AP, PDQ, and pH, respectively.

2.4. Species functional traits

A set of 14 morphological and physiological FT for the 21 study species were extracted from the literature (see Appendix A for sources used). Leaf level traits included maximum photosynthetic rate per unit mass (A_{mass}) and per unit area (A_{area}), maximum sto- matal conductance (G_{max}), intrinsic water use efficiency (WUE), leaf area (LA), specific leaf area (SLA), and nitrogen content per unit of mass (N_{mass}). Traits related to plant hydraulics and resistance to cavitation included Minimum Leaf Water Potential (MLWP, leaf water potential measured at midday during the driest period of the year), the water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), and the hydraulic safety margin (SM, the difference between MLWP and PLC_{50}). Maximum height (MH), seed dry weight (SDW), and wood density (WD), which are usually related with competition and life history strategies, were also included. When more than one value was found for the FT of a species, the average of the value was calculated and used in all further analyses. Trait plasticity was not considered in our study, as the number of trait values was not enough to characterize variability along climatic gradients for all species and traits.

2.5. *Data analysis*

Trait data normality was checked using Shapiro-Wilk normality tests, and we transformed data when it ensured normality (i.e. log transformation for A_{mass}, MH, SDW, SM, and SLA, and root square transformation for LA). The independency among traits was assessed by pairwise correlations and a PCA of FT. We assessed the relationships between single FT values and niche characteristics among species using Pearson correlation coefficient and their corresponding *P* values (Warton et al., 2006). The combined effects of multiple traits on niche characteristics were tested using multiple linear regressions. Because gymnosperms and angiosperms greatly differ in their wood anatomy and other relevant attributes (Brodribb et al., 2012; Carnicer et al., 2013), multiple regressions were performed including a dichotomic variable to assess the phyla effect. Traits were standardized to assess their weights on regressions, and the Akaike Information Criterion (AIC) was used as a measure of model performance in multi-model selection (Burnham and Anderson, 1998). All analyses were conducted using R software (version 3.2.0., R Development Core Team, 2015).

3. Results

3.1. *Species distribution models*

The accuracy of the SDM was generally satisfactory (Fielding and Bell, 1997): the best performance was obtained for *Quercus pubescens* and the worst for *Erica arborea* (Table 1). Considering all species, mean D^2 was 39% (min 20%, and max 66%), mean AUC was 0.88 (ranging from 0.79 to 0.96) and mean Kappa was 0.56 (ranging from 0.37 to 0.8).

3.2. *Functional traits*

Pairwise comparisons between traits showed that leaf traits were correlated among each other, whereas significant correlations among hydraulic traits were not always present (see Appendix D). There were no significant correlations between leaf and hydraulic traits, but some of them were related with life history traits (i.e. WD, was correlated with Aarea, Gmax, and Nmass; and MH was correlated with LA, MLWP and PLC50). A PCA performed on species FT showed similar results. Leaf traits were the largest contributors to the first axis (40% of variance explained), whereas the second axis was mainly determined by hydraulic traits and maximum height (20% of variance explained, Fig. 2).

3.3. *Functional traits and niche characteristics*

3.3.1. Single traits

FT showed correlations with the niche characteristics computed for each environmental variable considered (focus is given on aridity, i.e. the latent variable obtained from the PCA, since it integrates the effect of precipitation and temperature). However, not all of the fourteen FT were equally correlated to the niche characteristics of species. SLA was almost always the trait showing the strongest correlations (Table 2). All leaf traits, except Aarea, significantly scaled with niche aridity values. Thus, species with more arid niches were characterized by low SLA, Nmass, Amass, Gmax, and LA, and greater LLS and WUE (Fig. 3). The hydraulic traits that displayed the best correlations with the aridity niche were PLC50 and SM (Table 2), while MLWP was not correlated. SDW, MH, and WD did not show significant correlations with the aridity niche of species, and only MH and WD appeared to be related with the aridity niche when the phyla effect was considered. Overall, similar patterns were observed when analysing trait correlations with the niche characteristics of the other environmental variables, such as AP, PDQ, and AMT (i.e. traits values that decreased with aridity, also decreased with precipitations and increased with temperatures, see Appendix E for the complete correlation matrix).

Leaf traits were most strongly correlated with species maximum aridity (i.e. the most arid conditions reached by a species), whereas hydraulic traits were best correlated with the species optimum (i.e. the aridity conditions that a species occupies more frequently). None of the considered FT showed a correlation with the aridity range, but some traits were correlated with the niche ranges of other environmental variables e.g. WUE was inversely correlated with the annual precipitation range and SLA with the annual mean temperature range (see Appendix E).

3.3.2 . Trait combinations

Multiple regression analysis showed that SLA combined with other largely independent traits (Fig. 2) performed better than SLA alone in explaining species niche characteristics (except for mini- mum aridity, for which the best multiple trait model did not provide a significantly better fit than SLA alone, Table 3). The best-fitting model for the optimum was obtained when including SLA and SM as explanatory variables, while the best model for the maximum of aridity included SLA and PLC_{50}. SLA weights on these multi-ple regressions were almost always greater than for other traits, except for species optimum. Combinations with WD or MLWP did not increase the goodness of fit of the models. In addition, sep- arating gymnosperms from angiosperms did not enhance model performance (data not shown).

4. Discussion

The results of the present study highlight the close link between FT and species niches, confirming our first hypothesis and demonstrating how in the Mediterranean region traits com- monly associated with drought responses (i.e. SLA, PLC_{50}, and SM; Micco and Aronne 2012; Nardini et al., 2014) strongly affect species distribution and consequentlly their environmental niches. Such finding was possible thanks to the use of an appraoch that combined trait based ecology with niche modelling, highlighting the poten- tial of functional traits to predict species environmental niches and suggesting that an approach based on niche-trait relation- ships could improve our understanding of how traits govern species niche (McGill et al., 2006; Violle and Jiang, 2009; Westoby andWright, 2006). Furthermore, by setting the environmental limits of the species distribution, our approach reflects the physiological limits of species and, to a certain extent, the mechanisms behind them, which could contribute to greater robustness and accuracy in predictions of species distribution changes under climate change scenarios (Stahl et al., 2014; Williams et al., 2008).

Previous studies have analysed the relationships between species environmental niches and FT. Maharjan et al. (2011), for instance, observed that the optimum of rainforest species along a rainfall gradient scaled with wood density. Thuiller et al. (2004) observed that, in the Cape Florist Region, species from the Leu- cadendron taxa occupying more arid niches had lower leaf areas than those from more humid niches. Stahl et al. (2014), observed that WD, SDW, and MH of North American flora were related with species distribution limits regarding temperature and humidity, and Dvorský et al. (2015) identified that the subnival species in the Himalayas with narrower altitudinal ranges were also shorter in stature, held higher water content, and had higher water use efficiency.

Of all traits considered, SLA proved to be the one with the strongest ability to explain the distribution of species along the aridity gradient in Spain. It is perhaps not surprising for SLA to have a key role in setting the species niche in arid environments, since SLA has been associated with several important aspects of plant drought resistance. Low SLA values are mainly consequence of high leaf density, which is acquired by increasing concentration of lignin and structural carbohydrates in leaves (Poorter et al., 2009). Thus, SLA is considered a good index of leaf sclerophylly (Groom and Lamont, 1999): a tissue reinforcement that prevents mechanical cell damages during dry events and thus enhances leaf wilting resis- tance, which may allow maintaining leaf photosynthesis for longer under drought stress (Micco and Aronne, 2012). Overall, our results are consistent with global patterns showing that species from dry and hot environments (low water availability) tend to have low SLA values (Niinemets, 2001; Wright et al., 2005).

SLA is known to be causally linked with other leaf traits and to reflect trade-offs between construction and maintenance costs of leaves, and duration of photosynthetic returns from those invest- ments (Reich et al., 1997; Niinemets, 2001; Wright et al., 2004). It isthus not easy to isolate the individual contribution of a given trait to trait-environment relationships, particularly when traits with a disproportionate number of linkages with other traits, such as SLA, are involved. It may be better to view such ‘hub’ traits as parts of a constellation of traits, most of which are known to be involved in drought resistance mechanisms (Markesteijn et al., 2011; Nardini et al., 2014). Low SLA leaves are known to also have longer LLS, higher N_{mass} and lower A_{mass} and stomatal conductance (Wright et al., 2004). It is thus not surprising that also these leaf traits were correlated with the environmental niche in our study. The observed increment of WUE with aridity is consistent with species from drier sites having greater photosynthetic rates for a given stomatal conductance (Dudley, 1996), which is part of a water sav- ing strategy that involves N use efficiency (Wright et al., 2001). LA also decreased with aridity, most likely because it facilitates energyexchange and prevents excessive leaf temperature (Givnish, 1987; Thuiller et al., 2004).

Although SLA was the FT that showed the highest degree of correlation with the aridity niche (and in general with all environ- mental niche; see Appendix E), other functional traits, which did not co-vary with SLA, explained part of the variability in species aridity niche. These results are consistent with the fact that species from arid places tend to have a greater resistance to cavitation (i.e. low PLC_{50}, Maherali et al., 2004; Choat et al., 2012): low PLC_{50} allows species to maintain hydraulic functionality in dry conditions and thus to sustain leaf gas exchange, potentially improving their performances and survival (note however that drought-induced mortality mechanisms are complex, McDowell, 2011; Klein, 2015). Additionally, our results showed that species occupying more arid niches also maintain wider hydraulic safety margins, which is common in plants living in water limited environments, includ-ing the Mediterranean (Vilagrosa et al., 2012). This finding would suggest a higher resilience of drought adapted species to climate change. However, species with a higher WUE and a lower SLA were found to thrive over a narrower range of annual precipitations and annual mean temperatures, respectively, suggesting a lower intrin-sic adaptation potential to climate change by those species that are mostly specialized for warm and dry environments.

As initially hypothesized, our results also showed that trait com- binations (in our case SLA with PLC_{50} or SM) improved the ability to explain the different characteristics of species aridity niche and highlight the complementarity among drought resistance mech- anisms in Mediterranean environments. In addition, despite the known coordination between leaf transpiration and xylem water transport (Martinez-Vilalta et al., 2014), our results showed that SLA and hydraulic traits were poorly correlated. This is consis- tent with recent reports (Li et al., 2015) and with the evidence showing that SLA is largely independent from leaf hydraulic con- ductance, a key water relations trait that is frequently coordinated with stem hydraulic properties (Sack and Holbrook, 2006). All these results suggest that leaf structure, gas exchange and hydraulic traits may act somewhat independently. Brodribb et al. (2003) already observed that leaf wilting point and PLC_{50} are not neces- sarily related. Drought resistance and the ability to survive in arid environments are complex attributes that are clearly not conferred by a single trait. Therefore, specific combinations of traits may be adopted by species to maximize their performance under a given environment (Maire et al., 2013; Manzoni, 2014). Although they were not considered in this study, rooting habits are likely to be an important element to understand niche segregation over aridity gradients. Rooting depth gives access to water stored in deeper and moister soil layers, while superficial roots give access to sporadic and light rain events that may occur during summer (Mereu et al., 2009). Other root traits such as specific root length also seem to play a role in plant water relations (Burgess, 2006; Nardini et al., 2014).

Finally, leaf traits were better correlated with the arid limit of species niche rather than with the niche optimum. Similarly to our results, Stahl et al. (2014) also observed that some traits of North America flora are related with species' niche limits but not with their optimums. Previous studies have shown that species presence and abundance across gradients are not always driven by the same traits (Cingolani et al., 2007), supporting the idea that specific traits significantly determine the environmental lim- its of species distributions (Stahl et al., 2014), while other traits are mostly influencing species performance (Martínez-Vilalta et al., 2010) under less abiotic stressed conditions. Indeed, some studies have suggested that competition plays a major role at the high-resource end of species distributions, whereas the limits at the low-resource end of the distribution are set by physiological toler- ance (Brown et al., 1996; Normand et al., 2009). Despite their known role in drought resistance, hydraulic traits were best correlated with optimal niche conditions, again suggesting that drought resis- tance is multifaceted and that hydraulic traits *per se* are not enough to describe the species tolerance limits to drought, in agreement with previous results in Mediterranean ecosystems (Miranda et al., 2010). Our results also showed that species' ranges do not seem to be constrained by any of the traits considered in this study, likely evidencing that species environmental ranges are more related to trait variability or plasticity within species (not considered here) than with trait averages (Sultan, 2000).

5. Conclusions

Environmental filtering in the Mediterranean mostly affects leaf-level traits (mainly SLA) and hydraulic traits (such as SM or PLC_{50}), whereas traits such as MH or WD appeared to have a secondary role. Studied FT have a greater influence on the low resource limit of species' environmental niche (rather than its opti- mum), reinforcing the idea that such limit is mostly determined by physiological processes. Biotic interactions are likely to exerta more prominent role on less resource limited portions of the niche. Furthermore, environmental niches are better predicted by combinations of different FT, rather than any given FT, suggest- ing complementarity among traits and mechanisms to cope with drought. Future improvements in trait databases (e.g., TRY; Kattge et al., 2011) or remote sensing of plant functional diversity (Jetz et al., 2016) should allow including other potentially relevant traits and, importantly, trait plasticity in assessments of species environ- mental limits. These developments will contribute towards more robust assessments of the functional impacts of climatic changes using a more general, trait-based predictive framework (Dubuis et al., 2013; Stahl et al., 2014).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2016.05.001.

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Table 1

Performance indexes of Species Distribution Models. Calibration and accuracy parameters for each species, including Deviance explained (D^2), Kappa, and the Area Under the Curve (AUC).

Species	Number of presence	D^2	Kappa	AUC
Acer monspessulanum	1445	0.31	0.47	0.85
Arbutus unedo	8192	0.29	0.46	0.85
Erica arborea	9168	0.2	0.37	0.79
Erica multiflora	3171	0.46	0.67	0.92
Juniperus oxycedrus	20 694	0.41	0.57	0.9
Juniperus phoenica	9226	0.4	0.57	0.9
Olea europaea	7369	0.48	0.63	0.93
Pinus halepensis	16 386	0.62	0.76	0.96
Pistacia lentiscus	9172	0.51	0.66	0.93
Prunus spinosa	7443	0.25	0.42	0.83
Pistacia terebinthus	2565	0.27	0.47	0.84
Quercus faginea	14 885	0.23	0.42	0.82
Quercus pubescens	5040	0.66	0.8	0.96
Quercus pyrenaica	9829	0.4	0.59	0.9
Quercues suber	5694	0.49	0.66	0.93
Rosmarinus officinalis	17 851	0.44	0.62	0.92
Quercus coccifera.	12 311	0.44	0.62	0.91
Rhamnus alaternus	9703	0.35	0.52	0.88
Phyllerea latifolia	3245	0.39	0.55	0.9
Pinus pinea	5276	0.41	0.6	0.9
Quercus ilex	42 689	0.25	0.45	0.81

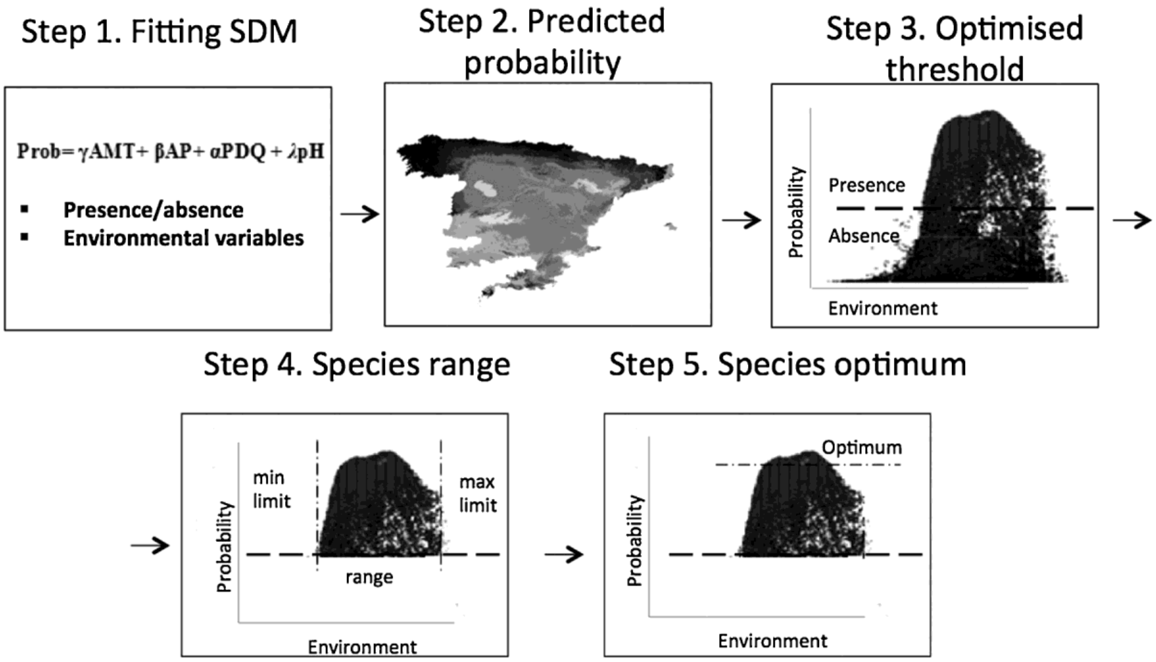

Fig. 1. Work flow to obtain niche characteristics. Step 1. For each species a SDM was fitted using the selected environmental variables in order to obtain the most accurate models. Step 2 and 3. The SDM was later projected into the Spanish territory and a threshold was set to remove locations where species probability was so low that it was predicted to not occur (i.e. predicted absences). Step 3. For each remaining location both presence probability and environmental variables were associated (i.e. each environmental variables used in the SDM and the latent variable, i.e. aridity). Step 4. Minimum and maximum limits were obtained selecting the 1st and 99th percentiles of environmental values, respectively. The range was calculated as the difference between both limits. Step 5. The optimum was calculated as the mean environmental value of the locations with the highest probability (i.e. locations with probability of occurrence over the 97th percentile).

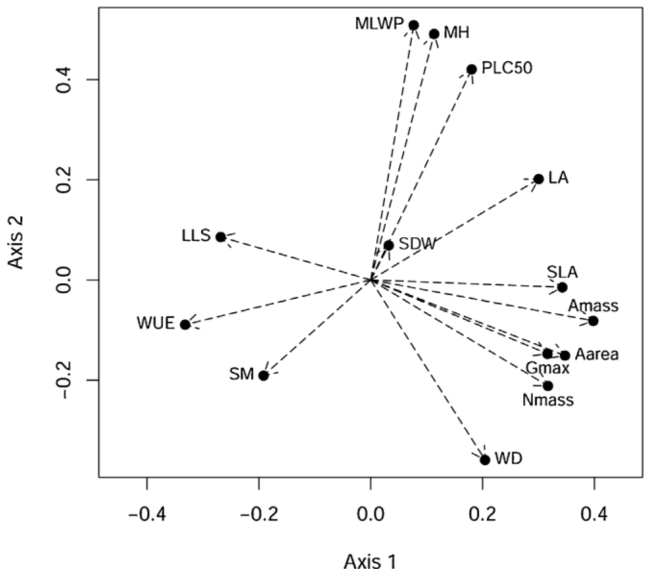

Fig. 2. Principal Component Analysis of plant functional traits, including: maximum photosynthetic rate per unit of mass (A_{mass}), and per unit of area (A_{area}), maximum stomata conductance (G_{max}), intrinsic Water Use Efficiency (WUE), Leaf Area (LA), Specific Leaf Area (SLA), Leaf LifeSpan, (LLS), nitrogen content per unit of mass (N_{mass}), Minimum Leaf Water Potential (MLWP), Maximum Height (MH), Seed Dry Weight (SDW), water potential at which 50% of hydraulic conductivity is lost (PLC_{50}), hydraulic safety margin (SM), and wood density (WD). The perpendicularity of hydraulic and leaf traits shows their relative independence. The first axis was mostly determined by leaf traits and explained 40% of the total variance; the second axis explained 20% of the variance%, and was mostly explained by hydraulic traits.

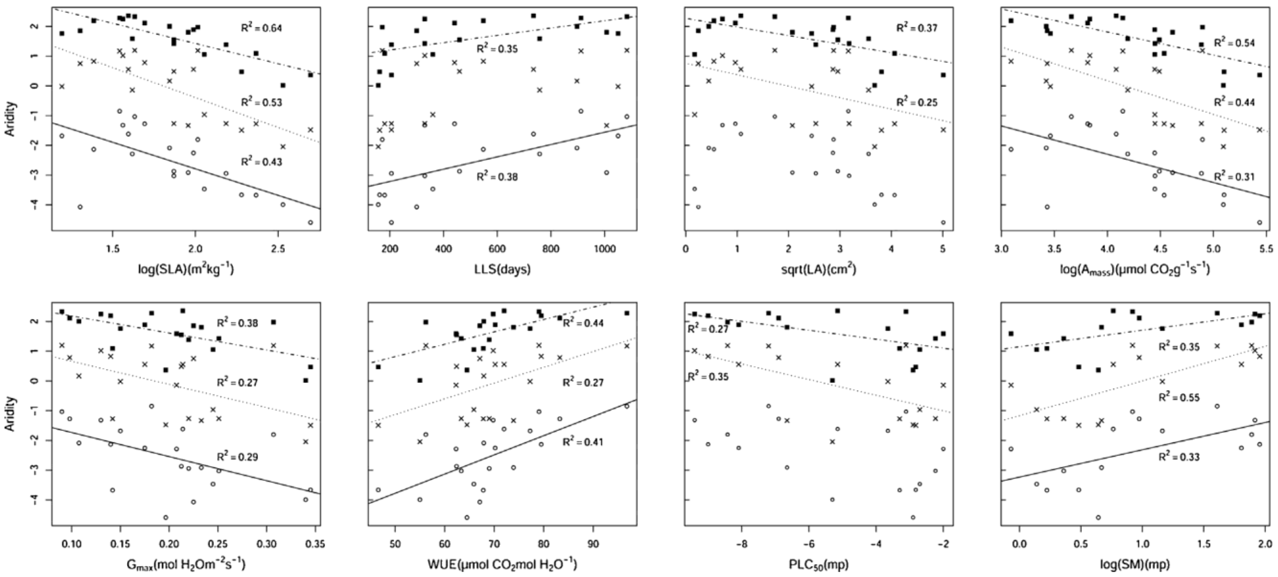

Fig. 3. Scatterplot and regression lines of different characteristics of the species' aridity niche as a function of species functional traits. Only the significant regression lines are shown (*P* values < 0.05). Crosses represent species optimum, and filled squares and open circles the species maximum (more arid) and minimum (less arid) limits, respectively. The variance explained is also given for each regression line. Abbreviations as in Fig. 2.

Table 3

ΔAIC for models of niche characteristics as a function of functional traits (ΔAIC > 2 supports differences among models, Burnham and Anderson, 1998). Models including only SLA as the explanatory variable (first column) are compared with models combining SLA with PLC_{50}, WD, SLA SM, and MLWP (columns 2–5, respectively). Traits are standardized. D^2 is the deviance explained. Abbreviations as in Fig. 2.

Aridity niche		Traits combined with SLA			
	SLA	+ PLC_{50}	+ WD	+ SM	+ MLWP
Optimum	7.4	2.7	9.4	0	9.3
Minimum	1.5	0.2	2.1	0	2.3
Maximum	6.1	0	7.2	4	3.2

Note: equations of the best models. Optimum = $-0.44 \times$ SLA + $0.55 \times$ SM; $D^2 = 69\%$. Minimum = $-0.71 \times$ SLA $+0.28 \times$ SM; $D^2 = 74\%$. Maximum = $-0.67 \times$ SLA $-0.41 \times PLC_{50}$; $D^2 = 78\%$.