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Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation

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Abstract

Vulnerability to climate change, and particularly to climate extreme events, is expected to vary across species ranges. Thus, we need tools to standardize the variability in regional climatic legacy and extreme climate across populations and species. Extreme climate events (e.g., droughts) can erode populations close to the limits of species' climatic tolerance. Populations in climatic-core locations may also become vulnerable because they have developed a greater demand for resources (i.e., water) that cannot be enough satisfied during the periods of scarcity. These mechanisms can become exacerbated in tree populations when combined with antagonistic biotic interactions, such as insect infestation. We used climatic suitability indices derived from Species Distribution Models (SDMs) to standardize the climatic conditions experienced across *Pinus edulis* populations in southwestern North America, during a historical period (1972–2000) and during an extreme event (2001–2007), when the compound effect of hot drought and bark beetle infestation caused widespread die-off and mortality. *Pinus edulis* climatic suitability diminished dramatically during the die-off period, with remarkable variation between years. *P. edulis* die-off occurred mainly not just in sites that experienced lower climatic suitability during the drought but also where climatic suitability was higher during the historical period. The combined effect of historically high climatic suitability and a marked decrease in the climatic suitability during the drought best explained the range-wide mortality. Lagged effects of climatic suitability loss in previous years and co-occurrence of *Juniperus monosperma* also explained *P. edulis* die-off in particular years. Overall, the study shows that past climatic legacy, likely determining acclimation, together with competitive interactions plays a major role in responses to extreme drought. It also provides a new approach to standardize the magnitude of climatic variability across populations using SDMs, improving our capacity to predict population's or species' vulnerability to climatic change.

KEYWORDS
climate change, climatic niche, core vs. edge populations, correlative niche models, drought-induced die-off, extreme climatic events, forest dieback, tree mortality

1 | INTRODUCTION

Regional episodes of extreme climatic variability associated to climate change, such as acute drought/heat events, are exacerbating tree mortality in forest ecosystems worldwide (Allen, Breshears, & McDowell, 2015; Allen et al., 2010; Neumann, Mues, Moreno, Hassenauer, & Seidl, 2017). However, many uncertainties remain about the spatial and temporal variability in tree populations vulnerability in front of such extreme climatic events (Allen et al., 2015; Clark et al., 2016). Extreme events are expected to affect tree, local populations differently within species' ranges because of the spatial variations in the physical conditions imposed by climatic anomalies (due to moist air circulation, local precipitation patterns, topography, soils, etc.) and also because of variations in the histories of colonization, adaptation, and acclimation experienced by different populations (Hampe & Petit, 2005). Thus, defining the vulnerability of tree populations across species ranges—which encompasses a variability in climatic legacy and weather conditions during extreme episodes—in the context of ongoing global environmental changes (Calvin & Jump, 2017; Fensham, Fraser, Macdermott, & Firn, 2015; Lloret et al., 2007) has vital implications for carbon balance (Anderegg, Schwalm et al., 2015; Mekonnnen, Grant, & Schwalm, 2017), resource management, and conservation (Seneviratne et al., 2012).

One of the main obstacles to unify principles and predictive capacity regarding when and where to expect increased tree mortality under altered climatic regimes is the fact that extreme climate phenomena, particularly those associated with water availability, are species/population-specific. The physiological mechanisms responsible of drought-induced tree mortality are still not completely established, but there is an agreement that they involve the impairment of the vascular transport system (i.e., hydraulic failure) and/or the C economy (Adams et al., 2017). In fact, the same absolute amount of water deficit can imply very different physiological, demographical, and ecological consequences, depending on the ecological and evolutionary context (Allen et al., 2015; Martínez-Vilalta & Lloret, 2016; Martínez-Vilalta, Lloret, & Breshears, 2012). One proposed solution to this problem has been the standardized measurement of event extremes (Kitzberger, 2013). Accordingly, water balance leading to drought conditions can be statistically standardized at different locations or time scales, following a probabilistic approach, for example, via the sc-PDSI (McDowell et al., 2008) or the SPEI indices (Vicente-Serrano, Begueria, & Lopez-Moreno, 2010). Climate-based indices allow us to establish common thresholds of drought "rarity" (Kitzberger, 2013) that cause tree die-off events irrespective of location and species (Greenwood et al., 2017; Mitchell, O'Grady, Hayes, & Pinkard, 2014). However, these climatic approaches only analyze how statistical deviations of the physical phenomenon in a given location relate to a population's biological response (e.g., mortality). However, they do not consider how spatial intra- or interspecific patterns of mortality emerge from the interaction between the species ecological and evolutionary adjustments and the climatic extreme.

Classic niche theory proposes that species perform less robustly when populations experience environmental conditions closer to the boundaries of the environmentally defined niche space (MacArthur, 1984; Martínez-Meyer, Díaz-Porras, Peterson, & Yáñez-Arenas, 2013). Thus, stochastic fluctuations or directional changes promoting harsher environmental conditions are expected to weaken population's performance near species climatic edges due to low assimilation and cumulative physiological damage (Morin, Augspurger, & Chuine, 2007; Seneviratne et al., 2012). However, populations living near the edges of climatic ranges may be more resistant to directional environmental changes and stochastic climatic extremes than core populations (Calvin & Jump, 2017) since they may have plastically or genetically adjusted to a chronically scarce and fluctuating limiting resource (e.g., water availability) (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Purves, 2009). In contrast, populations living at the core of the species' climatic range might exhibit a high demand for resources that, in the case of trees, could correspond to water due to elevated growth rates or high stand density or basal area. Then, during unusually extreme droughts, these characteristics can make them vulnerable to hydraulic failure and to water demand from competitors (Anderegg, Hicke et al., 2015; Jump et al., 2017; McDowell et al., 2008; Meddens et al., 2015). Nevertheless, the translation of population behavior across climatic ranges to species distribution may be eventually obscured by the coexistence of these alternative mechanisms and especially because the correspondence between demographic performance and species range may be multifaceted, depending on genetic, population, and biogeographic histories, biotic interactions, and microenvironment distribution (Abeli et al., 2014; Pironon, Villellas, Morris, Doak, & García, 2015; Purves, 2009).

Here, we adopt a novel approach to explain temporal and spatial patterns of tree die-off by standardizing the climatic event magnitude from the use of Species Distribution Models (SDMs) based on bioclimatic envelopes. SDMs (also known as bioclimatic niche models, correlative ecological niche models, or envelope models) consider the species' occurrence in sites across its distribution range as well as the climatic conditions of that range although other nonclimatic environmental variables can also be considered. SDMs are regularly used to interpret species' distribution patterns in relation to environmental variables, particularly climate (Elith & Leathwick, 2009; Franklin, 2010), and they have been applied in studies on turnover of vegetation composition across landscape (Jennings & Harris, 2017), regional patterns of growth (van der Maaten et al., 2017), community-level responses to experimental drought (Bilton, Metz, & Tielbörger, 2016), or projections of tree response to climate change (Cheaib et al., 2012). However, the use of SDMs requires caution since they do not address an explicit analysis of the functional mechanisms involved in the species distribution patterns, particularly ecophysiological performance, and dispersal and biotic interactions (Araújo & Luoto, 2007; Elith & Leathwick, 2009; Guisan & Thuiller, 2005). Furthermore, the occurrence of populations across the territory can be highly dependent of historical and geographical

contingency, including disturbance regime, human action, and interaction with other species (Elith & Leathwick, 2009; Latimer, Shan-shan, Gelfand, & Silander, 2006; Serra-Díaz et al., 2013). In spite of these deficiencies when constructing models of species' realized niche, SDMs reveals its ability to describe broad patterns of the relationship between climate and species occurrence (Franklin, 2010). Importantly for our purposes, SDMs provide estimates of the probability of a species' occurrence in a set of climatic conditions characterizing a particular locality. This value can thus be considered an integrative index of the climatic suitability historically experienced by populations living in a given site. Indeed, SDMs can also be used to describe climatic suitability for populations during a particular climatic event, providing a standardized measure of the event magnitude which can be contrasted across the species' geographic range. We use the term *bioclimatic deviation* to describe the specific climatic environment experienced by certain extant populations of a given species at a particular moment in relation to the whole range of climatic conditions in which a species is normally found. As climatic suitability is an occurrence-calibrated characterization of the suitable conditions across the landscape for a species long-term persistence, it can be used to explicitly evaluate intra- and interspecific responses (e.g., mortality, decline, establishment, masting, and insect outbreak.) to short-term climatic events across species' geographic ranges (Evans & Lyons, 2013; Fensham, Fairfax, & Ward, 2009; Sapes, Serra-Diaz, & Lloret, 2017). Moreover, temporal variability in climatic suitability can be used as a measure of environmental stability at any site in a species range. This approach is relevant because historical climatic stability is a key element to understanding an ecosystem's vulnerability to extreme climatic events (Gutschick & BassiriRad, 2003).

Here, we use an annual time series of downscaled bioclimatic data to assess the capacity of the output of a bioclimatic model based on historical (1972–2000) climatology (hereafter *historical climatic suitability*, *HCS*) to explain massive tree die-off and mortality due to the compound effect of drought and bark-beetle infestation of *Pinus edulis* (piñon pine) at a regional scale in southwest North America (Breshears et al., 2005; Clifford, Royer, Cobb, Breshears, & Ford, 2013; Gaylord et al., 2013; Macalady & Bugmann, 2014; Meddens et al., 2015) during the 2001–2007 period. Thus, *HCS* (ranging 0–1) is used as a long-term measure of *P. edulis* climatic suitability, so that higher/lower values coincide with core/edge bioclimatic conditions. We also project the model onto the conditions during the particular period of die-off (hereafter *episode climatic suitability*, *ECS*). *ECS* (ranging 0–1) is used as an absolute inverse measure of drought effects on climatic suitability so that values closer to zero/one indicate strong/weak drought magnitude, respectively. Additionally, as an inverse measure of site-specific climatic stability, we also calculate the long-term variability around the mean in climatic suitability (hereafter, *standard deviation in climatic suitability*, *HCS-SD*).

In this study, our goal is to assess tree vulnerability to drought episodes across a significant part of the species' range distribution, according to the variability in regional climatic legacy and weather conditions during the episode. This vulnerability raises from the combined effect of drought and insect attack. Hence, our purpose is to assess the relevance of population's bioclimatic characterization to understand this compound effect, but not to disentangle the separate contribution of these two factors. A negative or positive effect of *HCS* on die-off would support higher vulnerability of the populations living in the climatic edge or core, respectively, while negative effects of *ECS* would suggest that die-off is related to event's magnitude. *HCS x ECS* interactions would be indicative of a differing vulnerability during the event of climatic core or edge populations. Positive effects of *HCS-SD* on die-off would indicate increased population vulnerability in highly fluctuating climatic environments, heightening the cumulative effects of past deleterious periods (Anderegg, Schwalm et al., 2015; Lloret, Siscart, & Dalmases, 2004), despite the transitory recovery of suitable conditions. Interaction of *HCS-SD* with *HCS* would indicate whether climatic core or edge populations are more or less vulnerable to past bioclimatic variability, while interaction with *ECS* would indicate a reinforcing mechanism between past and current events.

2 | MATERIALS AND METHODS

2.1 | Study system

In the early 2000s, a die-off and mortality episode of *P. edulis* massively affected 12,000 km^2 in southwest North America, including forests dominated by this species and forests with co-occurrence of *Juniperus monosperma* (juniper) (Figure 1a). Tree mortality was triggered by the compound effect of a multiyear drought/warm episode with a Ips bark beetle outbreak (Breshears et al., 2005; Gaylord et al., 2013; Macalady & Bugmann, 2014; Clifford et al., 2013; Meddens et al., 2015).

2.2 | Calculation of historical and episode climatic suitability

To build, train, and test SDMs, we used pixels of *P. edulis* ocurrence downloaded from ForeCASTS Project Tree Atlas V5 (http://www.geobabble.org/~hnw/global/treeranges5/climate_change/site_lists/). This dataset includes 3,950 *P. edulis* occurrence locations from which 3,737 correspond to Forest Inventory and Analysis (FIA) Program plots and 213 from Global Information Facility (GBIF) sites. FIA data reflect predrought distribution of the species since inventories date back starting in the 1920s with yearly remeasurements after 1999 in most of the conterminous United States (https://www.fia.fs.fed.us). Climatic data consisted of yearly multiband raster time series (1971–2009) of the 20 standard bioclimatic predictors used in species distribution modeling downscaled to a 2 km pixel for the conterminous US by U.S. Geological Survey, Fort Collins Science Center from original 4 km PRISM climate data developed by the PRISM Climate Group at Oregon State University (O'Donnell & Ignizio, 2012; downloaded from: https://www.sciencebase.gov/catalog/). This pixel size is large enough to minimize the spatial inaccuracy in FIA plot coordinates due to noise added to protect their location ("fuzzing"),
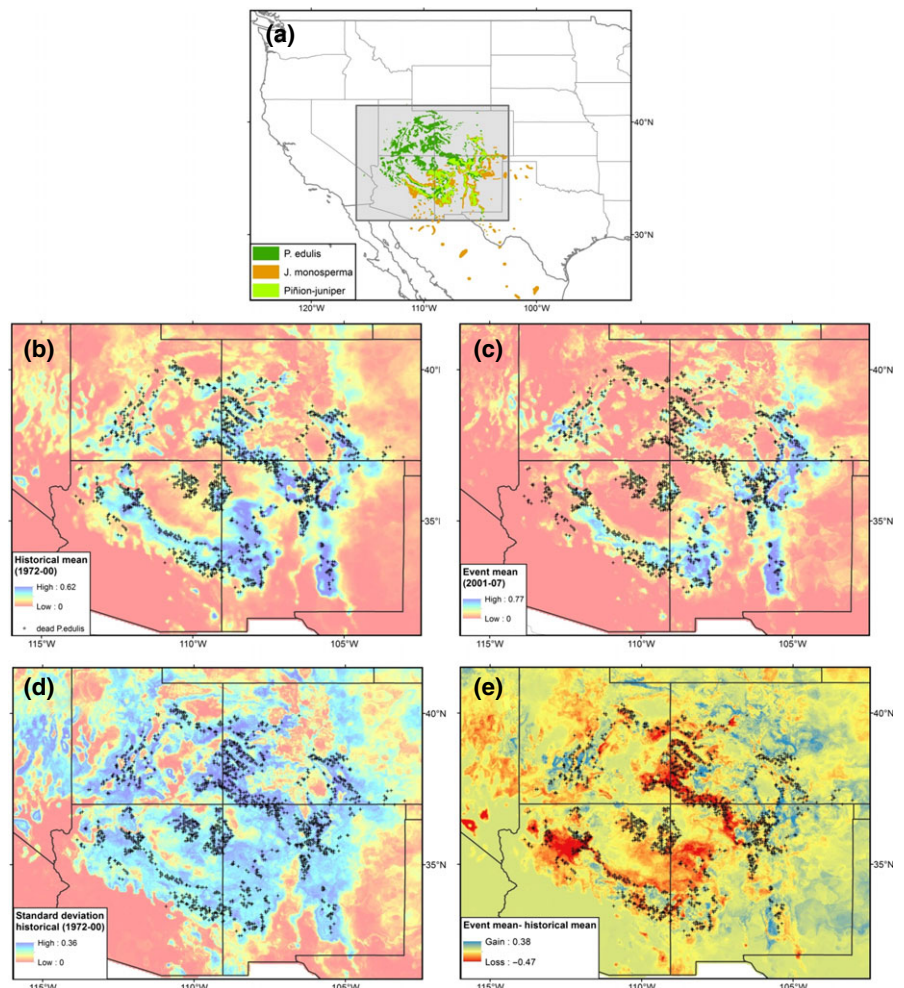
FIGURE 1 (a) Study area and distribution of *Pinus edulis* (piñon pine), *Juniperus monosperma* (juniper), and mixed piñon–juniper forests and woodlands; (b) historical, pre-episode (1972–2000) mean climatic suitability for *P. edulis* (*HCS*) (crosses indicate sites where *P. edulis* suffered die-off during the 2001–2007 episode); (c) mean climatic suitability for *P. edulis* during the 2001–2007 episode (*ECS*); (d) historical, pre-episode (1972–2000) standard deviation in climatic suitability for *P. edulis* (*HCS-SD*); (e) deviations (difference) in the climatic suitability of *P. edulis* during the 2001–2007 episode, compared to the historical, pre-episode suitability (1972–2000)

estimated approximately in a half a mile (https://www.fia.fs.fed. us/tools-data/spatial/Policy/index.php). Climatic and presence data were clipped to the 2,833,039 km² study area (30.59–45.32°N, 100.93–120.74°W; Figure 1). Historical climatic conditions (prior to the drought episode) were obtained by averaging yearly variables on a pixel-by-pixel basis over the pre-episode 1972–2000 period. To model species' historical climatic suitability (*HCS*), we used the maximum entropy approach implemented in the MAXENT software package (v3.3.3) (Phillips, Anderson, & Schapire, 2006). MaxEnt is a program for modeling species distributions from presence-only species records. The algorithm explores complex relationships with the environment minimizing the relative entropy between two probability densities (one estimated from the presence data and one from the landscape) defined in covariate space (Merow, Smith, & Silander, 2013). As in all correlative species distribution modeling approaches, the final result is not a unique model and must be taken as a hypothesis because sampling is incomplete and predictors do not necessarily capture all environmental constraints (Jarnevich, Stohlgren, Kumar, Morisette, & Holcombe, 2015). We used 50% presence points (1,964 points) within the study area for training and 50% for testing of the model. The total number of training points also including background pseudoabsences (generated randomly by MaxEnt and only used for model evaluation) was 11,934, representing 1.8%

of the study area. Modeling was repeated five times using bootstrap sampling from all the occurrence data. Model evaluation and final model output were based on averages of the five replicates. We retained all the variables in the final model, given that attempts at stepwise elimination always resulted in drops in regularized training gain lower than 1% for both species. After exploring a range of values (1, 0.5, 0.05, and 0) of the regularization multiplier (a constant used to fine tune the level of complexity of features to fit the data), we chose 0.05 as this value-maximized training gain (Merow et al., 2013). The model's final regularized training gains were 1.186 and the area under the curve (AUC) of the Receiver Operating Characteristic curve (ROC), a curve that reflects the ability of the model to correctly classify between presences and background points was 0.959, thus suggesting a relatively high predictive power of the model.

Then, the final models were projected to obtain yearly suitability for the surveyed pixels (classified as live or die-off, see below) in the entire 1972–2007 period including a historical reference period (1972–2000) and the die-off period (2001–2007). We calculated historical climate suitability (*HCS*) as the mean value of yearly suitability in the 1972–2000 period. The interannual variability in the historical suitability (*HCS-SD*) layer was estimated by calculating on a pixel-by-pixel basis the standard deviation in suitability during the 1972–2000

predrought period. For the 2001–2007 period, in addition to yearly values of climatic suitability, for each pixel classified as die-off, we also calculated in any given year of the period the mean value of climatic suitability from 2001 to the year in which die-off was reported (episode climate suitability, ECS); for pixels without die-off, this calculation was applied to the full 2001–2007 period. This ECS values represent an integrative measure of the climatic suitability during the episode, according to the state of the forest in any year.

Additionally, occurrences of *J. monosperma* in the region were gathered from the ForeCASTS Project Tree Atlas V5 including 1,763 *J. monosperma* occurrence locations (1,543 FIA Program plots + 220 GBIF sites). Co-occurrence of *J. monosperma* in *P.edulis* pixels was considered if *J. monosperma* was recorded within a radium <3 km of the *P. edulis* locations.

2.3 | *Pinus edulis* mortality maps

Yearly maps were obtained for the 2000–2007 period describing the mortality on *P. edulis* forests (Meddens, Hicke, & Ferguson,

2012) across its range (downloaded from http://databasin.org). This product was derived from aerial survey data of tree mortality caused by bark beetle concomitant with drought (Breshears et al., 2005; Meddens et al., 2015). As the data source (Meddens et al., 2012) relates the mortality to the year it was detected, we subtracted 1 year from the originally reported year to relate mortality to yearly climate data. Each yearly layer of mapped die-off (Albers Equal Area) was reprojected onto the coordinate system (geographic WGS84) in which *P. edulis* occurrence data were reported (see below). *P. edulis* occurrence pixels were classified as "die-off" (we use die-off hereafter to maintain consistence with literature reporting this event) during a given year if points in the mortality layer were within a radius of ≤3 km (i.e., representing eight surrounding neighbors to a given focal pixel) from a location where mortality was mapped in that same year (crossed in Figure 2). Alternatively, *P. edulis* occurrences were classified as "live," representing *P. edulis* populations that mostly survived, when they were >3 km away from any mapped mortality within the 2001–2007 period.
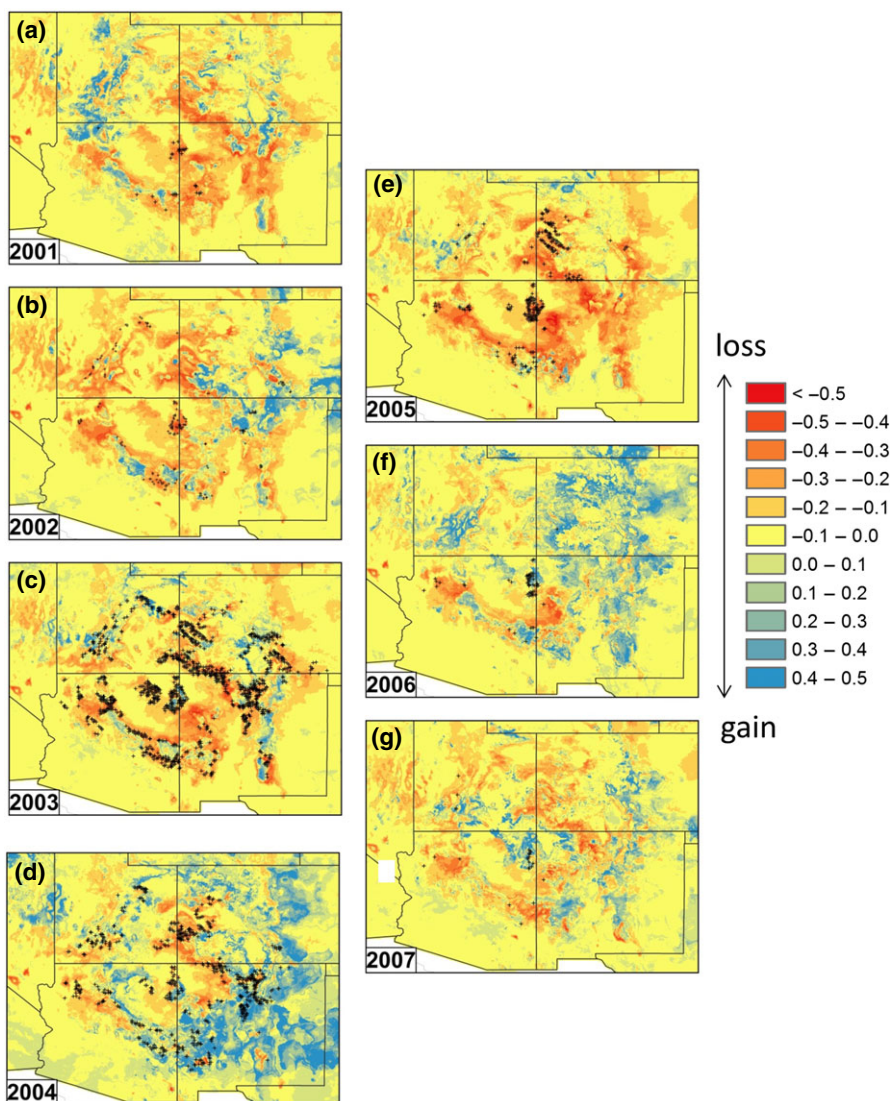

FIGURE 2 (a–g) 2001–2007 yearly bioclimatic deviations of *P. edulis* from historical, pre-episode climatic suitability (1972–2000). Crosses indicate *P. edulis* mortality sites recorded during a given year, red/blue colors indicate losses or gains, respectively, in climatic suitability during each year compared to the historical, pre-episode time series

2.4 | Statistical analysis

We assessed the role of HCS and ECS in determining P. edulis die-off by Generalized Linear Models GLMs (with a logit link function and a binomial distribution error structure) that considered "die-off" and "live" pixels categories as main variable and ECS, HCS, and HCS-SD as explicative factors. We also included bivariate interactions in the model. Longitude and latitude coordinates, and their product, were also included in the model to account for geographical trends. We also explored the effect of J. monosperma occurrence in P. edulis die-off by including in the model a binary variable describing J. monosperma presence or absence in the pixels as described above. We performed GLMs for each individual year from 2001 to 2007 and for the whole 2001–2007 period. In these individual yearly GLMs, we considered die-off pixels corresponding to that year, while live pixels were those remaining without die-off at the end of the 2001–2007 period. To account for temporal lags in die-off response to climate variability, we explored different models considering ECS as described above or alternatively replacing its value in the models by the climatic suitability for each pixel in the considered year (Year), in the two previous years (Year-1, Year-2), or by the mean value of these 3 years (Year, Year-1, Year-2) (Table S1). In the whole-period GLM, we pooled die-off pixels of the whole set of the years 2001–2007. Since J. monosperma occurrence did not produced a significant effect in the whole-period GLMs, this variable was eventually removed from the model. We previously checked the relevance of spatial autocorrelation by repeating 10 times the whole-period model in a subset of pixels that corresponded to one randomly selected pixel within each 10×10 km cells. The rationale for this procedure (Batllori, Parisien, Krawchuk, & Moritz, 2013; Moritz et al., 2012) is based on the fact that when significant effects disappear at larger pixel sizes, it means that spatial correlation is relevant to explain the significance of factors at higher resolution scales. Comparisons of climatic suitability indices during the 2001–2007 period were performed by Wilcoxon–Kruskal–Wallis test because residuals did not follow a normal distribution. All statistical analyses were carried on with JMP 10.0.0 (@2012 SAS Institute Inc.).

3 | RESULTS

3.1 | Bioclimatic influence on the pattern of P. edulis die-off

As expected, P. edulis ECS significantly dropped during the 2001–2007 period throughout the study area (Figure 1c) compared to the long-term HCS (Figure 1b,e) (mean $\pm$ SD suitability in 1972–2000: 0.309 ± 0.123, in 2001–2007: 0.226 ± 0.145, Wilcoxon–Kruskal–Wallis test, $P < .001$). This drop corresponded to extreme hot drought conditions as described in literature for this event (Breshears et al., 2005; Clifford et al., 2013; Meddens et al., 2015).

In addition to the general die-off pattern, the 2001–2007 drought period was temporally and spatially heterogeneous in the year-to-year bioclimatic conditions and the die-off response of P. edulis (Figure 2). Particularly low climatic suitability values were found in the year 2003 (Figure 2c), the one in which most P. edulis die-off occurred (50.7% of total pixels, detected in 2004 (Meddens et al., 2012)). Other years within the 2001–2007 period that had low climatic suitability, albeit with less widespread die-off, were 2001, 2002, and 2005 (Figure 2a,b,e). Despite low climatic suitability during 2001 and 2002, the die-off rate was not high in those years. The year 2004 was suitable in many localities, apart from some small unfavorable patches (Figure 2d), yet die-off for that year was the second highest in the 2001–2007 period (25.7% of total pixels, detected in 2005). After 2004, die-off declined. In 2005, climatic conditions were very unfavorable for P. edulis (Figure 2e), but die-off was not widespread (11.1% of total pixels, detected in 2006). Consistent with the low-reported die-off of P. edulis, the years 2006 and 2007 (detected in 2007 and 2008) were, overall, not extremely unfavorable (Figure 2f,g). Spatially, while the 2001–2007 period was characterized by a general reduction in climatic suitability, some areas located to the east showed gains in suitability (Figure 1c,e). These increases were concentrated during the years 2002, 2004, 2006, and 2007 and generally fell outside the die-off area (Figure 2d,f,g).

The correspondence between loss of climatic suitability and P. edulis die-off was statistically significant, as indicated by GLMs. Lower ECS had a negative effect on P. edulis populations for the whole period (Table 1; mean $\pm$ SD ECS in all die-off pixels = 0.190 ± 0.153, in all live pixels = 0.219 ± 0.150). In addition to ECS for the whole period, we also found an effect of low climatic suitability during the episode when analyzing each year separately, but this effect exhibited some lags since die-off pixels in 2001, 2002, 2003, 2005, and 2006 were determined by a decrease in climatic suitability values of previous years (Table S1). However, the delayed effect could not be unequivocally assigned to any lag period (Year-1, Year-2). Thus, we eventually considered ECS to further describe climatic suitability during the episode since it well integrates the accumulated effect of loss of climatic suitability and because models including this variable overall performed better in terms of the Akaike Information Criterion (Table S1). This better performance of ECS in relation to the other integrative estimation of the climatic suitability for the period (mean climatic suitability of the three recent years) was particularly clear when the respective models showed some discrepancy. Therefore, negative effect of ECS on P. edulis die-off also occurred in most individual years, with the exception of 2004 and 2007 (Figure 3b).

Historical climatic suitability for P. edulis showed a positive relationship with die-off. For the whole period, pixels that experienced die-off had higher HCS in the previous decades than pixels where P. edulis remained alive (Table 1; mean $\pm$ SD HCS in all die-off pixels = 0.656 ± 0.114, in all live pixels = 0.591 ± 0.168), and this pattern was consistent for both all pixels and for randomly selected pixels in 10×10 km cells. In fact, HCS was a stronger predictor of die-off than ECS, and the differences in HCS between die-off and live pixels were greater than those in ECS (Figure 3). This relationship between HCS and die-off held true for each year, except 2001

Term	All pixels			Random pixels-100 km^2		
	Estimate	χ^2	p	Estimate	χ^2	p
Intercept	−606.32	273.67	<.0001	−623.57	80.98	<.0001
Longitude	−5.54	271.47	<.0001	−5.69	79.88	<.0001
Latitude	16.97	288.79	<.0001	17.25	84.68	<.0001
Longitude*Latitude	0.16	288.55	<.0001	0.16	84.43	<.0001
HCS	3.72	168.18	<.0001	3.65	51.44	<.0001
ECS	−2.35	83.78	<.0001	−2.06	13.05	.0006
HCS-SD	3.46	12.17	.0005	5.91	10.38	.0062
HCS x ECS	4.20	4.30	.0381	9.03	5.86	.0404
HCS x HCS-SD	−16.61	9.72	.0018	2.10	0.24	.7382
ECS x HCS-SD	−6.80	1.03	.3107	−30.16	5.68	.0803

TABLE 1 Model describing die-off of *Pinus edulis* in relation to climatic suitability

GLM (with a logit link function and a binomial distribution error structure) results of die-off vs. live *P. edulis* state in all pixels (left columns) and mean values of results from 10 subsets of pixels, that corresponded to one randomly selected pixel within each 10 × 10 km cells (Random pixels-100 km^2, right columns). The whole set of surveys from 2001 to 2007 was considered. *HCS:* historical pre-event (1972–2000) mean climatic suitability for *P. edulis*; *ECS:* episode mean suitability, calculated since the start of the episode in 2001 until the year in which the die-off was detected or until 2007 for live pixels without die-off; *HCS-SD:* between year variability (SD) of climatic suitability during the 1972–2000 period. * indicates product, x indicates interaction between variables of the model.

(Figure 3a). Importantly, there was a significant interaction between *HCS* and *ECS* for the whole period (Table 1) and in most individual years (Table S1), indicating that *P. edulis* die-off pixels tended to combine high *HSC* and low *ESC* compared to live pixels (Figure 4).

Co-occurrence of *J. monosperma* had a negative effect on *P. edulis* performance in 2002, 2003, 2004, and 2006, particularly when considering the delayed effect of climatic suitability loss; this effect tended to disappear when considering *ECS* as an integrative estimation of the climatic suitability during the whole period (Table S1), except in 2016.

Between-year variability in climatic suitability (*HCS-SD*) was a positive predictor of *P. edulis* die-off, but its significance was in general lower than that of *HCS* and *ECS* (Tables 1 and S1). Die-off pixels had slightly greater interannual variability in suitability than live pixels (Figure S1 and Table S1). There was a negative effect of the interaction between *HCS* and *HCS-SD* when considering all pixels but not when analyzing randomly selected pixels in 10 × 10 km^2 cells (Table 1) for the whole period; at yearly level, this interaction was significant in 2002, 2003, and 2005. No significant effect of the interaction between *ECS* and *HCS-SD* was found for the whole period, but it was significantly negative in 2001 and 2002 (Table S1).

4 | DISCUSSION

Climatic suitability estimations allowed to explain regional patterns of *P. edulis* mortality, considering both combining historical climatic legacy (*HCS*) and loss of suitability during the extreme drought period (*ECS*). Noticeably, productive climatic conditions can increase vulnerability when combined with a dramatic increase in the current

drought intensity. The extreme climatic conditions of the 2001–2007 drought period were distinctly harsh for *P. edulis* populations in comparison with the previously experienced climate. The drop in *ECS* and its correspondence with die-off confirms the importance of climate (combined drought and heat) in the observed forest decline, recognizing its compounded effect with bark beetle infestation (Anderegg, Hicke et al., 2015), which in many cases eventually lead to tree mortality by phloem consumption. This result agrees with several studies of this system that have also disentangled the role of climate parameters, particularly high temperatures and water demand, in the spatial patterns of die-off (Adams et al., 2009; Breshears et al., 2005; Clifford et al., 2013; Williams et al., 2010), even considering the existing differences across geologic substrates, landscape patterns, and tree age (Floyd et al., 2009; Meddens et al., 2015).

The climatic suitability for *P. edulis* across the region showed an important between-year variability, indicating that multiyear droughts are spatially and temporally heterogeneous, both by nature and as regards the effects on tree die-off. For instance, in 2007, the lack of significant relationship between *ECS* and die-off can be explained because climatic suitability did not drop in many pixels (Figure 2g) and because the time of the last strong climatic suitability loss was 2 years before, in 2005; similarly, in 2004, *ECS* experienced less drop in comparison to the other years. Accordingly, there was no yearly close correspondence between low suitability and die-off, supporting the observed delayed effects of loss of climatic suitability and the widely reported existence of climate–mortality relationships that are blurred by time lags and cumulative effects acting on resource levels. This temporal decoupling may be related to physiological processes, involving resources storage and recovery of xylem
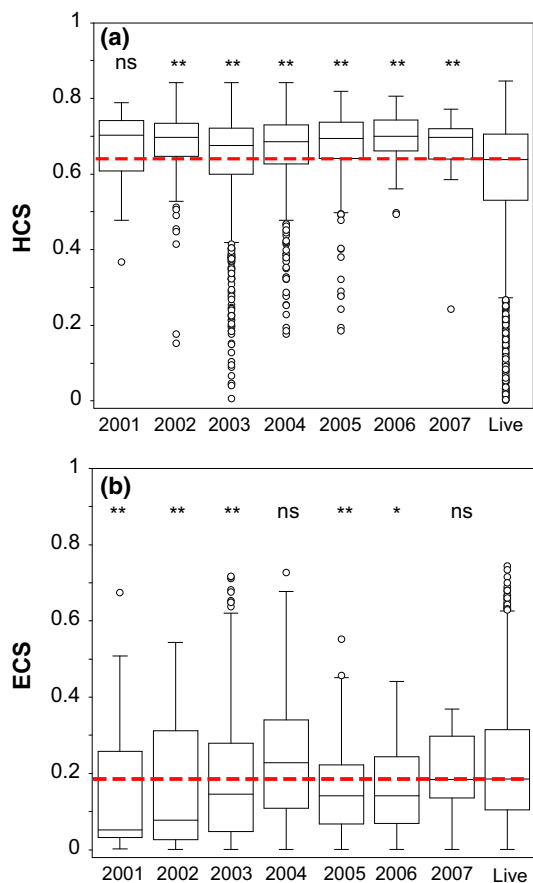
FIGURE 3 (a) Historical, pre-episode (1972–2000) mean suitability (*HCS*) and (b) episode mean suitability (2001–2007) (*ECS*) for *P. edulis* in all pixels with die-off and in live pixels (that remained without die-off after 2007). For die-off pixels, *ECS* was calculated as the mean value of climatic suitability from 2001 to the year in which die-off was detected; for live pixels, that period was 2001–2007. Significant effects of *HCS* and *ECS* on GLMs explaining die-off in the respective years are shown (ns: not significant; *p < .05; **p < .001). Dashed line indicates mean value of live pixels [Colour figure can be viewed at wileyonlinelibrary.com]

embolism (Anderegg, Berry, & Field, 2012; Galiano, Martínez-Vilalta, & Lloret, 2011; Meinzer & McCulloh, 2013), and demographical and spread rates of insect pests (Anderegg, Hicke et al., 2015; Raffa et al., 2008; Weed, Ayres, & Hicke, 2013). These processes often involve thresholds and nonlinear responses that explain delayed effects. In our study case, expansion of ips infestation may have been particularly relevant (Breshears et al., 2005). The use of *ECS* as the average suitability from the beginning of the drought period to the year in which die-off appeared allows to integrate the loss of suitability in time while including these cumulative and lag effects. Hence, die-off in this system seems to respond more to unfavorable multiyear bioclimatic conditions than to extreme conditions in a single year. For example, the massive die-off in 2003, and to a lesser extent 2004, was possibly a response to previous consecutive years of unfavorable conditions whereas the low die-off in 2005—despite extremely low suitability in the same year—was possible due to the preceding relatively favorable conditions in 2004 or the fact that the

more vulnerable populations had already declined. Alternatively, pest outbreak tends to produce a clumped pattern of mortality, particularly in sites and years where pine populations were more vulnerable to drought. Then, the spread of the pest outbreak may also have contributed to the observed spatial distribution of die-off across years, yet successful attack seems to need stressed trees (Meddens et al., 2015; Raffa et al., 2008).

The positive relationship between *P. edulis* HCS and die-off suggests that vulnerability to the combined effect of drought and bark beetles was higher in populations that historically have been living under more suitable conditions. This finding suggests that populations thriving in historically more suitable locations were more prone to decline in the die-off event than populations in sites subjected to chronic climatic stress. The lack of relationship between *HCS* and die-off at the beginning of the event period, in 2001, likely reflects the time lags needed by the combined effect of drought and ips infestation to produce dramatic tree mortality. It is noticeable that the more the suitability drops during the event, the more the vulnerability increases in these historically suitable locations. This trend is supported by the interaction between *HCS* and *ECS* that is consistent across subsets of randomly selected pixels of different size, although exhibited moderately significant values. This result contrasts with patterns documented at tree level (i.e., within populations) that reveal a marked decrease in growth prior to death during drought episodes (Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015; Macalady & Bugmann, 2014; Ogle, Whitham, & Cobb, 2000), but agrees with reported higher vulnerability to drought in populations established in damper sites (Sala & Tenhunen, 1994), particularly when interacting with competence (Clark et al., 2016). This vulnerability of climatic-core populations may implicate several nonexclusive mechanisms. First, it can be related to phenotypic plasticity, local adaptation (Moreira et al., 2014; Rose, Leuschner, Köckemann, & Buschmann, 2009), and/or acclimation to suitable conditions that led plants to poorly respond to water deficit conditions (Clark et al., 2016). The mechanisms involve molecular, physiological (vessel water transport, stomatal regulation, reserve storage), and structural (leaf area/size, leaf/sapwood area, hydraulic conductivity, above/below biomass) adjustments (Martínez-Vilalta et al., 2009; Morin et al., 2007; Peñuelas et al., 2013). For instance, some recent studies indicate that large isohydric trees should be more vulnerable to drought conditions (McDowell et al., 2015). Importantly, competence may also play a relevant role since high density or basal area developed under suitable climatic conditions would enhance imbalances between water demand and availability at stand or plant level during intense episodes of water scarcity (Clark et al., 2016; Jump et al., 2017). Indeed, several studies have documented a positive relationship between tree mortality and stand density associated to drought periods (Bell, Bradford, & Lauenroth, 2014; Klos, Wang, Bauerle, & Rieck, 2009), particularly in the study area (Greenwood & Weisberg, 2008). Our study also shows a potential influence of interspecific competition with *J. monosperma*. This effect seems associated to lag effects of previous years of unsuitable conditions, and it was likely diluted when considering the whole period, likely
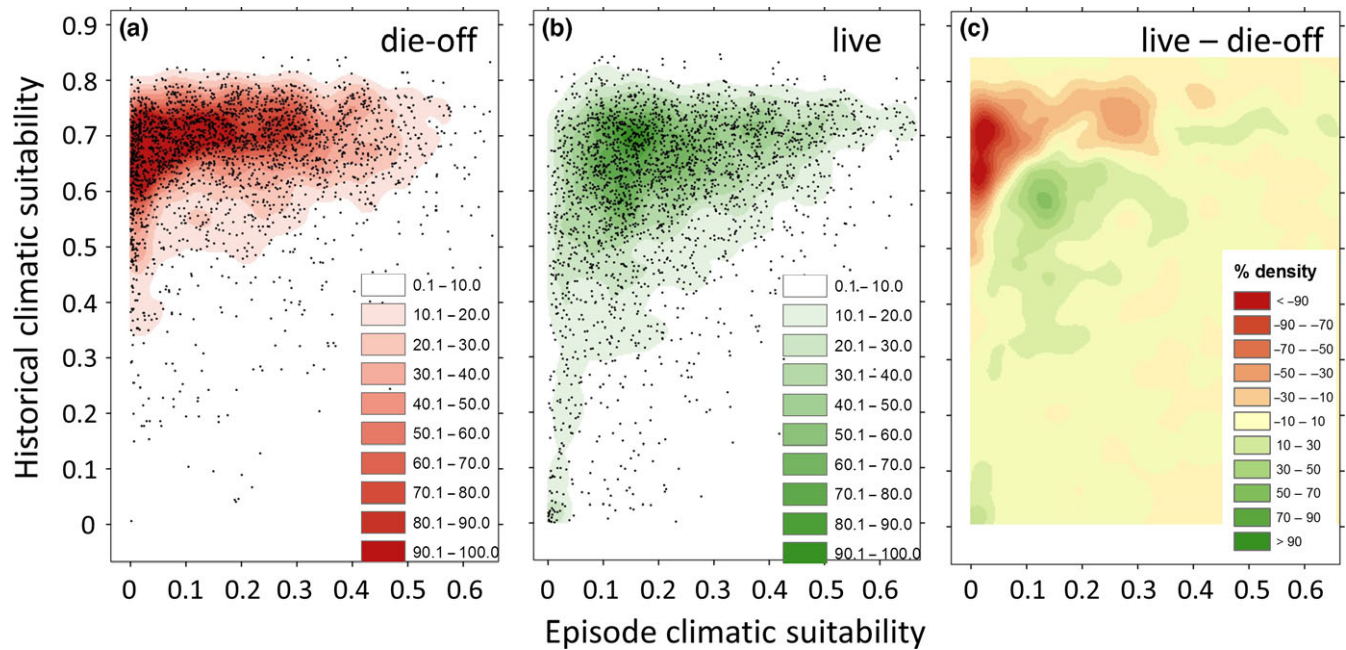
FIGURE 4 Interaction between historical, pre-episode (1972–2000) climatic suitability (*HCS*) and episode climatic suitability (*ECS*) (2001–2007) on occurrence (black dots) of *P. edulis*: (a) all pixels with die-off during 2001–2007, (b) all live pixels (those that remained without die-off after 2007), and (c) difference between live and die-off pixels (red or green areas indicate regions with negative or positive values of this difference, respectively; that is, red color indicates higher density (%) of die-off data points). Density contours reflect density of data points after fitting a smooth bivariate nonparametric density surface that estimates the bivariate probability (%) at each point

because the broad resolution of the study does not detect this effect at stand level when compensated across years. In contrast to the isohydric *P. edulis*, which tends to avoid low tissue water potentials —and the risk of cavitation—through stomatal regulation, *J. monosperma* is an anisohydric species better adapted to tolerating and continuing photosynthesis under low xylem water potentials (McDowell et al., 2008, 2015). These differences were also reflected in the local mortality rates of the two species (less than 25% in *J. monosperma*, while *P. edulis* achieved up to 95% from 2001 to 2007 (Shaw, Steed, & DeBlander, 2005; Bigler, Gavin, Gunning, & Veblen, 2007; McDowell et al., 2008)) and their distribution patterns, with a more xeric, low elevation and southeastern distribution for *J. monosperma* (Figure 1a) and can explain a worse performance of *P. edulis* when *J. monosperma* is present. Furthermore, higher tree density may represent resource limitations that would result in more vulnerability to insect attack, but this mechanism has not been unequivocally demonstrated in our system by previous studies (Floyd et al., 2009; Negron & Wilson, 2003). Overall, our results indicate that vulnerability to drought episodes is not confined to the ecotone closer to the dry/hot edges of tree species ranges (Allen & Breshears, 1998). Thus, our study therefore does not support worse demographic performance at the edge of a species' climatic range (Abeli et al., 2014; Martínez-Meyer et al., 2013). Instead, our results are consistent with the documented resistance of marginal populations to climate change (Doak & Morris, 2010; Hampe & Petit, 2005).

The significant interactions between *HCS* and *HCS-SD* when considering all pixels would suggest that *P. edulis* is more prone to die-off in both core-climatic areas with low year-to-year variability and edge areas with high year-to-year variability. This would agree with the interpretation that directional acclimation and increasing stand density under favorable, climatically stable conditions could increase vulnerability when unfavorable extreme conditions occur due to higher hydraulic failure (Anderegg, Schwalm et al., 2015) or competition (Jump et al., 2017). Likewise, vulnerability in *P. edulis* populations living near climatically unsuitable, highly variable edges endorses the relevance of the cumulative effects of past extreme events (Lloret et al., 2004) likely due to a depletion of stored reserves (Dickman, McDowell, Sevanto, Pangle, & Pockman, 2015) or the loss of meristems that allow regrowth (Zeppel et al., 2015). However, this result appears subjected to important spatial constraints since the interaction is not significant when we reduced autocorrelation effects by randomly selecting pixels at a larger spatial scale. For instance, between-year climatic variability in pixels may be governed by confounding factors such as topography, which in turn may determine die-off (e.g., mountain areas may exhibit both higher between-year climatic variability and shallower soils).

One drawback of applying measures of climatic suitability from SDMs is that the calculation is basically statistical, whereas species occurrence is determined by many factors other than climate (e.g., biotic interactions, past management, disturbance regime, dispersal constraints, and soil characteristics), so it cannot explicitly disentangle the suite of mechanisms involved in population success (Araújo & Luoto, 2007; Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Hampe, 2004; Serra-Díaz et al., 2013; Thuiller et al., 2008). In our case, *P. edulis* die-off was the compound result of drought and insect

outbreak (Anderegg, Hicke et al., 2015; Breshears et al., 2005; Macalady & Bugmann, 2014; McDowell et al., 2008, but see also Floyd et al., 2009) and their separate contributions cannot be well distinguished. The drop in climatic suitability during the 2001–2007 period confirms the importance of climate variability (drought and heat) in this interaction (Raffa et al., 2008). In fact, drought and insect infestation may produce synergistic effects that reinforce each other mutually (Anderegg, Hicke et al., 2015; Jactel et al., 2012; Macalady & Bugmann, 2014; McDowell et al., 2008). However, we cannot completely rule out the observed relationship between die-off and climatic suitability as a result of the effect of weather conditions on bark beetle populations, which led to infestation. The low *ECS* values observed during the 2001–2007 period corresponded to a warm period that may have broken down the control of bark beetle populations by cold temperatures (Raffa et al., 2008). Furthermore, resin ducts become less dense after drought periods, thus increasing vulnerability to biotic attack (Gaylord et al., 2013). Similarly, tree allocation to defenses against insect infestation (resin ducts number, size) may be lower in climatic-core populations, due to trade-offs between plant growth and resource allocation to defenses (Moreira et al., 2014) and their limited experience of droughts in the past may have reduced the production of these inducible defense structures (Gaylord et al., 2013). Furthermore, spatially continuous climatic-core populations may promote better dispersal of insect pests (e.g., ips) and eruptive dynamics (Raffa et al., 2008), compared to more fragmented and isolated climatic-edge populations. Since bark beetles are relatively poor dispersers, a highly correlated environmental factor that effectively increases the connectivity of suitable habitat is usually required to facilitate coalescence and spread (Aukema et al., 2006).

Despite the recognized limitations of correlational models, this study shows that species' climate niche is an appropriate approach to explain population responses that are functionally associated with climate, such as drought-induced die-off. This is particularly useful in a context of climate change and extreme climatic events. Bioclimatic indices may be suitable predictors of species-specific mortality, as they allow us to standardize climatic conditions from the population's point of view. They also could potentially be applied to other ecological processes that are driven by climate, such as invasion by exotics (Thuiller et al., 2005), insect outbreaks (Lantschner, Atkinson, Corley, & Liebhold, 2017; Sidder, Kumar, Laituri, & Sibold, 2016), or postdisturbance recovery. This application can investigate the variability in the response of a given species across environmental gradients or make a comparison between co-occurring species with different climatic suitability (Sapes et al., 2017). Although the correlation between demographical variables and outputs from SDMs can be subjected to considerable uncertainty, our study supports its validity when considering extreme situations in terms of climatic variability and demographic processes (i.e., mortality). However, further studies should be carried on to analyze the explanatory power of SDMs in comparison with direct climatic variables when assessing regional patterns of species' response to climate extremes.

In conclusion, this study shows that climatic suitability indices allow to relate populations' adequacy with the past climatic conditions with the current responses to climate change. Furthermore, these indices describe how the intensity of the drought episode as experienced from the species' point of view is correlated with the regional pattern of tree mortality. Our approach, therefore, highlights the vulnerability to climate change—and more particularly drought episodes—even in those populations established in sites with conditions close to the core of species' climatic niche. This vulnerability under future extreme drought episodes raises concerns about how conservation and management efforts have to be strategically developed to mitigate the impact of future climatic regimes. Thus, it may become necessary to move the focus toward considering smaller, more fragmented populations as conservation targets, in both climatic-edge and climatic-core areas. Indeed, populations from climatic-edge areas may be important not only as survival sites but also as potential sources of more drought-resistant genotypes that could potentially be used for repopulating sites decimated by drought-induced mortality (Hampe & Petit, 2005; Rehm, Olivas, Stroud, & Feeley, 2015). Furthermore, more research is necessary to determine the existence of common thresholds of bioclimatic suitability loss below which species consistently experience drought-induced die-off (Mitchell et al., 2014). If such bioclimatic thresholds could be determined, the consequences of drought events in species-rich forests could be predicted more accurately in accordance with different forecasted climate regime scenarios.

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