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

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Running head: Tree mortality and climatic suitability

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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 of 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 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 South Western 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 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

42   climatic variability across populations using SDMs, improving our capacity to predict

43   population's or species' vulnerability to climatic change.

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47   **Introduction**

48   Regional episodes of extreme climatic variability associated to climate change, such as acute

49   drought/heat events, are exacerbating tree mortality in forest ecosystems worldwide (Allen et al.,

50   2010; Allen et al., 2015; Neuman et al., 2017). However, many uncertainties remain about the

51   spatial and temporal variability of tree populations vulnerability in front of such extreme climatic

52   events (Allen et al., 2015; Clark et al., 2016). Extreme events are expected to affect tree local

53   populations differently within species' ranges because of the spatial variations in the physical

54   conditions imposed by climatic anomalies (due to moist air circulation, local precipitation

55   patterns, topography, soils, etc.), and also because of variations in the histories of colonization,

56   adaptation and acclimation experienced by different populations (Hampe & Petit, 2005). Thus,

57   defining the vulnerability of tree populations across species ranges - which encompasses a

58   variability of climatic legacy and weather conditions during extreme episodes - in the context of

59   ongoing global environmental changes (Lloret et al., 2007; Fensham et al., 2015; Calvin & Jump,

60   2017) has vital implications for carbon balance (Anderegg et al., 2015b; Mekonnen et al., 2017),

61   resource management and conservation (Seneviratne et al., 2012).

62   One of the main obstacles to unify principles and predictive capacity regarding when and

63   where to expect increased tree mortality under altered climatic regimes is the fact that extreme

64   climate phenomena, particularly those associated with water availability, are species/population-

65   specific. The physiological mechanisms responsible of drought-induced tree mortality are still

66   not completely established, but there is an agreement that they involve the impairment of the

67   vascular transport system (i.e hydraulic failure) and/or the C economy (Adams et al., 2017). In

68   fact, the same absolute amount of water deficit can imply very different physiological,

69   demographic and ecological consequences, depending on the ecological and evolutionary context

70   (Martínez-Vilalta et al., 2012; Allen et al., 2015; Martínez-Vilalta & Lloret, 2016). One proposed

71   solution to this problem has been the standardized measurement of event extremes (Kitzberger,

72   2013). Accordingly, water balance leading to drought conditions can be statistically standardized

73   at different locations or time scales, following a probabilistic approach - e.g., via the sc-PDSI

74   (McDowell et al., 2008), or the SPEI indices (Vicente-Serrano et al., 2010) -. Climate-based

75   indices allow us to establish common thresholds of drought 'rarity' (Kitzberger, 2013) that cause

76   tree die-off events irrespective of location and species (Mitchell et al., 2014; Greenwood et al.,

77   2017). However, these climatic approaches only analyze how statistical deviations of the

78   physical phenomenon in a given location relate to a population's biological response (e.g.

79   mortality). But, they do not consider how spatial intra- or inter-specific patterns of mortality

80   emerge from the interaction between the species ecological and evolutionary adjustments and the

81   climatic extreme.

82   Classic niche theory proposes that species perform less robustly when populations experience

83   environmental conditions closer to the boundaries of the environmentally defined niche space

84   (MacArthur, 1984; Martínez-Meyer et al., 2013). Thus, stochastic fluctuations or directional

85   changes promoting harsher environmental conditions are expected to weaken population's

86   performance near species climatic edges due to low assimilation and cumulative physiological

87   damage (Morin et al., 2007; Seneviratne et al., 2012). However, populations living near the

88   edges of climatic ranges may be more resistant to directional environmental changes and

89   stochastic climatic extremes than core populations (Calvin & Jump, 2017) since they may have

90   plastically or genetically adjusted to a chronically scarce and fluctuating limiting resource (e.g.

91   water availability) (Purves, 2009; Abeli et al., 2015). In contrast, populations living at the core of

92   the species' climatic range might exhibit a high demand for resources, that in the case of trees

93   could correspond to water due to elevated growth rates or high stand density or basal area. Then,

94   during unusually extreme droughts, these characteristics can make them vulnerable to hydraulic

95   failure, and to water demand from competitors (McDowell et al., 2008; Anderegg et al., 2015a;

96   Meddens et al., 2015; Jump et al. 2017). Nevertheless, the translation of population' behavior

97   across climatic ranges to species distribution may be eventually obscured by the coexistence of

98   these alternative mechanisms and specially because the correspondence between demographic

99   performance and species range may be multi-faceted, depending on genetic, population and

100   biogeographic histories, biotic interactions and microenvironment distribution (Purves, 2009;

101   Abeli et al., 2014; Pironon et al., 2015).

102   Here we adopt a novel approach to explain temporal and spatial patterns of tree die-off by

103   standardizing the climatic event magnitude from the use of Species Distribution Models (SDMs)

104   based on bioclimatic envelopes. SDMs (also known as bioclimatic niche models, correlative

105   ecological niche models, or envelope models) consider the species' occurrence in sites across its

106   distribution range, as well as the climatic conditions of that range, although other non-climatic

107   environmental variables can also be considered. SDMs are regularly used to interpret species'

108   distribution patterns in relation to environmental variables, particularly climate (Elith &

109   Leathwick, 2009; Franklin, 2010) and they have been applied in studies on turn-over of

110   vegetation composition across landscape (Jennings & Harris, 2017), regional patterns of growth

111   (Maaten et al., 2017), community-level responses to experimental drought (Bilton et al., 2017) or

112   projections of tree response to climate change (Cheaib et al., 2012). However, the use of SDMs

113   requires caution since they do not address an explicit analysis of the functional mechanisms

114   involved in the species distribution patterns, particularly ecophysiological performance, dispersal

115   and biotic interactions (Guisan and Thuiller 2005; Araujo and Luoto 2007; Elith & Leathwick

116   2009). Furthermore, the occurrence of populations across the territory can be highly dependent

117   of historical and geographical contingency, including disturbance regime, human action and

118   interaction with other species (Latimer et al. 2006; Elith & Leathwick 2009; Serra-Diaz et al.

119   2013). In spite of these deficiencies when constructing models of species' realized niche, SDMs

120   reveals its ability to describe broad patterns of the relationship between climate and species

121   occurrence (Franklin, 2010). Importantly for our purposes, SDMs provide estimates of the

122   probability of a species' occurrence in a set of climatic conditions characterizing a particular

123   locality. This value can thus be considered an integrative index of the climatic suitability

124   historically experienced by populations living in a given site. But SDMs can also be used to

125   describe climatic suitability for populations during a particular climatic event, providing a

126   standardized measure of the event magnitude which can be contrasted across the species'

127   geographic range. We use the term *bioclimatic deviation* to describe the specific climatic

128   environment experienced by certain extant populations of a given species at a particular moment

129   in relation to the whole range of climatic conditions in which a species is normally found.

130   Because climatic suitability is an occurrence-calibrated characterization of the suitable

131   conditions across the landscape for a species long-term persistence, it can be used to explicitly

132   evaluate intra- and inter-specific responses (e.g. mortality, decline, establishment, masting, insect

133   outbreak, etc.) to short-term climatic events across species' geographic ranges (Fensham et al.,

134   2009; Evans & Lyons 2013; Sapes et al., 2017). Moreover, temporal variability of climatic

135   suitability can be used as a measure of environmental stability at any site in a species range. This

136   approach is relevant because historical climatic stability is a key element to understanding an

137   ecosystem's vulnerability to extreme climatic events (Gutschick & BassiriRad 2003).

138   Here we use an annual time series of downscaled bioclimatic data to assess the capacity of

139   the output of a bioclimatic model based on historical (1972-2000) climatology (hereafter

140   *historical climatic suitability, HCS*) to explain massive tree die-off and mortality due to the

141   compound effect of drought and bark-beetle infestation of *Pinus edulis* (piñon pine) at a regional

142   scale in SW North America (Breshears et al., 2005; Gaylord et al., 2013; Macalady &

143   Bugmannm 2014; Clifford et al., 2015; Meddens et al., 2015) during the 2001-2007 period.

144   Thus, *HCS* (ranging 0-1) is used as a long-term measure of *P. edulis* climatic suitability, so that

145   higher/lower values coincide with core/edge bioclimatic conditions. We also project the model

146   onto the conditions during the particular period of die-off (hereafter *episode climatic suitability,*

147   *ECS*). *ECS* (ranging 0-1) is used as an absolute inverse measure of drought effects on climatic

148   suitability so that values closer to zero/one indicate strong/weak drought magnitude,

149   respectively. Additionally, as an inverse measure of site-specific climatic stability we also

150   calculate the long-term variability around the mean in climatic suitability (hereafter, *standard*

151   *deviation in climatic suitability, HCS-SD*).

152   In this study, our goal is to assess tree vulnerability to drought episodes across a significant

153   part of the species' range distribution, according to the variability of regional climatic legacy and

154   weather conditions during the episode. This vulnerability raises from the combined effect of

155   drought and insect attack. So, our purpose is to assess the relevance of population's bioclimatic

156 characterization to understand this compound effect, but not to disentangle the separate

157 contribution of these two factors. A negative or positive effect of *HCS* on die-off would support

158 higher vulnerability of the populations living in the climatic edge or core, respectively, while

159 negative effects of *ECS* would suggest that die-off is related to event's magnitude. *HCS x ECS*

160 interactions would be indicative of a differing vulnerability during the event of climatic core or

161 edge populations. Positive effects of *HCS-SD* on die-off would indicate increased population

162 vulnerability in highly fluctuating climatic environments, heightening the cumulative effects of

163 past deleterious periods (Lloret et al., 2004; Anderegg et al., 2015b), despite the transitory

164 recovery of suitable conditions. Interaction of *HCS-SD* with *HCS* would indicate whether

165 climatic-core or edge populations are more or less vulnerable to past bioclimatic variability,

166 while interaction with *ECS* would indicate a reinforcing mechanism between past and current

167 events.

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170 **Materials and methods**

171 *Study system*

172 In the early 2000s a die-off and mortality episode of *P. edulis* massively affected 12,000 km^2 in

173 SW North America, including forests dominated by this species and forests with co-occurrence

174 of *Juniperus monosperma* (juniper) (Fig. 1a). Tree mortality was triggered by the compound

175 effect of a multi-year drought/warm episode with a ips bark beetle outbreak (Breshears et al.,

176 2005; Gaylord et al., 2013; Macalady & Bugmann, 2014; Clifford et al., 2015; Meddens et al.,

177 2015).

Calculation of historical and episode climatic suitability

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179   To build, train and test SDMs we used pixels of *P. edulis* ocurrence downloaded from

180   ForeCASTS Project Tree Atlas V5

181   (http://www.geobabble.org/~hnw/global/treeranges5/climate_change/site_lists/). This dataset

182   includes 3,950 *P. edulis* occurrence locations from which 3,737 correspond to Forest Inventory

183   and Analysis (FIA) Program plots and 213 from Global Information Facility (GBIF) sites. FIA

184   data reflect pre-drought distribution of the species since inventories date back starting in the

185   1920s with yearly re-measurements after 1999 in most of the conterminous United States

186   (https://www.fia.fs.fed.us). Climatic data consisted of yearly multi-band raster time series

187   (1971-2009) of the 20 standard bioclimatic predictors used in species distribution modeling

188   downscaled to a 2-km pixel for the conterminous US by U.S. Geological Survey, Fort Collins

189   Science Center from original 4-km PRISM climate data developed by the PRISM Climate Group

190   at Oregon State University (O'Donnell & Ignizio 2012; downloaded from:

191   https://www.sciencebase.gov/catalog/). This pixel size is large enough to minimize the spatial

192   inaccuracy in FIA plot coordinates due to noise added to protect their location ("fuzzing"),

193   estimated approximately in a half a mile (https://www.fia.fs.fed.us/tools-

194   data/spatial/Policy/index.php). Climatic and presence data where clipped to the 2,833,039 km^2

195   study area (30.59-45.32°N, 100.93-120.74°W; Fig. 1). Historical climatic conditions (prior to the

196   drought episode) were obtained by averaging yearly variables on a pixel-by-pixel basis over the

197   pre-episode 1972-2000 period. To model species' historical climatic suitability (*HCS*) we used

198   the maximum entropy approach implemented in the MAXENT software package (v3.3.3)

199   (Phillips et al., 2006). MaxEnt is a program for modelling species distributions from presence-

200   only species records. The algorithm explores complex relationships with environment

201   minimizing the relative entropy between two probability densities (one estimated from the

202   presence data and one, from the landscape) defined in covariate space (Merow et al. 2013). As in

203   all correlative species distribution modeling approaches, the final result is not a unique model

204   and must be taken as a hypothesis because sampling is incomplete and predictors do not

205   necessarily capture all environmental constraints (Jarnevich et al. 2015). We used 50% presence

206   points (1,964 points) within the study area for training and 50% for testing of the model. The

207   total number of training points also including background pseudo-absences (generated randomly

208   by MaxEnt and only used for model evaluation) was 11,934, representing 1.8% of the study area.

209   Modeling was repeated five times using bootstrap sampling from all the occurrence data. Model

210   evaluation and final model output were based on averages of the five replicates. We retained all

211   the variables in the final model, given that attempts at stepwise elimination always resulted in

212   drops in regularized training gain lower than 1% for both species. After exploring a range of

213   values (1, 0.5, 0.05, and 0) of the regularization multiplier (a constant used to fine tune the level

214   of complexity of features to fit the data), we chose 0.05 as this value-maximized training gain

215   (Merow et al., 2013). The model's final regularized training gains were 1.186 and the area under

216   the curve (AUC) of the Receiver Operating Characteristic curve (ROC), a curve that reflects the

217   ability of the model to correctly classify between presences and background points was 0.959,

218   thus suggesting a relatively high predictive power of the model.

219

220   Then, the final models were projected to obtain yearly suitability for the surveyed pixels

221   (classified as live or die-off, see below) in the entire 1972-2007 period including a historical

222   reference period (1972-2000) and the die-off period (2001-2007). We calculated historical

223   climate suitability (*HCS*) as the mean value of yearly suitability in the 1972-2000 period. The

224   inter-annual variability in the historical suitability (*HCS-SD*) layer was estimated by calculating

225   on a pixel-by-pixel basis the standard deviation in suitability during the 1972-2000 pre-drought

226   period. For the 2001-2007 period, in addition to yearly values of climatic suitability, for each

227   pixel classified as die-off, we also calculated in any given year of the period the mean value of

228   climatic suitability from 2001 to the year in which die-off was reported (episode climate

229   suitability, *ECS*); for pixels without die-off, this calculation was applied to the full 2001-2007

230   period. This *ECS* values represent an integrative measure of the climatic suitability during the

231   episode, according to the state of the forest in any year.

232   Additionally, occurrences of *J. monosperma* in the region were gathered from the ForeCASTS

233   Project Tree Atlas V5 including 1,763 *J. monosperma* occurrence locations (1,543 FIA Program

234   plots + 220 GBIF sites). Co-occurrence of *J. monosperma* in *P.edulis* pixels was considered if *J.*

235   *monosperma* was recorded within a radium < 3 km of the *P. edulis* die-off locations.

236

237   *P. edulis mortality maps*

238   Yearly maps were obtained for the 2000-2007 period describing the mortality on *P. edulis* forests

239   (Meddens et al., 2013) across its range (downloaded from http://databasin.org). This product was

240   derived from aerial survey data of tree mortality caused by bark beetle concomitant with drought

241   (Meddens et al., 2015; Breshears et al., 2005). Because the data source (Meddens et al., 2012)

242   relates the mortality to the year it was detected, we subtracted one year from the originally

243   reported year in order to relate mortality to yearly climate data. Each yearly layer of mapped die-

244   off (Albers Equal Area) was re-projected onto the coordinate system (geographic WGS84) in

245   which *P. edulis* occurrence data was reported (see below). *P. edulis* occurrence pixels were

246 classified as "die-off" (we use die-off hereafter to maintain consistence with literature reporting

247 this event) during a given year if points in the mortality layer were within a radius of ≤ 3 km (i.e

248 representing 8 surrounding neighbors to a given focal pixel) from a location where mortality was

249 mapped in that same year (crossed in Fig. 2). Alternatively, *P. edulis* occurrences were classified

250 as "live", representing *P. edulis* populations that mostly survived, when they were >3 km away

251 from any mapped mortality within the 2001-2007 period.

252

253

254 *Statistical analysis*

255 We assessed the role of *HCS* and *ECS* in determining *P. edulis* die-off by Generalized Linear

256 Models GLMs (with a logit link function and a binomial distribution error structure) that

257 considered "die-off" and "live" pixels categories as main variable and *ECS*, *HCS* and *HCS-SD* as

258 explicative factors. We also included bivariate interactions in the model. Longitude and latitude

259 coordinates, and their product, were also included in the model to account for geographical

260 trends. We also explored the effect of *J. monosperma* occurrence in *P. edulis* die-off by

261 including in the model a binary variable describing *J. monosperma* presence or absence in the

262 pixels, as described above. We performed GLMs for each individual year from 2001 to 2007 and

263 for the whole 2001-2007 period. In these individual yearly GLMs we considered die-off pixels

264 corresponding to that year, while live pixels were those remaining without die-off at the end of

265 the 2001-2007 period. In order to account for temporal lags in die-off response to climate

266 variability, we explored different models considering *ECS* as described above or alternatively

267 replacing its value in the models by the climatic suitability for each pixel in the considered year

268 (Year), in the two previous years (Year-1, Year-2) or by the mean value of these three years

269   (Year, Year-1, Year-2) (Table S1). In the whole-period GLM we pooled die-off pixels of the

270   whole set of the years 2001-2007. Since *J. monosperma* occurrence did not produced a

271   significant effect in the whole-period GLMs, this variable was eventually removed from the

272   model. We previously checked the relevance of spatial autocorrelation by repeating ten times the

273   whole-period model in a subset of pixels, that corresponded to one randomly selected pixel

274   within each 10 x 10 km cells. The rationale for this procedure (Moritz et al., 2012; Batllori et al.,

275   2013) is based in the fact that when significant effects disappear at larger pixel sizes, it means

276   that spatial correlation is relevant to explain the significance of factors at higher resolution

277   scales. Comparisons of climatic suitability indices during the 2001-2007 period were performed

278   by Wilcoxon-Kruskal-Wallis test because residuals did not follow a normal distribution. All

279   statistical analyses were carried on with JMP 10.0.0 (@2012 SAS Institute Inc.).

280

281   **Results**

282   *Bioclimatic influence on the pattern of P. edulis die-off*

283   As expected, *P. edulis ECS* significantly dropped during the 2001-2007 period throughout the

284   study area (Fig. 1c) compared to the long-term *HCS* (Figs. 1b, e) (mean$\pm$ SD suitability in 1972-

285   2000: 0.309 ± 0.123, in 2001-2007: 0.226 ± 0.145, Wilcoxon-Kruskal-Wallis test, $P<0.001$). This

286   drop corresponded to extreme hot drought conditions as described in literature for this event

287   (Breshears et al., 2005; Clifford et al., 2015; Meddens et al., 2015).

288   In addition to the general die-off pattern, the 2001-2007 drought period was temporally and

289   spatially heterogeneous in the year-to-year bioclimatic conditions and the die-off response of *P.*

290   *edulis* (Fig. 2). Particularly low climatic suitability values were found in the year 2003 (Fig. 2c),

13

291   the one in which most *P. edulis* die-off occurred (50.7% of total pixels, detected in 2004

292   (Meddens *et al.* 2012)). Other years within the 2001-2007 period that had low climatic

293   suitability, albeit with less widespread die-off, were 2001, 2002 and 2005 (Figs. 2 a,b,e). Despite

294   low climatic suitability during 2001 and 2002, the die-off rate was not high in those years. The

295   year 2004 was suitable in many localities, apart from some small unfavourable patches (Fig. 2d),

296   yet die-off for that year was the second highest in the 2001-2007 period (25.7% of total pixels,

297   detected in 2005). After 2004, die-off declined. In 2005 climatic conditions were very

298   unfavourable for *P. edulis* (Fig. 2e) but die-off was not widespread (11.1% of total pixels,

299   detected in 2006). Consistent with the low reported die-off of *P. edulis*, the years 2006 and 2007

300   (detected in 2007 and 2008) were, overall, not extremely unfavourable (Fig. 2f, g). Spatially,

301   while the 2001-2007 period was characterized by a general reduction in climatic suitability, some

302   areas located to the east showed gains in suitability (Fig. 1c, e). These increases were

303   concentrated during years 2002, 2004, 2006 and 2007 and generally fell outside the die-off area

304   (Figs. 2d, f, g).

305   The correspondence between loss of climatic suitability and *P. edulis* die-off was statistically

306   significant, as indicated by GLMs. Lower *ECS* had a negative effect on *P. edulis* populations for

307   the whole period (Table 1; mean $\pm$ SD *ECS* in all die-off pixels = 0.190$\pm$ 0.153, in all live pixels

308   = 0.219$\pm$ 0.150). In addition to *ECS* for the whole period, we also found an effect of low climatic

309   suitability during the episode when analyzing each year separately, but this effect exhibited some

310   lags since die-off pixels in 2001, 2002, 2003, 2005 and 2006 were determined by a decrease of

311   climatic suitability values of previous years (Table S1). However, the delayed effect could not be

312   unequivocally assigned to any lag period (Year-1, Year-2). Thus, we eventually considered *ECS*

313   to further describe climatic suitability during the episode since it well integrates the accumulated

314   effect of loss of climatic suitability and because models including this variable overall performed

315   better in terms of the Akaike Information Criterion (Table S1). This better performance of *ECS*

316   in relation to the other integrative estimation of the climatic suitability for the period (mean

317   climatic suitability of the three recent years) was particularly clear when the respective models

318   showed some discrepancy. Therefore, negative effect of *ECS* on *P. edulis* die-off also occurred

319   in most individual years, with the exception of 2004 and 2007 (Fig. 3b).

320   *HCS* for *P. edulis* showed a positive relationship with die-off. For the whole period, pixels

321   that experienced die-off had higher *HCS* in the previous decades than pixels where *P. edulis*

322   remained alive (Table 1; mean $\pm$ SD *HCS* in all die-off pixels = 0.656$\pm$0.114, in all live pixels =

323   0.591$\pm$ 0.168), and this pattern was consistent for both all pixels and for randomly selected pixels

324   in 10 x 10 km^2 cells. In fact, *HCS* was a stronger predictor of die-off than *ECS*, and the

325   differences in *HCS* between die-off and live pixels were greater than those in *ECS* (Fig. 3). This

326   relationship between *HCS* and die-off held true for each year, except 2001 (Fig. 3a). Importantly,

327   there was a significant interaction between *HCS* and *ECS* for the whole period (Table 1) and in

328   most individual years (Table S1), indicating that *P. edulis* die-off pixels tended to combine high

329   *HSC* and low *ESC* compared to live pixels (Fig. 4).

330   Co-occurrence of *J. monosperma* had a negative effect on *P. edulis* performance in 2002,

331   2003, 2004 and 2006, particularly when considering the delayed effect of climatic suitability

332   loss; this effect tended to disappear when considering *ECS* as an integrative estimation of the

333   climatic suitability during the whole period (Table S1), except in 2016.

334   Between-year variability of climatic suitability (*HCS-SD*) was a positive predictor of *P.*

335   *edulis* die-off but its significance was in general lower than that of *HCS* and *ECS* (Tables 1 and

336　S1). Die-off pixels had slightly greater inter-annual variability of suitability than live pixels (Fig.

337　S1 and Table S1). There was a negative effect of the interaction between *HCS* and *HCS-SD*

338　when considering all pixels but not when analysing randomly selected pixels in 10 x 10 km^2 cells

339　(Table 1) for the whole period; at yearly level, this interaction was significant in 2002, 2003 and

340　2005. No significant effect of the interaction between *ECS* and *HCS-SD* was found for the whole

341　period, but it was significantly negative in 2001 and 2002 (Table S1).

342

343

344　**Discussion**

345　　Climatic suitability estimations allowed to explain regional patterns of *P. edulis* mortality,

346　considering both combining historical climatic legacy (*HCS*) and loss of suitability during the

347　extreme drought period (*ECS*). Noticeably, productive climatic conditions can increase

348　vulnerability when combined with a dramatic increase in the current drought intensity. The

349　extreme climatic conditions of the 2001-2007 drought period were distinctly harsh for *P. edulis*

350　populations in comparison with the previously experienced climate. The drop in *ECS* and its

351　correspondence with die-off confirms the importance of climate (combined drought and heat) in

352　the observed forest decline, recognizing its compounded effect with bark-beetle infestation

353　(Anderegg et al., 2015a), which in many cases eventually lead to tree mortality by phloem

354　consumption. This result agrees with several studies of this system that have also disentangled

355　the role of climate parameters, particularly high temperatures and water demand, in the spatial

356　patterns of die-off (Breshears et al., 2005; Adams et al., 2009; Williams et al., 2010; Clifford et

357   al., 2013), even considering the existing differences across geologic substrates, landscape

358   patterns, and tree age (Floyd et al., 2009; Meddens et al., 2015).

359   The climatic suitability for *P. edulis* across the region showed an important between-year

360   variability, indicating that multi-year droughts are spatially and temporally heterogeneous, both

361   by nature and as regards the effects on tree die-off. For instance, in 2007 the lack of significant

362   relationship between *ECS* and die-off can be explained because climatic suitability did not drop

363   in many pixels (Fig. 2g) and because the time of the last strong climatic suitability loss was two

364   years before, in 2005; similarly, in 2004 *ECS* experienced less drop in comparison to the other

365   years. Accordingly, there was no yearly close correspondence between low suitability and die-

366   off, supporting the observed delayed effects of loss of climatic suitability and the widely reported

367   existence of climate-mortality relationships that are blurred by time lags and cumulative effects

368   acting on resource levels. This temporal decoupling may be related to physiological processes,

369   involving resources storage and recovery of xylem embolism (Galiano et al., 2011; Anderegg et

370   al., 2012; Meinzer & McCulloh, 2013), and demographical and spread rates of insect pests

371   (Raffa et al., 2008; Weed et al., 2013; Anderegg et al., 2015a). These processes often involve

372   thresholds and non-linear responses that explain delayed effects. In our study case, expansion of

373   ips infestation may have been particularly relevant (Breshears et al., 2005). The use of *ECS* as

374   the average suitability from the beginning of the drought period to the year in which die-off

375   appeared allows to integrate the loss of suitability in time while including these cumulative and

376   lag effects. So, die-off in this system seems to respond more to unfavourable multi-year

377   bioclimatic conditions than to extreme conditions in a single year. For example, the massive die-

378   off in 2003, and to a lesser extent 2004, was possibly a response to previous consecutive years of

379   unfavourable conditions whereas the low die-off in 2005 - despite extremely low suitability in

380 the same year - was possible due to the preceding relatively favourable conditions in 2004 or the

381 fact that the more vulnerable populations had already declined. Alternatively, pest outbreak tends

382 to produce a clumped pattern of mortality, particularly in sites and years where pine populations

383 were more vulnerable to drought. Then, the spread of the pest outbreak may

384 have also contributed to the observed spatial distribution of die-off across years, yet successful

385 attack seems to need stressed trees (Raffa et al., 2008; Meddens et al. 2015).

386   The positive relationship between *P. edulis HCS* and die-off suggests that vulnerability to the

387 combined effect of drought and bark beetles was higher in populations that historically have been

388 living under more suitable conditions. This finding suggests that populations thriving in

389 historically more suitable locations were more prone to decline in the die-off event than

390 populations in sites subjected to chronic climatic stress. The lack of relationship between *HCS*

391 and die-off at the beginning of the event period, in 2001, likely reflects the time lags needed by

392 the combined effect of drought and ips infestation to produce dramatic tree mortality. It is

393 noticeable that the more the suitability drops during the event, the more the vulnerability

394 increases in these historically suitable locations. This trend is supported by the interaction

395 between *HCS* and *ECS* that is consistent across subsets of randomly selected pixels of different

396 size, although exhibited moderately significant values. This result contrasts with patterns

397 documented at tree level (i.e. within populations) that reveal a marked decrease in growth prior

398 to death during drought episodes (Ogle et al., 2012; Macalady & Bugmann, 2014; Camarero et

399 al., 2015), but agrees with reported higher vulnerability to drought in populations established in

400 damper sites (Sala & Tenhunen, 1994), particularly when interacting with competence (Clark et

401 al., 2016). This vulnerability of climatic-core populations may implicate several non-exclusive

402 mechanisms. First, it can be related to phenotypic plasticity, local adaptation (Rose et al., 2009;

403 Moreira *et al.* 2014) and/or acclimation to suitable conditions that led plants to poorly respond to

404 water deficit conditions (Clark et al. 2016). The mechanisms involve molecular, physiological

405 (vessel water transport, stomatal regulation, reserve storage) and structural (leaf area/size,

406 leaf/sapwood area, hydraulic conductivity, above/below biomass) adjustments (Morin et al.,

407 2007; Martínez-Vilalta et al., 2009; Peñuelas et al., 2013). For instance, some recent studies

408 indicate that large isohydric trees should be more vulnerable to drought conditions (McDowell *et*

409 *al.* 2015). Importantly, competence may also play a relevant role since high density or basal area

410 developed under suitable climatic conditions would enhance imbalances between water demand

411 and availability at stand or plant level during intense episodes of water scarcity (Clark et al.

412 2016; Jump et al., 2017). Indeed, several studies have documented a positive relationship

413 between tree mortality and stand density associated to drought periods (Klos et al., 2009; Bell et

414 al. 2014), particularly in the study area (Greenwood & Weisberg, 2008). Our study also shows a

415 potential influence of interspecific competition with *J. monosperma*. This effect seems

416 associated to lag effects of previous years of unsuitable conditions and it was likely diluted when

417 considering the whole period, likely because the broad resolution of the study does not detect this

418 effect at stand level when compensated across years. In contrast to the isohydric *P. edulis*, which

419 tends to avoid tissue low water potentials - and the risk of cavitation - through stomatal

420 regulation*, J. monosperma* is an anisohydric species better adapted to tolerating and continuing

421 photosynthesis under low xylem water potentials (McDowell *et al.* 2008; McDowell *et al.* 2015).

422 These differences were also reflected in the mortality rates of the two species (less than 25% in *J.*

423 *monosperma*, while *P. edulis* achieved up to 95% from 2001 to 2007 (Shaw *et al.* 2005; Bigler *et*

424 *al.* 2007; McDowell *et al.* 2008)) and their distribution patterns, with a more xeric, low elevation

425 and south-easterly distribution for *J. monosperma* (Fig. 1a) and can explain a worse performance

426   of *P. edulis* when *J. monosperma* is present. Also, higher tree density may represent resource

427   limitations that would result in more vulnerability to insect attack, but this mechanism has not

428   been unequivocally demonstrated in our system by previous studies (Negron & Wilson 2003;

429   Floyd et al. 2009). Overall, our results indicate that vulnerability to drought episodes is not

430   confined to the ecotone closer to the dry/hot edges of tree species ranges (Allen & Breshears,

431   1998). Thus, our study therefore does not support worse demographic performance at the edge of

432   a species' climatic range (Martínez-Meyer et al., 2013; Abeli *et al.,* 2014). Instead, our results

433   are consistent with the documented resistance of marginal populations to climate change (Hampe

434   & Petit, 2005; Doak & Morris, 2010).

435   The significant interactions between *HCS* and *HCS-SD* when considering all pixels would

436   suggest that *P. edulis* is more prone to die-off in both core climatic areas with low year-to-year

437   variability and edge areas with high year-to-year variability. This would agree with the

438   interpretation that directional acclimation and increasing stand density under favourable,

439   climatically stable conditions could increase vulnerability when unfavourable extreme conditions

440   occur due to higher hydraulic failure (Anderegg et al., 2015b) or competition (Jump et al. 2017).

441   Likewise, vulnerability in *P. edulis* populations living near climatically unsuitable, highly

442   variable edges endorses the relevance of the cumulative effects of past extreme events (Lloret &

443   Siscart, 2004) due to a depletion of stored reserves (Dickman et al., 2015) or the loss of

444   meristems that allow regrowth (Zeppel et al., 2015). However, this result appears subjected to

445   important spatial constraints, since the interaction is not significant when we reduced

446   autocorrelation effects by randomly selecting pixels at a larges spatial scale. For instance,

447   between-year climatic variability in pixels may be governed by confounding factors such as

448 topography, which in turn may determine die-off (e.g. mountain areas may exhibit both higher

449 between-year climatic variability and shallower soils).

450   One drawback of applying measures of climatic suitability from SDMs is that the calculation

451 is basically statistical, whereas species occurrence is determined by many factors other than

452 climate (e.g. biotic interactions, past management, disturbance regime, dispersal constraints and

453 soil characteristics), so it cannot explicitly disentangle the suite of mechanisms involved in

454 population success (Hampe, 2004; Guisan & Thuiller, 2005; Araújo & Luoto, 2007; Thuiller et

455 al., 2008; Elith & Leathwick, 2009; Serra-Díaz et al., 2013). In our case, *P. edulis* die-off was the

456 compound result of drought and insect outbreak (Breshears et al., 2005; MacDowell et al., 2008;

457 Macalady & Bugmann, 2014; Anderegg et al., 2015a, but see also Floyd et al., 2009) and their

458 separate contributions cannot be well distinguished. The drop in climatic suitability during the

459 2001-2007 period confirms the importance of climate variability (drought and heat) in this

460 interaction (Raffa et al. 2008). In fact, drought and insect infestation may produce synergistic

461 effects that reinforce each other mutually (MacDowell et al., 2008; Jactel et al., 2012; Macalady

462 & Bugmann, 2014; Anderegg et al., 2015a). However, we cannot completely rule out the

463 observed relationship between die-off and climatic suitability as a result of the effect of weather

464 conditions on bark beetle populations, which led to infestation. The low *ECS* values observed

465 during the 2001-2007 corresponded to a warm period that may have broken down the control of

466 bark beetle populations by cold temperatures (Raffa et al., 2008). Furthermore, resin ducts

467 become less dense after drought periods, thus increasing vulnerability to biotic attack (Gaylord et

468 al., 2013). Similarly, tree allocation to defences against insect infestation (resin ducts number,

469 size) may be lower in climatic-core populations, due to trade-offs between plant growth and

470 resource allocation to defences (Moreira et al., 2014) and their limited experience of droughts in

471   the past, thus reducing the production of these inducible defence structures (Gaylord et al.,

472   2013). Also, spatially continuous climatic-core populations may promote better dispersal of

473   insect pests (e.g. ips) and eruptive dynamics (Raffa et al., 2008), compared to more fragmented

474   and isolated climatic-edge populations. Since bark beetles are relatively poor dispersers, a highly

475   correlated environmental factor that effectively increases the connectivity of suitable habitat is

476   usually required to facilitate coalescence and spread (Aukema et al., 2006).

477   Despite the recognized limitations of correlational models, this study shows that species'

478   climate niche is an appropriate approach to explain population responses that are functionally

479   associated with climate, such as drought-induced die-off. This is particularly useful in a context

480   of climate change and extreme climatic events. Bioclimatic indices may be suitable predictors of

481   species-specific mortality, as they allow us to standardize climatic conditions from the

482   population's point of view. They also could potentially be applied to other ecological processes

483   that are driven by climate, such as invasion by exotics (Thuillier et al., 2005), insect outbreaks

484   (Sidder et al. 2016; Lantschner et al. 2017) or post-disturbance recovery. This application can

485   investigate the variability in the response of a given species across environmental gradients, or

486   make a comparison between co-occurring species with different climatic suitability (Sapes et al.,

487   2017). Although the correlation between demographical variables and outputs from SDMs can

488   be subject to considerable uncertainty, our study supports its validity when considering extreme

489   situations in terms of climatic variability and demographic processes (i.e. mortality). However,

490   further studies should be carried on to analyze the explanatory power of SDMs in comparison

491   with direct climatic variables when assessing regional patterns of species' response to climate

492   extremes.

493   In conclusion, this study shows that climatic suitability indices allow to relate populations'

494   adequacy with past climatic conditions with current responses to climate change. Furthermore,

495   these indices describe how the intensity of the drought episode as experienced from the species'

496   point of view is correlated with the regional pattern of tree mortality. Our approach therefore

497   highlights the vulnerability to climate change – and more particularly drought episodes - even in

498   those populations established in sites with conditions close to the core of species' climatic niche.

499   This vulnerability under future extreme drought episodes raises concerns about how conservation

500   and management efforts have to be strategically developed in order to mitigate the impact of

501   future climatic regimes. Thus, it may become necessary to move the focus towards considering

502   smaller, more fragmented populations as conservation targets, in both climatic-edge and core

503   areas. Indeed, populations from climatic-edge areas may be important not only as survival sites

504   but also as potential sources of more drought-resistant genotypes that could potentially be used

505   for repopulating sites decimated by drought-induced mortality (Hampe & Petit, 2005; Rehm et

506   al., 2015). Also, more research is necessary to determine the existence of common thresholds of

507   bioclimatic suitability loss below which species consistently experience drought-induced die-off

508   (Mitchell et al., 2014). If such bioclimatic thresholds could be determined, the consequences of

509   drought events in species-rich forests could be predicted more accurately in accordance with

510   different forecasted climate regime scenarios.

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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 ten subsets of pixels, that corresponded to one randomly selected pixel within each 10 x 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 vas 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.

	All pixels				Random pixels-100 km^2		
Term	Estimate	χ^2	*P*		Estimate	χ^2	*P*
Intercept	-606.32	273.67	<0.0001		-623.57	80.98	<0.0001
Longitude	-5.54	271.47	<0.0001		-5.69	79.88	<0.0001
Latitude	16.97	288.79	<0.0001		17.25	84.68	<0.0001
Longitude*Latitude	0.16	288.55	<0.0001		0.16	84.43	<0.0001
HCS	3.72	168.18	<0.0001		3.65	51.44	<0.0001
ECS	-2.35	83.78	<0.0001		-2.06	13.05	0.0006
HCS-SD	3.46	12.17	0.0005		5.91	10.38	0.0062
HCS x ECS	4.20	4.30	0.0381		9.03	5.86	0.0404
HCS x HCS-SD	-16.61	9.72	0.0018		2.10	0.24	0.7382
ECS x HCS-SD	-6.80	1.03	0.3107		-30.16	5.68	0.0803

Figure captions

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).

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.

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: no significant; *: $p<0.05$; **: $p<0.001$). Dashed line indicates mean value of live pixels.

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

799   negative or positive values of this difference, respectively; that is, red colour indicate higher

800   density (%) of die-off data points). Density contours reflect density of data points after fitting a

801   smooth bivariate nonparametric density surface that estimates the bivariate probability (%) at

802   each point.

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