



# Climatic Suitability Derived from Species Distribution Models Captures Community Responses to an Extreme Drought Episode

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## ABSTRACT

The differential responses of co-occurring species in rich communities to climate change—particularly to drought episodes—have been fairly 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 because this region constitutes 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 modeling algorithms (Mahalanobis distance, GAM, BRT, and MAXENT) to estimate species' climatic suitability before (1950–2000) and during the extreme drought. For each SDM, we related 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 the exceptional episode led to almost zero suitability values. Overall, our approach highlights climatic niche modeling 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.

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**Author Contributions** MAPN completed the fieldwork, modeled species' distributions, analyzed the data, and wrote the first draft. MAE conceived the study and wrote the paper. GS and EB contributed to analyze data and wrote the paper. JMSD wrote the paper and also conceived how to model species distribution. FL conceived the study, analyzed data and wrote the paper.

Data are available at <https://zenodo.org/record/1216812#.Ws4EjohuZPY>

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## HIGHLIGHTS

- Evidence of cross-scale link between biogeography and local responses under droughts
- Consistent predictions among different SDMs algorithms
- Species sensitivity to climate change even in ecosystems adapted to low precipitation

## 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 corresponds 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-Díaz 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 (that is, 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 (for example, 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 multiple episodes of vegetation die-off, including 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 (that is, lower suitability values compared to the niche's optimal value) are more vulnerable to such extreme events than populations living closer

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