

Temporal variability is key to modelling the climatic niche

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Abstract

Aim: Niche-based species distribution models (SDMs) have become a ubiquitous tool in ecology and biogeography. These models relate species occurrences with the environmental conditions found at these sites. Climatic variables are the most commonly used environmental data and are usually included in SDMs as averages of a reference period (30–50 years). In this study, we analyse the impact of including inter-annual climatic variability on the estimation of species niches and predicted distributions when assessing plant demographic response to extreme climatic episodes.

Location: Mediterranean basin, SE Iberian Peninsula.

Methods: We first characterized species niches with inter-annual and average climate in the same environmental space. We then compare the respective capacities of climatic suitability obtained from averaged climate-based and from inter-annual variability-based niches to explain population demographic responses to extreme drought. Furthermore, we assessed the relative increase in niche size when including climatic variability for a set of Mediterranean species exhibiting a wide range of distribution areas.

Results: We found that climatic suitability obtained from inter-annual variability-based niches showed higher explanatory capacity than average climate-based suitability, especially for populations living in climatically marginal conditions, although both niches quantifications significantly explained species demographic responses. In addition, species with restricted distribution ranges increased relatively more their niche space when considering climatic variability, probably because in widely distributed species spatial variability compensates for temporal variability.

Main conclusions: The common use of climatic averages when characterizing species niches could lead to underestimations of species distribution and misunderstanding of demographic behaviour, with implications for conservation plans derived from SDMs, for example, overestimations of species extinction risk under climate change, or underestimations of alien species invasion' risk. We highlight that including climatic variability in niche modelling can be particularly important when dealing with species with restricted distribution and populations at the margin of their species niche.

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KEYWORDS

climatic averages, climatic suitability, demography, inter-annual variability, niche modelling, species niche

1 | INTRODUCTION

In recent years, Species Distribution Models (SDMs) has become a very common tool in biogeography, ecology and conservation sciences (Araújo et al., 2019; Guisan et al., 2013). This technique has been widely used for many purposes (Guisan et al., 2017), such as niche quantification (Austin et al., 1990; Breiner et al., 2017), test of ecological and evolutionary hypotheses (Anderson et al., 2002; Graham et al., 2004; Leathwick, 1998; Mellert et al., 2011), prediction of the effects of global change on biodiversity (Thomas et al., 2004; Thuiller et al., 2005), support of conservation plans (Hannah et al., 2007; Tulloch et al., 2016), or estimation of invasive species risk (Peterson & Vieglais, 2001; Petitpierre et al., 2012).

Most of these studies generally use correlative SDMs that statistically correlate species' presences with the environmental conditions of sites where species occur (Franklin, 2010; Guisan et al., 2017; Peterson et al., 2011). These models are deeply rooted in Hutchinson's environmental niche concept (Guisan & Zimmermann, 2000), which implies that species' observed ranges are the geographical translation of species' environmental requirements in the N-dimensional space (i.e. the fundamental niche, sensu Hutchinson, 1957), discarding the areas where competitors impede the species presence (Soberón & Nakamura, 2009) and areas out of reach by dispersal (Barve et al., 2011; Pulliam, 2000). Several limitations of this method have been recognized, linked to both the underpinning theory and the commonly used methodologies. Some of the most criticized limitations include the equilibrium assumption (Guisan & Thuiller, 2005), which neglect any lag between environmental changes and species distributions (Blonder et al., 2015; Svenning & Skov, 2004); the niche conservatism assumption (Pearman et al., 2008), since these models implicitly consider that the niche remains constant when projected in time and space (Guisan et al., 2017); the lack of explicit inclusion of biotic interactions (Wiszniewski et al., 2013); or the frequent use of exclusively climatic predictors (Franklin, 2010; Mod et al., 2016; Thuiller, 2013), partly encouraged by their widespread availability in contrast to the relative lack of fine-grain resolution of other important and landscape-heterogeneous environmental variables (e.g. soils for plant distributions, Mod et al., 2016). Finally, SDMs usually include climatic variables as monthly or annual averages of reference periods of 30 to 50 years (Fick & Hijmans, 2017; Hijmans et al., 2005; Karger et al., 2017), in most cases, irrespective of whether modelled species' lifespan is significantly longer or shorter than these periods (Roubicek et al., 2010). This disregard for temporal variability of the climatic predictors at sites where occurrences have been collected, has been suggested to have a big impact on the accuracy of SDMs (Bateman et al., 2012; Zimmermann et al., 2009).

Characterizing the environmental requirements using exclusively averages over reference periods could lead to underestimations of

the real size of species' niche in the N-dimensional space. Not accounting for climate variability implies that, for example, two species withstanding the same average temperature for a given period have the same thermal niche, even if one of them lives under a constant climate every year, while the other suffers wide fluctuations in temperatures between years. Accordingly, the impact of including inter-annual variability in niche modelling may not be very important for species inhabiting areas with little temporal climatic variability (Hannah et al., 2014; Lembrechts et al., 2019). However, for species withstanding wide inter-annual climatic variability, differences between the niche characterized from climatic averages and the niche characterized including inter-annual variability is likely to be substantial (Hannah et al., 2014; Lembrechts et al., 2019). Similarly, species with small geographic distributions would be expected to show greater relative underestimation of their niche size when ignoring inter-annual variability than species with larger geographic distributions, where spatial variability could compensate for temporal variability (Hannah et al., 2014).

Underestimations of niche size caused by the non-inclusion of the inter-annual climate variability could have implications on different facets of ecology and biogeography. Since environmental suitability and population dynamics are theoretically related (Pulliam, 2000), niche breadth underestimation could contribute, among other ecological factors, to decouple climatic suitability from demographic processes (Csörgő et al., 2017; Thuiller et al., 2014). For instance, environmental suitability estimated from average climates could predict population absence or decline under some environmental conditions where the population intrinsic growth rate is positive during some years which ensures the persistence of the population (Dullinger et al., 2012; Eriksson, 1996). Also, climatic variability could be particularly relevant when predicting biodiversity changes under future climate change scenarios in which the recurrence of climatic extremes is increasing (Coumou & Rahmstorf, 2012; IPCC Working Group1, 2014). Depending on the magnitude of extreme climatic events, the position of populations in the environmental space could move away from niche centres and may even fall outside of the species niche (i.e. become sink populations), reducing populations' capacity to survive if these conditions persist. But if niches are wider than traditionally considered, for a given change in climatic conditions the probability of populations to be pushed out of their niche space would be reduced.

Despite these substantial implications, studies that accounted for inter-annual climatic variability are generally rare (Hannah et al., 2014; Zimmermann et al., 2009). Some mechanistic modelling approaches (Dormann et al., 2012; Kearney & Porter, 2009; Kearney, Matzelle, & Helmuth, 2012) may implicitly consider temporal variability in species distribution, by characterizing the physiological relationship between species responses and environmental variables.

In turn, range dynamics or dynamic occupancy models (Kéry, Guisera-Arroita, & Lahoz-Monfort, 2013; Pagel & Schurr, 2012; Royle & Kéry, 2007; Schurr et al., 2012) may include occurrences information from yearly re-surveys. However, these approaches are not possible for the vast majority of species, due to the lack of experimentally-derived physiological response curves (Araújo et al., 2013) or the absence of temporal systematic data collection (Schurr et al., 2012). Other studies have explicitly considered inter-annual climate to assess the relevance of temporal climatic variability on SDMs (Bateman et al., 2016; Bateman et al., 2012; Germain & Lutz, 2020; Margalef-Marrase, Pérez-Navarro, & Lloret, 2020; Zimmermann et al., 2009), but none of them has still provided an explicit comparison of the direct impact of including inter-annual climatic variability on niche size, and its impact when assessing the relationship between environmental niches and demographic responses.

Here, we attempted to fill these gaps by: (a) developing a novel procedure to characterize species niches based on long-term yearly climatic resolution and long-term climatic averages in a common environmental space; (b) assessing whether this inclusion of inter-annual variability improves the correspondence between niche-based environmental suitability modelled from averaged climate and population-level processes, illustrated by decay responses to an extreme drought event of *Pinus halepensis*' populations in southeast Spain; and (c), quantifying the relative change in niche size when considering inter-annual climatic variability versus averaged climate in 42 species with different distribution extents, corresponding to contrasting climatic ranges across the Mediterranean basin.

2 | MATERIAL AND METHODS

We quantified species' climatic niches by projecting geographic occurrences into a two- or three-dimensional environmental space and then estimating kernel densities (Blonder et al., 2014; Broennimann et al., 2012). We calculated an "inter-annual variability-based" niche by considering for each species' occurrence the climatic values for every single year of a reference period (e.g. 1979–2013). In contrast,

we obtained the "average-based" niche by considering only the average climate of every species' occurrence for the same period.

2.1 | Climatic suitability and demographic responses in *Pinus halepensis*

2.1.1 | Demographic response data

The study was carried out across forests of *Pinus halepensis* in the Murcia Region (southeast Spain) (Figure 1), an area which represents the arid limit of the species distribution. The average climate of this region is characterized by an annual mean temperature of 18°C, and annual rainfall ranging from 240 to 400 mm (Worldclim v 2.0, Fick & Hijmans, 2017). During the hydrological year 2013–2014, the region suffered the most intense drought on records, with on average less than 50% of the mean precipitation for the period 1970–2000 (AEMET, 2014) (Figure S1) and causing an extensive die-off and plant mortality in forest and woodlands ecosystems (Esteve-Selma et al., 2015).

P. halepensis decay data were collected for the whole Region of Murcia after the extreme drought episode by the Health Forest Unit of the Agriculture and Water Council of Murcia (Figure 1b) based on expert criteria of forest managers, who visually estimated canopy losses. Data were recorded and formatted in raster of 1 km² resolution covering a total of 4,378 km² including two categories: highly affected forests—mainly corresponding to stands with dead trees or visual evidence of canopy losses—, and unaffected forests—mainly corresponding to stands without evidence of canopy loss—(Figure 1b). Around 20% of the forest surface of the region was highly affected by drought. In addition, from this total surface, 264 plots of 1 km² were selected to measure the percentage of drought impact from High Resolution Orthoimagery (0.25 m) (PNOA - Aerial Orthophoto National Plan) in order to also have a continuous dataset which offers more information than the binary one (Figure 1c). Drought-induced decay percentages per plot were calculated by comparing tree cover surface before (PNOA for year 2011) and after

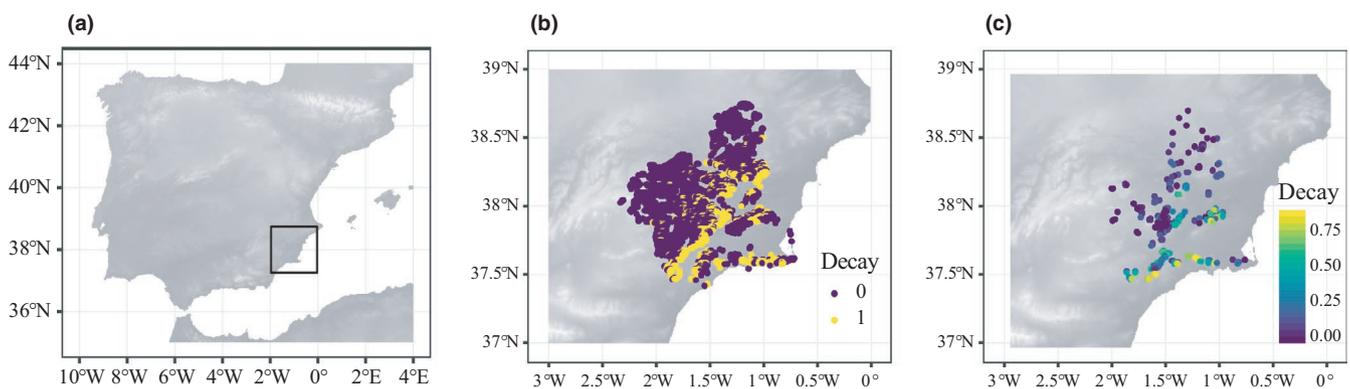


FIGURE 1 (a) Location of the study site in the SE of the Iberian Peninsula. (b) Location of decay plots with binary records (1-highly affected – 0-unaffected). Blue colours show plots not affected during the extreme year while yellow ones show highly affected plots. (c) Location of decay plots with continuous records, blue and yellow colours respectively show lowest and highest rates of impacts

(PNOA for year 2016) the extreme drought event, as the percentage of cover of dead and highly affected trees (dry canopy surface higher than 50%). These decay percentage values were then contrasted in the field for 14 plots of around 6,300 m² (total sampled surface of 87,964.59 m², Table S1), obtaining a Pearson correlation of 0.79. Thus, we used binary and continuous datasets to test our hypotheses.

2.1.2 | Species niche characterization based on climate average versus inter-annual variability

P. halepensis (hereafter *Pinus*) occurrences dataset used to characterize species niche were retrieved from the third Spanish National Forest Inventory (IFN3, 2007), with a total of 9,959 occurrences after removing *Pinus* plantations. This occurrence dataset covers most of *P. halepensis* range (Mauri et al., 2016).

As climatic dataset, we used 12 bioclimatic variables for every year of the period 1979–2007 (Chelsa database, Karger et al., 2017): bio1 (annual mean temperature), bio4 (temperature seasonality -standard deviation *100-), bio5 (maximum temperature of warmest month), bio6 (minimum temperature of coldest month), bio10 (mean temperature of warmest quarter), bio11 (mean temperature of coldest quarter), bio12 (annual precipitation), bio13 (precipitation of wettest month), bio14 (precipitation of driest month), bio15 (precipitation seasonality -coefficient of variation-), bio16 (precipitation of wettest quarter) and bio17 (precipitation of driest quarter); all of them with 1 km² resolution. We chose these variables in order to facilitate the interpretation of environmental axes and to remove climatic variables that correlate differently for the average 1979–2007 period and for the extreme drought year (i.e. precipitation of hottest quarter negatively correlated with temperature of hottest quarter during the average period, but positively during the extreme drought year since most precipitation was recorded precisely in summer during that year). The reference period of time was selected to match the occurrence database, that is until 2007, when IFN3 was carried out.

From these 12 bioclimatic variables, we obtained an inter-annual climatic dataset by extracting the climatic values of *Pinus* occurrences locations for every year of the period 1979–2007 (that is, 9,959 occurrences × 28 years) and an average climatic dataset by estimating the mean climate of the 28-year period for every occurrence location. From the inter-annual climatic dataset, we built the environmental space by using a PCA to reduce the climatic space of the 12 variables into a two-dimensional space (Figure S2) (Broennimann et al., 2012; Robertson et al., 2001). This approach represents a compromise between characterizing the climatic niche by a relatively large number of climatic variables and the use of a space with a reduced number of dimensions thus facilitating calculations and visual representation. Nevertheless, we also characterized the *Pinus* niche in three-dimensional environmental space in order to reduce the losses of total explained variability (see 3-d method explanation in Supplementary Material).

This two-dimensional environmental space was used to represent both the average *Pinus* niche and the *Pinus* inter-annual niche by projecting the scores of the climatic values of *Pinus* occurrences into this environmental space. We then used kernel density functions to determine the *Pinus* density for each cell of the two-dimensional environmental space, by applying a Gaussian kernel, selecting optimal bandwidth by cross-validation (Duong & Hazelton, 2005) and removing values below the 0.05 percentile. Finally, climatic suitability was estimated by dividing each density value in the niche space by the maximum density value within the niche, obtaining values ranging between 0 and 1.

We then extracted the climatic suitability of *Pinus* populations affected by drought for the extreme year 2013–2014, for which we had population decay data. Climatic conditions for this year were obtained from monthly precipitation and maximum, minimum and mean temperature records from between 68 and 114 weather stations of the Spanish Meteorological Agency (AEMET). This climatic dataset was translated into 1 km² resolution-maps following Ninyerola, Pons & Roure (2000) and using latitude, longitude and elevation as explanatory variables for climate. We then applied the “biovars” function (dismo package; Hijmans et al., 2016) to convert them into the final bioclimatic variables format. Finally, we selected the same 12 bioclimatic variables as used for niche characterization and translated these values into the two or three-dimension environmental space.

2.1.3 | Suitability-decay analyses

We applied GLMs with populations decay (binary or continuous) as response variable, and populations' climatic suitability during the extreme year (estimated from inter-annual or average niches) as explanatory variables. We produced four alternative GLMs: binary decay versus climatic suitability from average climatic niche, binary decay versus climatic suitability from inter-annual climatic niche, continuous decay versus climatic suitability from average climatic niche, continuous decay versus climatic suitability from inter-annual climatic niche. Each model used binomial error distribution and logit link. These models allowed us to compare the accuracy of the relationship between population decay and climatic suitability depending on niche characterization approach (inter-annual or average). These models were applied both for two-dimensional and three-dimensional niches.

In order to assess whether differences in accuracy between models were biased by the possible non-random locations of the observed populations in the environmental space, we compared the predictive capacity of both models (average niche based and inter-annual niche based) in 30,000 simulated decay datasets obtained by randomly creating subsets from the continuous decay dataset. In particular, differences in climatic suitability are expected to be maximal in the part of the environmental space not shared by average and inter-annual niches (Figure S3), since average niche predicts a suitability of 0 while inter-annual niche predicts positive suitability

values. So, for each randomly simulated dataset, we estimated the percentages of populations located in the non-shared space (ranging from 0% to 100%). Simulated dataset sizes ranged between 118 and 263 populations. For each simulated decay dataset, we also calculated the explanatory capacity of average and inter-annual niche-based climatic suitability, by applying GLM with continuous population decay as response variable and average or inter-annual climatic suitability as explanatory variables (see above explanation). Finally, we tested the differences of models explanatory capacity by applying GLM with R^2 as response variable, niche model (average or inter-annual climate based), percentage of population located in the non-shared space between two niches, the interaction of these two variables, and population size for each simulated dataset as explanatory variables. This last was included in order to correct the possible low performance of dataset with lower number of populations.

2.2 | Influence of range size on change in average versus inter-annual niche

We characterized the climatic niche of 42 Mediterranean plant species with range sizes varying from the whole Mediterranean basin to very small ranges for endemic species (i.e. Mediterranean, occidental Mediterranean, Iberoafrikan and Iberian Peninsula SE endemic species, Table S2), using the average and the inter-annual approaches described in the previous section. In addition, these species were selected for living under particularly variable climate between years. Species' occurrence data were collected from GBIF (GBIF, 2019, <http://www.gbif.org>) and from the herbarium of Jardí Botànic de Barcelona (<https://museu-ciencies.cat/es/area-ciencia/departamentos-ciencificos/jardin-botanico/>). Species' occurrence records were filtered to remove taxonomic inconsistencies (unappropriated species synonyms) and to reduce possible sampling bias and spatial autocorrelation. To do this, we selected each species filtering distance applying the `ecospat.mantel.correlogram` function (`ecospat` package; Di Cola et al., 2017) and selecting the minimal distance at which spatial autocorrelation is not significantly different than 0. Then, we retained only one occurrence per pixel of side equivalent to the selected filtering distance. For those species where the statistically selected filtering distance was lower than 1, we kept 1 km of pixel side, in order to maintain the spatial concordance between occurrence and climatic datasets. Species' final datasets ranged from 59 to 6,032 observations, with a total record of occurrences of 78,978.

Average and inter-annual climatic datasets were collected from CHELSA database (Karger et al., 2017) for the period 1979–2013. We selected the same 12 bioclimatic variables as selected above for *P. halepensis*. We obtained the inter-annual climatic dataset by extracting the climatic values of every occurrence for each year of the period 1979–2013 (that is, each species occurrence \times 35 years), and the average climatic dataset by estimating the mean climate of the 35-year period for every species occurrence. In this case, we calculated the common environmental space by using a PCA built using

the inter-annual climatic data from all the occurrences of all 42 analysed species (PCA-occ *sensu* Broennimann et al., 2012) (Table S6) since we wanted to compare different species niches among them. We estimated average and inter-annual niches by projecting the climatic values associated to each species occurrences into the first two PCA axes defining the climatic space, and using kernel density functions to determine species' density for each cell of the two-dimensional environmental space as described above, and removing density values below the 0.05 percentile.

We then calculated the ratio between the niche size (area) based on average and inter-annual approaches (niche area ratio = inter-annual niche area/average niche area). In order to test whether the relevance of including inter-annual variability varies depending on species average niche size, we applied a linear model (lm) with niches' area ratio as response variable and average-based niche area logarithmically transformed and species distribution range as response variables. Finally, we tested the linearity of the relationship between inter-annual niche size and average niche size using a log-log model (i.e. lm with log of inter-annual niche area as response variable and log of average niche area as explanatory variable) (Smith, 1980). We also analysed possible changes in niche size/background size ratio (i.e. the proportion that a species niche occupies of the available environmental space) when including inter-annual variability, by testing the linearity of the relationship between average niche size/average background size ratio and inter-annual niche size/background niche size ratio using a log-log model (see Supplementary Material niche/background ratio explanation).

3 | RESULTS

3.1 | Climatic suitability and demographic responses in *Pinus halepensis*

The first two PCA axes explained 60% of the variability of the 12 bioclimatic variables (Figure S2). The inter-annual niche of *P. halepensis* was 42% larger than the average niche. During the extreme climatic year, 93.3% of unaffected forests and 63.3% of highly affected forests were inside the *P. halepensis* inter-annual niche (Figure 2a). These values decreased to 52.8% for unaffected forests and 21.2% for highly affected ones when niche was calculated with average climate (Figure 2b).

Models relating species decay with species climatic suitability during the extreme year show that populations suitability significantly explained species decay irrespective of the decay dataset (binary or continuous) or the type of niche (average or inter-annual) (Figure 3, Table S2). However, models with inter-annual measures of climatic suitability better fitted with decay records, had considerably lower AIC, and slightly higher R^2 (particularly for continuous dataset, see Figure 3).

The explanatory capacity of models that include suitability from inter-annual climatic suitability was always higher than that of models including average climatic suitability, independently of the

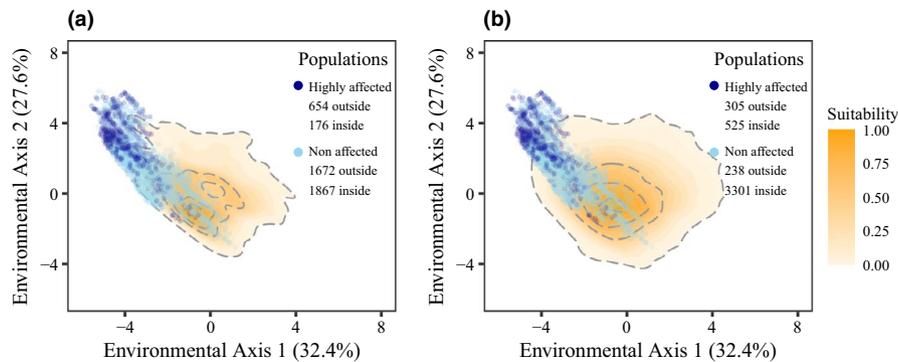


FIGURE 2 *P. halepensis* niche determined by two PCA environmental axes based on (a) average climate and (b) inter-annual climatic variability and location of highly affected and unaffected populations. Dark blue dots represent highly affected *P. halepensis* populations after the extreme event, while light blue dots represent unaffected *P. halepensis* populations after the extreme event. Orange palette indicates *P. halepensis* climatic suitability. Dashed lines represent in both cases 0.05, 0.5, 0.75 and 0.95 climatic suitability

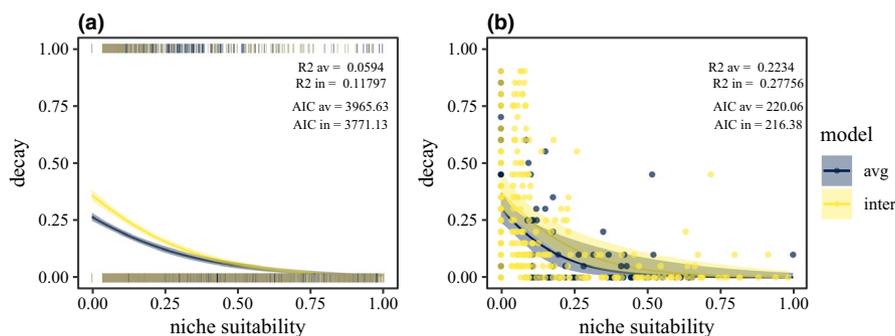


FIGURE 3 Drought-induced decay in *P. halepensis* populations in relation to population's climatic suitability estimated from average climate (dark blue colour, avg) and from inter-annual climatic variability (yellow colour, inter). Models considered drought-induced affectation as (a) a binary response variable (highly affected versus unaffected) or as (b) continuous response variable (percentage of affectation in plots)

proportion of populations located in the non-shared area defined by the average-based and inter-annual variability-based niches (Figure S3). Nevertheless, difference in explanatory capacity between the two type of models increased as the percentage of populations located in the non-shared area increased (Figure S4 and Table S3).

In case of three-dimensional species niche, the explained variability of the environmental space increased up to 76.15%. Climatic suitability derived from three-dimensional niche was highly correlated to two-dimensional niche-based climatic suitability (Pearson correlation > 0.8 for average climatic suitability and > 0.95 for inter-annual climatic suitability, see Table S4), leading to similar results when explaining *Pinus* populations decay after extreme drought (Figure S6 and Table S5).

3.2 | Influence of range size on change in average versus inter-annual niche

The two first PCA axes explained 60.8% of the variability of the 12 climatic variables describing the distribution of the set of 42 Mediterranean species (Figure S7). Linear models across species with different distribution ranges showed a significant negative

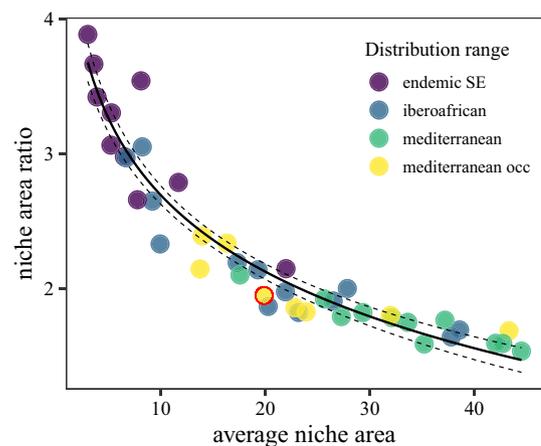


FIGURE 4 Species niche area ratio (inter-annual niche area / average niche area) in relation to average niche area for species with distinct distribution ranges across the Mediterranean basin. Green colour represents species widely distributed along the Mediterranean basin, yellow colour represents species mostly distributed in West Mediterranean basin, light blue colour represents Iberofafrican species, mostly distributed in North Africa and South Iberian Peninsula and dark blue colour represents species distributed in South East Iberian Peninsula. Red circle corresponds to *P. halepensis*

effect of the species average niche size logarithmically transformed on inter-annual/average niche size ratio, implying that species with smaller average-based niche area (corresponding to species with more restricted distribution ranges), increased more their niche area when considering inter-annual climatic suitability than species with larger average-based niche area (i.e. wider distribution ranges) (Figure 4 and Table S7). Accordingly, per distribution categories the endemic species were the ones which increased more their niche size when considering inter-annual variability. (Table S7). Log-log model results relating inter-annual variability-based niche size as a function of average-based niche size showed a regression slope significantly lower than 1 and higher than 0 (Table S8), which is associated to a positive but saturated relationship between average niche area and inter-annual niche area (Smith, 1980); so the higher values of average-based niche area, the lower increase of inter-annual niche size (Figure S8). Similarly, log-log model relating the average-based niche/background ratio and inter-annual variability-based niche/background ratio, also showed a regression slope lower than 1 and higher than 0 (Table S9), illustrating a saturated relationship rather than linear between the two ratios. Therefore, the higher the ratio of the study area occupied by species niche when including average climate, the lower the increase in the proportion that the inter-annual variability-based niches occupy within the inter-annual background region (Figure S10 and S11).

4 | DISCUSSION

4.1 | Including inter-annual variability in niche characterization

This study highlights some limitations of the predominant practice of characterizing species niches basing on average climate. Accounting for temporal climatic variability in locations where species occur increases the range and resolution of species climatic requirements constituting the climatic niche, expectedly leading to an increase in niche size. Differently from other studies which included climatic extremes or standard deviation of inter-year climate as a new dimension of the environmental hyperspace (Zimmermann et al., 2009) or as different environmental spaces (Bateman 2016), we included the whole distribution of climatic data across time for all occurrence sites in the same environmental space. This procedure allowed effectively quantifying differences in niche size. Certainly, during all the time that a population remains at a given site, climate conditions in some years could exceed temporarily the species tolerance limits. However, these macroclimatic extreme conditions do not necessarily result in population extinction, if more favourable conditions exist in microsites, or thanks to species local adaptation or facilitation from species interactions (Benito Garzón et al., 2011; De Frenne et al., 2013; Svenning & Sandel, 2013). Therefore, accounting for the whole temporal series of macroclimatic conditions encountered during a period of time, might include some climate extreme situations that overpass the species physiological tolerance limits, ultimately

leading to slight overestimations of species climatic niche sizes. This problem can be dealt by removing the most marginal percentile of niche density (in our case, the 5% percentile) when delimiting niche space. In addition to niche analyses in the environmental space, inter-annual variability could also be incorporated more generally into species distribution modelling approaches that allow for a hierarchical data structure (Kuznetsova et al., 2017; Wang & Maintainer, 2016) or by independently considering yearly climatic conditions at each site. Finally, including climatic variability when building SDMs is particularly promising in climate change studies since it will help to better determine future species distribution under a climatic context of increasing variability (Zimmermann et al., 2009).

4.2 | Climatic suitability and demographic responses

Our results emphasize the importance of climatic variability to explain the relationship between demographic processes and climatic suitability, specifically under extreme climatic events. We found that *P. halepensis*' climatic suitability estimated from niches characterized by inter-annual climatic variability better explained species decay under extreme events in comparison to climatic suitability estimated from niches that only considered climatic average (Figure 3). It is theoretically assumed that if species' climatic niches are properly represented, there should be a correspondence between population demographic processes (such as growth or mortality rates) and niche parameters (Csergő et al., 2017; Pulliam, 2000; Thuiller et al., 2014). Multiple studies have tried to assess this relationship (Csergő et al., 2017; Thuiller et al., 2014), particularly under extreme events (Lloret & Kitzberger, 2018; Margalef-Marrase et al., 2020; Pérez Navarro et al., 2018), but this correspondence does not always emerge (van der Maaten et al., 2017; Thuiller et al., 2014). Very often these niche-demography relationships, particularly in case of parameters related to growth, are affected by many local aspects—such as favourable microhabitats or biotic interactions—that impede identifying a clear relationship between niche and population performance (Csergő et al., 2017; Pearson & Dawson, 2003). Nevertheless, neglecting temporal variability in this kind of studies could also introduce a substantial error when predicting population performance in fluctuating environments (Niehaus et al., 2012). Although suitability derived from average-based niche may be robust enough to explain dramatic demographic responses under extreme climatic episodes, as we showed in our results (see also Lloret & Kitzberger, 2018; Pérez Navarro et al., 2018; Sapes et al., 2017), the better the characterization of the niche variability, the better the species fitness' predictions.

In addition, the inclusion of inter-annual variability when predicting species responses was especially relevant for populations located close to the niche margins where such populations can be included or excluded from the niche depending on yearly variation in climate (i.e. in the non-overlapping space between inter-annual and average-based niches) (Figure S3). This area of the species niche corresponds to unsuitable climatic conditions according to

average-based niche but suitable climatic conditions when climatic variability is included in niche characterization. The average-based niche does not show a good predictive capacity for demographic responses in this non-shared area (between the two types of niches), by considering this area unsuitable for species presence. Thus, if the study sample was composed only by populations from this non-shared area, the only model that could predict populations response correctly would be the one including inter-annual climatic variations (Figure S4). This mismatch also implies that populations located in this area, which in many cases (but not necessarily) also correspond to populations living at geographic range margins, could be wrongfully located out of the niche space when using average-based species niche.

4.3 | Influence of range size on change in average versus inter-annual niche

These above-mentioned implications of including inter-year variability could be even more important for species with narrow distribution ranges, which implies smaller average-based niches compared with those with broader distributions. Our results showed that, in the Mediterranean basin, species with smaller average-based niche areas increased relatively more their niche area when considering inter-annual climatic variability (Figure 4, Figure S8, S11 and Tables S8 and S9), probably because in species with narrow distribution ranges, spatial climatic variability does not compensate for temporal variability. Therefore, endemic and rare species tend to increase their niche size more when including yearly climatic variability, particularly when inhabiting highly fluctuating climates.

4.4 | Other implications of inter-annual variability versus average-based climatic models

This study highlights limitations, barely considered to date, of using climatic averaged datasets of 30–50 years' periods (Fick & Hijmans, 2017; Hijmans et al., 2005; Karger et al., 2017) when modelling species' niches and distributions (Hannah et al., 2014; Zimmermann et al., 2009). Not accounting for the whole temporal climatic resolution at sites of species occurrences when modelling climatic niche could result in errors affecting the characterization of species geographical distribution and losses of predictive power. Underestimations of then niche envelope could lead to underestimations of species' environmentally suitable areas in geographic space, and such errors could also be propagated into related management plans (e.g. selection of favourable areas for protecting species or assisted migrations; Guisan et al., 2013). Importantly, these possible niche underestimations could vary depending on species distribution ranges, being particularly relevant for rare species. In addition to the error derived from the non-inclusion of climatic variability, using systematically 30–50 years averaged climatic periods could be especially pernicious when characterizing the climatic niche of short-lived

species, as in pests (Jaime et al., 2019)—since these emerge explosively as a consequence of specific climatic conditions that appear in particular years of the period—, or in case of non-sessile organisms—which can buffer their environment variability by movement, thus only perceiving the climate of the locations during specific favourable time periods (Lembrechts et al., 2019)—. In these cases, it is particularly important to know the specific moment of species occurrence and use the corresponding temporal resolution (Bateman et al., 2016).

Estimates of invasion risk or extinction rate could also be affected by niche characterization errors. In this case, niche size underestimation could lead to underestimate the environmentally suitable habitat of invasive species in new regions, or to overestimate extinction risk (Feeley & Silman, 2011) as populations and species could be able to survive under changing climates or extreme events more than expected with average-based niches.

In addition to temporal climatic variability, there are other sources of climatic variability not included in the prevalent climatic datasets (Worldclim, CHELSA; Fick & Hijmans, 2017; Hijmans et al., 2005; Karger et al., 2017), such as the climatic heterogeneity held within geographic units due to a coarse spatial resolution (De Frenne et al., 2013; Geiger et al., 1995; Lembrechts et al., 2019; Lenoir et al., 2013). This lack of resolution, which could be particularly important for plants living in particularly favourable microhabitats (Maclean, Hopkins, Bennie, Lawson, & Wilson, 2015), and for small-stature plants which actually experience temperatures at ground-surface level (Lembrechts et al., 2019; Pradervand, Dubuis, Pellissier, Guisan, & Randin, 2014), may hinder our capacity to accurately portray species environmental requirements (Guisan et al., 2019) and lead us to neglect the important buffer capacity of microclimates on the responses of species, biodiversity and ecosystems to climate change (Ackerly et al., 2010; De Frenne et al., 2019; Maclean et al., 2015; Randin et al., 2015). Nevertheless, climatic datasets with high temporal climatic resolution are increasingly becoming available (Bramer et al., 2018; Lembrechts et al., 2019), from yearly (CHELSA scruts, Karger et al., 2017) to even weekly and daily scales (Wan, 2008; Wan et al., 2015), allowing for better oncoming consideration in niche characterization and distribution modelling.

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DATA AVAILABILITY STATEMENT

Authors have made available those databases and codes that are not yet publicly available in other public repositories in Dryad: <https://doi.org/10.5061/dryad.8kpr4xmd>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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