1 **Climatic suitability derived from species distribution models captures**

2 **community responses to an extreme drought episode**

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

4

5 [1] CREAF, Universitat Autònoma Barcelona, Cerdanyola del Vallès, 08193 Barcelona, Spain, 0034

6 935868087, e-mail: m.angeles582@gmail.com, Orcid id: 0000-0001-5553-995X

7 [2] Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA

8 [3] Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University,

9 8000, Aarhus C, Denmark

10 [4] UMR Silva, AgroParisTech, Université de Lorraine, INRA, 54000 Nancy, France.

11 [5] Department of Ecology and Hydrology, University of Murcia, Campus de Espinardo, 30100,

12 Murcia, Spain

13 [*] Corresponding author

14 Pérez-Navarro M.A. e-mail: m.angeles582@gmail.com. Ocid id: 0000-0001-5553-995X

15

16 **Abstract**

17 The differential responses of co-occurring species in rich communities to climate change -

18 particularly to drought episodes - have fairly been unexplored. Species Distribution Models

19 (SDMs) are used to assess changes in species suitability under environmental shifts, but whether

20 they can portray population and community responses is largely undetermined, especially in

21 relation to extreme events. Here we studied a shrubland community in SE Spain since this region

22 constitute an ecotone between the Mediterranean biome and subtropical arid areas, and it has

23 recently suffered its driest hydrological year on record. We used four different modelling

24 algorithms (Mahalanobis distance, GAM, BRT and MAXENT) to estimate species' climatic

25 suitability before (1950-2000) and during the extreme drought. For each SDM, we correlated

26 species' climatic suitability with their remaining green canopy as a proxy for species resistance

27 to drought. We consistently found a positive correlation between remaining green canopy and

28 species' climatic suitability before the event. This relationship supports the hypothesis of a

29 higher vulnerability of populations living closer to their species' limits of aridity tolerance.

30 Contrastingly, climatic suitability during the drought did not correlate with remaining green

31 canopy, likely because of the exceptional episode led to almost zero suitability values. Overall,

32 our approach highlights climatic niche modelling as a robust approach to standardizing and

33 comparing the behavior of different co-occurring species facing strong climatic fluctuations.

34 Although many processes contribute to resistance to climatic extremes, the results confirm the

35 relevance of populations' position in the species' climatic niche for explaining sensitivity to

36 climate change.

37

38 **Key words:** climatic suitability, SDMs, extreme climatic events, drought resistance, niche,

39 dieback.

40

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

3

67 relate the location of species occurrences to the environmental data on these sites (Franklin

68 2010). The SDM approach is based on the assumption that species occurrence portrays the

69 environmental and biotic conditions that are suitable for species to survive and reproduce (i.e.

70 the realized niche; Pulliam 2000; Soberón 2007; Peterson and others 2011), and so model

71 outputs are interpreted as a species-specific index of relative suitability or habitat suitability.

72 Accordingly, SDMs have been widely used under average climatic conditions (climatic norms) to

73 predict past or future distributional changes of species (Elith and Leathwick 2009). However, it

74 is not yet known whether these models are able to capture the impact of extreme climatic

75 events (e.g. droughts), especially in relation to community dynamics.

76 In the Mediterranean basin, vegetation has developed different strategies for dealing with

77 variable rainfall, such as shallow roots and deciduous summer leaves (Valladares and others

78 2004; Zunzunegui and others 2005). Nevertheless, these adaptive syndromes may not be

79 enough under the predicted scenarios of increased climatic extremes (IPCC 2013). In this

80 context, the southeast of the Iberian Peninsula has recently experienced the driest year on

81 record (AEMET 2014), causing an extensive vegetation die-off event in areas dominated by

82 shrubland (Esteve-Selma and others 2015). This Iberian region represents the ecotone between

83 the Mediterranean biome and subtropical shrublands of arid lands (Esteve-Selma and others

84 2010). This recent drought-induced mortality event therefore offers the possiblity to assess

85 community dynamics in relation to biogeographical paradigms at the limits – in this case, the

86 aridity margin - of the biome's distribution, which are areas considered to be very sensitive to

87 climate change (Guiot and Cramer 2016).

88 In this study, we use a shrubland community at the arid southern limit of the Mediterranean

89 biome to assess the differential response of coexisting species to an extreme drought event

90 according to species' climatic suitability, as determined from SDMs. Specifically, we test whether

91 populations living close to the edge of their species' climatic niche (i.e. lower suitability values

92 compared to the niche's optimal value) are more vulnerable to such extreme events than

93   populations living closer to their niche center. We use the remaining green canopy of species

94   after the drought event to examine the correlation between drought-induced die-off and

95   species' climatic suitability, considering both the historical suitability, as inferred from historical

96   climatic series, and the drought episode suitability, as reflected by the conditions during the

97   drought event. Given the considerable amount of uncertainty existing with respect to the

98   various SDM techniques, which use model-specific algorithms (Araújo and New 2007), we also

99   test whether the relationship between species' die-off and their climatic suitability depends on

100   the SDM algorithm applied. For this purpose, we applied four SDMs with highly contrasting

101   approaches (Mahalanobis distance, Generalized Additive Models –GAM–, Boosted Regression

102   Trees –BRT–, and Maximum Entropy approaches –MaxEnt–) to determine species suitability,

103   that was later correlated to species' die-off.

104   **Material and methods**

105   *Study area*

106   The study was carried out in two semi-arid shrubland areas in the province of Murcia (southeast

107   of the Iberian Peninsula) (Figure 1), Campo de Cagitán (38° 06' N, 1° 32' W) and Oro Mountain

108   (38° 11' N, 01° 30'W), 10 km apart but with similar soil characteristics and climatic conditions.

109   The Campo de Cagitán site was covered by a small expanse of scrubland embedded in an

110   agricultural matrix, and the Oro Mountain site was occupied by shrubland close to an open pine

111   forest on a hill slope. The overall sampled area amounted to 19 hm^2.

112   The potential vegetation comprises an open forest of *Pinus halepensis* L. and a sclerophyllous

113   shrubland (garrigue) dominated by *Quercus coccifera* L., *Pistacia lentiscus* L., *Olea europea* L.,

114   *Rhamnus lycioides* L. and *Juniperus oxycedrus* L., along with a highly diverse range of small

115   shrubs, such as *Thymus hyemalis* Lange and *Helianthemum spp.* (Braun-Blanquet and Bolòs

116   1957). The current landscape in these regions is a highly fragmented cropland that is either in

117   use or recently abandoned, with small patches of forest or shrubland interspersed between the

118   crops. The steep slopes in some areas preclude the presence of agricultural crops but they are

119   instead covered by scrublands, often containing the tussock grass *Stipa tenacissima L.* (which

120   was cultivated for fibers until the 1960s) and occasional open pine forests.

121   The region is included within the Mesomediterranean thermoclimatic belt and the

122   Mediterranean xeric bioclimatic region (Rivas-Martínez and others 2011), characterized by

123   annual mean temperatures of 18.5 °C and an annual rainfall of 200-350 mm. Precipitation in the

124   area is low and mainly concentrated in the fall, with great variability between years. During the

125   hydrological year 2013-2014 the Region of Murcia suffered the worst drought on record since

126   1941, demonstrating the extreme conditions of the event. During the drought event a mean

127   regional rainfall of 146.5 mm was recorded; this corresponds to just 46% of the average value

128   for the period 1971-2000 (Figure 1, AEMET 2014). This episode led to high mortality and

129   defoliation in different forests and shrublands (Esteve-Selma and others 2015).

130   *Field sampling*

131   In March 2015, a set of ten 50m^2 replicate plots were established in the study region, three in

132   the Campo de Cagitán and seven in the Oro Mountain, according to the shrubland surface area

133   available on each site. This sampling design reflects the region's highly fragmented habitat,

134   which prevented us from establishing ten replicates in a single location.

135   Sampling plots were established with the following criteria: 1) shrubland with no signs of recent

136   disturbance, with high species richness, different life forms, and low *S. tenacissima* density; and

137   2) low pine presence, in order to avoid wetter microenvironments caused by the shade of tree

138   canopies, which could affect the moisture in the air and soil. Each plot consisted of two linear

139   transects of 25 meters long by 1 wide. On each plot, we recorded the total number of individuals

140   per woody species, estimated their size by measuring two perpendicular diameters crossing at

141   the center of each individual and visually estimated the proportion of remaining green canopy

142   (RGC) per individual. A total of 22 species were sampled (Table 2). RGC levels were visually

143   estimated as a proxy for the species response to drought(die-off) as the percentage of green

144   leaves present relative to the amount in healthy individuals found in the study area (Sapes and

145   others 2017). To ensure that the green cover loss resulted from the drought of the previous

146   year, we avoided individuals with signs of older decay (e.g., stumps, decomposed stems,

147   branches with no thin tips). To determine the reliability of the visual RGC estimate, we also

148   measured the length (cm) of the segments occupied by green leaves and dry leaves (including

149   segments with no leaves) along a linear path from the tip to the base of two representative

150   branches of ten individuals per species, on every plot where a species was present. Then, a

151   directly measured RGC value was calculated per individual as [branch length with green leaves

152   (cm)/total branch length (cm)]*100. When ten individuals per species were not found within a

153   given plot, we measured the closest individuals to the sampled transects until ten replicates

154   were attained. Pearson's correlation between direct and visually estimated values of RGC was

155   calculated for plants from each species, always resulting in values higher than 0.7

156   (Supplementary material Appendix 1 Table 1). These analyses support the use of visual estimate

157   of RGC as a proxy for die-off (Sapes and others 2017, see Supplementary material Appendix 3).

158   Considering this high correlation and the limited number of individuals with real measures of

159   defoliation (10 per species and plot), we used the visually estimated RGC (made for every

160   individual) for the statistical analyses.

161   The variables described above were then scaled to the landscape level. First, we calculated the

162   following information for each plot: average percentage of visually estimated RGC for each

163   species; species frequency (the number of plots where each species was found over the total

164   number of plots) and the average size of each species (as the product of the two diameters

165   measured in the plants), since RGC could be affected by species size or relative abundance

166   (Lloret and others 2016; Sapes and others 2017). The values of species' RGC and size were then

167   averaged across plots. Finally, to account for the different species' strategies in relation to leaf

168   longevity and annual seasonality (Valladares and others 2004), all the species were classified

169   into one of the following foliar strategies: 1-evergreen, 2- semi-deciduous, 3-summer deciduous,

170   and 4-retamoid or leafless species.

7

171 *Climatic suitability modelling*

172 For the 22 sampled species, we built SDMs using four different algorithms - Mahalanobis

173 distance, GAM, BRT, and MaxEnt - to assess the robustness of the potential relationships

174 between visual estimates of RGC and the climatic suitability output of these models. These

175 models represent four highly differentiated modelling methods: distance-based models

176 (Mahalanobis distance), regression-based models (GAM), decision tree-based methods (BRT)

177 and a machine-learning technique based on the principle of maximum entropy (MaxEnt).

178 Therefore, they represent a gradient of complexity, where some models such as Mahalanobis

179 distance only consider linear relationships between predictors (Franklin 2010) whereas others

180 such as MaxEnt and BRT can include high-order interaction terms (Elith and others 2008; Phillips

181 and Dudík 2008).

182 The geographical occurrence data for each species were obtained from GBIF (Global Biodiversity

183 Information Facility: <www.gbif.org>). Occurrence data were filtered in order to remove

184 taxonomic and geographic inconsistencies and reduce dense local sampling by randomly

185 thinning species' records to one observation per 1x1 km grid cell. We considered the whole

186 distributional range of species; thus, the available number of occurrences was considerably

187 different from one species to the next, ranging from 200 to 6,000 after filtering. For each set of

188 filtered occurrences, 70% of presences were reserved for fitting the model (training data) and

189 the other 30% for the validation set (testing data), according to the number of environmental

190 predictors selected in our models and following the rule described by Huberty 1994 for

191 determining the optimum partitioning of training and test data. To improve the models'

192 performance accuracy (Barbet-Massin and others 2012), 100,000 random background points

193 were simulated for each species to fit both GAM and MaxEnt algorithms, and a random set of

194 pseudo-absences equivalent to the number of each species occurrences was simulated for BRT.

195 Since Mahalanobis distance works without simulated absences, no background points were

196 used in this case. The background extension was delineated in order to represent the current or

197   past available geographical space for the selected species (M dimension sensu Soberón 2007).

198   In our case, the geographical region used to establish species background was the

199   Mediterranean basin.

200   Six climatic variables representative of Mediterranean climate were used as predictors to

201   calibrate the suitability models: isothermality (mean diurnal temperature range/temperature

202   annual range), temperature seasonality, mean temperature of wettest quarter, mean

203   temperature of driest quarter, annual precipitation and precipitation seasonality, all of them

204   with 1 by 1 Km resolution. These variables were selected from the 19 bioclimatic variables

205   available in Worldclim.org (version 1.4) for the period 1950-2000 (Hijmans and others 2005),

206   according to the knowledge of the species' ecological requirements and in order to reduce

207   variables' collinearity. Pearson correlation and variation inflation factor (VIF) among variables

208   were always less than 0.75 and 5, respectively. Additionally, we used monthly precipitation and

209   maximum, minimum and mean temperature records over the 2013-2014 period from between

210   68 and 114 weather stations of the Spanish Meteorological Agency (AEMET) to elaborate the

211   climatic layers during the drought event (also in 1 by 1 km resolution), following Ninyerola and

212   others (2000), and using the 'biovars' function (dismo package; Hijmans and others 2016). To

213   minimize differences in the climatic interpolation methods between Worldclim and Ninyerola

214   and others (2000), only latitude, longitude and elevation were used as explanatory variables for

215   climatic data. In addition, we applied MESS analysis between these two data set over the Spanish

216   territory (where AEMET data are available) during the 1950-2000 period to assess dataset

217   dissimilarities, showing the high concordance and comparability of both climatic interpolation

218   methods over the entire extension and particularly over the study region (Supplementary

219   material Appendix 1 Figure A1). Finally, species' historic climatic suitability (HCS) was estimated

220   projecting the models over the climatic layers for the period 1950-2000, whereas species'

221   climatic suitability during the drought event (episode climatic suitability, ECS) was estimated by

222   projecting the calibrated models over the climate layers of the anomaly period 2013-2014.

223 For the four implemented SDM algorithms, model settings were selected following

224 recommendations from the literature, and partial dependence plots and predictive maps were

225 assessed to exclude those settings that produced unreliable response curves or distribution

226 maps. The final selected settings and main literature are showed in Table 1. To make all the

227 model outputs comparable (between 0 and 1 probability values), log raw output transformation

228 was applied for MaxEnt models (Phillips and Dudík 2008) and distance transformation into p-

229 values was applied for Mahalanobis distances (Clark and others 1993). Each model's predictive

230 performance was assessed by comparing model predictions with testing data, using the Area

231 Under Receiver Operating-characteristic Curve (AUC, Fielding and Bell 1997) and the Boyce index

232 (Boyce and others 2002; Hirzel and others 2006). These evaluation methods are considered a

233 reliable approach for our models and allowing comparison among them, since all the models

234 were fitted with the same species data set and environmental extension of layers (Hirzel and

235 others 2006; Franklin 2010). Finally, multivariate environmental similarity surface (MESS, Elith

236 and others 2010) analyses were carried out to measure the similarity between historical climate

237 and the extreme drought period in the occurrence locations; these analyses allowed to identify

238 extrapolation for predictions during the anomalous period as areas with high climatic

239 dissimilarities.

240 *Statistical analyses*

241 Generalized Linear Models (GLM) with normal distributions were performed to assess the

242 relationship between SDM-inferred HCS and ECS for each species and their die-off recorded in

243 the field. The visually estimated species RGC was used as a response variable whereas HCS, ECS,

244 the interaction between HCS and ECS, species size (logarithmically transformed), species

245 frequency, and species foliar category were introduced as explanatory variables. Difference

246 between HCS and ECS was discarded as an explanatory variable in the models, due to the high

247 correlation with ECS which produced same models results.

248   The final models were selected according to stepwise selection based on AIC (Akaike Information

249   Criterion). In addition, Phylogenetic Generalized Linear Models (PGLS) using Phylomatic

250   distances (Webb and Donoghue 2005) were performed in order to assess the potential effect of

251   phylogenetic species relationships in the selected model (Freckleton and others 2002). This PGLS

252   was finally discarded from the final analyses since phylogeny was not significant in any case

253   (lambda =0). Finally, consistency in the climatic suitability estimates (HCS, ECS) obtained from

254   each of the four implemented SDMs was tested by pairwise comparisons, using Pearson

255   correlation tests. All statistical analyses were carried out with R version 3.3.2 (R Core Team

256   2016).

257   **Results**

258   All the four SDMs algorithms developed showed high performance accuracy values with AUC

259   values higher than 0.75 and Boyce index' values being always positive and higher than 0.5 (Elith

260   and others 2002; Hirzel and others 2006; Supplementary material Appendix 1 Figure A2).

261   Particularly AUC mean values were 0.96±0.02 and Boyce index mean values were 0.93±0.07

262   MESS analyses showed that precipitation seasonality exhibited high dissimilarity between

263   extreme event climatic data and training predictor data near the coastal region. However, the

264   values corresponding to the drought episode were never outside training boundary values for

265   the study locations (Supplementary material Appendix 1 Figure A3). Climatic suitability dropped

266   dramatically during the drought episode for all species, irrespective of the SDM method, as

267   shown by the comparison between the respective HCS and ECS values (Figure 2, Supplementary

268   material Appendix 1 Table A2).

269   For the majority of SDM algorithms the stepwise GLM model selection determined that the most

270   parsimonious models explaining species' RGC were those including HCS, foliar category and

271   species size as explanatory variables. Only in the case of Mahalanobis distance did the stepwise

272   GLM model selection fail to remove any explanatory variables from the saturated model. There

273   was some variation in the significant variables associated with RGC in the different SDM

274　algorithms. All the selected variables were significant in BRT, while in MaxEnt HCS and foliar

275　category were significant, in GAM foliar category was significant and HCS was only marginally

276　significant, and in Mahalanobis only HCS and foliar category were marginally significant (Table

277　3).

278　In all cases RGC was positively related to HCS (Figure 2 and 3). Foliar categories 3 (summer

279　deciduous species) and 4 (leafless species) presented a significant, negative correlation with RGC

280　in BRT, GAM and MaxEnt models, while in the Mahalanobis distance model, foliar category 3

281　was only marginally significant. Finally, species size was only significantly negatively related with

282　RGC in BRT models (Table 3). Species frequency, ECS or the interaction between HCS and ECS

283　were not significant in any model (Table 3).

284　The values of species' HCS varied from model to model. BRT predicted the highest suitability

285　values for a given species and MaxEnt the lowest ones. This pattern was consistent for almost

286　all species (Supplementary material Appendix 1 Figure A4). For all species, the majority of

287　pairwise Pearson correlations between the HCS values inferred from the different SDM

288　algorithms were significant, with correlation values ranging between 0.45 and 0.78

289　(Supplementary material Appendix 1 Figure A5). However, the correlation between

290　Mahalanobis distance and BRT was not significant (Supplementary material Appendix 1 Figure

291　A5). In contrast, most pairwise correlations between models were not significant for ECS, likely

292　due to the extremely low ECS values exhibited by most species; in this case, when a significant

293　correlation was found, the relationship was driven by a single outlier value (Supplementary

294　material Appendix 1 Figure A6).

295　**Discussion**

296　We found a clear relationship between field measurements of species performance under an

297　extreme drought episode and the historical climatic suitability (HCS) of species derived from

298　SDMs. Within the studied community, co-occurring species living closer to their climatic

299　tolerance limit -identified by low HCS values compared to the optimal value of the distribution

12

300   range- proved more vulnerable to the extreme drought episode. This climatic limit corresponds

301   to the aridity margin of species' climatic niche (Supplementary material Appendix 2). These

302   results are consistent with the relationship observed between the decay of shrubland and

303   woodland species and the decrease in climatic suitability in other semi-arid areas in Spain (Sapes

304   and others 2017) and Southwestern North America (Lloret and Kitzberger 2018). This

305   relationship is also consistent with other studies which suggest that species' sensitivity to

306   climate change is related to niche characteristics such as mean niche position and niche breadth

307   (Thuiller and others 2005; Broennimann and others 2006). Species in the climatic niche margins

308   are generally assumed to exhibit lower survivorship and recruitment and higher extinction risk

309   because of the less favorable environmental conditions (Weber and others 2016). Precisely in

310   these situations of the environmental space closest to the physiological tolerance limits of the

311   species, the effect of climate variability is probably more severe (Zimmermann and others 2009),

312   promoting species' decline or range shifts at the trailing edge of species distribution (Bigler and

313   others 2006; Walther and others 2009).

314   *Species' drought responses and climatic suitability*

315   Studies that compare habitat suitability with different species' performances (population

316   density, growth, recruitment, fecundity, etc.) along the species distribution gradient are scarce

317   and still not fully conclusive with respect to general biogeographic paradigms (Centre-Periphery

318   hypothesis, Wright and others 2006; Sexton and others 2009; Thuiller and others 2010; Abeli

319   and others 2014; Csergő and others 2017). Likely species interaction, local variables or

320   adaptation mechanisms underlie the limited evidence of the relationship between species'

321   performance and climate suitability (Sexton and others 2009, 2014; Dallas and others 2017;

322   Lloret and Kitzberger 2018). Our results throw some light in this sense as they support the

323   relationship between species' performance when climatic conditions are extreme and

324   climatically-based descriptions of their suitability (i.e. HCS).

325   We also expected that populations experiencing higher displacement of climatic suitability

326   during the extreme event (low ECS) would experience greater leaf loses and higher mortality

327   rates. However, contrary to our expectations, we found that species' suitability during the

328   extreme episode (ECS) did not significantly explain species leaf loses in the studied community.

329   Our extremely low ECS levels observed for all species probably made it impossible to obtain

330   contrasted values of ECS among them. These low values indicate that the climatic episode was

331   extreme enough to displace all the studied populations far from their climatic optimum, even

332   for those species that were closer to this optimum during the historical period (Figure 2). In

333   addition to the exceptionality of the extreme event, the extremely low ECS values may derive

334   from 1) the averaged climatic data used for calibrating the models, which does not reflect the

335   variability or annual extremes during the considered 50-year period and 2) the limited ability of

336   models to predict suitability under climatic scenarios that are highly different from the period

337   used to fit the models (Elith and others 2010), as shown by the low MESS values, particularly for

338   precipitation seasonality –bio15- (although these were not negative in the study site)

339   (Supplementary material Appendix 1 Figure A3). This situation may also amplify the differences

340   between different algorithms and species' prevalence data in the predictions (Thuiller 2004;

341   Pearson and others 2006), as supported by the low correlations between the ECS predicted by

342   the different models (Supplementary material Appendix 1 Figure A6).

343   In addition to HCS, foliar categories were also significant in explaining the observed species' RGC,

344   suggesting that leaf strategy and seasonal senescence play a major role in understanding species

345   performance under strong drought conditions, at least in Mediterranean type ecosystems. Our

346   results show that summer-deciduous and leafless species always present significantly lower

347   values of RGC. This result is in part expected due to the general strategy in Mediterranean

348   species of dropping leaves during the dry, hot season to limit evapotranspiration and water loss

349   (de la Riva and others 2016a). In the Mediterranean basin this semideciduous mechanism

350   typically appears in combination with shallow roots and low water potentials as an anisohydric

14

351 syndrome, in contrast to species with hydrostable syndromes, which present sclerophyllous

352 leaves, more sensitive stomatal control and deeper roots (Zunzunegui and others 2005; de la

353 Riva and others 2016b). Thus, estimates of RGC as a proxy of drought resistance can be

354 misleading if these foliar strategies are not considered (Lloret and others 2016). In addition to

355 foliar strategies, other physiological features and local factors may modulate the interspecific

356 variability of responses to a given drought episode. For instance, species-specific resistance to

357 hydraulic failure and carbon economy (McDowell and others 2008; Anderegg and others 2012;

358 Adams and others 2017) and mutualistic and antagonistic biotic interactions (Lloret and others

359 2012; Valladares and others 2014).

360 *SDM algorithms and demographic performance*

361 Despite all these potential sources of variability, the four different SDM algorithms used in our

362 approach highlighted the positive relationship between climatic suitability (HCS) and resistance

363 to drought (RGC). These results were consistent across species, as shown by the high correlation

364 between the different models' HCS values (Supplementary material Appendix 1 Figure A5). The

365 agreement holds despite the wide variety of the modeling approaches. However, the 'simplest'

366 models (Mahalanobis distance and GAM) showed the lowest performance explaining species'

367 RGC compared to 'complex' ones (BRT and MaxEnt). This difference in algorithm performance

368 highlight the importance of the interactions between climatic variables and non-linear

369 relationships when assessing species' responses to climate, and thus, supporting the use of

370 SDMs versus simpler approaches based on univariate or multivariate correlations of

371 demographic performance with climatic variables. Moreover, algorithms that are generally

372 calibrated to produce smoother response curves, such as GLMs and GAMs, would be more

373 accurate to predict habitat suitability under new conditions (Elith and others 2010; Merow and

374 others 2014), while models based on presence-only data are more appropriate for predicting

375 the lowest suitability values in these scenarios (Pearson and others 2006). There is no general

376 agreement, however, about the most accurate algorithm in relation to situations of range shift

377   because even simpler models can lead to erroneous outputs (Elith and others 2010; Merow and

378   others 2014). We therefore urge ecologists to assess the degree of model complexity needed to

379   use SDMs as a proxy of ecological mechanisms, such as defoliation in this case.

380   Caution should also be taken when interpreting SDM predictions, given the assumptions that

381   these kind of models implicitly include (Pearson and Dawson 2003). Among other limitations,

382   these models commonly use only climatic predictors with a broad resolution (~1 km^2),

383   disregarding other meaningful abiotic factors, and they are also unable to capture microclimatic

384   effects at small spatial scales (Franklin and others 2013; Lenoir and others 2013; D'Amen and

385   others 2017). Microsite factors could be particularly important for our study, given that soil

386   features and depth, slope and orientation are especially relevant to species survival under

387   extreme drought (Colwell and others 2008; Hamerlynck and McAuliffe 2008). Furthermore,

388   SDMs assume that species respond homogeneously to climate change across their range, not

389   including intra-specific genetic variability and phenotypic plasticity, which may also favor

390   species' local adaptation under unfavorable conditions (Benito Garzón and others 2011; Lloret

391   and García 2016).

392   The drought episode experienced in the Region of Murcia in 2013-2014 was extraordinary in

393   historical terms, but these climatic situations are expected to become more frequent in the

394   future (Sheffield and Wood 2008). The ability of plant communities to withstand these events

395   and subsequently recover their green canopy will depend on both physiological traits related to

396   the adaptive syndromes of Mediterranean species (Peñuelas and others 2001) and the balance

397   between demographic processes such as mortality, growth, and recruitment (Lloret and others

398   2012). Under drier climatic scenarios, leafless and semi-deciduous species with shallow roots

399   (xerophytic malacophyllous) would be expected to be to take more advantage of scarce and

400   irregular rainfalls than sclerophyllous species with deeper roots. This is consistent with the

401   particularly high HCS values obtained for malacophyllous species (Figure 2 and 3). These

402   potential changes in species dominance within the community will likely lead to less productive

403   shrublands dominated by smaller species (Valladares and others 2004). Since species' climatic

404   suitability is broadly related to both physiological and demographic species performance

405   (Martinez-Meyer and others 2013), indexes describing climatic suitability can provide rough

406   estimates of species' vulnerability to extreme climatic episodes. While community resistance

407   and resilience could minimize ecological changes, the recurrence of these extreme drought

408   events could lead these Mediterranean communities to cross thresholds beyond which they

409   could collapse (Vicente-Serrano and others 2013; Valladares and others 2014). This depletion of

410   resilience in semi-arid shrubland communities could promote transitions to desert-like

411   ecosystems, as has been predicted by some climate change scenarios for southern areas of

412   Europe (Guiot and Cramer 2016). Accordingly, this study shows the impact of extreme drought

413   events even on communities supposedly well adapted to drought conditions (Lázaro and others

414   2001; Sapes and others 2017).

415   *Conclusion*

416   This study confirms the role of population position within its species climatic niche in explaining

417   populations' vulnerability to extreme climatic events. In the studied semi-arid shrubland, species

418   closer to their climatic tolerance limit were more vulnerable to extreme drought. Thus, the

419   predicted recurrence of severe drought events could reduce the community resilience,

420   increasing the risk of desertification in these arid lands. Our study empirically concurs with the

421   trends foreseen by theoretical models, based on predicted suitability and correlations with

422   drought response. This concurrence supports the use of SDMs to assess the impact of climate

423   change on plant communities, particularly in extreme climatic conditions. This approach, which

424   links species performance with regional biogeographic patterns, can probably be applied to

425   other processes heavily determined by strong climatic fluctuations.

426   **Acknowledgements**

References

AEMET, Spanish Weather Agency. 2014. Avance climatológico mensual mes de septiembre. Murcia.

Abeli T, Gentili R, Mondoni A, Orsenigo S, Rossi G. 2014. Effects of marginality on plant population performance. J Biogeogr 41:239–49.

Allen CD, Breshears DD. 1998. Drought-induced shift of a forest – woodland ecotone : Rapid landscape response to climate variation. Ecology 95:14839–42.

Allen CD, Breshears DD, McDowell NG. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:art129.

Anderegg WRL, Berry JA, Smith DD, Sperry JS, Anderegg LDL, Field CB. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proc Natl Acad Sci 109:233–7.

Araújo MB, New M. 2007. Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–7.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol Evol 3:327–38.

Benito Garzón M, Alía R, Robson TM, Zavala MA. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. Glob Ecol Biogeogr

Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A. 2006. Drought as an inciting mortality factor in scots pine stands of the Valais, Switzerland. Ecosystems 9:330–43.

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK. 2002. Evaluating resource selection functions. Ecol Modell 157:281–300.

457   Braun-Blanquet J, Bolòs O. 1957. The plant communities of the Central Ebro Basin and their

458   dynamics. An la Estac Exp Aula Dei 5:1–266.

459   Broennimann O, Thuiller W, Hughes G, Midgley GF, Alkemade JMR, Guisan A. 2006. Do

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

461   global change? Glob Chang Biol 12:1079–93.

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

463   episode: The role of seed bank and seedling emergence. Plant Biol 14:458–66.

464   Calenge C. 2015. Home Range Estimation in R : the adehabitatHR Package. R vignette:1–60.

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

466   Geographic Information System. J Wildl Manage 57:519.

467   Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT. 2008. Global Warming, Elevational

468   Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. Science (80-) 322:258–61.

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

470   Enquist BJ, McGill B, Svenning J-C, Violle C, Buckley YM. 2017. Less favourable climates

471   constrain demographic strategies in plants. Gurevitch J, editor. Ecol Lett 20:969–80.

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

473   level: From current approaches to future frameworks. Biol Rev 92:169–87.

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

475   geographic range or climatic niche. Anderson M, editor. Ecol Lett 20:1526–33.

476   Elith J, Burgman MA, Regan HM. 2002. Mapping epistematic uncertainties and vague conceps

477   in predictions of species distribution. Ecol Modell 157:313–29.

478   Elith J, Kearney M, Phillips S. 2010. The art of modelling range-shifting species. Methods Ecol

479   Evol 1:330–42.

480 Elith J, Leathwick JR. 2009. Species Distribution Models: Ecological Explanation and Prediction

481   Across Space and Time. Annu Rev Ecol Evol Syst 40:677–97.

482 Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. J Anim Ecol

483   77:802–13.

484 Esteve-Selma MA, Mart??nez-Fern??ndez J, Hern??ndez I, Mont??vez JP, Lopez JJ, Calvo JF,

485   Robledano F. 2010. Effects of climatic change on the distribution and conservation of

486   Mediterranean forests: The case of Tetraclinis articulata in the Iberian Peninsula.

487   Biodivers Conserv 19:3809–25.

488 Esteve-Selma MA, Martínez-Fernández J, Hernández I, Robledano F, Pérez-Navarro MA, Lloret

489   F. 2015. Cambio climático y biodiversidad en el contexto de la Región de Murcia. In:

490   Consejería de Agua Agricultura y Medio Ambiente, editor. Cambio climático en la Región

491   de Murcia. Evaluación basada en indicadores. Murcia. pp 105–32.

492 Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in

493   conservation presence/absence models. Environ Conserv 24:38–49.

494 Franklin J. 2010. Mapping species distributions. Spatial inference and prediction. New York:

495   Cambridge University Press.

496 Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L. 2013. Modeling plant

497   species distributions under future climates: how fine scale do climate projections need to

498   be? Glob Chang Biol 19:473–83.

499 Franklin J, Serra-Diaz JM, Syphard AD, Regan HM. 2016. Global change and terrestrial plant

500   community dynamics. Proc Natl Acad Sci 113:3725–34.

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

502   160:712–26.

503   Greenwood S, Ruiz-Benito P, Martínez-Vilalta J, Lloret F, Kitzberger T, Allen CD, Fensham R,

504   Laughlin DC, Kattge J, Bönisch G, Kraft NJB, Jump AS. 2017. Tree mortality across biomes

505   is promoted by drought intensity, lower wood density and higher specific leaf area. Ecol

506   Lett 20:539–53.

507   Guiot J, Cramer W. 2016. Climate change: The 2015 Paris Agreement thresholds and

508   Mediterranean basin ecosystems. Science (80-) 354:4528–32.

509   Hamerlynck EP, McAuliffe JR. 2008. Soil-dependent canopy die-back and plant mortality in two

510   Mojave Desert shrubs. J Arid Environ 72:1793–802.

511   Hijmans ARJ, Phillips S, Leathwick J, Elith J, Hijmans MRJ. 2016. Package ' dismo ' Species

512   Distribution Modeling.

513   Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated

514   climate surfaces for global land areas. Int J Climatol 25:1965–78.

515   Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A. 2006. Evaluating the ability of habitat

516   suitability models to predict species presences. Ecol Modell 199:142–52.

517   Huberty CJ. 1994. Applied discriminant analysis. New York: Wiley

518   IPCC, 2013. Climate change 2013: the physical science basis. contribution of working group I to

519   the fifth assessment report of the intergovernmental panel on climate change. In: Stocker

520   TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley

521   PM, Eds. Cambridge University Press, Cambridge, United Kingdom and New York, NY,

522   USA, 1535 pp.

523   Jump AS, Hunt JM, Peñuelas J. 2006. Rapid climate change-related growth decline at the

524   southern range edge of Fagus sylvatica. Glob Chang Biol 12:2163–74.

525   de la Riva EG, Olmo M, Poorter H, Ubera JL, Villar R. 2016a. Leaf Mass per Area (LMA) and Its

526   Relationship with Leaf Structure and Anatomy in 34 Mediterranean Woody Species along

527   a Water Availability Gradient. PLoS One 11:e0148788.

528   de la Riva EG, Pérez-Ramos IM, Tosto A, Navarro-Fernández CM, Olmo M, Marañón T, Villar R.

529   2016b. Disentangling the relative importance of species occurrence, abundance and

530   intraspecific variability in community assembly: a trait-based approach at the whole-plant

531   level in Mediterranean forests. Oikos 125:354–63.

532   Lázaro R, Rodrigo FS, Gutiérrez L, Domingo F, Puigdefábregas J. 2001. Analysis of a 30-year

533   rainfall record (1967–1997) in semi–arid SE Spain for implications on vegetation. J Arid

534   Environ 48:373–95.

535   Lenoir J, Graae BJ, Aarrestad PA, Alsos IG, Armbruster WS, Austrheim G, Bergendorff C, Birks

536   HJB, Bråthen KA, Brunet J, Bruun HH, Dahlberg CJ, Decocq G, Diekmann M, Dynesius M,

537   Ejrnaes R, Grytnes J-A, Hylander K, Klanderud K, Luoto M, Milbau A, Moora M, Nygaard B,

538   Odland A, Ravolainen VT, Reinhardt S, Sandvik SM, Schei FH, Speed JDM, Tveraabak LU,

539   Vandvik V, Velle LG, Virtanen R, Zobel M, Svenning J-C. 2013. Local temperatures inferred

540   from plant communities suggest strong spatial buffering of climate warming across

541   Northern Europe. Glob Chang Biol 19:1470–81.

542   Lesica P, Crone EE. 2016. Arctic and boreal plant species decline at their southern range limits

543   in the Rocky Mountains. Ecol Lett:166–74.

544   Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F. 2012. Extreme climatic events

545   and vegetation: The role of stabilizing processes. Glob Chang Biol 18:797–805.

546   Lloret F, García C. 2016. Inbreeding and neighbouring vegetation drive drought-induced die-off

547   within juniper populations. Field K, editor. Funct Ecol 30:1696–704.

548   Lloret F, Kitzberger T. 2018. Historical and event-based bioclimatic suitability predicts regional

549   forest vulnerability to compound effects of severe drought and bark beetle infestation.

550   Glob Chang Biol.

551   Lloret F, de la Riva EG, Pérez-Ramos IM, Marañón T, Saura-Mas S, Díaz-Delgado R, Villar R.

552   2016. Climatic events inducing die-off in Mediterranean shrublands: are species

553   responses related to their functional traits? Oecologia 180:961–73.

554   van der Maaten E, Hamann A, van der Maaten-Theunissen M, Bergsma A, Hengeveld G, van

555   Lammeren R, Mohren F, Nabuurs G-J, Terhürne R, Sterck F. 2017. Species distribution

556   models predict temporal but not spatial variation in forest growth. Ecol Evol 7:2585–94.

557   Martinez-Meyer E, Diaz-Porras D, Peterson AT, Yanez-Arenas C. 2013. Ecological niche

558   structure and rangewide abundance patterns of species. Biol Lett 9:20120637–20120637.

559   Martínez-Vilalta J, Lloret F. 2016. Drought-induced vegetation shifts in terrestrial ecosystems:

560   The key role of regeneration dynamics. Glob Planet Change 144:94–108.

561   Mcdowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A,

562   Williams DG, Yepez EA, Mcdowell N, Pockman WT, Allen CD, David D, Mcdowell N, Cobb

563   N, Kolb T, Plaut J, Sperry J. 2008. Mechanisms of Plant Survival and Mortality during

564   Drought : Why Do Some Plants Survive while Others Succumb to Drought ? New Phytol

565   178:719–39.

566   Merow C, Smith MJ, Edwards TC, Guisan A, Mcmahon SM, Normand S, Thuiller W, Wüest RO,

567   Zimmermann NE, Elith J. 2014. What do we gain from simplicity versus complexity in

568   species distribution models? Ecography (Cop) 37:1267–81.

569   Mouillot F, Rambal S, Joffre R. 2002. Simulating climate change impacts on fire frequency and

570   vegetation dynamics in a Mediterranean ecosystem. Glob Chang Biol 8:423–37.

571   Ninyerola M, Pons X, Roure JM. 2000. A methodological approach of climatological modelling

572   of air temperature and precipitation through GIS techniques. Int J Climatol 20:1823–41.

573   Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across

574   natural systems. Nature 421:37–42. http://www.ncbi.nlm.nih.gov/pubmed/12511946

575   Pearson RG, Dawson TP. 2003. Predicting the Impacts of Climate Change on the Distribution of

576   Species : Are Bioclimate Envelope Models Useful ? Glob Ecol Biogeogr 12:361–71.

577   Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L,

578   Segurado P, Dawson TP, Lees DC. 2006. Model-based uncertainty in species range

579   prediction. J Biogeogr 33:1704–11.

580   Peñuelas J, Lloret F, Montoya R. 2001. Severe drought effects on mediterranean woody flora in

581   Spain. For Sci 47:214–8.

582   Peterson AT (Andrew T, Soberón J, Pearson RG, Anderson RP, Martinez-Meyer E, Nakamura M,

583   Araújo MB. 2011. Ecological Niches and Geographic Distributions. Princeton.

584   Phillips SJ, Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and

585   a comprehensive evaluation. Ecography (Cop) 31:161–75.

586   Pironon S, Villellas J, Morris WF, Doak DF, García MB. 2015. Do geographic, climatic or

587   historical ranges differentiate the performance of central versus peripheral populations?

588   Glob Ecol Biogeogr 24:611–20.

589   Pulliam HR. 2000. On the relationship between niche and distribution. Ecol Lett 3:349–61.

590   Ridgeway G. 2007. Generalized Boosted Models : A guide to the gbm package. Compute 1:1–

591   12.

592   Rivas-Martínez S, Rivas-Sáenz S, Penas-Merino A. 2011. Worldwide bioclimatic classification

593   system. Glob Geobot 1:1–638.

594   Sapes G, Serra-Diaz JM, Lloret F. 2017. Species climatic niche explains drought-induced die-off

595   in a Mediterranean woody community. Ecosphere 8:e01833.

596   Serra-Diaz JM, Keenan TF, Ninyerola M, Sabaté S, Gracia C, Lloret F. 2013. Geographical

597   patterns of congruence and incongruence between correlative species distribution

598   models and a process-based ecophysiological growth model. J Biogeogr 40:1928–38.

599   Sexton JP, Hangartner SB, Hoffmann AA. 2014. Genetic isolation by environment or distance:

600   which pattern of gene flow is most common? Evolution (N Y) 68:1–15.

601   Sexton JP, Mcintyre PJ, Angert AL, Rice KJ. 2009. Evolution and Ecology of Species Range Limits.

602   Annu Rev Ecol Evol Syst 40:415–36.

603   Sheffield J, Wood ÆEF. 2008. Projected changes in drought occurrence under future global

604   warming from multi-model , multi-scenario , IPCC AR4 simulations. Clim Dyn 31:79–105.

605   Soberón J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecol

606   Lett 10:1115–23.

607   Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de

608   Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF,

609   Miles L, Ortega-Huerta MA, Townsend Peterson A, Phillips OL, Williams SE. 2004.

610   Extinction risk from climate change. Nature 427:145–8.

611   Thuiller W. 2004. Patterns and uncertainties of species' range shifts under climate change.

612   Glob Chang Biol 10:2020–7.

613   Thuiller W, Cile C, Albert H, Dubuis A, Randin C, Guisan A. 2010. Variation in habitat suitability

614   does not always relate to variation in species' plant functional traits. Biol Lett 6:120–3.

615   Thuiller W, Lavorel S, Araújo MB. 2005. Niche properties and geographical extent as predictors

616   of species sensitivity to climate change. Glob Ecol Biogeogr 14:347–57.

617   Valladares F, Benavides R, Rabasa SG, Diaz M, Pausas JG, Paula S, Simonson WD. 2014. Global

618   change and Mediterranean forests : current impacts and potential responses. In: Forests

619   and Global Change. pp 47–75.

620   Valladares F, Vilagrosa A, Peñuelas J, Ogaya R, Julio J, Corcuera L, Sisó S. 2004. CAPÍTULO 6

621   Estrés hídrico : ecofisiología y escalas de la sequía. In: Valladares F, editor. Ecologia del

622   bosque mediterráneo en un mundo cambiante. Ministerio. Madrid. pp 163–90.

623   Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI, Azorín-

624   Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E, Sanchez-Lorenzo A,

625   Dickinson RE. 2013. Response of vegetation to drought time-scales across global land

626   biomes. Proc Natl Acad Sci U S A 110:52–7.

627   Walther G-R, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát

628   Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarosík V, Kenis M, Klotz S, Minchin D, Moora

629   M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W,

630   Thuiller W, Vilà M, Vohland K, Settele J. 2009. Alien species in a warmer world: risks and

631   opportunities. Trends Ecol Evol 24:686–93.

632   Webb CO, Donoghue MJ. 2005. Phylomatic: Tree assembly for applied phylogenetics. Mol Ecol

633   Notes 5:181–3.

634   Weber MM, Stevens RD, Diniz-Filho JAF, Grelle CE V. 2016. Is there a correlation between

635   abundance and environmental suitability derived from ecological niche modelling? A

636   meta-analysis. Ecography (Cop) 40:817–28.

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

638   of semiparametric generalized linear models. J R Stat Soc 73:3–36.

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

640   niche modeling in a heterogeneous environment. Ecology 87:2433–9.

641 Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, Field CB, Mooney HA. 2003.

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

643   Deposition. Ecol Monogr 73:585–604.

644 Zimmermann NE, Yoccoz NG, Edwards TC, Meier ES, Thuiller W, Guisan A, Schmatz DR,

645   Pearman PB. 2009. Climatic extremes improve predictions of spatial patterns of tree

646   species. Proc Natl Acad Sci U S A 106 Suppl:19723–8.

647 Zunzunegui M, Díaz Barradas MC, Ain-Lhout F, Clavijo A, García Novo F. 2005. To live or to

648   survive in Doñana dunes: Adaptive responses of woody species under a Mediterranean

649   climate. Plant Soil 273:77–89.

650

651 Table captions

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

653 **Table 2** Main species information and attributes used in statistical analyses. See methods for

654 details about foliar strategy, RGC (Remaining Green Canopy), Size and Frequency.

655 **Table 3** Results of GLMs explaining remaining green canopy as a function of foliar strategy, size,

656 frequency, HCS (Historical Climatic Suitability), ECS (Episode Climatic Suitability) and the

657 interaction between the latter two (HCS:ECS) calculated from four different SDMs (Mahalabonis

658 distance, GAM, BRT, MaxEnt). AIC stepwise selection was applied to obtain the final models.

659 Significant or marginally significant P values are highlighted in bold.

660

Method	Key reference and main settings
Mahal **Mahalanobis distance**	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).
GAM **Generalized Additive Models**	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.
BRT **Boosted Regression Tree**	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).
MaxEnt **Maximum entropy**	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.

661

662

Family	Species	Code	Life form	Foliar strategy	RGC (%)	Size (cm^2)	Frequency
Anacardiaceae	Pistacia lentiscus	PLE	Microphanerophyte	Evergreen	25.33	0.0828	0.5
Asparagaceae	Asparagus horridus	AHO	Chamaephyte	Leafless	15.00	0.0291	0.1
Asteraceae	Artemisia barrelieri	ABA	Chamaephyte	Semideciduous	44.29	0.0043	0.9
	Artemisia campestris	ACA	Chamaephyte	Semideciduous	13.33	0.0115	0.1
Boraginaceae	Lithodora fruticosa	LFR	Nanophanerophyte	Semideciduous	47.27	0.0291	0.1
Chenopodiaceae	Salsola genistoides	SGE	Nanophanerophyte	Leafless	6.67	0.0795	0.2
Cistaceae	Cistus albidus	CAL	Nanophanerophyte	Semideciduous	77.50	0.0452	0.2
	Cistus clusii	CCL	Nanophanerophyte	Semideciduous	44.77	0.0456	0.9
	Helianthemum syriacum	HSY	Chamaephyte	Semideciduous	61.39	0.0018	0.3
Cupressaceae	Juniperus oxycedrus	JOX	Microphanerophyte	Evergreen	56.69	0.5503	0.6
	Juniperus phoenicea	JPH	Microphanerophyte	Evergreen	60.00	0.0736	0.1
Fagaceae	Quercus coccifera	QCO	Microphanerophyte	Evergreen	33.10	0.0091	0.7
Lamiaceae	Rosmarinus officinalis	ROF	Nanophanerophyte	Semideciduous	53.00	0.2353	1.0
	Sideritis leucantha	SLE	Nanophanerophyte	Semideciduous	44.77	3.0292	0.2
	Teucrium capitatum	TCA	Chamaephyte	Semideciduous	68.00	2.0186	0.6
	Thymus hyemalis	THY	Chamaephyte	Semideciduous	45.28	0.3894	1.0
Leguminosae	Anthyllis cytisoides	ACY	Nanophanerophyte	Semideciduous	21.46	0.3779	0.6
	Dorycnium pentaphyllum	DPE	Nanophanerophyte	Semideciduous	21.54	0.5769	0.5
	Ononis fruticosa	OFR	Nanophanerophyte	Semideciduous	10.11	0.4742	0.4
Poaceae	Stipa tenacissima	STE	Hemicryptophyte	Evergreen	61.89	0.0088	1.0
Rhamnaceae	Rhamnus lycioides	RLY	Microphanerophyte	Semideciduous	8.75	0.0560	0.3
Timeleaceae	Daphne gnidium	DGN	Nanophanerophyte	Semideciduous	15.00	0.0045	0.2

663

664

665

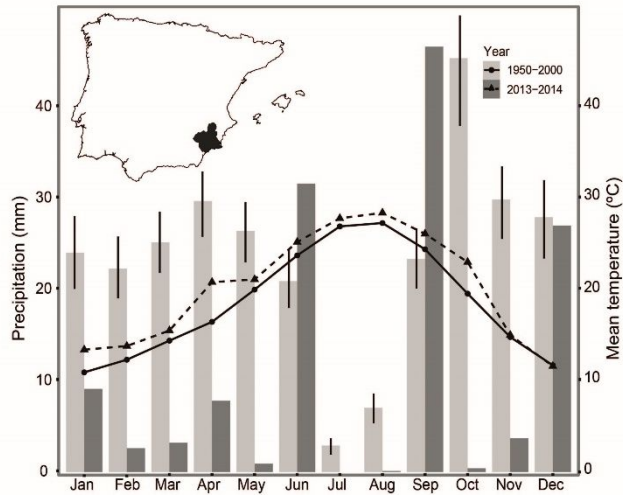|	MAHALANOBIS DISTANCE			GAM			BRT			MAXENT		
	AIC	197.97		AIC	196.10		AIC	187.33		AIC	194.15	
	R2 adj	0.32		R2 adj	0.33		R2 adj	0.55		R2 adj	0.39	
	β	Std.Error	P.value	β	Std.Error	P.value	β	Std.Error	P.value	β	Std.Error	P.value
INTERCEPT (FOLIAR.STR 1)	0.000	0.000	0.939	0.000	0.000	0.610	0.000	0.000	0.324	0.000	0.000	0.051
HCS	0.382	0.213	**0.096**	0.362	0.196	**0.083**	0.561	0.157	**0.003**	0.446	0.199	**0.039**
FOLIAR.STR 2	0.062	0.299	0.838	-0.317	0.241	0.207	-0.317	0.198	0.130	-0.364	0.234	0.139
FOLIAR.STR 3	-0.435	0.230	**0.081**	-0.563	0.210	**0.016**	-0.618	0.172	**0.002**	-0.706	0.223	**0.006**
FOLIAR.STR 4	-0.254	0.254	0.336	-0.688	0.218	**0.006**	-0.690	0.173	**0.001**	-0.628	0.199	**0.006**
LOG(SIZE)	-0.244	0.212	0.271	-0.318	0.201	0.133	-0.373	0.167	**0.039**	-0.330	0.1934	0.107
FREQUENCY	0.369	0.225	0.125									
ECS	27.618	18.640	0.162									
HCS:ECS	-27.360	18.590	0.165									

666

667

668   Figure captions

669   **Figure 1** Study region within the Iberian Peninsula (Murcia region: black shading in the inset,

670   upper left map) and monthly temperature (lines) and precipitation (bars) data during the

671   historical 1950-2000 period (light grey bars and dots) and the 2013-2014 hydrological year

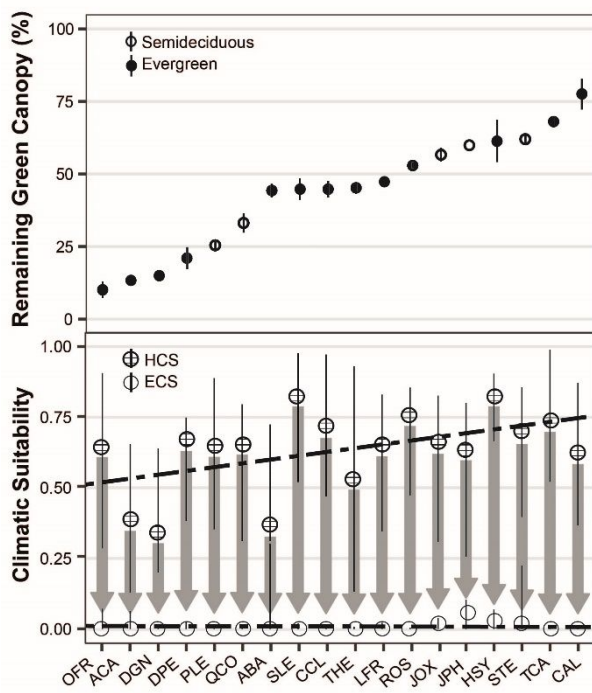672   (anomaly period; dark grey bars and triangles).

673   **Figure 2** Averaged proportion of Remaining Green Canopy (RGC) in shrub species with foliar

674   strategies 1 and 2 (top graph) for the ten studied plots. Species' RGC values are sorted in

675   increasing order (x-axis) and error bars are shown. Red and blue dots represent foliar strategies.

676   The lower graph shows the Historical Climatic Suitability (HCS) and the drought Episode Climatic

677   Suitability (ECS) values for each species. Blue and red dots represent median suitability values

678   of HCS and ECS, respectively, and the error bars correspond to the range between maximum

679   and minimum suitability values predicted by the four applied SDM algorithms (see text for

680   details).

681   **Figure 3** Partial residual plot of RGC (Remaining Green Canopy) in relation to HCS (Historical

682   Climatic Suitability) obtained for each SDM model. B (standardized estimate value) and P values

683   for HCS in these models are shown in the left corner of each plot. Species codes are shown in

684   Table 2.

685

686
687

34

688
689

690