

# ECOGRAPHY

## Research

### Comparing climatic suitability and niche distances to explain populations responses to extreme climatic events

Maria A. Perez-Navarro, Olivier Broennimann, Miguel Angel Esteve, Guillem Bagaria, Antoine Guisan and Francisco Lloret

M. A. Perez-Navarro (<https://orcid.org/0000-0001-5553-995X>) ✉ ([m.angeles582@gmail.com](mailto:m.angeles582@gmail.com)), Dept of Geography, King's College London, London, UK. – MAP-N and F. Lloret, CREA, Bellaterra (Cerdanyola del Vallès), Catalonia, Spain. FL also at: Ecology Unit, Univ. Autonomous of Barcelona, Bellaterra (Cerdanyola del Vallès), Catalonia, Spain. – O. Broennimann and A. Guisan (<https://orcid.org/0000-0002-3998-4815>), Dept of Ecology and Evolution (DEE), Univ. of Lausanne, Lausanne, Switzerland. – M. A. Esteve, Dept of Ecology and Hydrology, Univ. of Murcia, Murcia, Spain. – G. Bagaria (<https://orcid.org/0000-0001-6465-2866>), Xarxa per a la Conservació de la Natura (XCN), Vic, Spain.

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Habitat suitability calculated from species distribution models (SDMs) has been used to assess population performance, but empirical studies have provided weak or inconclusive support to this approach. Novel approaches measuring population distances to niche centroid and margin in environmental space have been recently proposed to explain population performance, particularly when populations experience exceptional environmental conditions that may place them outside of the species niche. Here, we use data of co-occurring species' decay, gathered after an extreme drought event occurring in the southeast of the Iberian Peninsula which highly affected rich semiarid shrubland communities, to compare the relationship between population decay (mortality and remaining green canopy) and 1) distances between populations' location and species niche margin and centroid in the environmental space, and 2) climatic suitability estimated from frequently used SDMs (here MaxEnt) considering both the extreme climatic episode and the average reference climatic period before this. We found that both SDMs-derived suitability and distances to species niche properly predict populations performance when considering the reference climatic period; but climatic suitability failed to predict performance considering the extreme climate period. In addition, while distance to niche margins accurately predict both mortality and remaining green canopy responses, centroid distances failed to explain mortality, suggesting that indexes containing information about the position to niche margin (inside or outside) are better to predict binary responses. We conclude that the location of populations in the environmental space is consistent with performance responses to extreme drought. Niche distances appear to be a more efficient approach than the use of climate suitability indices derived from more frequently used SDMs to explain population performance when dealing with environmental conditions that are located outside the species environmental niche. The use of this alternative metrics may be particularly useful when designing conservation measures to mitigate impacts of shifting environmental conditions.

Keywords: extreme drought, mediterranean shrubland, niche, plant decay, population performance, SDMs



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## Introduction

In his concluding remarks, Hutchinson (1957) defined the species niche as the  $n$ -dimensional hypervolume – an abstract range of multiple environmental conditions – that allows species to persist indefinitely. Despite the contemporary limitations of niche formalization and representation at that time, Hutchinson also suggested that within this hypervolume, all points would not have equal probability for species' persistence, considering that there would be 'an optimal part of the niche with markedly suboptimal conditions near the boundaries'. This expectation could be considered as inspiration for a largely known paradigm in biogeography: the centre-periphery hypothesis (CPH) (Hengeveld and Haeck 1982, Brown 1984, Pironon et al. 2017). This hypothesis predicts that species' abundance and fitness progressively decline from the geographic distribution center towards the distribution margins, by assuming the concordance between environmental and geographic spaces, given that population performance would decline along with the decrease of environmental suitability, from the niche optimum towards the margins (Maguire 1973, Brown 1984).

Since their emergence, correlative species distribution models (SDMs; Guisan and Zimmermann 2000, Franklin 2010, Guisan et al. 2017) have become one of the most pervasive tools to determine species habitat suitability (Guisan et al. 2013, Araújo et al. 2019). They are statistical models that correlate species occurrences to environmental conditions of the sites where they occur. They provide estimates that can be interpreted as species probability of occurrence or habitat suitability (Guisan and Thuiller 2005, Elith et al. 2011) (ranging between 0 – non suitable environment – and 1 – optimal environmental conditions), which are assumed to correspond to species realized niche when species is in equilibrium with environment (Guisan and Zimmermann 2000, Soberón and Nakamura 2009). SDMs have been used to assess population performance and abundance (VanDerWal et al. 2009, Ureña-Aranda et al. 2015, Csergő et al. 2017). Nevertheless, the correlation between habitat suitability and population abundance or performance is not consistently supported by literature (Sexton et al. 2009, Pironon et al. 2016, Dallas et al. 2017, Chevalier et al. 2021). These poor correlations could be due to negative effects of density-dependence in more densely occupied suitable areas (Thuiller et al. 2014), the lack of consideration of some relevant local microhabitat conditions (such as soils or biotic interactions) in niche estimation (Gurevitch et al. 2016, Csergő et al. 2017, Lembrechts et al. 2019b), the existence of non-equilibrium dynamics (such as high population growth in recently colonized areas even though these locations are scarcely environmentally suitable, Thuiller et al. 2014, Osorio-Olvera et al. 2019), the presence of demographic compensation processes (Doak and Morris 2010), species phenotypic plasticity and adaptation to local conditions (Benito Garzón et al. 2011), or due to data and methodological issues, e.g. missing predictors, linear versus non-linear models, etc. (Yañez-Arenas et al. 2012, Chevalier et al. 2021). The existence of these decoupling

factors, however, does not invalidate the potential role of niche estimates explaining population performance (Csergő et al. 2017), particularly when performance is strongly influenced by climate (Doak and Morris 2010).

Another potential source of discrepancy between species population performance and habitat suitability, could emerge from the limitations of SDMs for spatial and temporal extrapolations. Although SDMs are reasonably accurate for characterizing current natural distributions of species (Elith and Leathwick 2009, Guisan et al. 2013), they could lead to non-reliable suitability estimates when projecting under environmental conditions highly dissimilar from those used to calibrate the models (Dormann 2007, Elith et al. 2010). This risk in extrapolation could be even higher in case of complex models, which often include variables' interaction and could lead to overfitting, increasing the uncertainty when projecting to new scenarios (Thuiller et al. 2004, Merow et al. 2014). In addition, since SDMs outputs are constrained between 0 and 1, they systematically produce zero values when environmental conditions are unfavorable (i.e. below a determined species tolerance threshold), thus hindering the correlation between suitability and population performance (Perez-Navarro et al. 2018).

According to the niche theory, species probability of occurrence would be null outside of the niche space, but there are several circumstances that may allow populations to temporarily occur outside of their fundamental niche boundaries. For instance, they could persist under unfavorable conditions (sink habitats, with a negative population growth) if they are sustained by immigration from source habitats (Pulliam 2000). Similarly, plant longevity may also lead to population persistence when environmental conditions become unsuitable, delaying climate-induced changes in species distribution (i.e. extinction debt, Svenning and Sandel 2013). Finally, pulses of abrupt climatic changes can temporarily locate populations outside of the species niche (Perez-Navarro et al. 2018). In this case, the combination of the magnitude (i.e. distance to species niche) and duration of the temporal climatic shift will determine populations mortality and survival rates, allowing species to recover after the episode if the climatic drift is not too long and intense. For those populations living temporarily 'outside' their niche, it could be expected to find higher decay and lower growth rates in populations located farther away from the niche margins compared to populations located outside but closer to the niche margins. This implies that, as the capacity to host a species within its niche is different at each site across niche space (Hutchinson 1957, Maguire 1973, Brown 1984), sites outside the species niche may not have the same potential for hindering species occurrence.

Consequently, niche parameters or indexes other than standard SDM suitability predictions, not constrained between 0 and 1, are required to assess and predict demographic responses for populations located outside of the species niche (where SDM-based suitability is zero), such as sink populations, alien species invasions or populations suffering extreme climatic episodes. For instance, environmental distances to niche centroids and margins are not floored at zero and

provide continuous values even if the population is located outside of the species niche. While niche centroids represents the optimal conditions for species persistence, niche margins represent the expected threshold separating species persistence from extinction, that is, positive from negative growth rates (Pulliam 2000, Soberón 2007). Recent studies have used distances to niche margins to explain invasion success (Broennimann et al. 2021), or distances to niche centroid to explain populations' abundances (Martínez-Meyer et al. 2013, Osorio-Olvera et al. 2020, Chevalier et al. 2021), growth rates (Manthey et al. 2015) and genetic diversity (Lira-Noriega and Manthey 2014). However, no study has yet provided an explicit comparison between SDM-derived climatic suitability and both distances to niche centroid and margin in the environmental space to explain populations' performance. Here, we fill this gap and compare the use of 1) Euclidean distances between population locations and species niche centroids and margins in environmental space (Fig. 1) and 2) SDMs-derived climatic suitability, to explain populations performance.

In order to contrast the predictive capacity of SDMs derived suitability and niche distances, we use species defoliation and mortality datasets collected just after an extreme drought year occurring in the southeast of the Iberian Peninsula. Specifically, here we 1) tested, across 38 woody species, whether populations located farther from the species' niche centroid and margins during the extreme event showed higher population decay, measured as remaining green canopy (RGC) and mortality; 2) compared the capacity of distances to climatic niche centroid and distances to climatic niche margins to explain decay; 3) compared niche-based distances and SDM derived suitability as predictors of populations decay.

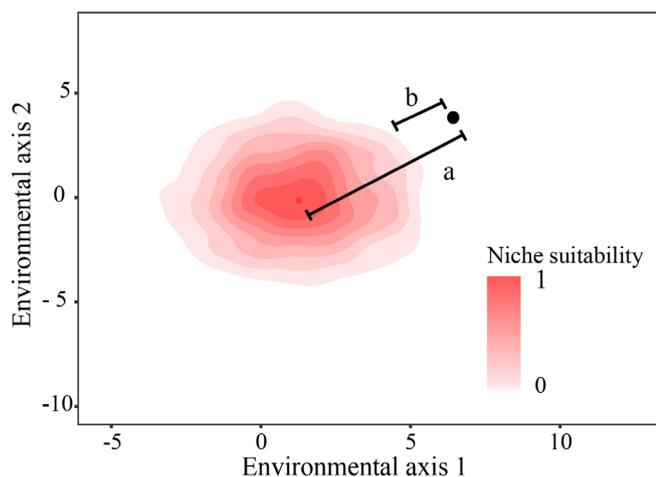


Figure 1. Example of species niche in an environmental space defined by two environmental axes. White to red color gradient represents species climatic suitability, where 1 (red) corresponds to niche optimum and 0 (white) to the environmental space outside of the niche envelope. The black dot represents a population located outside of species niche boundaries, and 'a' and 'b' are distances to the niche centroid and to the closest point of the niche margin, respectively.

## Material and methods

### Study area

The study was carried out in three shrubland areas in the southeast of the Iberian Peninsula (Fig. 2): Cuatro Calas (1.63°W, 37.38°N), Moreras mountain (1.32°W, 37.56°N) and Calblanque Natural Park (0.74°W, 37.61°N). These areas share similar plant communities, dominated by semi-arid native shrubland species – belonging to genus *Genista* (Fabaceae), *Helianthemum* (Cistaceae), *Teucrium* (Lamiaceae) or *Thymus* (Lamiaceae) – mixed with tussock grasses (mostly *Macrochloa tenacissima* (L.) (Poaceae)).

The study sites are included within the Mediterranean xeric bioclimate (Rivas-Martínez et al. 2017), experiencing a mean annual temperature of 17°C, and annual rainfalls of 245–300 mm (reference period 1971–2000, AEMET and IP 2011). During the hydrological year 2013–2014 the Iberian southeast suffered its driest year on record, leading to extensive plant communities' die-off (Perez-Navarro et al. 2018). Particularly, Cuatro Calas and Moreras Mountain accumulated less than 30% of the average precipitation for the reference period 1971–2000 and Calblanque Natural Park less than 70% (Supporting information, AEMET 2014).

### Decay data

During January–March 2016, 30 replicated plots of 5 × 5 m were established within each area. Plots were separated from each other by at least 25 m. All plots shared similar topographic characteristics with moderate to slight slope and south or southeast orientation. Within each plot, we recorded the total number of individuals per woody species (total of 38 species) and visually estimated the proportion of remaining green canopy (RGC) per individual (as a proxy of species decay, according to Sapes et al. 2017 and Perez-Navarro et al. 2018). To ensure that the green cover loss resulted from the recent drought, we avoided individuals with signs of older decay (e.g. stumps, decomposed stems, branches with no thin tips). In case of plants with photosynthetic stems and no leaves, defoliation was considered as the presence of dry stems. Finally, each individual was also categorized as alive (RGC > 0%) or dead (RGC = 0%). We recorded a total of 12 123 individuals.

### Species' occurrences data

We compiled the geographical distribution data of the 38 sampled species from the Global Biodiversity Information Facility (GBIF) (GBIF 2019, <www.gbif.org>) and the herbarium of the Institut Botànic de Barcelona. We filtered species occurrences to remove taxonomic and geographic inconsistencies and to reduce possible sampling bias by randomly thinning species' records to one observation per km<sup>2</sup> (in concordance with the spatial resolution of the climatic dataset). Final species occurrences datasets ranged from 60 to 7000 observations.

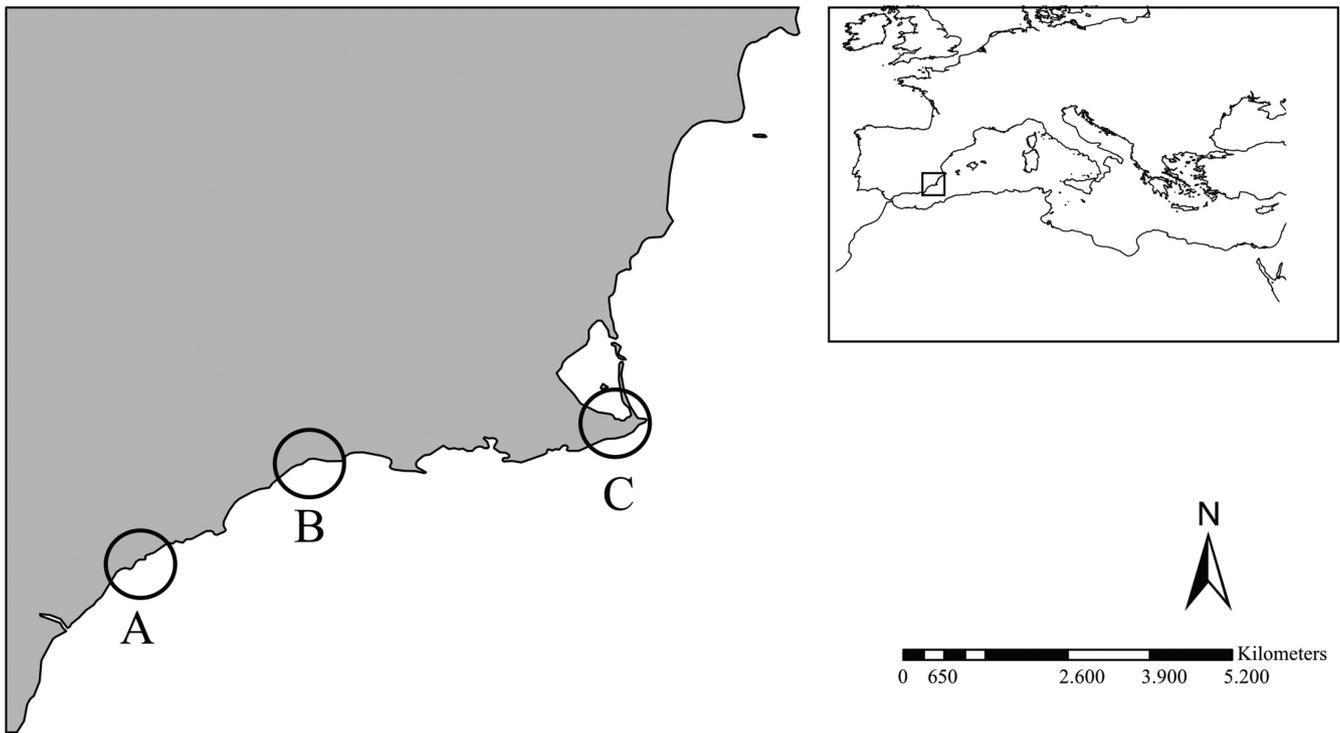


Figure 2. Top right panel shows the location of the study region in the Mediterranean basin. Left panel shows the expanded map of the study area, indicating the study sites: (A) Cuatro Calas (sandstone bedrock), (B) Moreras' mountain (limestone bedrock) and (C) Calblanque Natural Park (schist metamorphic bedrock).

### Climatic data

We used 12 bioclimatic variables at 1 km<sup>2</sup> resolution for the climatic period 1979–2012 (34 years): annual mean temperature (bio 1), temperature seasonality (bio 4), maximum temperature of warmest month (bio 5), minimum temperature of coldest month (bio 6), mean temperature of warmest quarter (bio 10), mean temperature of coldest quarter (bio 11), annual precipitation (bio 12), precipitation of wettest month (bio 13), precipitation of driest month (bio 14), precipitation seasonality (bio 15), precipitation of wettest quarter (bio 16) and precipitation of driest quarter (bio 17). These variables were obtained after retrieving monthly temperature and precipitation variables for every year of the period 1979–2012 from the Chelsa yearly climate database (Karger et al. 2017), by applying the biovars function (dismo package Hijmans et al. 2016). We selected these 12 bioclimatic variables instead of the total 19 variables available in the Chelsa database in order to simplify axes interpretation, avoiding variables corresponding to the interaction between temperature and precipitation (e.g. maximum temperature of driest quarter), which may correlate differently depending on species distribution areas and time period. From this yearly climatic data, we established two alternative climatic datasets: 1) one with interannual climatic resolution to calibrate the environmental climatic space for niche characterization (so the common climatic space can be in concordance with the temporal resolution of the extreme drought year), and 2) one with average climatic resolution, by averaging the yearly

values of the former dataset, to characterize species niches and fit SDMs.

For the extreme year 2013–2014 we obtained the climatic variables at 1 km<sup>2</sup> resolution from monthly precipitation and maximum, minimum and mean temperature records from 68 to 114 weather stations of the Spanish Meteorological Agency (AEMET), by applying Ninyerola et al. (2000) procedure (Supporting information) and the 'biovars' function (dismo package, Hijmans et al. 2016). We also selected the same 12 bioclimatic variables.

### Niche characterization and estimation of environmental distances

We first built the common climatic space by using a principal component analysis (PCA) to convert the environmental space constituted by the 12 bioclimatic variables into a two-dimensional surface defined by the first and second PCA components (Broennimann et al. 2012). The PCA was calibrated with ade4 package (Dray and Dufour 2007) using the climatic values for every single year of the 1979–2012 period at all the sites where at least one of the 38 analyzed species occurred (PCA-occ sensu Broennimann et al. 2012) (Supporting information). We built the common environmental space considering inter-annual variability in order to avoid the extreme year to be outside of the environmental space. The first and second axes of the PCA explained together the 60.8% of the climatic variability (Supporting information).

In this common climatic space, we characterized each species' niche using average climatic data. We used average climate in order to keep the concordance with MaxEnt as this cannot be fitted with temporal hierarchical data. We characterized the species niche using 2d kernel density function (Duong 2018) and following Broennimann et al. (2021), see Supporting information for further details. Then, we estimated the species niche centroid as the gravity center of species' niche (i.e. mean of climatic PCA axis values weighted by species' density), and the species niche margin as the perimeter of species' niche space after discarding densities below the 0.05 lowest percentile.

Finally, we estimated population distances to species niche centroid and limits during both the average climatic period and the extreme drought episode. To do that, we first calculated the PCA scores (i.e. the coordinates in the climatic space) of each studied population (population climate, hereafter) during the reference average period and during the extreme year using the function `suprow` of package `ade4` (Dray and Dufour 2007). Distance to species' niche centroid was estimated as the Euclidean distance between population climate (average or extreme climate) and species niche centroid (Martínez-Meyer et al. 2013). Distance to species niche margin was estimated following three steps similarly to Broennimann et al. (2021). We first assigned positive sign (i.e. multiply by +1) to distances of populations located outside of the niche, and negative sign (i.e. multiply by -1) to those located within the niche. Second, we calculated the Euclidean distance between the population climate (average or extreme climate) and the closest point in niche margin. Finally, in order to compare distances across species, we standardized population distances to species niche size. Here, we scaled margin distances in two different ways. First, by dividing margin distance by the distance between population's closest point in the niche margin and niche centroid (i.e. niche amplitude in the direction of population location in the environmental space, hereafter scaled by centroid–margin distance). According to Fig. 1, distance between niche centroid and population's closest point in the niche margin could be calculated as:  $a - b$  when population is located outside of species niche, and  $a + b$  when population is located inside of the species niche. Second, by dividing margin distance by total niche area (hereafter niche scaled by area). Finally, we also estimated the Mahalanobis distance for each population to the species niche also using the same two PCA axes in order to test its differences with Euclidean distances. All four approaches were used in subsequent analyses but only Euclidean distance to niche centroid and to niche margin scaled by centroid–margin distance are showed in the main results. Results of models including Euclidean distances to niche margin scaled by area and Mahalanobis distance are given in the Supporting information. Note that it is also possible to scale distances to niche centroid by niche size, however here we kept them as absolute values in order to allow comparisons with the niche centroid use in current literature (Martínez-Meyer et al. 2013, Martínez-Gutiérrez et al. 2018, Osorio-Olvera et al. 2020) and to avoid overlapping information with distance to niche margin index.

## SDM-derived suitability

From the species occurrence data and climatic average datasets described above, we further built standard species distribution models (SDMs) for every species to estimate populations' climatic suitability both during the average and the extreme drought episode. We specifically used the MaxEnt algorithm (Phillips and Dudík 2008) in R (`dismo` package Hijmans et al. 2016), with the same 12 variables used in niche characterization. Each species model was built with 20 000 background points randomly distributed in the biogeographic study region. The geographic background area was defined by applying trend surface analyses (TSA, Acevedo et al. 2012) over all species occurrences, see Supporting information for further details. In addition, `ENMEeval` package (Muscarella et al. 2014) was used on 8 different representative species to find the most accurate model predictors according to AIC, AUC and Boyce index criteria (Supporting information). Final MaxEnt models were fitted including regularization multiplier (index penalizing model complexity) of 2, and hinge, product, linear and quadratic features. Five-fold cross-validation was applied and final climatic suitability was estimated as the average of the 5-fold replicates for MaxEnt logistic output (equivalent to species probability of occurrence) (Phillips and Dudík 2008). No threshold was applied over the continuous suitability. Models' accuracy was evaluated using the area under of the receiver operating characteristic curve (ROC) curve (AUC; Hanley and McNeil 1982), and Boyce index (Boyce et al. 2002, Hirzel et al. 2006). Each species' model was finally projected on the average reference climate, as well as on the extreme climatic conditions, to obtain populations' climatic suitability during the reference and the extreme climate period. Supporting information summarizes the different steps of MaxEnt modeling approach.

## Statistical analyses

We applied generalized linear mixed models (GLMM fitted with `lmerTest` R package, ver. 3.1.0, Kuznetsova et al. 2017) with species decay (RGC or mortality) as response variable, and population distances to species niche (to centroid, margin or Mahalanobis) or population climatic suitability derived from MaxEnt as explanatory variables, with species and plot nested within site as crossed random effects. These models were applied both for the climatic average period and the extreme drought year. To reduce noise in model residuals, we aggregated the original dataset (12 124 total individuals) at the species  $\times$  plot level and added the number of individuals per species and plot as a weighting factor in the mixed models. Due to the high impact of drought on plant species during the extreme drought year, RGC showed a zero-inflated distribution (Martin et al. 2005), so we separately model RGC  $> 0$  and mortality percentage as response variables (similarly to Guisan et al. 1998 with ordinal data), both with binomial error distribution (i.e. a form of 2-steps zero-inflated model; Barry and Welsh 2002). We finally built the next ten

models, both for the average and the extreme climatic period: 1) RGC as a function of niche centroid Euclidean distance, 2) RGC as a function of niche margin Euclidean distance scaled by centroid–margin distance, 3) RGC as a function of niche margin Euclidean distance scaled by niche area, 4) RGC as a function of Mahalanobis distance, 5) RGC as a function of SDM-derived climatic suitability, 6) mortality as a function of niche centroid Euclidean distance, 7) mortality as a function of niche margin Euclidean distance scaled by centroid–margin distance, 8) mortality as a function of niche margin Euclidean distance scaled by niche area, 9) mortality as a function of Mahalanobis distance and 10) mortality as a function of SDM-derived climatic suitability.

## Results

Regarding to populations' position in the environmental space, we found that the 58.8% of analyzed populations were located within their respective species niche during the average reference period 1979–2012, while this percentage decreased to 3.3% during the extreme drought period 2013–2014. Accordingly, mean relative distance to species niche margin (scaled by centroid–margin distance) was  $-0.057 \pm 0.256$  during the reference period, where negative distance means that on average populations were located within species niche, while mean distance to species niche margin was  $0.550 \pm 0.311$  during the extreme drought, where positive distance means that on average populations were located outside of their species niche. Average distance to species niche centroid was  $2.951 \pm 1.720$  during the reference period and  $5.204 \pm 1.667$  during the extreme period. Regarding to the SDM (MaxEnt) derived climatic suitability, 0% of population had close to 0 suitability value (i.e. less than 0.01) during the average reference period, while this percentage was 29.32% during the extreme year. Accordingly, average climatic suitability was  $0.524 \pm 0.21$  during the reference period and  $0.086 \pm 0.18$  during the extreme period (Supporting information). AUC values were on average  $0.98 \pm 0.01$  for all the analyzed species and boyce index was  $0.93 \pm 0.03$ .

### Remaining green canopy as response to drought

Both Euclidean distance to species niche margin (scaled by distance centroid–margin distance), Mahalanobis distance and climatic suitability estimated for the reference period 1979–2012 significantly explained the observed remaining green canopy (RGC) after the extreme events (Fig. 3, Supporting information). Populations distances to species niche centroid and to niche margin scaled by niche area were marginally significant during the average reference period. All niche distances showed negative relationship with RGC, while climatic suitability positively related with RGC.

When considering the climatic conditions of the extreme episode, RGC was significantly explained by populations Euclidean distances to niche margin (scaled by both approaches; Methods) and Mahalanobis distance and

marginally explained by population Euclidean distances to niche centroid (Fig. 3 and Supporting information), indicating that those populations displaced farther from species niche during the extreme period suffered higher canopy losses. Contrastingly, climatic suitability during the extreme event did not correlate with RGC, presumably due to the extremely low suitability values obtained for almost all populations (Fig. 3).

### Mortality as response variable

When analyzing mortality as response variable, we found that both population Euclidean distances to species niche margin scaled by distance between margin and centroid, Mahalanobis distance and climatic suitability predicted on the average reference period 1979–2012 significantly explained mortality percentage. Distance to species niche margin estimated during the reference period showed positive relationship with mortality percentage, while climatic suitability showed a negative relationship. Contrastingly, we did not find any significant correlation between mortality and population Euclidean distances to niche centroid (Fig. 4) nor to niche margin scaled by niche area (Supporting information).

In the case of population climatic conditions during the extreme drought event, we observed that Euclidean distance to species niche margin (both scaled by centroid–margin distance and scaled by niche area) significantly and positively related to species mortality (Fig. 4 and Supporting information), whereas population distance to niche centroid and climatic suitability derived from MaxEnt were not significant (Fig. 4). Mahalanobis distance also significantly explained mortality during the extreme event, although showed lower explanatory capacity than distance to niche margin (Supporting information).

## Discussion

### Niche estimates and demographic responses under extreme climatic events

In this study, we show that population distances to species' niche margin and centroid in environmental space, both during the extreme event and during the historical reference period, explained differences in the performance of populations of different species during an extreme drought episode (Fig. 3, 4), with those populations located farther from species niche showing higher decay during drought. Particularly, while distances to species niche centroid significantly explains remaining green canopy (RGC), relative distances to species niche margin significantly and more strongly explained both mortality percentage and RGC. In spite of the weak literature support to the correlation between species demographic performance and climatic niche parameters (Sexton et al. 2009, Dallas et al. 2017, Chevalier et al. 2021), several studies have shown better population performance or higher populations abundance at the species niche center compared

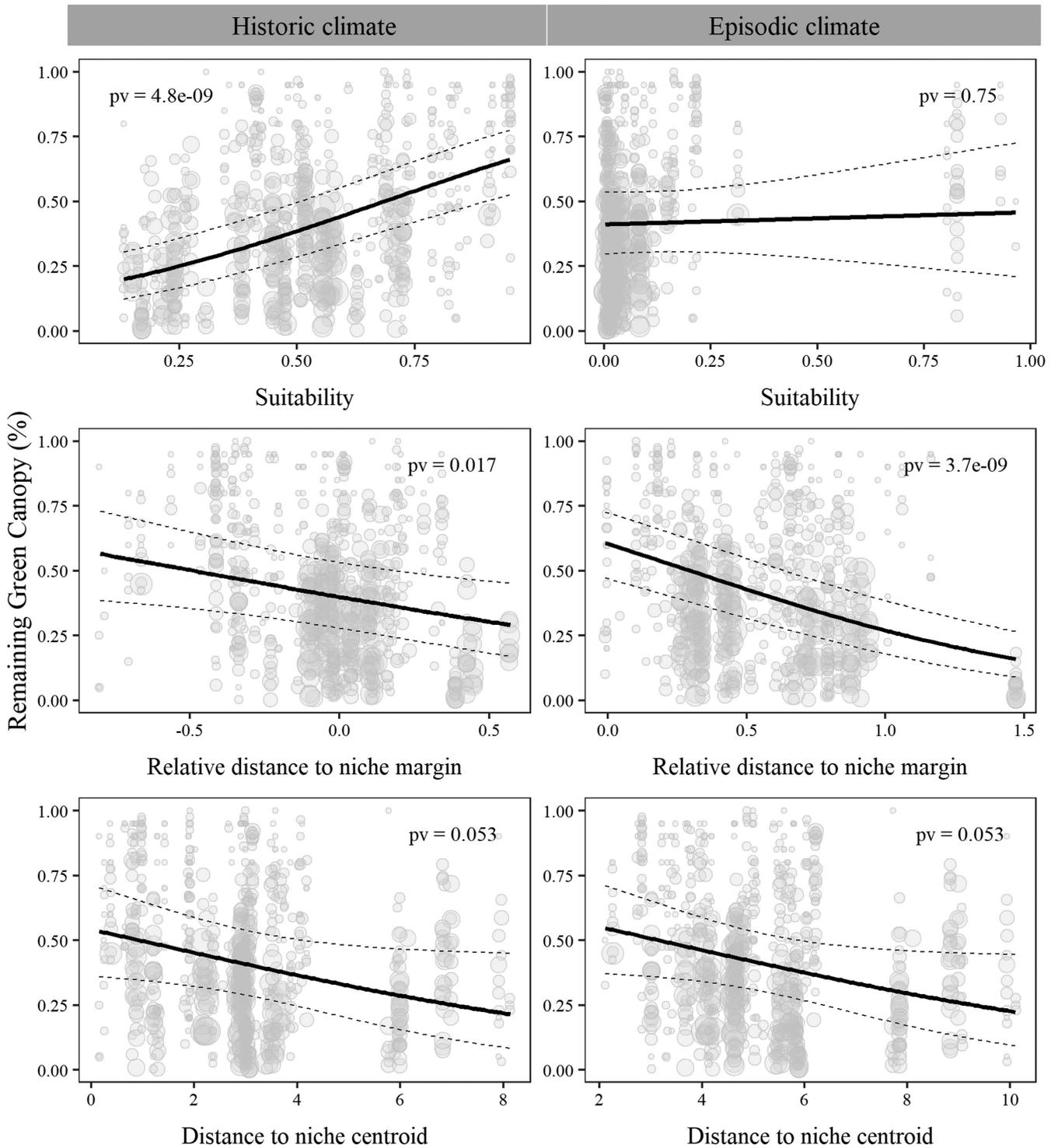


Figure 3. Remaining green canopy (RGC) in relation to population distances to species niches and climatic suitability. Left column shows RGC responding to niche metrics and climatic suitability, both estimated for the average reference period 1979–2012. Right column shows RGC responding to niche metrics and climatic suitability estimated for the extreme drought period 2013–2014. Top panel row shows climatic suitability derived from MaxEnt as explanatory variable, middle panel row shows populations distances to species niche margin scaled by distance between niche centroid and populations' closest margin point as explanatory variable, and bottom panel row shows populations distances to niche centroid as explanatory variable. Plot points represent each different analyzed population (i.e. species  $\times$  plot) and are sized by populations' number of individuals. Each panel also shows ANOVA p-values (pv) for testing significance.

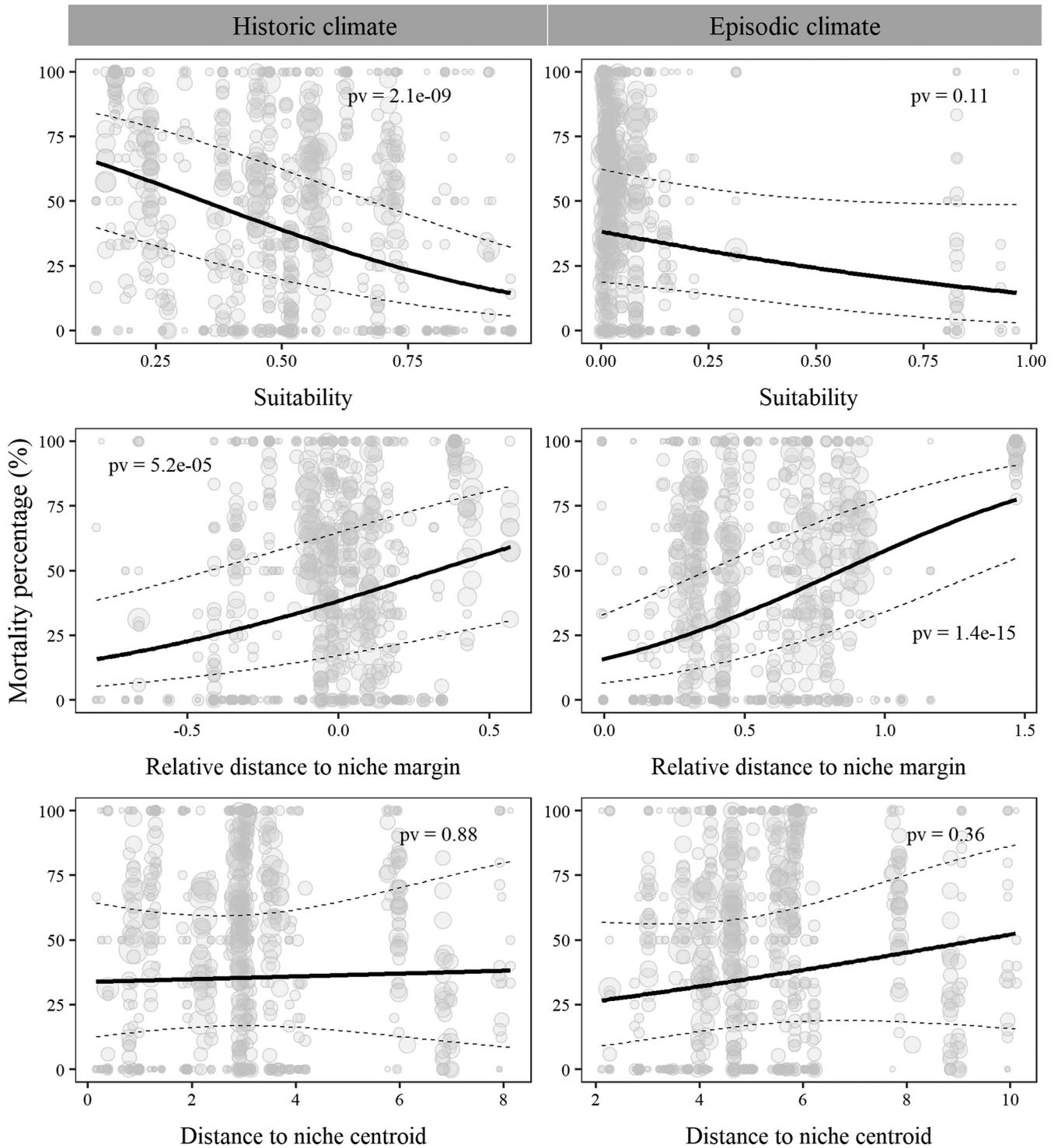


Figure 4. Mortality percentage in relation to population distances to species niches and climatic suitability. Left column shows mortality percentage responding to niche metrics and climatic suitability, both estimated for the average reference period 1979–2012. Right column shows mortality percentage responding to niche metrics and climatic suitability estimated for the extreme drought period 2013–2014. Top panel row shows climatic suitability derived from MaxEnt as explanatory variable, middle panel row shows populations distances to species niche margin scaled by distance between niche centroid and populations' closest margin point as explanatory variable, and bottom panel row shows populations distances to niche centroid as explanatory variable. Plot points represent each different analyzed population (i.e. species  $\times$  plot) and are sized by populations' number of individuals. Each panel also shows ANOVA p-values (pv) for testing significance.

to the species range margins (Jump and Woodward 2003, Martínez-Meyer et al. 2013, Sangüesa-Barreda et al. 2018, Osorio-Olvera et al. 2020), especially under extreme climatic conditions (Sapes et al. 2017, Lloret and Kitzberger 2018, Perez-Navarro et al. 2018). These latter studies evidenced a negative correlation between climatic suitability under historical reference conditions and population decay during extreme drought, pointing that populations historically located farther from species' climatic optimums showed higher sensitivity to extreme climatic events. Here, we show that the use of distances in environmental space allows to demonstrate that also those populations that resulted more displaced from the species niche – especially from the margins – during the extreme climatic episode are more prone to decay, regardless from the population location within the species niche during the reference period. In fact, population distances to niche margin during the extreme episode explained a slightly higher percentage of variability in decay models than the same distance metrics during the reference period (Supporting information). The relationship between population performance and niche distances could emerge more evidently during extreme climatic episodes than during normal years because demographic responses under exceptionally extreme climatic episodes are likely more influenced by climate than by other environmental forces, such as unmeasured microhabitat conditions, species interactions or favorable community structure (Dallas et al. 2017).

Interestingly, distances to niche margin or centroid seemed not to be completely interchangeable when explaining continuous responses (RGC) or binary states (dead–alive). Whereas both distances to niche centroid and margins significantly explained population differences in RGC (Fig. 3, Supporting information), distances to species niche centroid were not significant to explain population mortality. Consistent with the niche concept, this result suggests that demographic binary responses directly related to plant occurrence, such as mortality, are better informed by population position in niche space (within or outside the niche), which is implicitly contained in populations distances to niche margins (Fig. 4, Supporting information). These findings are consistent with general biogeographic paradigms assuming a gradient of population fitness within the niche, decreasing from niche centroid towards the margins (Maguire 1973, Pironon et al. 2016), with mortality being particularly relevant outside of species niche boundaries, where environmental conditions do not fulfill species' requirements (Hutchinson 1957, Maguire 1973).

Populations distances to species niche margins scaled by niche area showed lower explanatory capacity than those scaled by centroid–margin distance, and they only significantly explained population performance when they were estimated for the extreme climatic episode (Supporting information). Although niche area represents the actual size of species realized niche, it does not include information about the position of niche optimum within niche boundaries, giving same results for skewed and symmetrical niches. Populations distances to niche margin scaled by centroid–margin

distance, otherwise, captures population position regarding to niche centroid, thus giving different results if population is located outside of species niche but closer or farther to niche centroid. We suggest here that, given that realized niches are often asymmetrical (Brown et al. 1996), niche distances scaled by centroid–margin distance constitute the most informative index to explain populations performance. In fact, we also found that Mahalanobis distance (which measures distance to species niche centroid but controlling by the dispersion of the rest of species occurrences, and thus, implicitly account for populations relative position in niche space), also explained decay better than Euclidean distance to niche centroid and to niche margin scaled by niche area.

### **Distances in the environmental space versus climatic suitability**

While our findings support the use of niche distances under climatic conditions for both reference and extreme period, populations' climatic suitability based on standard SDM approaches only explained population observed decay responses (both mortality and green cover losses) when projected on the average reference period 1979–2012. In case of climatic suitability obtained for the extreme climatic period, the near-zero suitability values obtained from MaxEnt for most species (Supporting information) presumably prevented from obtaining a significant correlation between decay and suitability. These extremely low climatic suitability values expectedly emerged as a consequence of the exceptionality of the extreme conditions that actually displaced most populations outside of their species niche, even for those species typically distributed in arid regions (Perez-Navarro et al. 2018). In addition, traditional SDMs may exhibit a limited ability to predict suitability under climatic scenarios highly dissimilar from calibration climatic conditions (Elith et al. 2010, Merow et al. 2014), as in the analyzed drought (Supporting information). Although MaxEnt does not lead to response curves particularly unrealistic outwards training data (Elith and Graham 2009, Elith et al. 2010), it implicitly assumes that modelled parameters and variables interactions obtained for calibration dataset will be maintained in shifting environmental scenarios (Phillips and Dudík 2008, Merow et al. 2013), which could potentially lead to extrapolation errors. Nonetheless, the use of more complex regression models such as GAMMs could help to more accurately relate performance and niche estimates, particularly when looking at extreme conditions.

Conversely, other simpler SDM methods that can provide output values beyond niche limits, such as Mahalanobis distances (Hirzel et al. 2002, Calenge et al. 2008), or distance to niche margins (i.e. if turned into a predictive distribution approach; Broennimann et al. 2021) or distance to niche centroid (Robertson et al. 2009, Osorio-Olvera et al. 2020), could be particularly useful to explain demographic responses under highly dissimilar environmental conditions to those use to calibrate the models, as they produce continuous values beyond the niche. These approaches could

be tested to predict decay under extreme climatic events (Perez-Navarro et al. 2018), determine negative growth rates for populations located outside of species niche (sink populations; Pulliam 2000), or assess climatic preadaptation of invasive species when introduced to novel environments (Broennimann et al. 2021).

Nevertheless, SMDs may lead to highly reliable predictions when projecting over environmental conditions lying within the range of those conditions used to calibrate the models (Elith et al. 2010, Merow et al. 2013), as suggested by the higher explanatory capacity of climatic suitability derived from MaxEnt when projecting the models on the reference climatic period 1979–2012 (Fig. 3, 4, Supporting information). According to that, we do not discourage the use of SDMs to predict population performance unless target populations are likely to be located outside of species niche. In addition, our estimations of Mahalanobis and Euclidean niche distance has also some limitations such as the lack of consideration of the variance explained by each PCA axes, the sensitivity of niche estimation to occurrence bias and the low number of environmental axes used. Although we used this simple approach for better representation and interpretation it is possible to create environmental spaces of higher dimensions and to account the explained variability of each environmental axes when applying Euclidean or Mahalanobis distance formulas. In addition, determining species niche margin discarding more than 5% could help to estimate more robust niche boundaries.

Finally, it is worth noting some considerations concerning both traditional SDMs and niche distance approaches. On the one hand, they may not necessarily depict real species physiological optimums and margins, as far as they derive from current geographical species occurrences, implicitly including species interactions, dispersal limitations and human habitat modifications (Colwell and Rangel 2009). Therefore, both niche characterization and SDMs are closer to represent the species realized niche rather than the fundamental one (Pearman et al. 2008). In addition, the impossibility of distinguishing between source and sink populations in most occurrence databases (Osorio-Olvera et al. 2019), as well as the possible sampling biases (Bystrakova et al. 2012), make it difficult to exactly portray species' realized niches. Here, we tried to overcome this latter limitation by randomly thinning species records to 1 occurrence per km<sup>2</sup> and by visually checking every species' niche and SDM response curves. In addition, our niche estimations did not account for environmental conditions actually experienced at plant or population level (Lenoir et al. 2013, Lembrechts et al. 2019a), since global environmental databases frequently present a relatively coarse spatial resolution (i.e. 1 km<sup>2</sup>). Finally, both niche distances and SDM outputs were highly sensitive to the selected climatic variables defining niche dimensions, since different climatic variables' subsets are differently related among them – both temporally and spatially (Elith et al. 2010) – leading to different environmental hypspaces.

## Conclusion

Our study empirically supports the use of distances to niche centroids or margins in the environmental space, rather than more traditional SDM-based climatic suitability indices, as a measure to explain population responses under extreme conditions that can fall outside the usual range of species' requirements. Our results specifically highlight that species located farther from niche centroid and niche margin during extreme drought episodes were more prone to show canopy losses and higher mortality. Thus, niche distances in environmental space may constitute a useful alternative tool to more traditional SDM-derived suitability to support conservation measures focused on mitigating the impacts of shifting environmental conditions or dealing with populations living outside of their realized niches, such as sink populations or invasive species.

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## Author contributions

**Maria A. Perez-Navarro:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead). **Olivier Broennimann:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Miguel Angel Esteve-Selma:** Conceptualization (equal); Data curation (supporting); Supervision (supporting); Writing – review and editing (equal). **Guillem Bagaria:** Data curation (equal); Methodology (supporting); Writing – review and editing (equal). **Antoine Guisan:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Francisco Lloret:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Supervision (equal); Writing – review and editing (equal).

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## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.2bvq83btc>> (Perez-Navarro et al. 2022).

## Supporting information

The Supporting information associated with this article is available with the online version.

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