This is the accepted version of the article:

Pérez Navarro, María Ángeles; Sapes, Gerard; Batllori, Enric; [et al.]. Climatic suitability derived from species distribution models captures community responses to an extreme drought episode. DOI 10.1007/s10021-018-0254-0

This version is available at https://ddd.uab.cat/record/203570

under the terms of the © copyright license
Climatic suitability derived from species distribution models captures community responses to an extreme drought episode

Pérez-Navarro M.A.¹, Sapes G.², Batllori E.¹, Serra-Diaz J.M.³,⁴, Esteve M.A.⁵, Lloret F.¹

¹CREAF, Universitat Autònoma Barcelona, Cerdanyola del Vallès, 08193 Barcelona, Spain, 0034 935868087, e-mail: m.angeles582@gmail.com, Orcid id: 0000-0001-5553-995X

²Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA

³Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, 8000, Aarhus C, Denmark

⁴UMR Silva, AgroParisTech, Université de Lorraine, INRA, 54000 Nancy, France.

⁵Department of Ecology and Hydrology, University of Murcia, Campus de Espinardo, 30100, Murcia, Spain

*Corresponding author

Pérez-Navarro M.A. e-mail: m.angeles582@gmail.com, Orcid id: 0000-0001-5553-995X
**Abstract**

The differential responses of co-occurring species in rich communities to climate change - particularly to drought episodes - have fairly been unexplored. Species Distribution Models (SDMs) are used to assess changes in species suitability under environmental shifts, but whether they can portray population and community responses is largely undetermined, especially in relation to extreme events. Here we studied a shrubland community in SE Spain since this region constitute an ecotone between the Mediterranean biome and subtropical arid areas, and it has recently suffered its driest hydrological year on record. We used four different modelling algorithms (Mahalanobis distance, GAM, BRT and MAXENT) to estimate species’ climatic suitability before (1950-2000) and during the extreme drought. For each SDM, we correlated species’ climatic suitability with their remaining green canopy as a proxy for species resistance to drought. We consistently found a positive correlation between remaining green canopy and species’ climatic suitability before the event. This relationship supports the hypothesis of a higher vulnerability of populations living closer to their species’ limits of aridity tolerance. Contrastingly, climatic suitability during the drought did not correlate with remaining green canopy, likely because of the exceptional episode led to almost zero suitability values. Overall, our approach highlights climatic niche modelling as a robust approach to standardizing and comparing the behavior of different co-occurring species facing strong climatic fluctuations. Although many processes contribute to resistance to climatic extremes, the results confirm the relevance of populations’ position in the species’ climatic niche for explaining sensitivity to climate change.

**Key words:** climatic suitability, SDMs, extreme climatic events, drought resistance, niche, dieback.
**Introduction**

The climatic trends observed over the last decades are promoting vegetation shifts (Parmesan and Yohe 2003), phenological changes (Zavaleta and others 2003) and modifications to disturbance regimes (Mouillot and others 2002; Allen and others 2015), as well as altering the interactions between these processes (Franklin and others 2016). However, the adjustment of populations to changing climatic conditions may be more influenced by the extremes of climatic variability than by average climate trends. For instance, mortality and recruitment processes – which shape species’ distributions and ranges – may be largely conditioned by pulses of extreme climatic conditions such as extreme drought events (del Cacho and Lloret 2012; Greenwood and others 2017).

Vegetation mortality and die-off processes associated with climatic warming have often been observed at ecotones corresponding to the rear edge of species’ distributions (Allen and Breshears 1998; Bigler and others 2006; Jump and others 2006; Lesica and Crone 2016), supporting the assumption that a decline in plant populations may be more significant at their equatorial latitudinal or lowland altitudinal margins (Thomas and others 2004). Translated into the perspective of a plant community, marked by the coexistence of species that have adapted differently to environmental conditions, mortality processes would have a greater influence on the populations of species located close to their tolerance limits, to the benefit of other species that find the new environment more suitable (Martínez-Vilalta and Lloret 2016). This hypothesis implicitly correspond to the biogeographic paradigm that species perform better in their geographical center of distribution than they do in the margins (Centre-Periphery hypothesis, see Sexton and others 2009; but see Dallas and others 2017), with the further assumption that geographical and environmental spaces are mostly concordant (Pironon and others 2015).

Species Distribution Models (SDMs) have been used to test the relationship between species’ climatic niche and their physiological or demographic performance (Serra-Diaz and others 2013; Pironon and others 2015; van der Maaten and others 2017). These are statistical models that
relate the location of species occurrences to the environmental data on these sites (Franklin 2010). The SDM approach is based on the assumption that species occurrence portrays the environmental and biotic conditions that are suitable for species to survive and reproduce (i.e. the realized niche; Pulliam 2000; Soberón 2007; Peterson and others 2011), and so model outputs are interpreted as a species-specific index of relative suitability or habitat suitability. Accordingly, SDMs have been widely used under average climatic conditions (climatic norms) to predict past or future distributional changes of species (Elith and Leathwick 2009). However, it is not yet known whether these models are able to capture the impact of extreme climatic events (e.g. droughts), especially in relation to community dynamics.

In the Mediterranean basin, vegetation has developed different strategies for dealing with variable rainfall, such as shallow roots and deciduous summer leaves (Valladares and others 2004; Zunzunegui and others 2005). Nevertheless, these adaptive syndromes may not be enough under the predicted scenarios of increased climatic extremes (IPCC 2013). In this context, the southeast of the Iberian Peninsula has recently experienced the driest year on record (AEMET 2014), causing an extensive vegetation die-off event in areas dominated by shrubland (Esteve-Selma and others 2015). This Iberian region represents the ecotone between the Mediterranean biome and subtropical shrublands of arid lands (Esteve-Selma and others 2010). This recent drought-induced mortality event therefore offers the possibility to assess community dynamics in relation to biogeographical paradigms at the limits – in this case, the aridity margin - of the biome’s distribution, which are areas considered to be very sensitive to climate change (Guiot and Cramer 2016).

In this study, we use a shrubland community at the arid southern limit of the Mediterranean biome to assess the differential response of coexisting species to an extreme drought event according to species’ climatic suitability, as determined from SDMs. Specifically, we test whether populations living close to the edge of their species’ climatic niche (i.e. lower suitability values compared to the niche's optimal value) are more vulnerable to such extreme events than
populations living closer to their niche center. We use the remaining green canopy of species after the drought event to examine the correlation between drought-induced die-off and species’ climatic suitability, considering both the historical suitability, as inferred from historical climatic series, and the drought episode suitability, as reflected by the conditions during the drought event. Given the considerable amount of uncertainty existing with respect to the various SDM techniques, which use model-specific algorithms (Araújo and New 2007), we also test whether the relationship between species' die-off and their climatic suitability depends on the SDM algorithm applied. For this purpose, we applied four SDMs with highly contrasting approaches (Mahalanobis distance, Generalized Additive Models –GAM–, Boosted Regression Trees –BRT–, and Maximum Entropy approaches –MaxEnt–) to determine species suitability, that was later correlated to species' die-off.

Material and methods

Study area

The study was carried out in two semi-arid shrubland areas in the province of Murcia (southeast of the Iberian Peninsula) (Figure 1), Campo de Cagitán (38° 06’ N, 1° 32’ W) and Oro Mountain (38° 11’ N, 01° 30’W), 10 km apart but with similar soil characteristics and climatic conditions. The Campo de Cagitán site was covered by a small expanse of scrubland embedded in an agricultural matrix, and the Oro Mountain site was occupied by shrubland close to an open pine forest on a hill slope. The overall sampled area amounted to 19 hm².

The potential vegetation comprises an open forest of Pinus halepensis L. and a sclerophyllous shrubland (garrigue) dominated by Quercus coccifera L., Pistacia lentiscus L., Olea europea L., Rhamnus lycioides L. and Juniperus oxycedrus L., along with a highly diverse range of small shrubs, such as Thymus hyemalis Lange and Helianthemum spp. (Braun-Blanquet and Bolòs 1957). The current landscape in these regions is a highly fragmented cropland that is either in use or recently abandoned, with small patches of forest or shrubland interspersed between the crops. The steep slopes in some areas preclude the presence of agricultural crops but they are
instead covered by scrublands, often containing the tussock grass *Stipa tenacissima* L. (which was cultivated for fibers until the 1960s) and occasional open pine forests.

The region is included within the Mesomediterranean thermoclimatic belt and the Mediterranean xeric bioclimatic region (Rivas-Martínez and others 2011), characterized by annual mean temperatures of 18.5 °C and an annual rainfall of 200-350 mm. Precipitation in the area is low and mainly concentrated in the fall, with great variability between years. During the hydrological year 2013-2014 the Region of Murcia suffered the worst drought on record since 1941, demonstrating the extreme conditions of the event. During the drought event a mean regional rainfall of 146.5 mm was recorded; this corresponds to just 46% of the average value for the period 1971-2000 (Figure 1, AEMET 2014). This episode led to high mortality and defoliation in different forests and shrublands (Esteve-Selma and others 2015).

**Field sampling**

In March 2015, a set of ten 50m² replicate plots were established in the study region, three in the Campo de Cagitán and seven in the Oro Mountain, according to the shrubland surface area available on each site. This sampling design reflects the region’s highly fragmented habitat, which prevented us from establishing ten replicates in a single location.

Sampling plots were established with the following criteria: 1) shrubland with no signs of recent disturbance, with high species richness, different life forms, and low *S. tenacissima* density; and 2) low pine presence, in order to avoid wetter microenvironments caused by the shade of tree canopies, which could affect the moisture in the air and soil. Each plot consisted of two linear transects of 25 meters long by 1 wide. On each plot, we recorded the total number of individuals per woody species, estimated their size by measuring two perpendicular diameters crossing at the center of each individual and visually estimated the proportion of remaining green canopy (RGC) per individual. A total of 22 species were sampled (Table 2). RGC levels were visually estimated as a proxy for the species response to drought(die-off) as the percentage of green leaves present relative to the amount in healthy individuals found in the study area (Sapes and
others 2017). To ensure that the green cover loss resulted from the drought of the previous year, we avoided individuals with signs of older decay (e.g., stumps, decomposed stems, branches with no thin tips). To determine the reliability of the visual RGC estimate, we also measured the length (cm) of the segments occupied by green leaves and dry leaves (including segments with no leaves) along a linear path from the tip to the base of two representative branches of ten individuals per species, on every plot where a species was present. Then, a directly measured RGC value was calculated per individual as \([\text{branch length with green leaves (cm)} / \text{total branch length (cm)}] \times 100\). When ten individuals per species were not found within a given plot, we measured the closest individuals to the sampled transects until ten replicates were attained. Pearson’s correlation between direct and visually estimated values of RGC was calculated for plants from each species, always resulting in values higher than 0.7 (Supplementary material Appendix 1 Table 1). These analyses support the use of visual estimate of RGC as a proxy for die-off (Sapes and others 2017, see Supplementary material Appendix 3).

Considering this high correlation and the limited number of individuals with real measures of defoliation (10 per species and plot), we used the visually estimated RGC (made for every individual) for the statistical analyses.

The variables described above were then scaled to the landscape level. First, we calculated the following information for each plot: average percentage of visually estimated RGC for each species; species frequency (the number of plots where each species was found over the total number of plots) and the average size of each species (as the product of the two diameters measured in the plants), since RGC could be affected by species size or relative abundance (Lloret and others 2016; Sapes and others 2017). The values of species’ RGC and size were then averaged across plots. Finally, to account for the different species’ strategies in relation to leaf longevity and annual seasonality (Valladares and others 2004), all the species were classified into one of the following foliar strategies: 1-evergreen, 2-semi-deciduous, 3-summer deciduous, and 4-retamoid or leafless species.
For the 22 sampled species, we built SDMs using four different algorithms - Mahalanobis distance, GAM, BRT, and MaxEnt - to assess the robustness of the potential relationships between visual estimates of RGC and the climatic suitability output of these models. These models represent four highly differentiated modelling methods: distance-based models (Mahalanobis distance), regression-based models (GAM), decision tree-based methods (BRT) and a machine-learning technique based on the principle of maximum entropy (MaxEnt). Therefore, they represent a gradient of complexity, where some models such as Mahalanobis distance only consider linear relationships between predictors (Franklin 2010) whereas others such as MaxEnt and BRT can include high-order interaction terms (Elith and others 2008; Phillips and Dudík 2008).

The geographical occurrence data for each species were obtained from GBIF (Global Biodiversity Information Facility: <www.gbif.org>). Occurrence data were filtered in order to remove taxonomic and geographic inconsistencies and reduce dense local sampling by randomly thinning species' records to one observation per 1x1 km grid cell. We considered the whole distributional range of species; thus, the available number of occurrences was considerably different from one species to the next, ranging from 200 to 6,000 after filtering. For each set of filtered occurrences, 70% of presences were reserved for fitting the model (training data) and the other 30% for the validation set (testing data), according to the number of environmental predictors selected in our models and following the rule described by Huberty 1994 for determining the optimum partitioning of training and test data. To improve the models' performance accuracy (Barbet-Massin and others 2012), 100,000 random background points were simulated for each species to fit both GAM and MaxEnt algorithms, and a random set of pseudo-absences equivalent to the number of each species occurrences was simulated for BRT. Since Mahalanobis distance works without simulated absences, no background points were used in this case. The background extension was delineated in order to represent the current or
past available geographical space for the selected species (M dimension sensu Soberón 2007).

In our case, the geographical region used to establish species background was the Mediterranean basin.

Six climatic variables representative of Mediterranean climate were used as predictors to calibrate the suitability models: isothermality (mean diurnal temperature range/temperature annual range), temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, annual precipitation and precipitation seasonality, all of them with 1 by 1 Km resolution. These variables were selected from the 19 bioclimatic variables available in Worldclim.org (version 1.4) for the period 1950-2000 (Hijmans and others 2005), according to the knowledge of the species’ ecological requirements and in order to reduce variables’ collinearity. Pearson correlation and variation inflation factor (VIF) among variables were always less than 0.75 and 5, respectively. Additionally, we used monthly precipitation and maximum, minimum and mean temperature records over the 2013-2014 period from between 68 and 114 weather stations of the Spanish Meteorological Agency (AEMET) to elaborate the climatic layers during the drought event (also in 1 by 1 km resolution), following Ninyerola and others (2000), and using the ‘biovars’ function (dismo package; Hijmans and others 2016). To minimize differences in the climatic interpolation methods between Worldclim and Ninyerola and others (2000), only latitude, longitude and elevation were used as explanatory variables for climatic data. In addition, we applied MESS analysis between these two data set over the Spanish territory (where AEMET data are available) during the 1950-2000 period to assess dataset dissimilarities, showing the high concordance and comparability of both climatic interpolation methods over the entire extension and particularly over the study region (Supplementary material Appendix 1 Figure A1). Finally, species’ historic climatic suitability (HCS) was estimated projecting the models over the climatic layers for the period 1950-2000, whereas species’ climatic suitability during the drought event (episode climatic suitability, ECS) was estimated by projecting the calibrated models over the climate layers of the anomaly period 2013-2014.
For the four implemented SDM algorithms, model settings were selected following recommendations from the literature, and partial dependence plots and predictive maps were assessed to exclude those settings that produced unreliable response curves or distribution maps. The final selected settings and main literature are showed in Table 1. To make all the model outputs comparable (between 0 and 1 probability values), log raw output transformation was applied for MaxEnt models (Phillips and Dudík 2008) and distance transformation into p-values was applied for Mahalanobis distances (Clark and others 1993). Each model’s predictive performance was assessed by comparing model predictions with testing data, using the Area Under Receiver Operating-characteristic Curve (AUC, Fielding and Bell 1997) and the Boyce index (Boyce and others 2002; Hirzel and others 2006). These evaluation methods are considered a reliable approach for our models and allowing comparison among them, since all the models were fitted with the same species data set and environmental extension of layers (Hirzel and others 2006; Franklin 2010). Finally, multivariate environmental similarity surface (MESS, Elith and others 2010) analyses were carried out to measure the similarity between historical climate and the extreme drought period in the occurrence locations; these analyses allowed to identify extrapolation for predictions during the anomalous period as areas with high climatic dissimilarities.

**Statistical analyses**

Generalized Linear Models (GLM) with normal distributions were performed to assess the relationship between SDM-inferred HCS and ECS for each species and their die-off recorded in the field. The visually estimated species RGC was used as a response variable whereas HCS, ECS, the interaction between HCS and ECS, species size (logarithmically transformed), species frequency, and species foliar category were introduced as explanatory variables. Difference between HCS and ECS was discarded as an explanatory variable in the models, due to the high correlation with ECS which produced same models results.
The final models were selected according to stepwise selection based on AIC (Akaike Information Criterion). In addition, Phylogenetic Generalized Linear Models (PGLS) using Phylomatic distances (Webb and Donoghue 2005) were performed in order to assess the potential effect of phylogenetic species relationships in the selected model (Freckleton and others 2002). This PGLS was finally discarded from the final analyses since phylogeny was not significant in any case (lambda =0). Finally, consistency in the climatic suitability estimates (HCS, ECS) obtained from each of the four implemented SDMs was tested by pairwise comparisons, using Pearson correlation tests. All statistical analyses were carried out with R version 3.3.2 (R Core Team 2016).

Results

All the four SDMs algorithms developed showed high performance accuracy values with AUC values higher than 0.75 and Boyce index’ values being always positive and higher than 0.5 (Elith and others 2002; Hirzel and others 2006; Supplementary material Appendix 1 Figure A2). Particularly AUC mean values were 0.96±0.02 and Boyce index mean values were 0.93±0.07 MESS analyses showed that precipitation seasonality exhibited high dissimilarity between extreme event climatic data and training predictor data near the coastal region. However, the values corresponding to the drought episode were never outside training boundary values for the study locations (Supplementary material Appendix 1 Figure A3). Climatic suitability dropped dramatically during the drought episode for all species, irrespective of the SDM method, as shown by the comparison between the respective HCS and ECS values (Figure 2, Supplementary material Appendix 1 Table A2). For the majority of SDM algorithms the stepwise GLM model selection determined that the most parsimonious models explaining species’ RGC were those including HCS, foliar category and species size as explanatory variables. Only in the case of Mahalanobis distance did the stepwise GLM model selection fail to remove any explanatory variables from the saturated model. There was some variation in the significant variables associated with RGC in the different SDM
algorithms. All the selected variables were significant in BRT, while in MaxEnt HCS and foliar category were significant, in GAM foliar category was significant and HCS was only marginally significant, and in Mahalanobis only HCS and foliar category were marginally significant (Table 3).

In all cases RGC was positively related to HCS (Figure 2 and 3). Foliar categories 3 (summer deciduous species) and 4 (leafless species) presented a significant, negative correlation with RGC in BRT, GAM and MaxEnt models, while in the Mahalanobis distance model, foliar category 3 was only marginally significant. Finally, species size was only significantly negatively related with RGC in BRT models (Table 3). Species frequency, ECS or the interaction between HCS and ECS were not significant in any model (Table 3).

The values of species’ HCS varied from model to model. BRT predicted the highest suitability values for a given species and MaxEnt the lowest ones. This pattern was consistent for almost all species (Supplementary material Appendix 1 Figure A4). For all species, the majority of pairwise Pearson correlations between the HCS values inferred from the different SDM algorithms were significant, with correlation values ranging between 0.45 and 0.78 (Supplementary material Appendix 1 Figure A5). However, the correlation between Mahalanobis distance and BRT was not significant (Supplementary material Appendix 1 Figure A5). In contrast, most pairwise correlations between models were not significant for ECS, likely due to the extremely low ECS values exhibited by most species; in this case, when a significant correlation was found, the relationship was driven by a single outlier value (Supplementary material Appendix 1 Figure A6).

**Discussion**

We found a clear relationship between field measurements of species performance under an extreme drought episode and the historical climatic suitability (HCS) of species derived from SDMs. Within the studied community, co-occurring species living closer to their climatic tolerance limit -identified by low HCS values compared to the optimal value of the distribution
range-proved more vulnerable to the extreme drought episode. This climatic limit corresponds to the aridity margin of species' climatic niche (Supplementary material Appendix 2). These results are consistent with the relationship observed between the decay of shrubland and woodland species and the decrease in climatic suitability in other semi-arid areas in Spain (Sapes and others 2017) and Southwestern North America (Lloret and Kitzberger 2018). This relationship is also consistent with other studies which suggest that species' sensitivity to climate change is related to niche characteristics such as mean niche position and niche breadth (Thuiller and others 2005; Broennimann and others 2006). Species in the climatic niche margins are generally assumed to exhibit lower survivorship and recruitment and higher extinction risk because of the less favorable environmental conditions (Weber and others 2016). Precisely in these situations of the environmental space closest to the physiological tolerance limits of the species, the effect of climate variability is probably more severe (Zimmermann and others 2009), promoting species' decline or range shifts at the trailing edge of species distribution (Bigler and others 2006; Walther and others 2009).

Species' drought responses and climatic suitability

Studies that compare habitat suitability with different species' performances (population density, growth, recruitment, fecundity, etc.) along the species distribution gradient are scarce and still not fully conclusive with respect to general biogeographic paradigms (Centre-Periphery hypothesis, Wright and others 2006; Sexton and others 2009; Thuiller and others 2010; Abeli and others 2014; Csergő and others 2017). Likely species interaction, local variables or adaptation mechanisms underlie the limited evidence of the relationship between species' performance and climate suitability (Sexton and others 2009, 2014; Dallas and others 2017; Lloret and Kitzberger 2018). Our results throw some light in this sense as they support the relationship between species’ performance when climatic conditions are extreme and climatically-based descriptions of their suitability (i.e. HCS).
We also expected that populations experiencing higher displacement of climatic suitability during the extreme event (low ECS) would experience greater leaf loses and higher mortality rates. However, contrary to our expectations, we found that species' suitability during the extreme episode (ECS) did not significantly explain species' leaf loses in the studied community. Our extremely low ECS levels observed for all species probably made it impossible to obtain contrasted values of ECS among them. These low values indicate that the climatic episode was extreme enough to displace all the studied populations far from their climatic optimum, even for those species that were closer to this optimum during the historical period (Figure 2). In addition to the exceptionality of the extreme event, the extremely low ECS values may derive from 1) the averaged climatic data used for calibrating the models, which does not reflect the variability or annual extremes during the considered 50-year period and 2) the limited ability of models to predict suitability under climatic scenarios that are highly different from the period used to fit the models (Elith and others 2010), as shown by the low MESS values, particularly for precipitation seasonality –bio15– (although these were not negative in the study site) (Supplementary material Appendix 1 Figure A3). This situation may also amplify the differences between different algorithms and species' prevalence data in the predictions (Thuiller 2004; Pearson and others 2006), as supported by the low correlations between the ECS predicted by the different models (Supplementary material Appendix 1 Figure A6).

In addition to HCS, foliar categories were also significant in explaining the observed species' RGC, suggesting that leaf strategy and seasonal senescence play a major role in understanding species performance under strong drought conditions, at least in Mediterranean type ecosystems. Our results show that summer-deciduous and leafless species always present significantly lower values of RGC. This result is in part expected due to the general strategy in Mediterranean species of dropping leaves during the dry, hot season to limit evapotranspiration and water loss (de la Riva and others 2016a). In the Mediterranean basin this semideciduous mechanism typically appears in combination with shallow roots and low water potentials as an anisohydric
syndrome, in contrast to species with hydrostable syndromes, which present sclerophyllous leaves, more sensitive stomatal control and deeper roots (Zunzunegui and others 2005; de la Riva and others 2016b). Thus, estimates of RGC as a proxy of drought resistance can be misleading if these foliar strategies are not considered (Lloret and others 2016). In addition to foliar strategies, other physiological features and local factors may modulate the interspecific variability of responses to a given drought episode. For instance, species-specific resistance to hydraulic failure and carbon economy (Mcdowell and others 2008; Anderegg and others 2012; Adams and others 2017) and mutualistic and antagonistic biotic interactions (Lloret and others 2012; Valladares and others 2014).

**SDM algorithms and demographic performance**

Despite all these potential sources of variability, the four different SDM algorithms used in our approach highlighted the positive relationship between climatic suitability (HCS) and resistance to drought (RGC). These results were consistent across species, as shown by the high correlation between the different models' HCS values (Supplementary material Appendix 1 Figure A5). The agreement holds despite the wide variety of the modeling approaches. However, the ‘simplest’ models (Mahalanobis distance and GAM) showed the lowest performance explaining species’ RGC compared to ‘complex’ ones (BRT and MaxEnt). This difference in algorithm performance highlight the importance of the interactions between climatic variables and non-linear relationships when assessing species’ responses to climate, and thus, supporting the use of SDMs versus simpler approaches based on univariate or multivariate correlations of demographic performance with climatic variables. Moreover, algorithms that are generally calibrated to produce smoother response curves, such as GLMs and GAMs, would be more accurate to predict habitat suitability under new conditions (Elith and others 2010; Merow and others 2014), while models based on presence-only data are more appropriate for predicting the lowest suitability values in these scenarios (Pearson and others 2006). There is no general agreement, however, about the most accurate algorithm in relation to situations of range shift...
because even simpler models can lead to erroneous outputs (Elith and others 2010; Merow and others 2014). We therefore urge ecologists to assess the degree of model complexity needed to use SDMs as a proxy of ecological mechanisms, such as defoliation in this case. Caution should also be taken when interpreting SDM predictions, given the assumptions that these kind of models implicitly include (Pearson and Dawson 2003). Among other limitations, these models commonly use only climatic predictors with a broad resolution (~1 km²), disregarding other meaningful abiotic factors, and they are also unable to capture microclimatic effects at small spatial scales (Franklin and others 2013; Lenoir and others 2013; D’Amen and others 2017). Microsite factors could be particularly important for our study, given that soil features and depth, slope and orientation are especially relevant to species survival under extreme drought (Colwell and others 2008; Hamerlynck and McAuliffe 2008). Furthermore, SDMs assume that species respond homogeneously to climate change across their range, not including intra-specific genetic variability and phenotypic plasticity, which may also favor species' local adaptation under unfavorable conditions (Benito Garzón and others 2011; Lloret and García 2016).

The drought episode experienced in the Region of Murcia in 2013-2014 was extraordinary in historical terms, but these climatic situations are expected to become more frequent in the future (Sheffield and Wood 2008). The ability of plant communities to withstand these events and subsequently recover their green canopy will depend on both physiological traits related to the adaptive syndromes of Mediterranean species (Peñuelas and others 2001) and the balance between demographic processes such as mortality, growth, and recruitment (Lloret and others 2012). Under drier climatic scenarios, leafless and semi-deciduous species with shallow roots (xerophytic malacophyllous) would be expected to be to take more advantage of scarce and irregular rainfalls than sclerophyllous species with deeper roots. This is consistent with the particularly high HCS values obtained for malacophyllous species (Figure 2 and 3). These potential changes in species dominance within the community will likely lead to less productive
shrublands dominated by smaller species (Valladares and others 2004). Since species' climatic
suitability is broadly related to both physiological and demographic species performance
(Martinez-Meyer and others 2013), indexes describing climatic suitability can provide rough
estimates of species' vulnerability to extreme climatic episodes. While community resistance
and resilience could minimize ecological changes, the recurrence of these extreme drought
events could lead these Mediterranean communities to cross thresholds beyond which they
could collapse (Vicente-Serrano and others 2013; Valladares and others 2014). This depletion of
resilience in semi-arid shrubland communities could promote transitions to desert-like
ecosystems, as has been predicted by some climate change scenarios for southern areas of
Europe (Guiot and Cramer 2016). Accordingly, this study shows the impact of extreme drought
events even on communities supposedly well adapted to drought conditions (Lázaro and others
2001; Sapes and others 2017).

Conclusion
This study confirms the role of population position within its species climatic niche in explaining
populations' vulnerability to extreme climatic events. In the studied semi-arid shrubland, species
closer to their climatic tolerance limit were more vulnerable to extreme drought. Thus, the
predicted recurrence of severe drought events could reduce the community resilience,
increasing the risk of desertification in these arid lands. Our study empirically concurs with the
trends foreseen by theoretical models, based on predicted suitability and correlations with
drought response. This concurrence supports the use of SDMs to assess the impact of climate
change on plant communities, particularly in extreme climatic conditions. This approach, which
links species performance with regional biogeographic patterns, can probably be applied to
other processes heavily determined by strong climatic fluctuations.

Acknowledgements
The research underlying this work has been supported by the Spanish Ministry of Education
through a doctoral grant (FPU14/03519) and by the Spanish Ministry of Economy and
Competitiveness through the BIOCLIM project (CGL2015-67419-R). We thank GBIF and WorldClim for making their data freely available online. We are also grateful to our colleagues at the University of Murcia and several friends who helped during field sampling. Finally, we want to thank the two anonymous reviewers for their helpful comments.
References


Braun-Blanquet J, Bolòs O. 1957. The plant communities of the Central Ebro Basin and their
dynamics. An la Estac Exp Aula Dei 5:1–266.

geographic distribution, niche property and life form explain plants’ vulnerability to

del Cacho M, Lloret F. 2012. Resilience of Mediterranean shrubland to a severe drought


Clark JD, Dunn JE, Smith KG. 1993. A Multivariate Model of Female Black Bear Habitat Use for a


Csergő AM, Salguero-Gómez R, Broennimann O, Coutts SR, Guisan A, Angert AL, Welk E, Stott I,

D’Amen M, Rahbek C, Zimmermann NE, Guisan A. 2017. Spatial predictions at the community

Dallas T, Decker RR, Hastings A. 2017. Species are not most abundant in the centre of their


Evol 1:330–42.


Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic Analysis and Comparative Data:


Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation

Wright JW, Davies KF, Lau JA, Mccall A, Mckay JK. 2006. Experimental verification of ecological

Grassland Responses To Three Years of Elevated Temperature, Co 2 , Precipitation, and N

Zimmermann NE, Yoccoz NG, Edwards TC, Meier ES, Thuiller W, Guisan A, Schmatz DR,
Pearman PB. 2009. Climatic extremes improve predictions of spatial patterns of tree

Zunzunegui M, Díaz Barradas MC, Ain-Lhout F, Clavijo A, García Novo F. 2005. To live or to
survive in Doñana dunes: Adaptive responses of woody species under a Mediterranean
Table captions

Table 1 Main settings used in the different SDM modeling approaches.

Table 2 Main species information and attributes used in statistical analyses. See methods for details about foliar strategy, RGC (Remaining Green Canopy), Size and Frequency.

Table 3 Results of GLMs explaining remaining green canopy as a function of foliar strategy, size, frequency, HCS (Historical Climatic Suitability), ECS (Episode Climatic Suitability) and the interaction between the latter two (HCS:ECS) calculated from four different SDMs (Mahalanobis distance, GAM, BRT, MaxEnt). AIC stepwise selection was applied to obtain the final models. Significant or marginally significant P values are highlighted in bold.
<table>
<thead>
<tr>
<th>Method</th>
<th>Key reference and main settings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mahal</td>
<td>adehabitatHS package (Calenge 2015). Modification of the original function mahasuhab in order to obtain distance and probability values from other layers not used to calculate variables’ mean vector. This function makes it possible to determine probability values, assuming that under multivariate normality, squared Mahalanobis distance is approximately distributed as Chi-square with n-1 degrees of freedom, which makes it possible to calculate p-value maps (Clark and others 1993).</td>
</tr>
<tr>
<td>Mahalanobis distance</td>
<td></td>
</tr>
<tr>
<td>GAM</td>
<td>mgcv package v.1.8-16 (Wood 2011). Weighted background number: 100,000 points. The optimal number of edf for each variable was selected between 1 and 4 by cross-validation, using gam function. The number of knots for those species where response curves being biologically counterintuitive was also reduced.</td>
</tr>
<tr>
<td>Generalized Additive Models</td>
<td></td>
</tr>
<tr>
<td>BRT</td>
<td>gbm package v. 2.1.1 (Ridgeway 2007). Pseudoabsence number equivalent to presence species data. Tree complexity of 5 for those species with more than 250 occurrences and 3 for those species with less than 250. The learning rate of 0.005 was chosen because it made it possible to achieve at least 1,000 trees in every case, following Elith and others (2008).</td>
</tr>
<tr>
<td>MaxEnt</td>
<td>MaxEnt v. 3.3.1 (Phillips and Dudík 2008) used with default setting with the exception of: 100,000 background points, 10-fold cross-validation, regularization multiplier of 3, and threshold feature unselect in order to produce smoother response curves.</td>
</tr>
<tr>
<td>Family</td>
<td>Species</td>
</tr>
<tr>
<td>-------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td>Pistacia lentiscus</td>
</tr>
<tr>
<td>Asparagaceae</td>
<td>Asparagus horridus</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>Artemisia barrelieri</td>
</tr>
<tr>
<td></td>
<td>Artemisia campestris</td>
</tr>
<tr>
<td>Boraginaceae</td>
<td>Lithodora fruticosa</td>
</tr>
<tr>
<td>Chenopodiaceae</td>
<td>Salsola genistoides</td>
</tr>
<tr>
<td>Cistaceae</td>
<td>Cistus albidus</td>
</tr>
<tr>
<td></td>
<td>Cistus clusii</td>
</tr>
<tr>
<td></td>
<td>Helianthemum syriacum</td>
</tr>
<tr>
<td>Cupressaceae</td>
<td>Juniperus oxycedrus</td>
</tr>
<tr>
<td></td>
<td>Juniperus phoenicea</td>
</tr>
<tr>
<td>Fagaceae</td>
<td>Quercus coccifera</td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>Rosmarinus officinalis</td>
</tr>
<tr>
<td></td>
<td>Sideritis leucantha</td>
</tr>
<tr>
<td></td>
<td>Teucrium capitatum</td>
</tr>
<tr>
<td></td>
<td>Thymus hyemalis</td>
</tr>
<tr>
<td>Leguminosae</td>
<td>Anthyllis cytisoides</td>
</tr>
<tr>
<td></td>
<td>Dorycnium pentaphyllum</td>
</tr>
<tr>
<td></td>
<td>Ononis fruticosa</td>
</tr>
<tr>
<td>Poaceae</td>
<td>Stipa tenacissima</td>
</tr>
<tr>
<td>Rhamnaceae</td>
<td>Rhamnus lycioides</td>
</tr>
<tr>
<td>Timeleeaceae</td>
<td>Daphne gnidiwm</td>
</tr>
<tr>
<td>MAHALANOBIS DISTANCE</td>
<td>GAM</td>
</tr>
<tr>
<td>-----------------------</td>
<td>-----</td>
</tr>
<tr>
<td>AIC 197.97</td>
<td>AIC 196.10</td>
</tr>
<tr>
<td>R2 adj 0.22</td>
<td>R2 adj 0.33</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>INTERCEPT (FOLIAR.STR 1)</th>
<th>β</th>
<th>Std.Error</th>
<th>P.value</th>
<th>β</th>
<th>Std.Error</th>
<th>P.value</th>
<th>β</th>
<th>Std.Error</th>
<th>P.value</th>
<th>β</th>
<th>Std.Error</th>
<th>P.value</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTERCEPT (FOLIAR.STR 1)</td>
<td>0.000</td>
<td>0.000</td>
<td>0.939</td>
<td>0.000</td>
<td>0.000</td>
<td>0.610</td>
<td>0.000</td>
<td>0.000</td>
<td>0.324</td>
<td>0.000</td>
<td>0.000</td>
<td>0.051</td>
</tr>
<tr>
<td>HCS</td>
<td>0.382</td>
<td>0.213</td>
<td><strong>0.096</strong></td>
<td>0.362</td>
<td>0.196</td>
<td><strong>0.083</strong></td>
<td>0.561</td>
<td>0.157</td>
<td><strong>0.003</strong></td>
<td>0.446</td>
<td>0.199</td>
<td><strong>0.039</strong></td>
</tr>
<tr>
<td>FOLIAR.STR 2</td>
<td>0.062</td>
<td>0.299</td>
<td>0.838</td>
<td>-0.317</td>
<td>0.241</td>
<td>0.207</td>
<td>-0.317</td>
<td>0.198</td>
<td>0.130</td>
<td>-0.364</td>
<td>0.234</td>
<td>0.139</td>
</tr>
<tr>
<td>FOLIAR.STR 3</td>
<td>-0.435</td>
<td>0.230</td>
<td><strong>0.081</strong></td>
<td>-0.563</td>
<td>0.210</td>
<td><strong>0.016</strong></td>
<td>-0.618</td>
<td>0.172</td>
<td><strong>0.002</strong></td>
<td>-0.706</td>
<td>0.223</td>
<td><strong>0.006</strong></td>
</tr>
<tr>
<td>FOLIAR.STR 4</td>
<td>-0.254</td>
<td>0.254</td>
<td>0.336</td>
<td>-0.688</td>
<td>0.218</td>
<td><strong>0.006</strong></td>
<td>-0.690</td>
<td>0.173</td>
<td><strong>0.001</strong></td>
<td>-0.628</td>
<td>0.199</td>
<td><strong>0.006</strong></td>
</tr>
<tr>
<td>LOG(SIZE)</td>
<td>-0.244</td>
<td>0.212</td>
<td>0.271</td>
<td>-0.318</td>
<td>0.201</td>
<td>0.133</td>
<td>-0.373</td>
<td>0.167</td>
<td><strong>0.039</strong></td>
<td>-0.330</td>
<td>0.193</td>
<td>0.107</td>
</tr>
<tr>
<td>FREQUENCY</td>
<td>0.369</td>
<td>0.225</td>
<td>0.125</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ECS</td>
<td>27.618</td>
<td>18.640</td>
<td>0.162</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HCS:ECS</td>
<td>-27.360</td>
<td>18.590</td>
<td>0.165</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure captions

Figure 1 Study region within the Iberian Peninsula (Murcia region: black shading in the inset, upper left map) and monthly temperature (lines) and precipitation (bars) data during the historical 1950-2000 period (light grey bars and dots) and the 2013-2014 hydrological year (anomaly period; dark grey bars and triangles).

Figure 2 Averaged proportion of Remaining Green Canopy (RGC) in shrub species with foliar strategies 1 and 2 (top graph) for the ten studied plots. Species’ RGC values are sorted in increasing order (x-axis) and error bars are shown. Red and blue dots represent foliar strategies. The lower graph shows the Historical Climatic Suitability (HCS) and the drought Episode Climatic Suitability (ECS) values for each species. Blue and red dots represent median suitability values of HCS and ECS, respectively, and the error bars correspond to the range between maximum and minimum suitability values predicted by the four applied SDM algorithms (see text for details).

Figure 3 Partial residual plot of RGC (Remaining Green Canopy) in relation to HCS (Historical Climatic Suitability) obtained for each SDM model. B (standardized estimate value) and P values for HCS in these models are shown in the left corner of each plot. Species codes are shown in Table 2.