# DROUGHT-INDUCED EFFECTS IN COEXISTING MEDITERRANEAN SHRUBS IN RELATION TO SPECIES' BIOCLIMATIC NICHE

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# Abstract

Climate-induced drought is one of the principal factors altering plant community dynamics and composition as well as species' geographic distributions in the Mediterranean basin. The use of bioclimatic models that consider both bioclimatic conditions and species' geographic distributions to predict potential scenarios under these climatic conditions have recently become extensively developed. However, studies relating the effects of drought over community dynamics with regional-scale patterns are very scarce. Here I relate field observations made in a Mediterranean community (NE Iberian Peninsula) on the effects of a climatic drought anomaly over local-population traits driving community dynamics (abundance and resistance to drought estimated from defoliation) with the species bioclimatic niche assessed at regional scale from Species Distribution Models. Results highlight that species' abundance increases when the average bioclimatic conditions are more suitable. Resistance to drought is not related with species' bioclimatic suitability at such locality, estimated from average climatic conditions, but it diminishes when the displacement induced by the climatic anomaly over the species' bioclimatic suitability is higher. Less frequent species appears more resistant than more common ones, suggesting the relevance of acclimation or natural selection over populations, and thus determining community dynamics under climate change scenarios. These results suggest that a drought climate scenario could lead to shifts in community dynamics and species' distributions and the emergence of new communities better adapted to the new conditions. I conclude that bioclimatic models can reflect both regional and local scale patterns and can be useful to predict community shifts in front of bioclimatic anomalies and I provide a procedure to link patterns at such distant scales. Further investigation is needed to assess and improve the prediction ability of this procedure as well as the importance of these climatic anomalies.

## Introduction

During the last century, the climate of the whole planet has warmed up approximately 0.74 ºC. IPCC predictions about climatic change have shown that temperatures could increase between 1.1 and 6.4 ºC during the next 100 years (IPCC 2007). These predictions suggest higher future desertification rates (D'Odorico *et al.*, 2013; Sardans & Peñuelas, 2013) and longer drought perturbation periods (IPCC 2001). Some studies are detecting that these perturbations are affecting plant communities and ecosystems in several ways such as species distribution shifts (Hughes, 2000; McCarty, 2001), changes in species composition of communities (Condit, 1998; Sebastià *et al.*, 2008; Lloret *et al.*, 2009) and changes in the structure and functioning of ecosystems (McCarty, 2001). Especially, several cases of drought-induced dieback have been detected around the world (Allen *et al.*, 2010) that could lead to ecosystem changes caused by higher mortality than tree regeneration (Lloret *et al.*, 2012) or due to new combinations of native and invasive exotic species (Jiménez *et al.*, 2011).

It is known that a directional climate change could affect the community vegetation structure (i.e. plant covering and volume), for instance by worsening the living conditions of several species as their performance diminish together with community structure degradation (Lloret *et al.*, 2009; Saccone *et al.*, 2009; del Cacho *et al.*, 2012) or improving vegetation living conditions in cold ecosystems (Hobbie & Chapin, 1998; Jonsdottir *et al.*, 2005; Peñuelas *et al.*, 2007). In other cases, studies have seen that some species could be benefited from these new climatic conditions. Extremely stress-tolerant species that have better drought-resistance mechanisms or that find the new climate more suitable could find the opportunity to succeed over other species, conducing to species displacements or community composition shifts (Van Der Veken *et al.*, 2004; Ogaya & Peñuelas, 2006).

In particular, climatic change perturbations like drought episodes could affect communities' species composition through impacts on physiological and demographic processes that eventually will influence community dynamics (Galiano *et al.*, 2013). But these effects are often difficult to study because of the inertia of plant communities produced by stabilizing processes (Lloret *et al.*, 2012). Nevertheless, here are some studies pointing out that new climatic dynamics could bring to composition shifts and succession dynamics like community reshuffling and community decline (Foster, 2001). As a result, under future drier conditions I expect that communities will experience changes in species composition and will be formed by drought-adapted species capable of surviving in the new climatic scenario (Sanz-Elorza, 2003). Also, several studies point that climatic change perturbations could have effects on species biogeographic distributions (Thomas *et al.*, 2004; Hobbs *et al.*, 2006; Scholze *et al.*, 2006) by expanding (Woodward, 1987) or reducing its range (Huntley *et al.*, 1995) and promoting altitudinal (Jump *et al.*, 2007) or latitudinal shifts (Jump *et al.*, 2009).

The intrinsic complexity of these processes has propitiated the use of new tools like Species Distribution Models (SDMs) capable of integrating huge amounts of data about climatic change when predicting its effects. SDMs use bioclimatic distributions (Hintikka, 1963; Dahl, 1980; Woodward, 1988) - based on the Hutchinson's ecologic niche concept (Hutchinson, 1957) - and geographic distributions of species to model both geographic and bioclimatic species' distributions given a specific climatic scenario for the next decades (Guisan & Zimmermann, 2000). These models estimate the relationship between species geographical occurrence and the environmental and/or spatial characteristics of the sites where species occurs (Franklin, 2009). Among different modelling approaches, MaxEnt platform (Phillips *et al.*, 2006) is widely used, given its feasibility and versatility (Phillips & Dudík, 2008; Elith *et al.*, 2011). This software basically allows developing temporal and spatial predictions about the potential distribution of species based on presence-only data. Presence-only data based models are subjected to errors because absences are not analysed and should be uses with caution (Phillips *et al.*, 2009; Ward

*et al.*, 2009), but they allow the use of large flora datasets and provides a useful tool to quantitatively explore species' bioclimatic niche.

Nevertheless, there are very few studies that analyse the effects of climatic change over species at community level and hardly any specifically using MaxEnt (f.i., Pacheco *et al.*, 2010; Laughlin *et al.*, 2011). In fact, most of them consider climatic change effects over one or very few species with different requirements in order to assess the differences that climatic change has over species with different ecological characteristics (Buermann *et al.*, 2008; Collevatti *et al.*, 2011; Simpson & Prots, 2013), but this approach can hardly afford the response of communities based on the behaviour of coexisting species.

In this study, I aim to relate the response to drought periods of population-level traits observed at local scale with regional assessment obtained from bioclimatic models. I compare for several coexisting woody species (i) the abundance of their populations to the position of these populations in the respective species' bioclimatic niche, (ii) the resistance of populations to drought to their position in the species' bioclimatic niche. I conducted this study at the Monegros countryside in the central Ebro valley, NE of the Iberian Peninsula. This area is a semiarid place bioclimatically located in an extreme of the Mediterranean biome that has recently suffered from persistent drought since 2006 (see Annex, Figure 1).

I follow two approaches to compare population-level traits, including plant abundance and resistance to drought – estimated by remaining green canopy –, to the position in the bioclimatic niche: 1) estimation of species' bioclimatic suitability from bioclimatic distributions modelled using MaxEnt, obtained from current geographic distributions and the average climatic conditions in the past 50 years and 2) estimation of species' bioclimatic suitability using the same procedure but considering the climatic conditions recorded during the drought period (2006-2010); this estimation describes the deviation induced by such drought period from the average bioclimatic niche of the species -hereafter, bioclimatic anomaly -. Specifically,

our hypotheses will be: 1) those species that occur farther from their bioclimatic distribution average have lower population densities, 2a) those species that occur farther from their bioclimatic distribution average have lower resistance to drought, 2b) the most abundant species have higher resistance to drought levels and 3) those species for which the conditions experienced during the bioclimatic anomaly period represent a higher proportional displacement from their bioclimatic niche experienced lower resistance to drought levels.

## Methods

<u>Study area</u>

The study site is located in the Monegros countryside, in the central Ebro valley, NE of the Iberian Peninsula (41°25'N, 0°4'E), at ca. 280 m above sea level (see Annex, Figure 1).

The climate is Mediterranean with semiarid tendency. Mean annual rainfall is about 396 mm and shows great seasonal variability with higher precipitation values in spring (ca. 30 %) and autumn (ca. 32 %) and lower values in winter (ca. 18 %) and summer (ca. 20 %), causing a chronic summer drought. Mean annual temperature is 14.8 °C with high seasonal variation; from 6.1 °C in the coldest month (January) to 23.8 °C in the hottest month (July) and extreme values ranging from -12 °C (December) to 41 °C (July) (Figure 1).

The studied stands present Mediterranean and steppe vegetation belonging to the *Rhamneto-Cocciferetum pistacietosum* association (Braun-Blanquet & Bolòs, 1957), a continental open shrubland with occasional occurrence of trees (*Pinus halepensis* Mill. and *Juniperus phoenicea* L.). Some of the dominant species are the shrubs *Rosmarinus officinalis* L.*, Rhamnus lycioides* L.*, Helianthemum syriacum* (Jacq.) Dum. Cours.*, Cistus clusii* Dunal*, Quercus coccifera* L. and *Genista scorpius* (L.) DC. (Braun-Blanquet & Bolòs, 1957). These species typically show a Mediterranean distribution, although many of them are located in their bioclimatic distribution edge, such as *Juniperus phoenicea* L. and *Quercus coccifera* L..

<u>Abundance variables and drought resistance</u>

I set one 50 x 50 m stand in each of ten shrubland zones across the study area (see Annex, Figure 2). In each stand, I selected woody species according to the following criteria: i) they cover a wide range of life forms; from small chamaephytes such as *Helianthemum* sp pl to phanerophytes such as *Juniperus phoenice*a, ii) drought-induced defoliation could be visually assessed. I focus our study on adult plants since seedlings and saplings may be differently affected by drought than adults and because recruit abundance may be overrepresented in relation to adults. For each population different measures of abundance such as density, cover, biomass and frequency were estimated (see Annex, Table 1, Table 2 and Table 3). I randomly sited 20 points in each stand and I measured the distance from each point to the closest plant belonging to each species with at least 20 adult individuals growing within the stand. Then, stand density for each species - here representing the average number of plants of each species existing in those stands where a species was found - was estimated as the stand area divided by the mean minimum circular area that must be explored to find the closest plant, determined by the distances from the points to the closest plant. This method to measure species' densities from the distance from a random point to the closest individual could underestimate rare species as it prevents from detecting species with density lower than 80 individuals per hectare. Therefore, for species with less than 20 individuals within the stand, density was estimated by counting all individuals present in two perpendicular transects located in the middle of the stand. For small sized species (less than ca. 20 cm high), transects were of 1 x 50 m, while for medium sized species (between ca. 20 cm and ca. 50 cm high) transects were of 2 x 50 m. Then, regional density was calculated averaging the values of all the stands, that is, including those stands where the species was not found and where stand density was equal to zero.

Species stand cover was estimated for each stand where a given species was present as the average ellipsoidal projection obtained from 15 plants multiplied by species' stand density. Ellipsoidal projections were defined by the largest radius of a plant and its perpendicular one at the centre. Species stand biomass was estimated for each stand where a given species was present by multiplying the species' average ellipsoidal projection by their height and by species stand density. Then, species stand cover and stand biomass were calculated at regional scale as the mean of all stands (including those ones where the species was not found). I also calculated species' frequency of occurrence as the number of stands in which a species was found – hereafter frequency of occurrence -.

Drought resistance levels were visually estimated in the same plants sampled before through the randomly sited point method as the percentage of the remaining leaves (see Annex, Table 3). I only sampled recently defoliated plants (see Annex, Figure 3) to ensure that defoliation was caused by the last drought anomaly. Visual estimations were previously calibrated in order to ensure accuracy (see Annex, Table 4). Calibrations were done by comparing visual estimations with calculated estimations of drought resistance for a representative part of the studied species. Calculated estimations were based on 40 individuals of each species and were defined as the quotient between the weight of the remaining leaves in four standard branches of a given diameter (see Annex Table 4) out of the total weight of these branches (including leaves). Calculated estimations of drought resistance were standardized dividing the values by the highest value found in the same species and then converted into a percentage.

Climatic suitability models and Bioclimatic Anomaly Drought Index

For each species, I obtained occurrence data from whole Europe and the Mediterranean zone at 10 Km resolution from GBIF database (GBIF Data Portal, 2012). This database is formed by two types of data: information about the occurrence of species at particular dates and places, and information about the classification of those organisms into taxonomic hierarchies. A

typical issue when using this databases is getting accurate and reliable data (Marcer *et al.*, 2012) making it difficult to create unbiased models. These data banks use to have taxonomic and recording inconsistencies, such as different types of spatial resolution and entry formats and, thus, in many cases, they are too coarse to be used (McPherson *et al.*, 2006; Niamir *et al.*, 2011). Therefore, it is easy that the resulting model underestimates poor sampled areas and overestimates those that are highly sampled (Phillips *et al.*, 2009). However, reliable information can be obtained after filtering inconsistencies. Values of predictive bioclimatic variables from average conditions period (1950 – 2000) at 1 Km$^2$ pixel resolution were obtained from WorldClim (Hijmans *et al.*, 2005) while values of bioclimatic variables from the climate drought anomaly period (2006-2010) at 1 x 1 UTM resolution were obtained from the AEMET database for the whole Iberian peninsula (AEMET). Then, bioclimatic variables from the average conditions period and the climate drought anomaly period were transformed to 10 Km and 10 x 10 UTM respectively using MiraMon GIS (Pons, 2013) and Quantum GIS software (QGIS Development Team, 2009). Bioclimatic variables from climate drought anomaly period were not transformed to Km as the latitudinal variation of the UTM grids within the modelled background is negligible.

I selected a group of 14 bioclimatic variables for modelling. These variables were : "mean temperature of wettest quarter", "mean temperature of driest quarter", "mean temperature of warmest quarter", "mean temperature of coldest quarter", "max temperature of warmest month", "min temperature of coldest month", "temperature seasonality", "precipitation seasonality", "precipitation of wettest month", "precipitation of driest month", "precipitation of wettest quarter", "precipitation of driest quarter", "precipitation of warmest quarter" and "precipitation of coldest quarter". Then, I built a SDM for each species under average climatic conditions for the European territory and under anomaly conditions for the Iberian Peninsula region using MaxEnt (see Annex, Figure 4 and Figure 5).

I calculated the mean occurrence probability values for all species and both periods from SDM models averaging the occurrence probability values of all the stands. Then, I used these values as a measure of the adequacy of the climatic conditions of these periods for each species in relation to their respective bioclimatic niche - hereafter average or anomaly climatic suitability. Finally, I used the ratio between these two variables to build a normalized Bioclimatic Anomaly Drought Index (BADI) (Equation 1) which represents the impact of the drought anomaly for each species, that is, the displacement that each species has proportionally suffered from their previous bioclimatic suitability in the study area (see Annex, Table 3).

Statistical analyses

Hypothesis 1 (which states that those species that occur farther from their bioclimatic distribution average are the less abundant), was evaluated with a GLM with regional density logarithmically transformed as dependent variable; average climatic suitability as factor and regional biomass logarithmically transformed as a covariable. Regional biomass was included in the model to control possible demographic biases since higher density is expected in short-lifespan or small-sized species. I also performed a log-normal GLZM with frequency of occurrence as dependent variable, average climatic suitability as factor and regional biomass as covariable.

Hypotheses 2a and 2b (which state that those species that are farther from their bioclimatic distribution average have low drought resistance levels and that the most abundant species have higher resistance to drought levels, respectively) were assessed by a log-normal GLZM with drought resistance as dependent variable; average climatic suitability and frequency of occurrence as factors and regional biomass as covariable to control demographic factors, as explained above.

Hypothesis 3 (which states that those species for which the conditions experienced during the bioclimatic anomaly represent a higher proportional displacement from their average

bioclimatic niche experienced lower drought resistance levels) was evaluated with a GLZM with drought resistance as dependent variable; BADI and frequency of occurrence as factors and regional biomass as a covariable to control demographic factors effects.

All these models were subsequently simplified to the significant ones by dropping out non-significant variables (see Table 1). Stand density was not included in our models as it was highly correlated with regional density ($r = 0.91$). Also, stand cover, regional cover and stand biomass were not included as they were highly correlated with regional biomass ($r = 0.84$, $r = 0.97$ and $r = 0.96$ respectively).

I discarded in the analyses those species that showed potential sampling errors, low sample size and high Cooks' distances (after searching for outliers). *Helianthemum apenninum* was excluded from all analyses as it was difficult to distinguish from *Helianthemum hirtum*. Due to high Cooks' distance, *Genista biflora* was excluded from all analyses excepting the GLZM considering drought resistance in relation to BADI, frequency of occurrence and regional biomass. *Buxus sempervirens* was excluded by high Cooks' distance from the GLM considering regional density in relation to the average climatic suitability and regional biomass and, also from the GLZM considering frequency of occurrence in relation to the average climatic suitability and regional biomass. *Juniperus phoenicea* was also excluded due to high Cooks' distance from this last analysis. Finally, *Ononis tridentata* was also excluded due to high Cooks' distance from the GLZM considering drought resistance in relation to the average climatic suitability, frequency of occurrence and regional biomass and from the GLZM considering drought resistance in relation to BADI, frequency of occurrence and regional biomass.

# Results

Assessing models and variables:

Bioclimatic models were consistent and were well adjusted with AUC values over 0.8, except in *Lithospermum fruticosum* (AUC = 0.538) (Table 2). Thus, they had good prediction capacity except in this species, which that was dismissed for subsequent calculations and analyses.

Models built for the period 2006-2010 show clear evidence of a worsening of the climatic conditions for all studied populations growing in the considered area, as supported by the values of anomaly climatic suitability (Figure 2). This is consistent with precipitation and temperature data from the studied region obtained during the average conditions and the bioclimatic anomaly periods (Figure 1).

BADI is sensitive to species that are more threatened by the bioclimatic anomaly, that is with lower probability of occurrence under conditions of climatic anomaly, as supported by high correlations between BADI and species probability of occurrence during the anomaly period (*p-value* < 0.05, *r* = 0.97).

Abundance and bioclimatic niche

GLM analysis considering regional density in relation to average climatic suitability and regional biomass was significant (*p-value* = 0.01, $r^2$ = 0.51). Effects sizes show that both average climatic suitability and regional biomass are significant (*p-value* = 0.011 and *p-value* = 0.005 respectively). Average climatic suitability shows a positive relationship with regional density, indicating that species' population increases as bioclimatic conditions improve (Figure 3). As expected there is also a positive correlation between regional density and biomass. GLZM analysis between frequency of occurrence in relation to average climatic suitability and regional biomass was also significant (*p-value* = 0.042, AIC = 73.53). But effects sizes show that only regional biomass is significant (*p-value* = 0.007).

GLZM analysing drought resistance in relation to average climatic suitability, frequency of occurrence and regional biomass was significant (*p-value* = 0.002, AIC = 118.38). Effects sizes show that only frequency of occurrence is significant (*p-value* = 0.024), being negatively related to drought resistance, thus indicating that more frequent species in the area tend to experience lower drought resistance levels than rare ones (Figure 4).

Drought resistance and deterioration of bioclimatic niche during the climatic anomaly

GLZM analysing drought resistance in relation to BADI, frequency of occurrence and regional biomass was significant (*p-value* = 0.001, AIC = 124.54). Effects sizes show that both BADI and frequency of occurrence are significant (*p-value* = 0.01 and *p-value* = 0.003 respectively). BADI was negatively correlated with drought resistance - following a negative logarithmic-type function -, indicating that those species that experienced larger drought impact in terms of defoliation were also proportionally more displaced from their bioclimatic niche when comparing average and anomaly climatic conditions (Figure 5). Also, drought resistance and frequency of occurrence show a negative relationship as seen before.

## Discussion

This study shows that population-level responses observed at local scales, such population density or defoliation after drought periods, are linked to the bioclimatic niche of the species, estimated from species' regional patterns of distribution. Thus, the results support the hypothesis that local species' abundance in the Valcuerna valley - here, regional density - agrees with the species' bioclimatic suitability in such locality. This relationship appears when the bioclimatic suitability is estimated from the average Valcuerna climatic conditions, which are those that species' populations have endured during decades. This means that this pattern could have been mediated by medium to long-term ecological processes affecting species'

demography, including establishment of species (Meiners *et al.*, 2002), or species' reproductive performance (Muñoz-Vallés *et al.*, 2013), which in turn also determine species' geographic distributions through immigration and extinction processes (Collins & Glenn, 1991). Also, these results support the existence of environmental filters - in our case climatic ones - determining community assembly, according with species niche differentiation (Chesson, 2000). Thus, I observe that some species would achieve dominance - in terms of population density - when climatic conditions fit with their bioclimatic niche, suggesting that the species composition of these communities is driven by species functional differences. This pattern is expected in lastly-successional states (Stokes & Archer, 2010), in contraposition to early-successional states which would be more determined by stochastic dispersal-colonization processes, which in turn are driven by species abundance at larger spatial scales (Volkov *et al.*, 2003). The observed relationship between local abundance and regional occurrence provides insight about the population-level relevance in the likely changes of the species geographic distributions as a consequence of new drought-climate scenarios and, in consequence, of communities' composition (Rehfeldt *et al.*, 2006; Mckenney *et al.*, 2007).

However, the species' ability to resist drought persistent conditions – in terms of avoiding defoliation – was not related to the average bioclimatic suitability of the Valcuerna area for each species. Therefore, the results apparently do not support the hypothesis establishing that those species that occur farther from their bioclimatic distribution average have lower resistance to drought conditions. This could be due to the fact that drought resistance was not measured during the average climatic conditions but during the bioclimatic anomaly, and the relationship would only appear with the last one. But this result also makes sense if I take into account that species subjected to sub-optimal average conditions during a long time could have become acclimated (Gauthier & Jacobs, 2011). Then, the effect of a bioclimatic anomaly could have a reduced impact on those populations that have previously been subjected to

similar conditions during large periods of time (Richter *et al.*, 2012) and, thus, I could not distinguish their effect when estimating drought resistance.

Also differently to the expectations, drought resistance was negatively related to species' frequency, indicating that those species that are more extensively distributed in the area tend to experience lower drought resistance levels than rare ones. Again acclimation can explain this trends, taking into account that those species living in the near-edge of their bioclimatic distribution and being less common in the area have had to face more extreme relative climatic conditions than other species better suited for the same climatic conditions (Brown, 1996; Lennon *et al.*, 2002). Then, less common species could have been acclimated better to drought climatic conditions (Gauthier & Jacobs, 2011), thus developing more drought-resistant phenotypes. Thus, when the bioclimatic anomaly that took place during the period of 2006 – 2010 occurred, near-edges, less common living species could have resisted better the bioclimatic anomaly.

Also, rare species living in the near-edge of their bioclimatic distribution could have been experiencing higher selection pressure due to the drought conditions of the area (Lindner *et al.*, 2010), meanwhile, abundant species located nearer the centre of the bioclimatic distribution are likely to present higher diversity of genotypes as selection pressure acts smoother (Vergeer *et al.*, 2003). Thus, abundant species could present a higher amount of less-adapted genotypes in front of climate-drought anomaly.

However, when considering the displacement that the climatic anomaly produced in the bioclimatic niche of the species (BADI), a clear relationship with drought resistance appeared, as hypothesized. This reaffirms the reported existence of a recent climatic drought period correlated with a loss of green canopy in the region (Vicente-Serrano *et al.*, 2012). The fact that a better correspondence was obtained when relating drought resistance with BADI, but not with the average climatic suitability, points out that defoliation is a response emerging after anomalous drought periods, which in fact perform as analogous of short-term processes

like disturbances (Grimm & Wissel, 1997), but not with the inherent drought of the Mediterranean climate. Also the geographical range used to estimate anomaly bioclimatic suitability (Iberian peninsula) is smaller and closer to the Monegros country than the area considered to calculate the average bioclimatic suitability (Europe and Mediterranean region), and it probably reflects better population-level processes operating in the Valcuerna valley.

The relationship between drought resistance and BADI follows a negative logarithmic-type function (Figure 5) that indicates that the rate of drought resistance increases faster under low BADI values. As drought resistance is the inverse of defoliation, this could be indicating that leaf shedding is a fast response mechanism to drought, as previously known (Pook, 1985): when drought conditions appear, plants could reduce quickly the amount of standing leaves, keeping the minimum to maintain vegetative structures while avoiding water losses (Bullock & Solis-Magallanes, 1990; McDowell, 2011; Pineda-García *et al.*, 2011).

I must take into account that BADI is a quotient, and consequently it is sensitive to low values of species' climatic suitability during the bioclimatic anomaly. This implies that our calculations for the most affected species could be overestimated, that is, our approach could stress the sensitivity to the drought of the more vulnerable species. Other calculations like the difference of the climatic suitability between average and anomaly conditions could not be enough sensitive to detect the effects of bioclimatic drought anomaly in those species that were located near their bioclimatic distribution limit and that present low probability of occurrence values. Finally, species abundance and drought resistance at stand level may be determined by factors other than climate, particularly soil gypsum levels. Although I focused on the overall performance in the Valcuerna study area and this variability was accounted by averaging stand observations, the contribution of these factors merits further exploration when analysing the relationship between population-level performance and bioclimatic niche assessed from regional distributions.

## Conclusions

Here it is shown that regional observations analysed through SDMs reflect species' population abundance and drought resistance patterns at local scale. Particularly, drought resistance is well explained through models that consider the decline in the bioclimatic conditions during extreme drought periods. Drought resistance patterns are determined by short-term ecological processes defined by the bioclimatic conditions existing during drought anomalies. Abundance patterns are correlated with the average bioclimatic conditions typically existing at the location, suggesting that it is well determined by medium to long-term ecological processes, such as species' establishment and reproductive performance. The interrelation between abundance, drought resistance and response to bioclimatic conditions suggests the existence of phenotypic or genotypic selection pressure over populations driving community assembly and dynamics during perturbations, such as extreme climatic periods. This could lead to community shifts and eventually the emergence of new communities with more resemblance with those currently found in more arid regions than in the typical Mediterranean one (Ruiz-Labourdette *et al.*, 2013). Further investigations are needed to assess the importance of these climatic anomalies in the context of upcoming drought-climate scenarios and to assess the possibility of creating a new tool for predicting community dynamics based on this new methodology.

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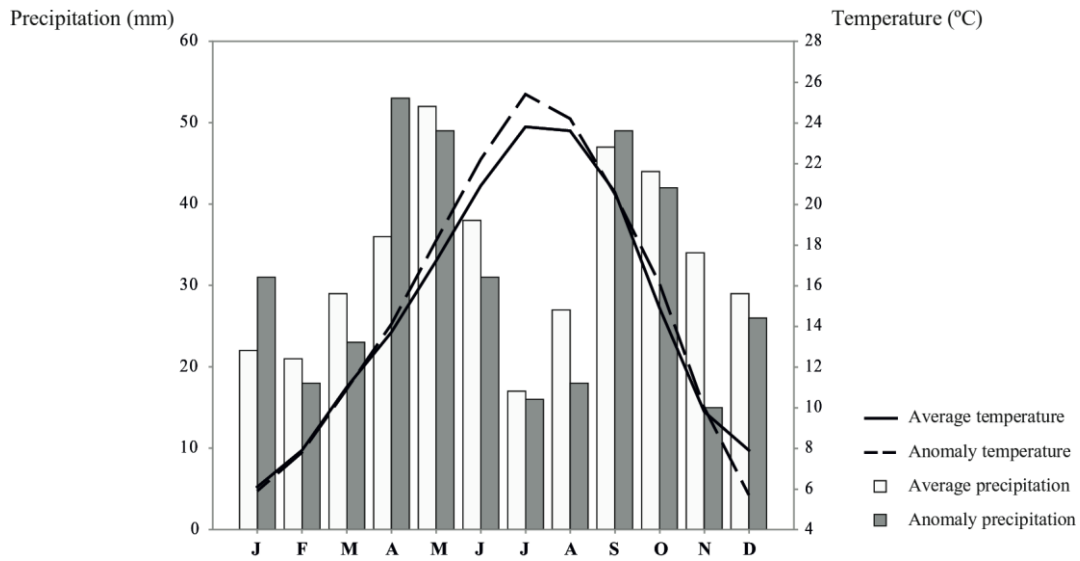
# Tables and figures



**Figure 1** Valcuerna valley monthly precipitation (bars) and temperature (lines) under average conditions (1950-2000) and during the climate drought anomaly (2006 – 2010). Precipitation and temperature values obtained from the AEMET database (AEMET).

$$BADI = \frac{\text{occurrence probability under average conditions } (P\ average)}{\text{occurrence probability under conditions of climatic anomaly } (P\ anomaly)}$$

**Equation 1** Bioclimatic Anomaly Drought Index (BADI). BADI is calculated for a given species as the ratio between its modelled occurrence under average conditions and its modelled occurrence under conditions of climatic anomaly. These values are calculated for a given locality, which in this case corresponds to the Valcuerna valley. The occurrence probability values are calculated at 10 Km$^2$ from a regional bioclimatic distribution model (MaxEnt).

| Model and significant effects | Analysis type | positive/negative effect | *p-value* | r² or AIC |
|---|---|---|---|---|
| **Species' abundance in relation to species' bioclimatic suitability** | | | | |
| **Log(Regional density) = average climatic suitability + Log(Regional Biomass)** | GLM | | 0.010 | 0.51 |
| Average climatic suitability | | + | 0.011 | - |
| Log(Regional Biomass) | | + | 0.005 | - |
| **Frequency of occurrence = average climatic suitability + Regional Biomass** | GLZM | | 0.042 | 73.53 |
| Regional Biomass | | + | 0.007 | - |
| **Species' resistance to drought in relation to species' bioclimatic suitability** | | | | |
| **Drought Resistance = average climatic suitability + Frequency of occurrence + Regional Biomass** | GLZM | | 0.002 | 118.38 |
| Frequency of occurrence | | - | 0.024 | - |
| **Species' resistance to drought in relation to the bioclimatic anomaly** | | | | |
| **Drought Resistance = BADI + Frequency of occurrence + Regional Biomass** | GLZM | | 0.001 | 124.54 |
| BADI | | - | 0.01 | - |
| Frequency of occurrence | | - | 0.003 | - |

**Table 1** Assessment of statistic models performed for each hypothesis. The type of analysis,

significant effects, p-values and positive/negative effects are shown for each model.

| Species | Family | Training data AUC | Test data AUC |
|---|---|---|---|
| *Bupleurum fruticescens* L. | Apiaceae | 0.952 | 0.94 |
| *Lithospermum fruticosum* L. | Boraginaceae | 0.838 | 0.538* |
| *Buxus sempervirens* L. | Buxaceae | 0.924 | 0.909 |
| *Herniaria fruticosa* L. | Caryofyllaceae | 0.98 | 0.939 |
| *Cistus clusii* Dunal | Cistaceae | 0.959 | 0.954 |
| *Fumana ericoides* (Cab.) Gand. | Cistaceae | 0.938 | 0.931 |
| *Fumana thymifolia* (L.) Webb | Cistaceae | 0.933 | 0.931 |
| *Helianthemum apenninum* (L.) Mill. | Cistaceae | 0.932 | 0.888 |
| *Helianthemum syriacum* (Jacq.) Dum. Cours. | Cistaceae | 0.981 | 0.927 |
| *Helianthemum myrtifolium* (Lam.) Samp. | Cistaceae | 0.992 | 0.995 |
| *Helianthemum squamatum* (L.) Dum. Cours. | Cistaceae | 0.975 | 0.971 |
| *Juniperus phoenicea* L. | Cupressaceae | 0.933 | 0.921 |
| *Genista biflora* (Desf.) DC. | Fabaceae | 0.982 | 0.969 |
| *Genista scorpius* (L.) DC. | Fabaceae | 0.928 | 0.918 |
| *Ononis tridentata* L. | Fabaceae | 0.969 | 0.949 |
| *Quercus coccifera* L. | Fagaceae | 0.916 | 0.905 |
| *Globularia alypum* L. | Globulariaceae | 0.97 | 0.952 |
| *Rosmarinus officinalis* L. | Lamiaceae | 0.903 | 0.894 |
| *Thymus vulgaris* L. | Lamiaceae | 0.929 | 0.916 |
| *Rhamnus lycioides* L. | Rhamnaceae | 0.931 | 0.92 |

**Table 2** Assessment of the agreement between modelled and predicted distributions for each sampled species. Training data is the portion of the data used to test the goodness of the model explaining the data used to fit the model. Test data is the portion of the data used to test the goodness of the model predicting independent data. Statistics given are the Area Under the Curve (AUC). Accuracy classification: 1 > AUC > 0.8: good ; 0.8 > AUC > 0.7: fair; 0.7 > AUC: poor (see Phillips *et al.*, 2006).
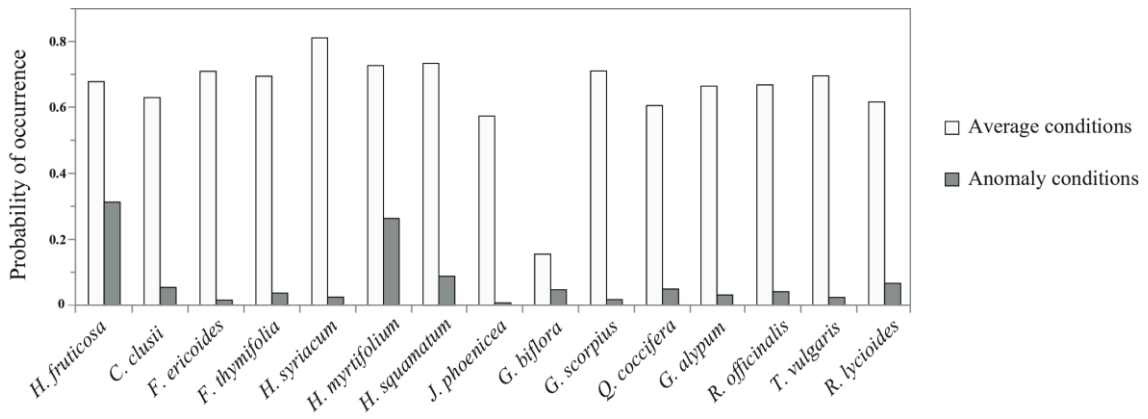
**Figure 2** Probability of occurrence of each species for the average bioclimatic conditions and under conditions of climatic anomaly.
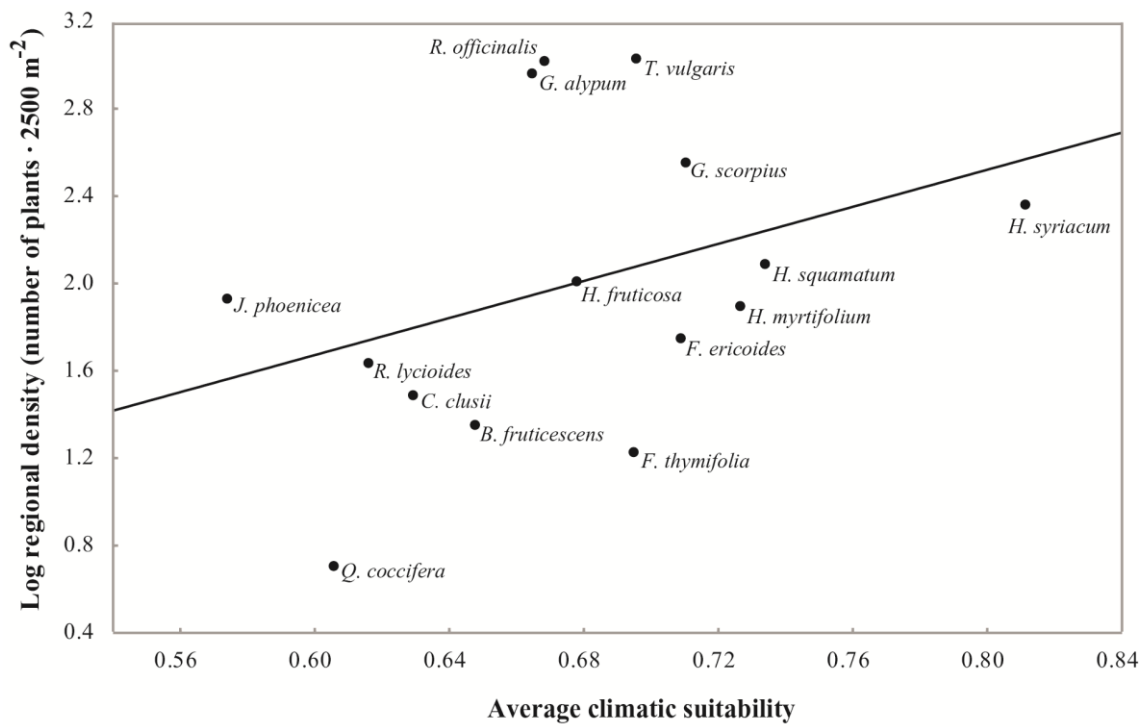


**Figure 3** Relationship between regional density and the average climatic suitability. Regional density values are logarithmically presented.
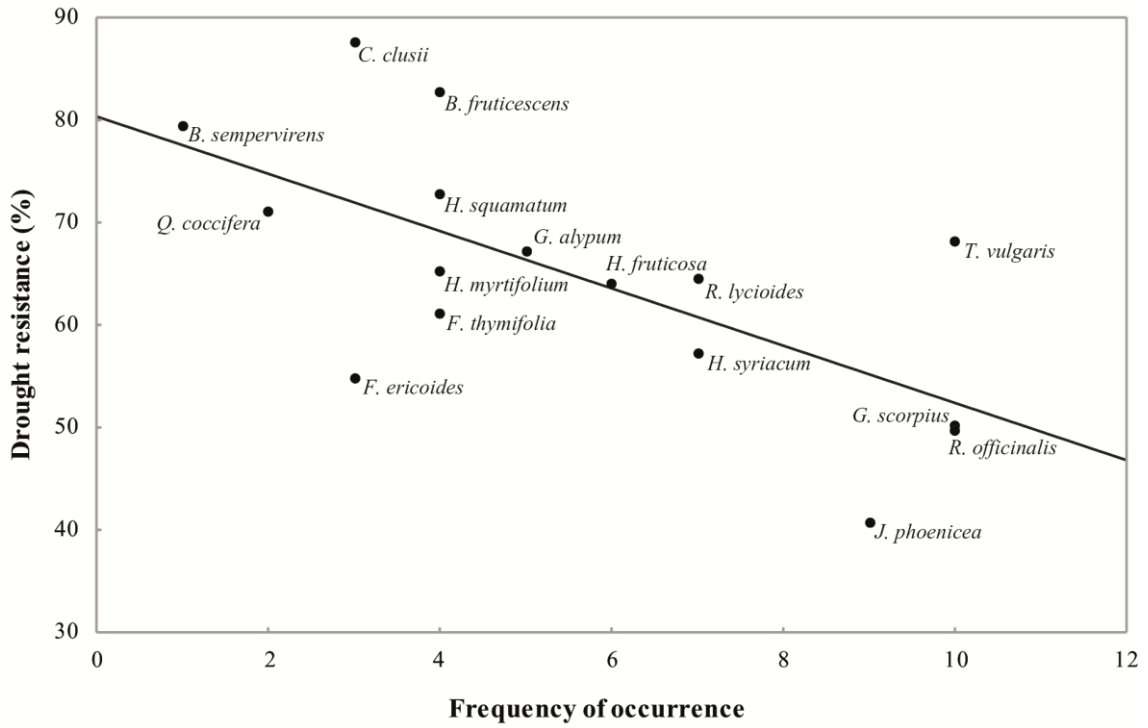
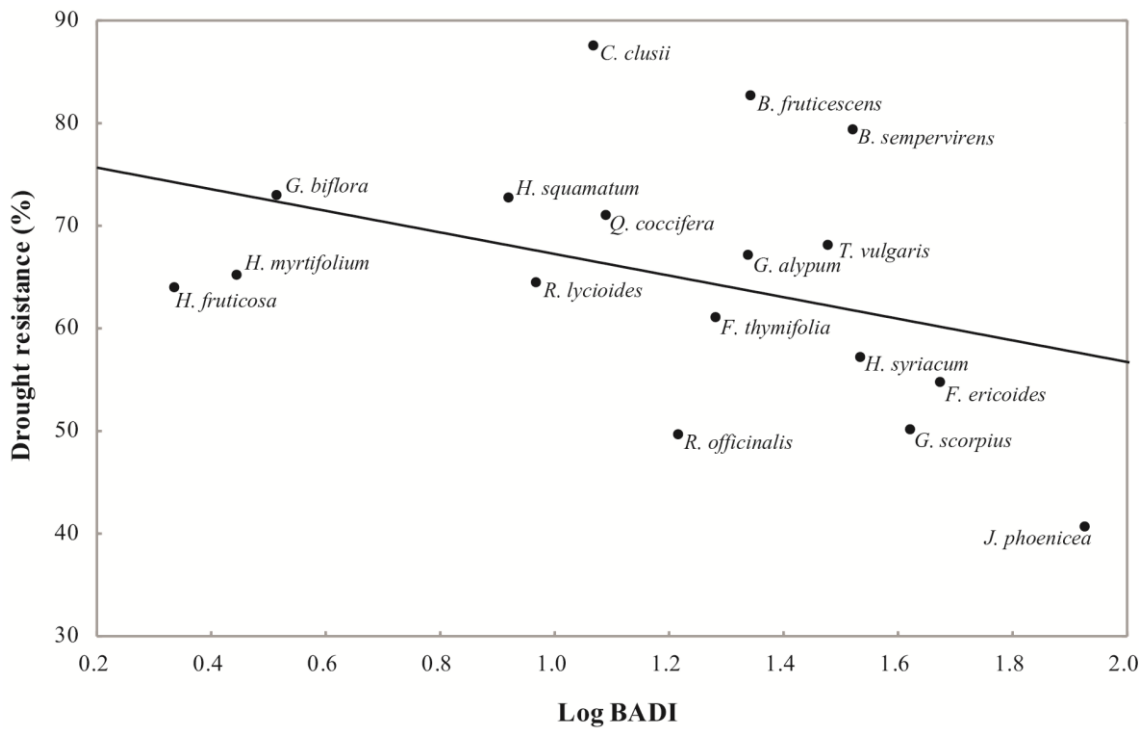**Figure 4** Relationship between drought resistance and species' frequency of occurrence.



**Figure 5** Relationship between drought resistance and Bioclimatic Anomaly Drought Index

(BADI). BADI represents the drought impact level of the anomaly in a given species and the

grade of displacement that a species' bioclimatic distribution has proportionally suffered. BADI

values are logarithmically presented.

**Figure 1** Location of the study area in the Iberian Peninsula.

**Figure 2** View of two of the sites at the beginning of the study when the anomaly was taking place.

| Species | Family | Rejection criteria |
| --- | --- | --- |
| *Pistacia lentiscus* L. | Anacardiaceae | Not enough individuals |
| *Pistacia terebinthus* L. | Anacardiaceae | Not enough individuals |
| *Helicrysum stoechas* (L.) Moench | Asteraceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Staehelina dubia* L. | Asteraceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Boleum asperum* Desv. | Brassicaceae | Aerial structures die every year |
| *Helianthemum hirtum* (L.) Mill. | Cistaceae | Hard to differentiate from H. apenninum without flowers |
| *Juniperus oxicedrus* L. | Cupressaceae | Not enough individuals |
| *Ephedra distachya* L. | Ephedraceae | Higher photosynthetic parts tend to break down making difficult to estimate resistance levels |
| *Ephedra fragilis* Desf. | Ephedraceae | Higher photosynthetic parts tend to break down making difficult to estimate resistance levels |
| *Ononis minutissima* L. | Fabaceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Retama sphaerocarpa* (L.) Boiss. | Fabaceae | Not enough individuals |
| *Phlomis lychnitis* L. | Lamiaceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Salvia lavandulifolia* Vahl | Lamiaceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Sideritis spinulosa* Barnades ex Asso | Lamiaceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Teucrium polium* L. | Lamiaceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Teucrium polium subs. capitatum* L. | Lamiaceae | Leaf morphology and colours make difficult to estimate resistance levels properly |
| *Pinus halepensis* Mill. | Pinaceae | Not enough individuals |
| *Rhamnus alaternus* L. | Rhamnaceae | Not enough individuals |
| *Thymelaea tinctoria* (Pourr.) Endl. | Thymelaeaceae | Not enough individuals |

**Table 1** Species present in the Valcuerna valley that were excluded from the study according to different criteria.

| Species | Family |
|---|---|
| *Bupleurum fruticescens* L. | Apiaceae |
| *Lithospermum fruticosum* L. | Boraginaceae |
| *Buxus sempervirens* L. | Buxaceae |
| *Herniaria fruticosa* L. | Caryofyllaceae |
| *Cistus clusii* Dunal | Cistaceae |
| *Fumana ericoides* (Cab.) Gand. | Cistaceae |
| *Fumana thymifolia* (L.) Webb | Cistaceae |
| *Helianthemum apenninum* (L.) Mill. | Cistaceae |
| *Helianthemum myrtifolium* (Lam.) Samp. | Cistaceae |
| *Helianthemum squamatum* (L.) Dum. Cours. | Cistaceae |
| *Helianthemum syriacum* (Jacq.) Dum. Cours. | Cistaceae |
| *Juniperus phoenicea* L. | Cupressaceae |
| *Genista biflora* (Desf.) DC. | Fabaceae |
| *Genista scorpius* (L.) DC. | Fabaceae |
| *Ononis tridentata* L. | Fabaceae |
| *Quercus coccifera* L. | Fagaceae |
| *Globularia alypum* L. | Globulariaceae |
| *Rosmarinus officinalis* L. | Lamiaceae |
| *Thymus vulgaris* L. | Lamiaceae |
| *Rhamnus lycioides* L. | Rhamnaceae |

**Table 2** Sampled species.

| Variable name | Units | Tranformation type |
|---|---|---|
| Stand density | Number of individuals $\cdot$ 2500 m$^{-2}$ | - |
| Regional density | Number of individuals $\cdot$ 2500 m$^{-2}$ | Logarithmical |
| Stand cover | Percentage | - |
| Regional cover | Percentage | - |
| Stand biomass | m$^3 \cdot$ 2500 m$^{-2}$ | - |
| Regional biomass | m$^3 \cdot$ 2500 m$^{-2}$ | Logarithmical |
| Frequency of occurrence | Count | - |
| Drought resistance | % | - |
| Average climatic suitability | Per unit basis | - |
| Anomaly climatic suitability | Per unit basis | - |
| BADI | Undimensional | - |

**Table 3** Variables used in the study with their units and transformation type when used in a GLM.

**Figure 3** Image of a *Rosmarinus officinalis* L. and *Helianthemum squamatum* (L.) Dum. Cours. individuals that have recently suffered from defoliation.

Recently defoliated leaves are not degraded yet and can be found on the ground near to the plant.

| Species | Family | Standard branch diameter (mm) | $r^2$ |
|---------|--------|-------------------------------|-------|
| *Lithospermum fruticosum* L. | Boraginaceae | 0.12 | 0.5140 |
| *Helianthemum myrtifolium* (Lam.) Samp. | Cistaceae | 0.1 | 0.507 |
| *Juniperus phoenicea* L. | Cupressaceae | 0.42 | 0.5525 |
| *Genista scorpius* (L.) DC. | Fabaceae | 0.2 | 0.6414 |
| *Quercus coccifera* L. | Fagaceae | 0.4 | 0.4723 |
| *Globularia alypum* L. | Globulariaceae | 0.24 | 0.5232 |
| *Rosmarinus officinalis* L. | Lamiaceae | 0.31 | 0.6876 |
| *Thymus vulgaris* L. | Lamiaceae | 0.14 | 0.7056 |
| *Rhamnus lycioides* L. | Rhamnaceae | 0.45 | 0.6269 |

**Table 4** Correlations between visual-estimated resistance and mathematical-based resistance carried out for a representative part of our studied species.

The diameter of the branches used to estimate the ratio between the dry weight of the remaining leaves and the dry weight of the whole branches

(including leaves) is provided (see main text).

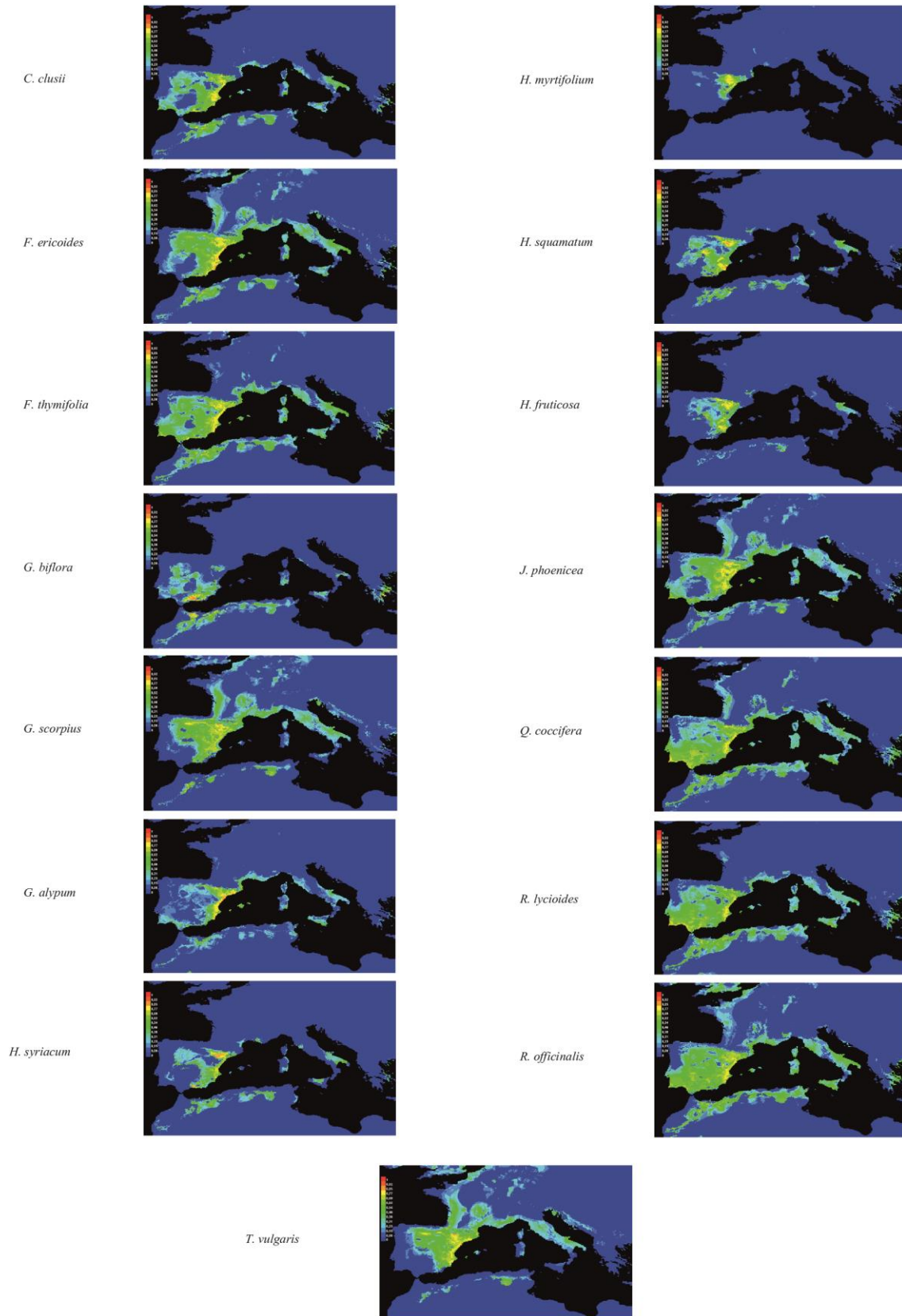**Predicted suitability during normal conditions**



**Figure 4** SDMs for each species under climatic average conditions for the European and Mediterranean region territory. Legend: Probability of occurrence (Blue: 0 – Red: 1).
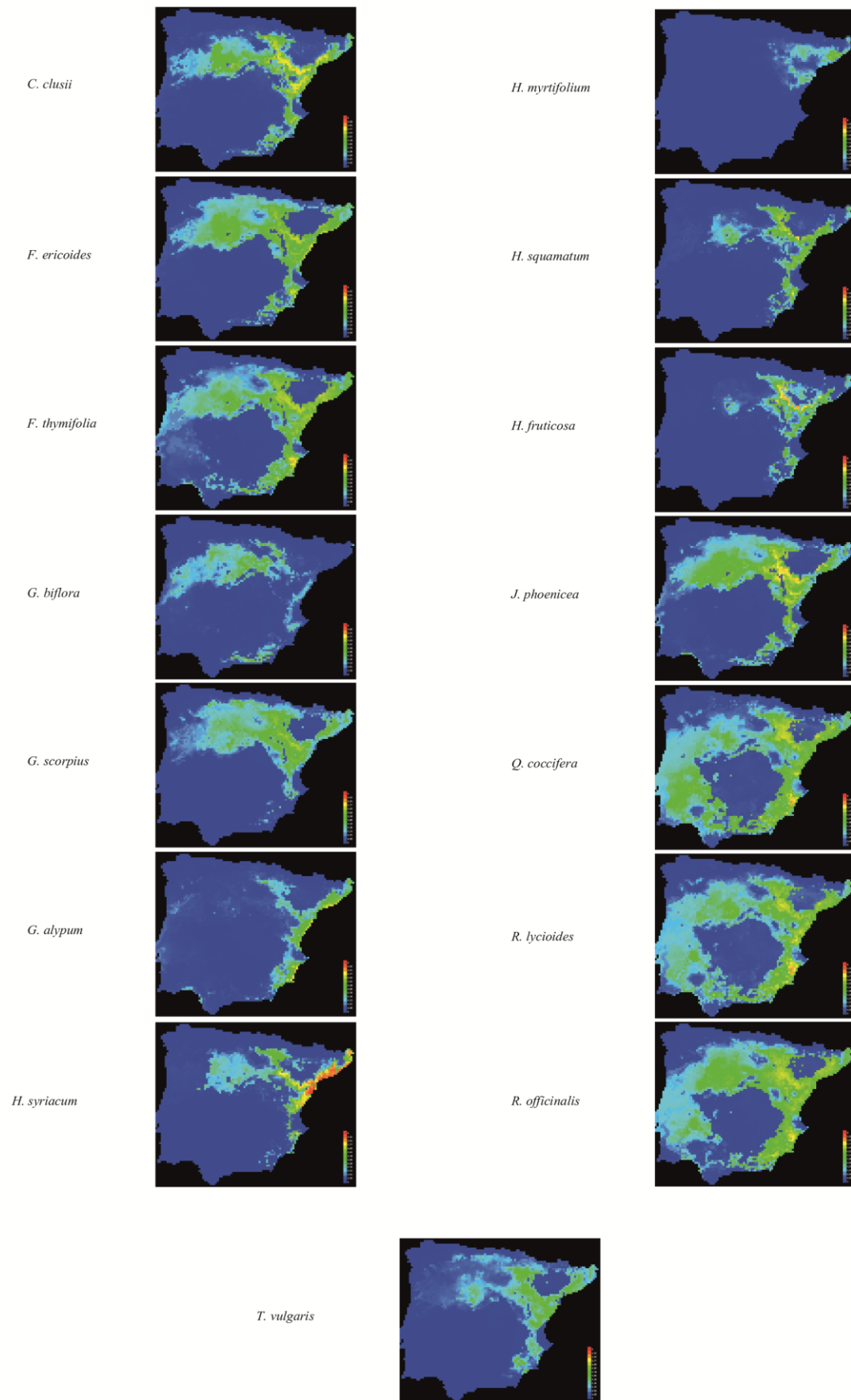
**Figure 5** SDMs for each species under climatic anomaly conditions in the Iberian Peninsula.
Legend: Probability of occurrence (Blue: 0 – Red: 1).

**Figure 6** Example of two individuals of *J. phoenicea* L. from the same site showing great differences on their resistance levels.

**Figure 7** Example of two sites with similar conditions showing contrasting drought resistance (defoliation) patterns.

## Agraïments:

Sembla mentida que de tot el treball això sigui el més difícil d'escriure... necessitaria 8000 paraules més per fer-hi cabre tot el que voldria dir... perdoneu si ara sóc caòtic i desordenat però penso escriure-ho tal com surti:

Primer de tot gràcies a tots aquells que m'heu recolzat durant aquest treball. Laia, Arnau, gràcies per aguantar els meus moments d'èxtasi en els que em poso a explicar la vida de les plantetes i en els que el cap m'explota i tampoc puc parar la verborrea que em caracteritza. Mar, gràcies per fer que la meva vida tingui una mica d'ordre i no sigui el caos personificat, et prometo que em compraré una agenda l'any vinent! I un despertador! Se'm farà molt difícil separar-me de vosaltres després de tants anys junts creixent com a persones i com a científics... (CIENTÍFICS!! Ara semblem gent important!!)

A la meva germana: Gemma, gràcies per acollir-me les mil vegades que he anat a mostrejar als Monegros, ni t'imagines com ajuda tenir un plat calent a taula i un llit tou on dormir cada nit, així com el sentir-se a casa (el meu director crec que també li ha agradat que no li porti tantes factures de dietes).

A en Paco, han passat 3 anys des que vaig entrar al CREAF a fer pràctiques amb tu. He fet feines dures a vegades però sempre ha estat molt fructífer i gratificant. No podria sentir-me més agraït per la dedicació que has tingut amb mi. Has estat el meu mentor i he après moltíssim amb tu. Marxo a fer ciència a un lloc espectacular gràcies a les teves recomanacions. No podria haver tingut un director millor. Per tot i més, gràcies.

A tots els que m'han ajudat durant el treball: Pep Ninot, ha estat un plaer treballar amb tu als Monegros. Amb les teves historietes les hores passen volant. Pep Serra, et dec una birra i una rosa de Sant Jordi (que aquella no era per a tu!) per les hores de paciència explicant-me

MaxEnt. Als estudiants de pràctiques: Bea, Laura i Belén gràcies per ajudar-me! Bel, para ti un muy especial "Muito Obrigado".

I per acabar, a tot el CREAF. Perquè durant 3 anys he après de tots i tothom. El que cadascú m'ha ensenyat, forma una petita part del que sóc avui com a biòleg. Així doncs, m'enduc una part de tots vosaltres a Montana, enlloc em podria haver sentit tan a gust. Entre tots heu fet que el CREAF sigui casa meva. Gràcies.