

# New Forests

## Interactions between climate, growth and seed production in Spanish black pine (*Pinus nigra* Arn. ssp *salzmannii*) forests in Cuenca Mountains (Spain).

--Manuscript Draft--

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<b>Abstract:</b>	<p>Climate cues and tree age usually interact to determine secondary growth and seed production by masting species. This study aims to evaluate first, tree age and local and regional climate effects on tree ring width and seed production of Spanish black pine forest in Cuenca Mountains (Spain). Secondly, we aim to assess the relationship between seed production and secondary growth of Spanish black pine. Seed fall was estimated using 60 rectangular seed traps (40×50×15 cm) from 2000 to 2014, randomly distributed along the study area. Standardized tree-ring index chronologies were calculated using 106 randomly distributed trees grouped in three age classes (&gt;80 years; 26 to 80 years and ≤25 years). Local climate was obtained from a meteorological station whereas regional climate was calculated using the CRU-TS 3.1 dataset. <i>P. nigra</i> seed production ranged from 2 to 189 seeds m<sup>-2</sup> on average (coefficient of variation =157%) and classification based on percentile seed production identified four masting years (2000, 2003, 2006, and 2014). <i>P. nigra</i> secondary growth and seed production were influenced by climate (regional and local). Generally, we found a negatively relationship between seed production and secondary growth. However, masting did not appear to directly influence growth-climate responses in the study site. Forest management plans should take into account that <i>P. nigra</i> is a climate sensitive tree and with a bimodal masting behaviour.</p>
<b>Suggested Reviewers:</b>	<p>Bernard Prevosto, Dr Researcher, Irstea bernard.prevosto@irstea.fr Dr. Prevosto has conducted different research works and publications related to natural regeneration, tree growth and climate change in Mediterranean effects on Mediterranean forest ecosystems</p> <p>Andy Hackett Pain, Dr Researcher and lecturer, University of Cambridge ajh220@cam.ac.uk Dr. Andy has been working on masting and tree growth relationship in forest ecosystems</p>

**Response to Reviewers:**

Authors: First of all, we would like to thank the editor in Chief and Associate editor for providing the opportunity to review our manuscript and improve its quality. We would also like to thank the reviewers for their time and efforts in providing critical and constructive comments. We believe we have carefully addressed all the issues raised by the reviewers. Detailed responses to comments are provided below:

Editor-in-Chief: Thank you for submitting your manuscript, which has now been re-appraised by an Associate Editor and the same two expert reviewers. Your manuscript will be acceptable after you have carried out minor revisions according to comments below. In addition to these, I notice you have no citations to New Forests although we publish related papers quite often; please have a look at recent issues and see if you can mention some papers to ensure that the context of your work is framed clearly within scope of the journal. Please provide a covering letter detailing your changes. Thank you for the opportunity to consider your work.

Authors: Thank you very much for your suggestions. We have addressed all of them in the new version of the manuscript. In addition, please note that some references regarding masting condition recently published in New Forest Journal has been added. More in detail:

- Parker WC, Noland TL, Morneau, AE (2013). Comparative mast seed production in unmanaged and shelterwood white pine (*Pinus strobus* L.) stands in central Ontario. *New For* 44 (4): 613–628.
- Resco de Dios V, Fischer C, Colinas C. (2007). Climate Change Effects on Mediterranean Forests and Preventive Measures. *New For* 33: 1, 29–40

Associate editor: I concur with the comments by the reviewer#1, and suggest the authors to address the concern raised by the reviewer before the manuscript can be considered for publication.

Associate editor: I concur with comments' of reviewer #1. The authors should address the concern raised by the reviewer

Authors: Thank you very much for your suggestions. Please see response to reviewer #1.

Reviewer #1: I think the authors have solved most of the proposed changes well, but I have serious doubts about the stand density influence. I consider that "woody increment by standardized tree-ring index" method is adequate to control the variation induced by the age on the tree growth, but not the stand density. The authors should include this variable in the statistical analysis as a covariate, to determine accurately the climate influence. It is a key point in this manuscript.

Authors: Thank you very much for your suggestions. We totally agree with your comment and the data has been newly analysed. Please note that the new detrending worked in excluding competition effects on growth climate relationships, as can be seen by the similarity of the climate response functions when calculated for all trees, dominant trees (basal area in larger trees < 25 m<sup>2</sup>/ha) and suppressed trees (>25). Please see the manuscript figures. In addition, new paragraphs have been added.

- 1.- For example, in the methods, we have replace "using a negative exponential fit to filter out the effects of tree age" by the following: "using a cubic spline where the frequency response is 0.50 at a wavelength of 0.67 time the series length in years. This ensures that both age-related trends and non-climatic bias due to different competition status are removed, while preserving the climatic signal. The effectiveness of this detrending in removing competition-related bias is showed by the fact that linear regression of mean individual tree-ring index for the period 1994-2014 against basal area in larger trees (BAL) as a competition index produced a non-significant regression coefficient (p = 0.933); when the same regression was run using raw tree-ring width, a significant and negative slope (p <0.001) was obtained".
- 2.- The last paragraph of the Results has been replaced by the following: "Masting had a negligible effect on sensitivity of tree growth to climate. In fact, the slope of climate-growth regressions was always flatter in masting relative to non-masting years, both at the time of seed production and in the following year (Figure 6)."
- 3.- In the abstract, we have replaced "Moreover, It is worthily to note that tree age modulate climate sensitivity, increasing tree-ring width in older trees." by the following: "However, masting did not appear to directly influence growth-climate responses in the study site".

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1 **Interactions between climate, growth and seed production in Spanish black pine**  
2 **(*Pinus nigra* Arn. ssp *salzmannii*) forests in Cuenca Mountains (Spain).**

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20 12 **ABSTRACT**

21  
22 13 Climate cues and tree age usually interact to determine secondary growth and seed  
23 14 production by masting species. This study aims to evaluate first, tree age and local and  
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30 21 ≤25 years). Local climate was obtained from a meteorological station whereas regional  
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36 27 production and secondary growth. ~~Moreover, It is worthily to note that tree age modulate~~  
37 28 ~~climate sensitivity, increasing tree ring width in older trees~~ However, masting did not  
38 29 appear to directly influence growth-climate responses in the study site. Forest  
39 30 management plans should take into account that *P. nigra* is a climate sensitive tree and  
40 31 with a bimodal masting behaviour.

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## 1. INTRODUCTION

Global climate observations and predictions for the 21<sup>st</sup> century show the existence of a warming trend, as well as higher frequency of extreme climatic events and longer and more severe droughts, particularly in Mediterranean areas (IPCC 2013). Decreasing precipitation, increasing temperatures and extreme drought events have the potential to increase forest vulnerability to mortality agents, alter plant phenology and growth patterns, and shift the distribution of many tree populations in Mediterranean ecosystems ([Resco de Dios et al. 2007](#); Béllard et al. 2014; Candel-Perez et al. 2012; Vacchiano et al. 2014; Castagneri et al. 2015). Extreme droughts will lead to reduced forest productivity, regeneration bottlenecks, and changes in forest species composition (Martínez-Vilalta et al. 2008; Allen et al. 2009). Even though warmer temperatures could extend the available growing period (Wullschleger et al. 2002; Boisvenue and Running 2006), a simultaneous increase of extreme drought events may reduce the amount of time the plants are able to keep their stomata open, therefore reducing carbon uptake and shortening the time span for plant growth and development (McDowell et al. 2008).

The ability of plant species to tolerate such changing conditions is influenced by many factors such as phenotypic plasticity, genetic variability within and among populations, and interactions with site factors and disturbances. The future composition of plant communities remains difficult to predict reliably, and some authors have shown apparent contradictions (Lloret et al. 2012). For example, different studies showed an increase in abundance or cover of certain species with rising temperatures or aridity (Benavides et al. 2013), or even argued for the absence of drought sensitivity under warming conditions (Candel-Perez et al. 2012). Thus, suggesting that favourable establishment syndromes may mitigate or compensate the negative effects induced by climate change on the growth and vitality of adult trees.

Climate is the main factor controlling plant establishment, either by a direct effect on the regeneration micro-environment (Pearson and Dawson 2003; Linares *et al.*2010), or indirectly via its effects on disturbance timing and severity (Ascoli et al. 2015). Assessing how water stress and warming temperatures interact with local site conditions or forest structure to affect establishment and growth is essential to understand the response of

69 many key forest ecosystems to climate change (Vaganov et al. 2006; Vacchiano et al.  
70 2015).

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72 Additionally, many studies have shown a strong relationship between ring width and local  
73 climate (Camarero et al. 1998; Briffa et al. 2002; Candel-Perez et al. 2012). Tree growth  
74 and ring width are controlled by carbon supply, cell division and expansion (Fritts et al.  
75 1991). These processes may be near-instantaneous (e.g. photosynthesis controlling  
76 carbon supply), or involve carry-over processes from previous years (e.g. remobilisation  
77 of carbon reserves), being strongly influenced by local and regional climatic conditions.  
78 The simultaneous assessment of secondary growth variability and natural regeneration  
79 success may serve to gauge the climatic resilience of trees in the face of increasing  
80 climatic variability across different life stages at the local and regional level (Matias and  
81 Jump 2012; Candel-Perez et al. 2012). In particular, processes such as flowering, fruiting,  
82 and seed rain are both key controlling factors of natural recruitment of tree populations,  
83 and are tightly coupled with the year-to-year variability in the allocation of resources  
84 (Allen et al. 2010).

85

86 Many tree species display strong inter-annual variation in allocation to reproduction  
87 (Schauber et al. 2002), a phenomenon known as masting. The synchronized annual  
88 variability displayed by masting is explained by several theories (Kelly 1994; Herrera et  
89 al. 1998; Koenig and Knops 2000; [Parker et al. 2013](#)), although no consensus exists.  
90 Masting years (heavy seed production across many individuals and populations) are  
91 “cued” by particular climatic conditions (Vacchiano et al. 2017), and can generate  
92 “switching” of resources between growth and reproduction. Masting episodes (heavy  
93 seed production across many individuals and populations) are “cued” by particular  
94 climatic conditions in the antecedent years. Masting seem to involve a resource trade-off  
95 between growth and reproduction, i.e, producing a narrower ring in the year of masting  
96 (Piovesan and Schirone 2000). On top of this, the effect of individual tree variables such  
97 as age is still poorly understood.

98

99 The species examined in this study, Spanish black pine (*Pinus nigra* Arn. ssp *salzmannii*),  
100 has been described as a masting species (Lucas-Borja et al. 2012). However, there is a  
101 need to better understand local and regional climate influences on both tree ring width  
102 and seed production of this as well as other pine species (Koenig and Knops 2000;

103 Redmond et al. 2012). In this article we aim to evaluate (i) if and how tree ring width and  
104 seed production of Spanish black pine are influenced by climate; (ii) which type of  
105 climate (regional vs. local) has a stronger influence on masting; (iii) if there is any  
106 relationship between seed production and secondary growth of Spanish black pine; (iv)  
107 if tree age modulates climate sensitivity and reproduction-growth tradeoffs.

108

## 109 **2. MATERIAL AND METHODS**

110

### 111 **2.1. Target species**

112 *Pinus nigra* Arn. is the most widely distributed pine species in high altitudinal areas of  
113 Mediterranean Basin, and the subspecies *salzmannii* occurs in central and eastern Spain  
114 and southern France. The Convention for the Conservation of European Wildlife and  
115 Natural Habitats (EC Resolution 4/1996) classified Spanish black pine forests as “habitats  
116 of European interest” requiring specific conservation measures, partly due to the lack of  
117 basic understanding on the regeneration biology of this long-lived species (Kerr 2000).  
118 Different climate change signals on black pine have been found in drought-prone areas  
119 as warmer temperatures and water deficit can induce lower radial growth (Nabuurs et al.  
120 2013) and reduced seed rain (Lucas-Borja et al. 2012).

121

122 *P. nigra* can reach sexual maturity from 15 years of age onwards (Vidakovic 1974).  
123 Pollen is usually released from May to June; fertilization takes place 13 months after  
124 pollination (Van Haverbeke 1990), cone and seed maturation during the second year, and  
125 seed dispersal during late winter of the second year up to the spring of the third year.  
126 Different problems such as irregular masting, seed mass dependence on climatic  
127 conditions, seed predation, repeated dry summers over a period of at least three years,  
128 excessive grazing, and uncontrolled ploughing activities have been suggested as  
129 regeneration obstacles for *P.nigra* (Del Cerro et al. 2009; Tíscar and Linares 2014).

130

131 European populations of *P. nigra* are known to have highly variable fecundity through  
132 time (Coutts et al. 2012). Kerr (2000) reported that *P. nigra subsp. laricio* has the capacity  
133 to produce seeds every year, but good seed years occur only every 3–5 years. Large  
134 fluctuations in cone and seed production are also reported for *P. nigra* populations in  
135 Spain (Ordóñez et al. 2006; Del Cerro et al. 2009). Early reports indicated that Spanish  
136 *P. nigra* produces large seed outputs every 3-4 years and small crops in between (Ruiz de

137 la Torre 1979). Tree-level observations showed that many trees produce consistently few  
138 cones and a small number of trees produce many cones (Tiscar and Linares 2011; Coutts  
139 et al. 2012), but individual level data was not available in these studies.

140

## 141 **2.2 Study area**

142 This study was conducted from 2000 to 2014 in the Palancares y Agregados forest (1177  
143 to 1233 m above sea level, 40°01'50"N; 1°59'10"W, Cuenca Mountains, Spain, Figure  
144 1). Cuenca Mountains is a mountainous area located in the region of Castilla-La-Mancha  
145 (central-eastern Spain). According to Allué (1990), the climate is classified as  
146 Mediterranean humid, with a mean annual temperature of 11.9°C (mean lowest  
147 temperatures of the coldest month: -0.5°C; mean highest temperatures of the hottest  
148 month: 30.5°C) and a mean annual precipitation of 595 mm (99 mm in summer).  
149 Calcareous, sandy soils dominate the study area (Table 1).

150

151 Spanish black pine is naturally distributed in this area between 1000 and 1500 m a.s.l.  
152 where it dominates forest stand composition (Del Cerro et al. 2009). The studied forest is  
153 composed by a mosaic of even-aged stands of different mean age, due to the effect of past  
154 management. Stands are usually dense (955 trees ha<sup>-1</sup>), with a mean diameter of 22 cm  
155 (Table 1) and canopy cover usually between 70% and 85%. Due to the presence of both  
156 dense forest and open gaps, the understory vegetation includes shade-tolerant species  
157 (such as *Geranium sylvaticum*, *Corylus avellana*, *Crataegus monogyna*, *Teucrium*  
158 *chamaedrys*, *Teucrium gnaphalodes*) as well as more typical open-space species  
159 (*Centaurea paniculata*, *Plantago media*, *Lotus corniculatus*, *Juniperus oxycedrus*,  
160 *Genista scorpius*, *Amelanchier ovalis*, *Acer campestre*, *Viburnum lantana*, *Rubus idaeus*,  
161 *Rosa spp.*, and *Prunus spinosa*).

162

163 Spanish Black pine forests in the Cuenca Mountains have traditionally been managed  
164 using the shelterwood method, with a shelter-phase of 20–25 years and a rotation period  
165 of 100–125 years (Tíscar Oliver et al. 2011). The regeneration method used involves a  
166 uniform opening of the canopy without soil preparation. The first management plan of  
167 Palancares y Agregados forest was written in 1895. The whole area of the forest was then  
168 divided into compartments up to 50 hectares in surface, delineated by roads, streams,  
169 rocky outcrops and other spatial features. Individual compartments or a number of  
170 aggregated ones were established as management units, and for each management unit

171 tactical planning considerations, i.e. *where* and *when* silvicultural treatments would be  
172 applied, were defined. Palancares y Agregados forest plans were valid for a decade and  
173 have been revised 10 times. Each of those revisions was accomplished by a forest  
174 inventory from which forest structure at the compartment level can be known for different  
175 moments in the past.

176

### 177 **2.3. Seed rain, ring width and climate data**

178 Seed fall was estimated using 60 rectangular seed traps (40×50×15 cm), randomly  
179 distributed along the Palancares y Agregados forest. The number of traps is set so as to  
180 limit the relative error around the mean ( $e_r$ ) to  $\pm 25\%$  assuming that the coefficient of  
181 variation (CV) of the measured variable is lower or equal to 1 ( $N = 200^2 CV^2 e_r^{-2}$ , after  
182 Mace 1964). The only canopy species was Spanish black pine. The minimum distance  
183 between seed traps was 200 m, allowing them to be considered as independent data sets  
184 in the analyses. The top of the traps was protected with wire netting (1×1 cm mesh size)  
185 to avoid seed predation. Dispersed and filled seeds were collected in years 2000-2014 on  
186 seven dates/year, beginning in early January and continuing until the final collection in  
187 late May, i.e., the season when seed fall was observed (Del Cerro et al. 2009). Yearly  
188 seed rain intensity was computed by summing seed counts from all traps. Due to the strict  
189 bimodal pattern of black pine fructification (Lucas-Borja 2011), seed rain data were  
190 converted to a binary series (masting / non-masting) using the 75<sup>th</sup> percentile as a cutoff  
191 (Kelly et al. 1994).

192

193 For the quantification of secondary growth, we sampled 106 randomly distributed trees  
194 with a diameter at breast height (dbh) larger than 7.5 cm, avoiding those with  
195 asymmetrical growth and a non-circular bole. In a circular area (radius = 15 m) centered  
196 on each sample tree, we measured percent canopy cover and the diameter and height of  
197 all trees with dbh >7.5 cm, then calculated tree density, total basal area, quadratic mean  
198 diameter, and mean tree height. Each tree was measured for dbh and bark thickness; then,  
199 two cores per tree were extracted perpendicular to the terrain slope at breast height (Fritts  
200 1976). Sampled trees were closely located to the seed traps. Cores were sanded and  
201 visually cross-dated, and their ring-width series were counted and measured to the nearest  
202 0.001 mm with the help of a stereomicroscope mounted above a LINTAB™ 5  
203 RINNTECH® device linked to a computer. Cross-dating was checked using COFECHA  
204 (Holmes 1983). We averaged tree-ring widths from the same trees and detrended tree



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205 ~~chronologies using a negative exponential fit to filter out the effects of tree age~~  
206 ~~using a cubic spline where the frequency response is 0.50 at a wavelength of 0.67 time the series~~  
207 ~~length in years. This ensures that both age-related trends and non-climatic bias due to~~  
208 ~~different competition status are removed, while preserving the climatic signal. The~~  
209 ~~effectiveness of this detrending in removing competition-related bias is showed by the~~  
210 ~~fact that linear regression of mean individual tree-ring index for the period 1994-2014~~  
211 ~~against basal area in larger trees (BAL) as a competition index produced a non-significant~~  
212 ~~regression coefficient ( $p = 0.933$ ); when the same regression was run using raw tree-ring~~  
213 ~~width, a significant and negative slope ( $p < 0.001$ ) was obtained.~~ Finally, we built a site  
214 chronology by averaging the yearly tree-ring index across all trees, and three age-  
215 dependent chronologies by summing the tree-ring index of only old (breast height age  $> 80$   
216 years), medium (26 to 80 years) and young ( $\leq 25$  years) trees, respectively

217  
218 Local climate data (mean monthly temperature T and total monthly precipitation P) were  
219 obtained from a meteorological station located inside the study forest for the period 1997-  
220 2014. Regional climate data were obtained at a daily resolution for the same period from  
221 the CRU-TS 3.1 dataset (Harris et al. 2014) using the 1x1 km cell where the local weather  
222 station was located. Daily climate data were summarized by monthly average  
223 (temperature) or sum (precipitation). As an additional climate variable potentially  
224 associated to masting, we computed the temperature difference between two subsequent  
225 years (DT) at a monthly resolution (Kelly et al. 2013).

#### 226 227 **2.4. Data analysis**

228 Yearly seed, tree-ring index, and climate series (P, T and  $\Delta T$  from each month) were  
229 checked for temporal autocorrelation with a lag of one year by fitting a linear regression  
230 between each year's value and the value of the previous year. Also, all data series were  
231 check for temporal trends by linear regression of each series against time. If a significant  
232 ( $p < 0.05$ ) value was found in a series for the autocorrelation coefficient or the slope of  
233 the regression against time, the series were pre-whitened by taking the residuals from an  
234 autoregressive model (lag 1) or a time-dependent linear model, respectively. Local and  
235 regional monthly climate series were compared by Pearson's correlation ( $p < 0.05$ ).

236  
237 The influence of climate on masting was assessed by composite analysis. Local and  
238 regional monthly climate variables (P, T, DT) were tested for significant differences

239 between masting and non-masting years by a two-sample t-test. The Was  
240 homoscedasticity assumption was satisfied. Due to the specific flowering ecology of  
241 black pine, climate in the year of seed production (0) and up to three years before (-3)  
242 was tested. The influence of climate on secondary growth was tested by Pearson's  
243 correlations between the mean site chronology and local and regional monthly climate  
244 variables between June of year -1 and September of the current year, by using the function  
245 dcc( ) of the treeclim package (Zhang and Biondi 2015) for the R statistical framework  
246 (R Core Team 2008).

247

248 Trade-offs between seed production and growth were assessed first by composite analysis  
249 (t-test) of tree-ring index (of both year 0 and year +1, i.e., one year after seed production)  
250 in masting vs. non-masting years. Subsequently, to disentangle the influence of climate  
251 and masting on tree growth, we ran selected climate-growth correlations (sum of P April-  
252 May in year 0 from regional climate, average T March-June in year 0 from local climate)  
253 separately for masting and non-masting years (using tree-ring index of both year 0 and  
254 year +1), under the competing hypotheses that climate-growth relationships in or after  
255 masting years would be either significantly stronger (due to resource limitation) or  
256 significantly weaker (due to resource depletion) than in or after non-masting years.

257

258 Finally, climate-growth correlations and masting-growth composites were run separately  
259 for old, medium, and young tree chronologies to ascertain the effect of age on climate  
260 sensitivity and masting-growth trade-offs.

261

### 262 3. RESULTS

263 Seed production in the study area was markedly bimodal during the studied period 2000-  
264 2014, ranging from 2 to 189 seeds m<sup>-2</sup> on average (coefficient of variation =157%);  
265 classification based on percentile seed production identified four masting years (2000,  
266 2003, 2006, and 2014) (Figure 2). The series exhibited a weak negative temporal trend  
267 and a weak negative temporal autocorrelation at lag 1, but both were non-significant (p  
268 =0.68 and 0.46, respectively).

269

270 Cored trees exhibited some age-dependent difference in standardized growth (Figure 3),  
271 with medium trees showing higher average tree-ring index than old trees for the period  
272 1997-2014 (Table 2).

273

274 Monthly climate series did not exhibit any significant temporal trends between 1997 and  
275 2014, except for decreasing local precipitation in February, decreasing local temperature  
276 in April, and decreasing CRU temperature in February and March ( $p < 0.05$ ). Local  
277 climatologies in the study period indicated on average 14.9% more precipitation and 7.6%  
278 higher temperatures than CRU. Correlations between local and regional climate were  
279 higher for precipitation ( $R$  between 0.48 and 0.94 depending on the month), lower for  
280 temperature (0.20 – 0.90), and lowest for DT (-0.35 – 0.46) (Figure 4).

281

282 The climate, both local and regional, significantly affected tree-ring index. The effect was  
283 greater for winter-spring precipitation of the same year (positive correlation), fall-winter  
284 temperatures of the previous years (positive correlation) and spring-summer temperatures  
285 of the current year (negative correlation). Regional precipitation data produced higher  
286 correlations than local, while regional temperature data produced lower correlation than  
287 the local analogue. Old and medium-aged trees exhibited consistent climate relationships,  
288 while the effects of the previous summer and current spring P and T were weaker in  
289 younger trees (Figure 5).

290

291 In the study period, climate had a limited influence on fructification. Three years before  
292 fructification, DT in June (local climatology) and temperature in December (regional)  
293 had a positive effect on seed production. Two years before fructification, we could detect  
294 a negative influence of April temperature (local) and June (regional) or August (local)  
295 precipitation, and finally a positive influence of current year's temperature (in January  
296 using local climate, and May using regional climate) (Figure 6).

297

298 All chronologies (all trees, old, medium, young) showed a lower tree-ring index in the  
299 year of masting relative to the average of non-masting years, and a higher tree-ring index  
300 in the year following masting, although such differences were never larger than the 95%  
301 significance threshold. Young trees exhibited the smallest differences in growth (t-  
302 statistic: +0.43 and -0.53 in year 0 and year+1, respectively), old trees the highest (t-  
303 statistic: +1.68 and -1.24, respectively) between masting and non-masting years.

304

305 ~~Masting had a noticeable effect in increasing the sensitivity of tree growth to climate in~~  
306 ~~year 0, i.e., making growth more dependent on high spring precipitation and limited~~

307 ~~spring temperature in the year of seed production. In both cases, the slopes of the climate-~~  
308 ~~growth relationships differed significantly ( $p < 0.05$ ). In year +1 the relationship between~~  
309 ~~precipitation and growth was steeper but not significantly different between masting and~~  
310 ~~non-masting years, whereas the effect of spring-summer temperature on growth was~~  
311 ~~significantly reversed, i.e., negative instead on positive after a masting year (Figure 7)~~  
312 Masting had a negligible effect on sensitivity of tree growth to climate. In fact, the slope  
313 of climate-growth regressions was always flatter in masting relative to non-masting years,  
314 both at the time of seed production and in the following year (Figure 6).

## 316 4. DISCUSSION

### 317 4.1 Masting and climate

318 Our findings on correlations between climate and seed production can be interpreted in  
319 the light of the specific reproductive ecology of *P. nigra* and its interactions with the  
320 proximate causes of masting, i.e., the processes and resources (water, carbon, nitrogen)  
321 involved in the two- to three-year long seed development. The positive influence of DT  
322 in June-3 and T in December -2, as well as the negative effect of T in April and June -2,  
323 can be related to resource accumulation and faster mineralization rate of needle litter by  
324 soil organisms (this involves especially nitrogen, Allen et al. 2017). Cool summers two  
325 years before flowering induce resource accumulation in many other species, e.g. *Fagus*  
326 and *Picea* (Vacchiano et al. 2017). The negative effect of P in August -2 may be related  
327 to lower pollination efficiency in presence of rain; no temperature effects were detected  
328 in summer -2 to justify an effect on flower induction. The absence of effects in year -1  
329 could have to do with the fact that fecundation (13 months after pollination) is not  
330 influenced by climate, as it happens inside the cone scales. Finally, the positive effect of  
331 current January and May T can have to do with seeds release mechanisms. In the genus  
332 *Pinus*, seeds are often released as cones dry out (cones are xerochastic; Greene et al. 2008),  
333 and several cases have documented dry and windy conditions, i.e., when conditions for  
334 long distance dispersal were favourable, promoting seed abscission in conifer species  
335 (Dawson et al. 1997; Counts et al. 2012).

336  
337 In the study area, seed production between 2000 and 2014 was markedly bimodal, and  
338 tree rings were significantly narrower in mast years (composite analysis), which is  
339 consistent with findings by Linares and Tíscar (2010). According to the classification by  
340 Kelly (1994), “normal” masting species are characterised by (i) a marked bimodal seed

1 341 output throughout the years, and (ii) the presence of switching, i.e., in years of large crops,  
2 342 resources are diverted from vegetative growth or reserves. As other *Pinus* species, *P.*  
3 343 *nigra* conforms to this description. The coefficient of variation for seed output found in  
4 344 this study (1.57), which is extremely similar to that previously found by Tiscar and  
5 345 Linares (2011) in a 4-year study, indicates the likely occurrence of resource switching (if  
6 346  $CV > 1.6$  according to Kelly, 1994). Moreover, high production years were always  
7 347 followed by scarce or null seed production, consistent with findings in both Spain  
8 348 (Mackay 1926 in Sierra de Cazorla) and elsewhere (Coutts 2012 in New Zealand invasive  
9 349 populations). This is a tell-tale sign of switching and depletion of resources during  
10 350 masting.

11 351 This study does not directly inquire the ultimate causes of masting in *P. nigra*. However,  
12 352 existing observations of *P. nigra* reproductive ecology may support both the pollination  
13 353 coupling and the predator satiation hypotheses for masting (Pearse et al. 2016). The wind  
14 354 pollination hypothesis states that wind-pollinated plants obtain reproductive benefits by  
15 355 synchronizing large flowering efforts, because it increases the probability of pollination  
16 356 (Smith et al. 1990). It has been observed that *Pinus nigra* produces higher percentages of  
17 357 empty seeds (unpollinated) in low flowering years (Tíscar, 2007). Similarly, the predator  
18 358 satiation hypothesis states that large seed crops are likely to satiate seed predators, which  
19 359 thus destroy a lower percentage of crop (Kelly 1994). Most *Pinus nigra* dispersed-seeds  
20 360 are predated by rodents and birds in low seed years, while a higher percentage survives  
21 361 predation in high seed years (Tíscar 2007). In a similar study, predation rates were found  
22 362 to be influenced by the seed crop size, as predators consumed more than 75 % of seeds  
23 363 in years with lower production and less than 15 % in a mast year (Lucas Borja et al. 2012).

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## 26 366 **4.2 Secondary growth and climate**

27 367 There is abundant literature (also in the Mediterranean forest) that relates growth response  
28 368 to species' resilience to climate change and potential vitality declines (Linares et al. 2009;  
29 369 de Luis et al. 2013). However, the relationship is far from linear, as climate-growth  
30 370 responses may depend on many tree- and stand-level factors, and individuals or  
31 371 populations of sensitive species are also capable of showing remarkable resilience (i.e.,  
32 372 growth release) when adverse climate stresses relax (Hackett-Pain 2016).

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374 In Spain, *P. nigra* has been found to be a drought-sensitive species (Candel-Pérez, 2012).  
375 Winter-spring precipitation of the dissemination year showed a positive and significant  
376 correlation with secondary growth. It is in accordance with Matin-Benito et al (2008),  
377 who showed that a cool, wet autumn and spring, and/or mild winter enhanced radial  
378 growth. In addition, fall-winter temperatures of the previous year and spring-summer  
379 temperatures of the dissemination year showed a positive and negative significant  
380 correlation, respectively, with secondary growth. It is also in accordance with Martín-  
381 Benito et al (2008 and 2012), who demonstrated that tree-ring growth was negatively  
382 correlated with spring temperatures and that current summer temperatures decreased  
383 secondary growth (Matin-Benito et al (2012). In late winter or early spring, warmer  
384 temperatures may cause cambium activation, which favour secondary growth and periods  
385 of water stress allow less carbon being diverted for growth (Chaves et al. 2003; Matin-  
386 Benito et al. 2008).

387

#### 388 **4.3 Regional vs. local climate**

389 As was stated by Shestakova et al (2016), understanding how climate change affects tree  
390 ecosystems is important for anticipating its impacts on terrestrial ecosystems. Our results  
391 demonstrated that correlations between local and regional climate were on average higher  
392 for precipitation, lower for temperature, and lowest for DT. Climate had a limited  
393 influence on fructification, varying for example from positive effect of June-3 DT (local)  
394 to a negative effect of June-2 (regional). In addition, the influence of climate on tree ring  
395 width showed that regional precipitation data produced higher correlations than local,  
396 whereas regional temperature data produced lower correlation than the local climate.  
397 Thus, no clear trend was found and it is difficult to evaluate which type of climate  
398 (regional vs. local) has a stronger influence on secondary growth and masting. In the case  
399 of *P. nigra*, no evidence has been found reflecting that regional climate generates higher  
400 tree growth or fructification periods than local climate.

401

#### 402 **4.4 Masting-growth tradeoffs**

403 Climate in year -1 does not seem to influence masting as it does growth. However, T in  
404 year 0 has self-reinforcing effects (positive effect on seed release and output, and negative  
405 on growth). A reason for this study was also to warn dendroclimatologist about the  
406 potential effects of masting on tree ring width and the risk of confounding climatically

407 negative years with high production years. Growth reductions indeed happen in the  
408 masting year, so this is useful to report.

409

#### 410 **4.5 Age effects**

411 As has been showed in other *P. nigra* forests (Candel-Pérez et al. 2012), climate–growth  
412 relationships are modulated by forest age. Our results showed that tree-ring index in older  
413 and medium-aged trees presented higher correlation with climate than in younger trees  
414 for the period 1997-2014. It is worthily to note that the age of cored trees used on this  
415 study are relatively young when observing the life span of *P. nigra*, which is one of the  
416 longest-lived European tree species with extant individuals more than 1000 years old  
417 (Creus 1998).

418

419 Due to the study design (i.e., traps collecting seeds from trees of various ages), we could  
420 not directly test the effect of age on reproductive output. From the literature, minimum  
421 seed bearing age is 15 to 40 years, while maximum production is reached between 100  
422 and 120 years of age (Tiscar 2002). The relationship between fertility and tree age has  
423 been studied in the neighbouring Cazorla-Segura mountain range, where trees >200 years  
424 old showed significantly reduced fertility (i.e., the capacity to produce sound seeds able  
425 to germinate) compared to that of trees with ages <120 years (Tiscar 2002). The  
426 possibility that the overall seed output could be smaller in old trees was not tested here,  
427 but is ruled out by empirical observations of trees up to 600 years old still producing  
428 abundant crops in masting years (Tiscar and Linares 2011). Therefore, it makes sense to  
429 pool the reproductive output of all three sexually mature tree age classes, even if in reality  
430 stands will regenerate after the seed cut stage of the shelterwood system (80-100 years).

431

432 The production of seeds can also be driven by other factors. During the mast year of 2006,  
433 higher seedfall was observed at lower elevation and in higher density stands (Lucas Borja  
434 et al. 2012). However, the effect of tree density is contradictory, as Ordóñez et al. (2005)  
435 reported that both cone production and the proportion of years that each tree produced  
436 cones decreased in very dense stands - a fact that can be attributed to less photosynthetic  
437 surface and more limited access to resources for fruit development due to increased intra-  
438 specific competition (Arista and Talavera, 1996).

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440 However, if seed output can be considered independent of tree age in the analyzed stands,  
441 resource allocation tradeoffs were sensitive to age, with older trees exhibiting the largest  
442 differences in standardized tree-ring width when masting vs. non-masting years were  
443 compared, both in the year of seed production and in the following one. A resource  
444 allocation schedule specifies the proportion of energy allocated to reproduction as a  
445 fraction of the total energy available, at each size or age. The increased size and structural  
446 complexity of older trees raise maintenance respiration costs and lower the efficiency of  
447 the hydraulic pathway, which may explain the largest differences in tree-ring width when  
448 masting vs. non-masting years were compared (Candel-Perez et al. 2012).

449

#### 450 **4.6 Ecological significance**

451 Seed production and tree growth are important indicators of species resilience to climate  
452 change and *P. nigra* has been found to be a drought-sensitive species. However, the  
453 existing evidence suggest that seed availability seems not to avoid natural regeneration  
454 success. *P. nigra* fructification and subsequent dissemination together with the long-lived  
455 span may ensure forest stand persistence. Thus, It could be said that the main bottleneck  
456 in the recruitment dynamics of *P. nigra* may in fact be related to microclimatic conditions  
457 and suitable sites for initial seedling recruitment (Tiscar and Linares 2011). Management  
458 consideration should be highlighted, promoting proper silvicultural guidelines and for  
459 example synchronizing regeneration cuts with masting years in order to ensure natural  
460 regeneration.

461

#### 462 **6. CONCLUSION**

463 Our findings on correlations between climate and seed production can be interpreted in  
464 the light of the specific reproductive ecology of *P. nigra* and its interactions with the  
465 proximate causes of masting, i.e., the processes and resources (water, carbon, nitrogen)  
466 involved in the two- to three-year long seed development. Our results demonstrated that  
467 *P. nigra* tree ring width and seed production were influenced by climate and that generally,  
468 there is a negatively relationship between seed production and secondary growth.  
469 Moreover, It is worthily to note that tree age modulate climate sensitivity, increasing  
470 correlations between climate and tree-ring index in older trees. *P. nigra* has been showed  
471 to be climate sensitive tree and a bimodal masting behaviour, which should be taking into  
472 account for management purposes and silvicultural guidelines.

473



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1 **Interactions between climate, growth and seed production in Spanish black pine**  
2 **(*Pinus nigra* Arn. ssp *salzmannii*) forests in Cuenca Mountains (Spain).**

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20 12 **ABSTRACT**

21  
22 13 Climate cues and tree age usually interact to determine secondary growth and seed  
23 14 production by masting species. This study aims to evaluate first, tree age and local and  
24 15 regional climate effects on tree ring width and seed production of Spanish black pine  
25 16 forest in Cuenca Mountains (Spain). Secondly, we aim to assess the relationship between  
26 17 seed production and secondary growth of Spanish black pine. Seed fall was estimated  
27 18 using 60 rectangular seed traps (40×50×15 cm) from 2000 to 2014, randomly distributed  
28 19 along the study area. Standardized tree-ring index chronologies were calculated using 106  
29 20 randomly distributed trees grouped in three age classes (>80 years; 26 to 80 years and  
30 21 ≤25 years). Local climate was obtained from a meteorological station whereas regional  
31 22 climate was calculated using the CRU-TS 3.1 dataset. *P. nigra* seed production ranged  
32 23 from 2 to 189 seeds m<sup>-2</sup> on average (coefficient of variation =157%) and classification  
33 24 based on percentile seed production identified four masting years (2000, 2003, 2006, and  
34 25 2014). *P. nigra* secondary growth and seed production were influenced by climate  
35 26 (regional and local). Generally, we found a negatively relationship between seed  
36 27 production and secondary growth. However, masting did not appear to directly influence  
37 28 growth-climate responses in the study site. Forest management plans should take into  
38 29 account that *P. nigra* is a climate sensitive tree and with a bimodal masting behaviour.

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54 31 **Keywords:** Masting; climate change; seed production; ring width; natural regeneration

35 **1. INTRODUCTION**

36 Global climate observations and predictions for the 21<sup>st</sup> century show the existence of a  
37 warming trend, as well as higher frequency of extreme climatic events and longer and  
38 more severe droughts, particularly in Mediterranean areas (IPCC 2013). Decreasing  
39 precipitation, increasing temperatures and extreme drought events have the potential to  
40 increase forest vulnerability to mortality agents, alter plant phenology and growth  
41 patterns, and shift the distribution of many tree populations in Mediterranean ecosystems  
42 (Resco de Dios et al. 2007; Béllard et al. 2014; Candel-Perez et al. 2012; Vacchiano et al.  
43 2014; Castagneri et al. 2015). Extreme droughts will lead to reduced forest productivity,  
44 regeneration bottlenecks, and changes in forest species composition (Martínez-Vilalta et  
45 al, 2008; Allen et al. 2009). Even though warmer temperatures could extend the available  
46 growing period (Wullschleger et al. 2002; Boisvenue and Running 2006), a simultaneous  
47 increase of extreme drought events may reduce the amount of time the plants are able to  
48 keep their stomata open, therefore reducing carbon uptake and shortening the time span  
49 for plant growth and development (McDowell et al. 2008).

50  
51 The ability of plant species to tolerate such changing conditions is influenced by many  
52 factors such as phenotypic plasticity, genetic variability within and among populations,  
53 and interactions with site factors and disturbances. The future composition of plant  
54 communities remains difficult to predict reliably, and some authors have shown apparent  
55 contradictions (Lloret et al. 2012). For example, different studies showed an increase in  
56 abundance or cover of certain species with rising temperatures or aridity (Benavides et al.  
57 2013), or even argued for the absence of drought sensitivity under warming conditions  
58 (Candel-Perez et al. 2012). Thus, suggesting that favourable establishment syndromes  
59 may mitigate or compensate the negative effects induced by climate change on the growth  
60 and vitality of adult trees.

61  
62 Climate is the main factor controlling plant establishment, either by a direct effect on the  
63 regeneration micro-environment (Pearson and Dawson 2003; Linares *et al.*2010), or  
64 indirectly via its effects on disturbance timing and severity (Ascoli et al. 2015). Assessing  
65 how water stress and warming temperatures interact with local site conditions or forest  
66 structure to affect establishment and growth is essential to understand the response of  
67 many key forest ecosystems to climate change (Vaganov et al. 2006; Vacchiano et al.  
68 2015).

1  
2 70 Additionally, many studies have shown a strong relationship between ring width and local  
3 71 climate (Camarero et al. 1998; Briffa et al. 2002; Candel-Perez et al. 2012). Tree growth  
4 72 and ring width are controlled by carbon supply, cell division and expansion (Fritts et al.  
5 73 1991). These processes may be near-instantaneous (e.g. photosynthesis controlling  
6 74 carbon supply), or involve carry-over processes from previous years (e.g. remobilisation  
7 75 of carbon reserves), being strongly influenced by local and regional climatic conditions.  
8 76 The simultaneous assessment of secondary growth variability and natural regeneration  
9 77 success may serve to gauge the climatic resilience of trees in the face of increasing  
10 78 climatic variability across different life stages at the local and regional level (Matias and  
11 79 Jump 2012; Candel-Perez et al. 2012). In particular, processes such as flowering, fruiting,  
12 80 and seed rain are both key controlling factors of natural recruitment of tree populations,  
13 81 and are tightly coupled with the year-to-year variability in the allocation of resources  
14 82 (Allen et al. 2010).

83

27 84 Many tree species display strong inter-annual variation in allocation to reproduction  
28 85 (Schauber et al. 2002), a phenomenon known as masting. The synchronized annual  
29 86 variability displayed by masting is explained by several theories (Kelly 1994; Herrera et  
30 87 al. 1998; Koenig and Knops 2000; Parker et al. 2013), although no consensus exists.  
31 88 Masting years (heavy seed production across many individuals and populations) are  
32 89 “cued” by particular climatic conditions (Vacchiano et al. 2017), and can generate  
33 90 “switching” of resources between growth and reproduction. Masting episodes (heavy  
34 91 seed production across many individuals and populations) are “cued” by particular  
35 92 climatic conditions in the antecedent years. Masting seem to involve a resource trade-off  
36 93 between growth and reproduction, i.e, producing a narrower ring in the year of masting  
37 94 (Piovesan and Schirone 2000). On top of this, the effect of individual tree variables such  
38 95 as age is still poorly understood.

96

51 97 The species examined in this study, Spanish black pine (*Pinus nigra* Arn. ssp *salzmannii*),  
52 98 has been described as a masting species (Lucas-Borja et al. 2012). However, there is a  
53 99 need to better understand local and regional climate influences on both tree ring width  
54 100 and seed production of this as well as other pine species (Koenig and Knops 2000;  
55 101 Redmond et al. 2012). In this article we aim to evaluate (i) if and how tree ring width and  
56 102 seed production of Spanish black pine are influenced by climate; (ii) which type of

103 climate (regional vs. local) has a stronger influence on masting; (iii) if there is any  
104 relationship between seed production and secondary growth of Spanish black pine; (iv)  
105 if tree age modulates climate sensitivity and reproduction-growth tradeoffs.

## 107 **2. MATERIAL AND METHODS**

### 109 **2.1. Target species**

110 *Pinus nigra* Arn. is the most widely distributed pine species in high altitudinal areas of  
111 Mediterranean Basin, and the subspecies *salzmannii* occurs in central and eastern Spain  
112 and southern France. The Convention for the Conservation of European Wildlife and  
113 Natural Habitats (EC Resolution 4/1996) classified Spanish black pine forests as “habitats  
114 of European interest” requiring specific conservation measures, partly due to the lack of  
115 basic understanding on the regeneration biology of this long-lived species (Kerr 2000).  
116 Different climate change signals on black pine have been found in drought-prone areas  
117 as warmer temperatures and water deficit can induce lower radial growth (Nabuurs et al.  
118 2013) and reduced seed rain (Lucas-Borja et al. 2012).

119  
120 *P. nigra* can reach sexual maturity from 15 years of age onwards (Vidakovic 1974).  
121 Pollen is usually released from May to June; fertilization takes place 13 months after  
122 pollination (Van Haverbeke 1990), cone and seed maturation during the second year, and  
123 seed dispersal during late winter of the second year up to the spring of the third year.  
124 Different problems such as irregular masting, seed mass dependence on climatic  
125 conditions, seed predation, repeated dry summers over a period of at least three years,  
126 excessive grazing, and uncontrolled ploughing activities have been suggested as  
127 regeneration obstacles for *P.nigra* (Del Cerro et al. 2009; Tíscar and Linares 2014).

128  
129 European populations of *P. nigra* are known to have highly variable fecundity through  
130 time (Coutts et al. 2012). Kerr (2000) reported that *P. nigra subsp. laricio* has the capacity  
131 to produce seeds every year, but good seed years occur only every 3–5 years. Large  
132 fluctuations in cone and seed production are also reported for *P. nigra* populations in  
133 Spain (Ordóñez et al. 2006; Del Cerro et al. 2009). Early reports indicated that Spanish  
134 *P. nigra* produces large seed outputs every 3-4 years and small crops in between (Ruiz de  
135 la Torre 1979). Tree-level observations showed that many trees produce consistently few

136 cones and a small number of trees produce many cones (Tiscar and Linares 2011; Coutts  
137 et al. 2012), but individual level data was not available in these studies.

138

## 139 **2.2 Study area**

140 This study was conducted from 2000 to 2014 in the Palancares y Agregados forest (1177  
141 to 1233 m above sea level, 40°01'50"N; 1°59'10"W, Cuenca Mountains, Spain, Figure  
142 1). Cuenca Mountains is a mountainous area located in the region of Castilla-La-Mancha  
143 (central-eastern Spain). According to Allué (1990), the climate is classified as  
144 Mediterranean humid, with a mean annual temperature of 11.9°C (mean lowest  
145 temperatures of the coldest month: -0.5°C; mean highest temperatures of the hottest  
146 month: 30.5°C) and a mean annual precipitation of 595 mm (99 mm in summer).  
147 Calcareous, sandy soils dominate the study area (Table 1).

148

149 Spanish black pine is naturally distributed in this area between 1000 and 1500 m a.s.l.  
150 where it dominates forest stand composition (Del Cerro et al. 2009). The studied forest is  
151 composed by a mosaic of even-aged stands of different mean age, due to the effect of past  
152 management. Stands are usually dense (955 trees ha<sup>-1</sup>), with a mean diameter of 22 cm  
153 (Table 1) and canopy cover usually between 70% and 85%. Due to the presence of both  
154 dense forest and open gaps, the understory vegetation includes shade-tolerant species  
155 (such as *Geranium sylvaticum*, *Corylus avellana*, *Crataegus monogyna*, *Teucrium*  
156 *chamaedrys*, *Teucrium gnaphalodes*) as well as more typical open-space species  
157 (*Centaurea paniculata*, *Plantago media*, *Lotus corniculatus*, *Juniperus oxycedrus*,  
158 *Genista scorpius*, *Amelanchier ovalis*, *Acer campestre*, *Viburnum lantana*, *Rubus idaeus*,  
159 *Rosa spp.*, and *Prunus spinosa*).

160

161 Spanish Black pine forests in the Cuenca Mountains have traditionally been managed  
162 using the shelterwood method, with a shelter-phase of 20–25 years and a rotation period  
163 of 100–125 years (Tiscar Oliver et al. 2011). The regeneration method used involves a  
164 uniform opening of the canopy without soil preparation. The first management plan of  
165 Palancares y Agregados forest was written in 1895. The whole area of the forest was then  
166 divided into compartments up to 50 hectares in surface, delineated by roads, streams,  
167 rocky outcrops and other spatial features. Individual compartments or a number of  
168 aggregated ones were established as management units, and for each management unit  
169 tactical planning considerations, i.e. *where* and *when* silvicultural treatments would be

170 applied, were defined. Palancares y Agregados forest plans were valid for a decade and  
171 have been revised 10 times. Each of those revisions was accomplished by a forest  
172 inventory from which forest structure at the compartment level can be known for different  
173 moments in the past.

174

### 175 **2.3. Seed rain, ring width and climate data**

176 Seed fall was estimated using 60 rectangular seed traps (40×50×15 cm), randomly  
177 distributed along the Palancares y Agregados forest. The number of traps is set so as to  
178 limit the relative error around the mean ( $e_r$ ) to  $\pm 25\%$  assuming that the coefficient of  
179 variation (CV) of the measured variable is lower or equal to 1 ( $N = 200^2 CV^2 e_r^{-2}$ , after  
180 Mace 1964). The only canopy species was Spanish black pine. The minimum distance  
181 between seed traps was 200 m, allowing them to be considered as independent data sets  
182 in the analyses. The top of the traps was protected with wire netting (1×1 cm mesh size)  
183 to avoid seed predation. Dispersed and filled seeds were collected in years 2000-2014 on  
184 seven dates/year, beginning in early January and continuing until the final collection in  
185 late May, i.e., the season when seed fall was observed (Del Cerro et al. 2009). Yearly  
186 seed rain intensity was computed by summing seed counts from all traps. Due to the strict  
187 bimodal pattern of black pine fructification (Lucas-Borja 2011), seed rain data were  
188 converted to a binary series (masting / non-masting) using the 75<sup>th</sup> percentile as a cutoff  
189 (Kelly et al. 1994).

190

191 For the quantification of secondary growth, we sampled 106 randomly distributed trees  
192 with a diameter at breast height (dbh) larger than 7.5 cm, avoiding those with  
193 asymmetrical growth and a non-circular bole. In a circular area (radius = 15 m) centered  
194 on each sample tree, we measured percent canopy cover and the diameter and height of  
195 all trees with dbh >7.5 cm, then calculated tree density, total basal area, quadratic mean  
196 diameter, and mean tree height. Each tree was measured for dbh and bark thickness; then,  
197 two cores per tree were extracted perpendicular to the terrain slope at breast height (Fritts  
198 1976). Sampled trees were closely located to the seed traps. Cores were sanded and  
199 visually cross-dated, and their ring-width series were counted and measured to the nearest  
200 0.001 mm with the help of a stereomicroscope mounted above a LINTAB<sup>TM</sup> 5  
201 RINNTECH<sup>®</sup> device linked to a computer. Cross-dating was checked using COFECHA  
202 (Holmes 1983). We averaged tree-ring widths from the same trees and detrended tree  
203 chronologies using a cubic spline where the frequency response is 0.50 at a wavelength of

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204 0.67 time the series length in years. This ensures that both age-related trends and non-  
205 climatic bias due to different competition status are removed, while preserving the  
206 climatic signal. The effectiveness of this detrending in removing competition-related bias  
207 is showed by the fact that linear regression of mean individual tree-ring index for the  
208 period 1994-2014 against basal area in larger trees (BAL) as a competition index  
209 produced a non-significant regression coefficient ( $p = 0.933$ ); when the same regression  
210 was run using raw tree-ring width, a significant and negative slope ( $p < 0.001$ ) was  
211 obtained. Finally, we built a site chronology by averaging the yearly tree-ring index  
212 across all trees, and three age-dependent chronologies by summing the tree-ring index of  
213 only old (breast height age  $> 80$  years), medium (26 to 80 years) and young ( $\leq 25$  years)  
214 trees, respectively

215

216 Local climate data (mean monthly temperature T and total monthly precipitation P) were  
217 obtained from a meteorological station located inside the study forest for the period 1997-  
218 2014. Regional climate data were obtained at a daily resolution for the same period from  
219 the CRU-TS 3.1 dataset (Harris et al. 2014) using the 1x1 km cell where the local weather  
220 station was located. Daily climate data were summarized by monthly average  
221 (temperature) or sum (precipitation). As an additional climate variable potentially  
222 associated to masting, we computed the temperature difference between two subsequent  
223 years (DT) at a monthly resolution (Kelly et al. 2013).

224

225 **2.4. Data analysis**

226 Yearly seed, tree-ring index, and climate series (P, T and  $\Delta T$  from each month) were  
227 checked for temporal autocorrelation with a lag of one year by fitting a linear regression  
228 between each year's value and the value of the previous year. Also, all data series were  
229 check for temporal trends by linear regression of each series against time. If a significant  
230 ( $p < 0.05$ ) value was found in a series for the autocorrelation coefficient or the slope of  
231 the regression against time, the series were pre-whitened by taking the residuals from an  
232 autoregressive model (lag 1) or a time-dependent linear model, respectively. Local and  
233 regional monthly climate series were compared by Pearson's correlation ( $p < 0.05$ ).

234

235 The influence of climate on masting was assessed by composite analysis. Local and  
236 regional monthly climate variables (P, T, DT) were tested for significant differences  
237 between masting and non-masting years by a two-sample t-test. The Was



1 238 homoscedasticity assumption was satisfied. Due to the specific flowering ecology of  
2 239 black pine, climate in the year of seed production (0) and up to three years before (-3)  
3 240 was tested. The influence of climate on secondary growth was tested by Pearson's  
4 241 correlations between the mean site chronology and local and regional monthly climate  
5 242 variables between June of year -1 and September of the current year, by using the function  
6 243 dcc( ) of the treeclim package (Zhang and Biondi 2015) for the R statistical framework  
7 244 (R Core Team 2008).

8 245  
9 246 Trade-offs between seed production and growth were assessed first by composite analysis  
10 247 (t-test) of tree-ring index (of both year 0 and year +1, i.e., one year after seed production)  
11 248 in masting vs. non-masting years. Subsequently, to disentangle the influence of climate  
12 249 and masting on tree growth, we ran selected climate-growth correlations (sum of P April-  
13 250 May in year 0 from regional climate, average T March-June in year 0 from local climate)  
14 251 separately for masting and non-masting years (using tree-ring index of both year 0 and  
15 252 year +1), under the competing hypotheses that climate-growth relationships in or after  
16 253 masting years would be either significantly stronger (due to resource limitation) or  
17 254 significantly weaker (due to resource depletion) than in or after non-masting years.

18 255  
19 256 Finally, climate-growth correlations and masting-growth composites were run separately  
20 257 for old, medium, and young tree chronologies to ascertain the effect of age on climate  
21 258 sensitivity and masting-growth trade-offs.

22 259

### 23 260 **3. RESULTS**

24 261 Seed production in the study area was markedly bimodal during the studied period 2000-  
25 262 2014, ranging from 2 to 189 seeds m<sup>-2</sup> on average (coefficient of variation =157%);  
26 263 classification based on percentile seed production identified four masting years (2000,  
27 264 2003, 2006, and 2014) (Figure 2). The series exhibited a weak negative temporal trend  
28 265 and a weak negative temporal autocorrelation at lag 1, but both were non-significant (p  
29 266 =0.68 and 0.46, respectively).

30 267

31 268 Cored trees exhibited some age-dependent difference in standardized growth (Figure 3),  
32 269 with medium trees showing higher average tree-ring index than old trees for the period  
33 270 1997-2014 (Table 2).

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272 Monthly climate series did not exhibit any significant temporal trends between 1997 and  
273 2014, except for decreasing local precipitation in February, decreasing local temperature  
274 in April, and decreasing CRU temperature in February and March ( $p < 0.05$ ). Local  
275 climatologies in the study period indicated on average 14.9% more precipitation and 7.6%  
276 higher temperatures than CRU. Correlations between local and regional climate were  
277 higher for precipitation ( $R$  between 0.48 and 0.94 depending on the month), lower for  
278 temperature (0.20 – 0.90), and lowest for DT (-0.35 – 0.46) (Figure 4).

279  
280 The climate, both local and regional, significantly affected tree-ring index. The effect was  
281 greater for winter-spring precipitation of the same year (positive correlation), fall-winter  
282 temperatures of the previous years (positive correlation) and spring-summer temperatures  
283 of the current year (negative correlation). Regional precipitation data produced higher  
284 correlations than local, while regional temperature data produced lower correlation than  
285 the local analogue. Old and medium-aged trees exhibited consistent climate relationships,  
286 while the effects of the previous summer and current spring P and T were weaker in  
287 younger trees (Figure 5).

288  
289 In the study period, climate had a limited influence on fructification. Three years before  
290 fructification, DT in June (local climatology) and temperature in December (regional)  
291 had a positive effect on seed production. Two years before fructification, we could detect  
292 a negative influence of April temperature (local) and June (regional) or August (local)  
293 precipitation, and finally a positive influence of current year's temperature (in January  
294 using local climate, and May using regional climate) (Figure 6).

295  
296 All chronologies (all trees, old, medium, young) showed a lower tree-ring index in the  
297 year of masting relative to the average of non-masting years, and a higher tree-ring index  
298 in the year following masting, although such differences were never larger than the 95%  
299 significance threshold. Young trees exhibited the smallest differences in growth (t-  
300 statistic: +0.43 and -0.53 in year 0 and year+1, respectively), old trees the highest (t-  
301 statistic: +1.68 and -1.24, respectively) between masting and non-masting years.  
302 Masting had a negligible effect on sensitivity of tree growth to climate. In fact, the slope  
303 of climate-growth regressions was always flatter in masting relative to non-masting years,  
304 both at the time of seed production and in the following year (Figure 6).

306 **4. DISCUSSION**

307 **4.1 Masting and climate**

308 Our findings on correlations between climate and seed production can be interpreted in  
309 the light of the specific reproductive ecology of *P. nigra* and its interactions with the  
310 proximate causes of masting, i.e., the processes and resources (water, carbon, nitrogen)  
311 involved in the two- to three-year long seed development. The positive influence of DT  
312 in June-3 and T in December -2, as well as the negative effect of T in April and June -2,  
313 can be related to resource accumulation and faster mineralization rate of needle litter by  
314 soil organisms (this involves especially nitrogen, Allen et al. 2017). Cool summers two  
315 years before flowering induce resource accumulation in many other species, e.g. *Fagus*  
316 and *Picea* (Vacchiano et al. 2017). The negative effect of P in August -2 may be related  
317 to lower pollination efficiency in presence of rain; no temperature effects were detected  
318 in summer -2 to justify an effect on flower induction. The absence of effects in year -1  
319 could have to do with the fact that fecundation (13 months after pollination) is not  
320 influenced by climate, as it happens inside the cone scales. Finally, the positive effect of  
321 current January and May T can have to do with seeds release mechanisms. In the genus  
322 *Pinus*, seeds are often released as cones dry out (cones are xerochastic; Greene et al. 2008),  
323 and several cases have documented dry and windy conditions, i.e., when conditions for  
324 long distance dispersal were favourable, promoting seed abscission in conifer species  
325 (Dawson et al. 1997; Counts et al. 2012).

326  
327 In the study area, seed production between 2000 and 2014 was markedly bimodal, and  
328 tree rings were significantly narrower in mast years (composite analysis), which is  
329 consistent with findings by Linares and Tíscar (2010). According to the classification by  
330 Kelly (1994), “normal” masting species are characterised by (i) a marked bimodal seed  
331 output throughout the years, and (ii) the presence of switching, i.e., in years of large crops,  
332 resources are diverted from vegetative growth or reserves. As other *Pinus* species, *P.*  
333 *nigra* conforms to this description. The coefficient of variation for seed output found in  
334 this study (1.57), which is extremely similar to that previously found by Tíscar and  
335 Linares (2011) in a 4-year study, indicates the likely occurrence of resource switching (if  
336  $CV > 1.6$  according to Kelly, 1994). Moreover, high production years were always  
337 followed by scarce or null seed production, consistent with findings in both Spain  
338 (Mackay 1926 in Sierra de Cazorla) and elsewhere (Coultts 2012 in New Zealand invasive

339 populations). This is a tell-tale sign of switching and depletion of resources during  
340 masting.

341 This study does not directly inquire the ultimate causes of masting in *P. nigra*. However,  
342 existing observations of *P. nigra* reproductive ecology may support both the pollination  
343 coupling and the predator satiation hypotheses for masting (Pearse et al. 2016). The wind  
344 pollination hypothesis states that wind-pollinated plants obtain reproductive benefits by  
345 synchronizing large flowering efforts, because it increases the probability of pollination  
346 (Smith et al. 1990). It has been observed that *Pinus nigra* produces higher percentages of  
347 empty seeds (unpollinated) in low flowering years (Tíscar, 2007). Similarly, the predator  
348 satiation hypothesis states that large seed crops are likely to satiate seed predators, which  
349 thus destroy a lower percentage of crop (Kelly 1994). Most *Pinus nigra* dispersed-seeds  
350 are predated by rodents and birds in low seed years, while a higher percentage survives  
351 predation in high seed years (Tíscar 2007). In a similar study, predation rates were found  
352 to be influenced by the seed crop size, as predators consumed more than 75 % of seeds  
353 in years with lower production and less than 15 % in a mast year (Lucas Borja et al. 2012).

354

355

#### 356 **4.2 Secondary growth and climate**

357 There is abundant literature (also in the Mediterranean forest) that relates growth response  
358 to species' resilience to climate change and potential vitality declines (Linares et al. 2009;  
359 de Luis et al. 2013). However, the relationship is far from linear, as climate-growth  
360 responses may depend on many tree- and stand-level factors, and individuals or  
361 populations of sensitive species are also capable of showing remarkable resilience (i.e.,  
362 growth release) when adverse climate stresses relax (Hackett-Pain 2016).

363

364 In Spain, *P. nigra* has been found to be a drought-sensitive species (Candel-Pérez, 2012).  
365 Winter-spring precipitation of the dissemination year showed a positive and significant  
366 correlation with secondary growth. It is in accordance with Martín-Benito et al (2008),  
367 who showed that a cool, wet autumn and spring, and/or mild winter enhanced radial  
368 growth. In addition, fall-winter temperatures of the previous year and spring-summer  
369 temperatures of the dissemination year showed a positive and negative significant  
370 correlation, respectively, with secondary growth. It is also in accordance with Martín-  
371 Benito et al (2008 and 2012), who demonstrated that tree-ring growth was negatively  
372 correlated with spring temperatures and that current summer temperatures decreased

373 secondary growth (Matin-Benito et al (2012). In late winter or early spring, warmer  
374 temperatures may cause cambium activation, which favour secondary growth and periods  
375 of water stress allow less carbon being diverted for growth (Chaves et al. 2003; Matin-  
376 Benito et al. 2008).

377

### 378 **4.3 Regional vs. local climate**

379 As was stated by Shestakova et al (2016), understanding how climate change affects tree  
380 ecosystems is important for anticipating its impacts on terrestrial ecosystems. Our results  
381 demonstrated that correlations between local and regional climate were on average higher  
382 for precipitation, lower for temperature, and lowest for DT. Climate had a limited  
383 influence on fructification, varying for example from positive effect of June-3 DT (local)  
384 to a negative effect of June-2 (regional). In addition, the influence of climate on tree ring  
385 width showed that regional precipitation data produced higher correlations than local,  
386 whereas regional temperature data produced lower correlation than the local climate.  
387 Thus, no clear trend was found and it is difficult to evaluate which type of climate  
388 (regional vs. local) has a stronger influence on secondary growth and masting. In the case  
389 of *P. nigra*, no evidence has been found reflecting that regional climate generates higher  
390 tree growth or fructification periods than local climate.

391

### 392 **4.4 Masting-growth tradeoffs**

393 Climate in year -1 does not seem to influence masting as it does growth. However, T in  
394 year 0 has self-reinforcing effects (positive effect on seed release and output, and negative  
395 on growth). A reason for this study was also to warn dendroclimatologist about the  
396 potential effects of masting on tree ring width and the risk of confounding climatically  
397 negative years with high production years. Growth reductions indeed happen in the  
398 masting year, so this is useful to report.

399

### 400 **4.5 Age effects**

401 As has been showed in other *P. nigra* forests (Candel-Pérez et al. 2012), climate–growth  
402 relationships are modulated by forest age. Our results showed that tree-ring index in older  
403 and medium-aged trees presented higher correlation with climate than in younger trees  
404 for the period 1997-2014. It is worthily to note that the age of cored trees used on this  
405 study are relatively young when observing the life span of *P. nigra*, which is one of the

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406 longest-lived European tree species with extant individuals more than 1000 years old  
407 (Creus 1998).

408

409 Due to the study design (i.e., traps collecting seeds from trees of various ages), we could  
410 not directly test the effect of age on reproductive output. From the literature, minimum  
411 seed bearing age is 15 to 40 years, while maximum production is reached between 100  
412 and 120 years of age (Tiscar 2002). The relationship between fertility and tree age has  
413 been studied in the neighbouring Cazorla-Segura mountain range, where trees >200 years  
414 old showed significantly reduced fertility (i.e., the capacity to produce sound seeds able  
415 to germinate) compared to that of trees with ages <120 years (Tiscar 2002). The  
416 possibility that the overall seed output could be smaller in old trees was not tested here,  
417 but is ruled out by empirical observations of trees up to 600 years old still producing  
418 abundant crops in masting years (Tiscar and Linares 2011). Therefore, it makes sense to  
419 pool the reproductive output of all three sexually mature tree age classes, even if in reality  
420 stands will regenerate after the seed cut stage of the shelterwood system (80-100 years).

421

422 The production of seeds can also be driven by other factors. During the mast year of 2006,  
423 higher seedfall was observed at lower elevation and in higher density stands (Lucas Borja  
424 et al. 2012). However, the effect of tree density is contradictory, as Ordóñez et al. (2005)  
425 reported that both cone production and the proportion of years that each tree produced  
426 cones decreased in very dense stands - a fact that can be attributed to less photosynthetic  
427 surface and more limited access to resources for fruit development due to increased intra-  
428 specific competition (Arista and Talavera, 1996).

429

430 However, if seed output can be considered independent of tree age in the analyzed stands,  
431 resource allocation tradeoffs were sensitive to age, with older trees exhibiting the largest  
432 differences in standardized tree-ring width when masting vs. non-masting years were  
433 compared, both in the year of seed production and in the following one. A resource  
434 allocation schedule specifies the proportion of energy allocated to reproduction as a  
435 fraction of the total energy available, at each size or age. The increased size and structural  
436 complexity of older trees raise maintenance respiration costs and lower the efficiency of  
437 the hydraulic pathway, which may explain the largest differences in tree-ring width when  
438 masting vs. non-masting years were compared (Candel-Perez et al. 2012).

439

#### 440 **4.6 Ecological significance**

1 441 Seed production and tree growth are important indicators of species resilience to climate  
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3 442 change and *P. nigra* has been found to be a drought-sensitive species. However, the  
4  
5 443 existing evidence suggest that seed availability seems not to avoid natural regeneration  
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7 444 success. *P. nigra* fructification and subsequent dissemination together with the long-lived  
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9 445 span may ensure forest stand persistence. Thus, It could be said that the main bottleneck  
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11 446 in the recruitment dynamics of *P. nigra* may in fact be related to microclimatic conditions  
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13 447 and suitable sites for initial seedling recruitment (Tiscar and Linares 2011). Management  
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15 448 consideration should be highlighted, promoting proper silvicultural guidelines and for  
16  
17 449 example synchronizing regeneration cuts with masting years in order to ensure natural  
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19 450 regeneration.

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#### 21 452 **6. CONCLUSION**

22 453 Our findings on correlations between climate and seed production can be interpreted in  
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24 454 the light of the specific reproductive ecology of *P. nigra* and its interactions with the  
25  
26 455 proximate causes of masting, i.e., the processes and resources (water, carbon, nitrogen)  
27  
28 456 involved in the two- to three-year long seed development. Our results demonstrated that  
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30 457 *P. nigra* tree ring width and seed production were influenced by climate and that generally,  
31  
32 458 there is a negative relationship between seed production and secondary growth.  
33  
34 459 Moreover, It is worthily to note that tree age modulate climate sensitivity, increasing  
35  
36 460 correlations between climate and tree-ring index in older trees. *P. nigra* has been showed  
37  
38 461 to be climate sensitive tree and a bimodal masting behaviour, which should be taking into  
39  
40 462 account for management purposes and silvicultural guidelines.

41 463

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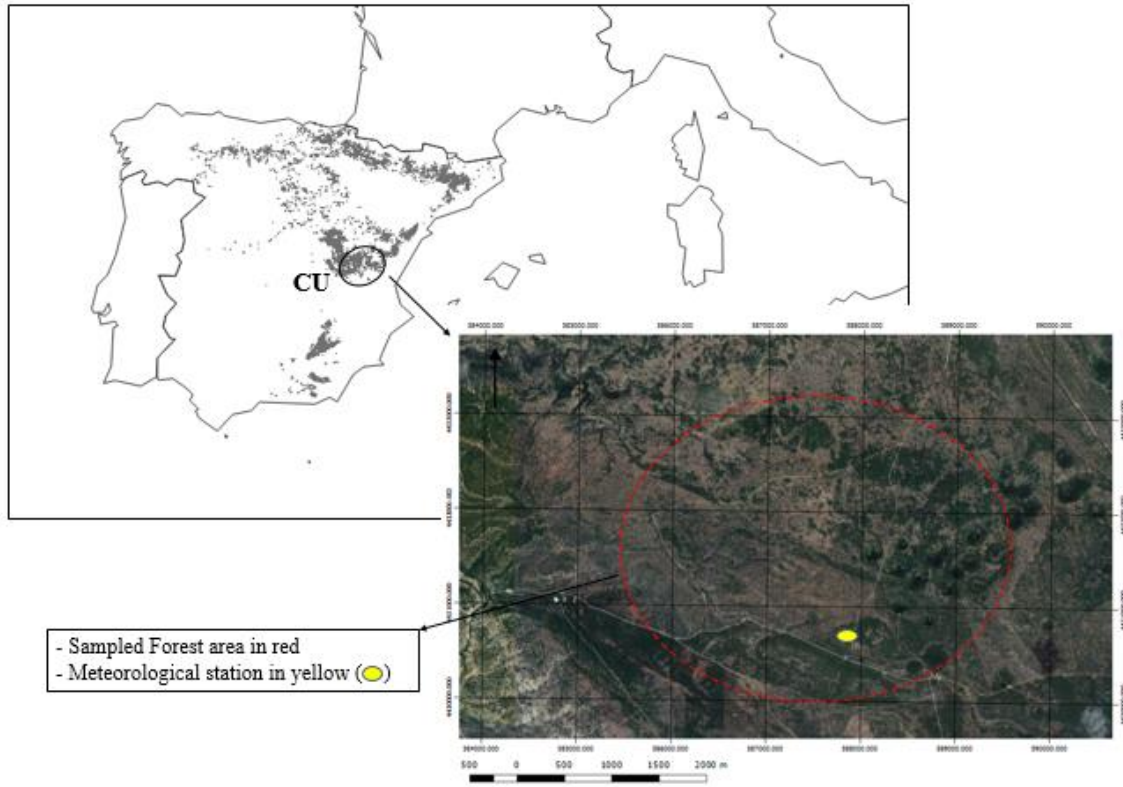
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1 **Figures**

2

3 **Figure 1.** Geographic location of the study site Cuenca (CU) Mountains. *P.nigra*  
4 distribution (natural and planted forest) in shaded.



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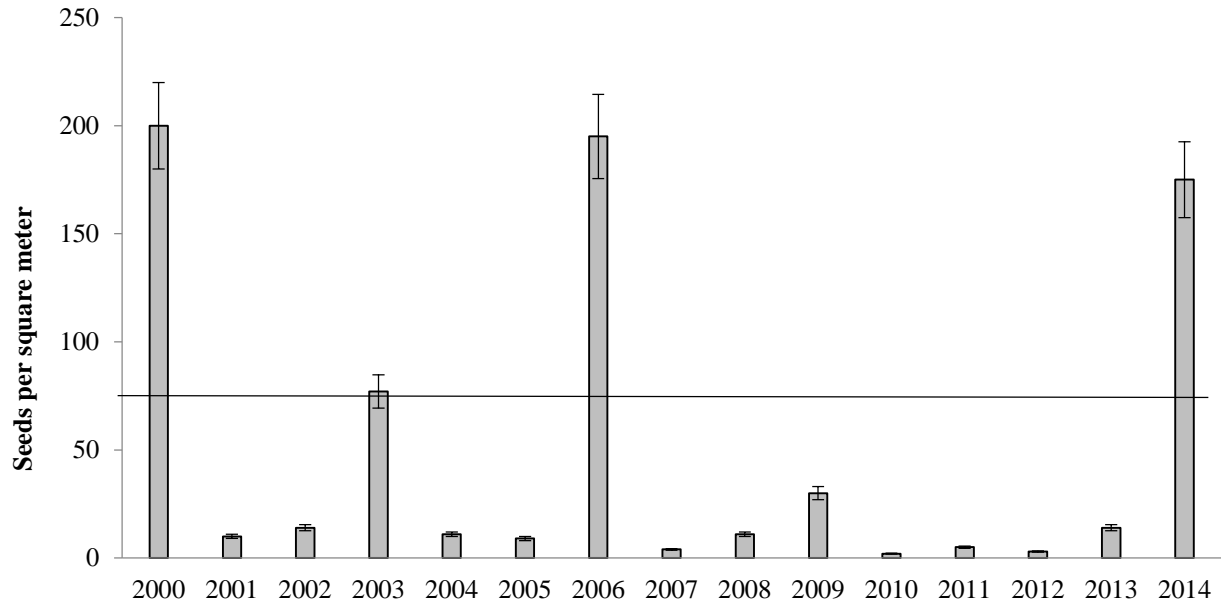
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16 **Figure 2.** Mean seed production data from seed traps for 2000-2014; 75th percentile  
17 threshold to define masting years

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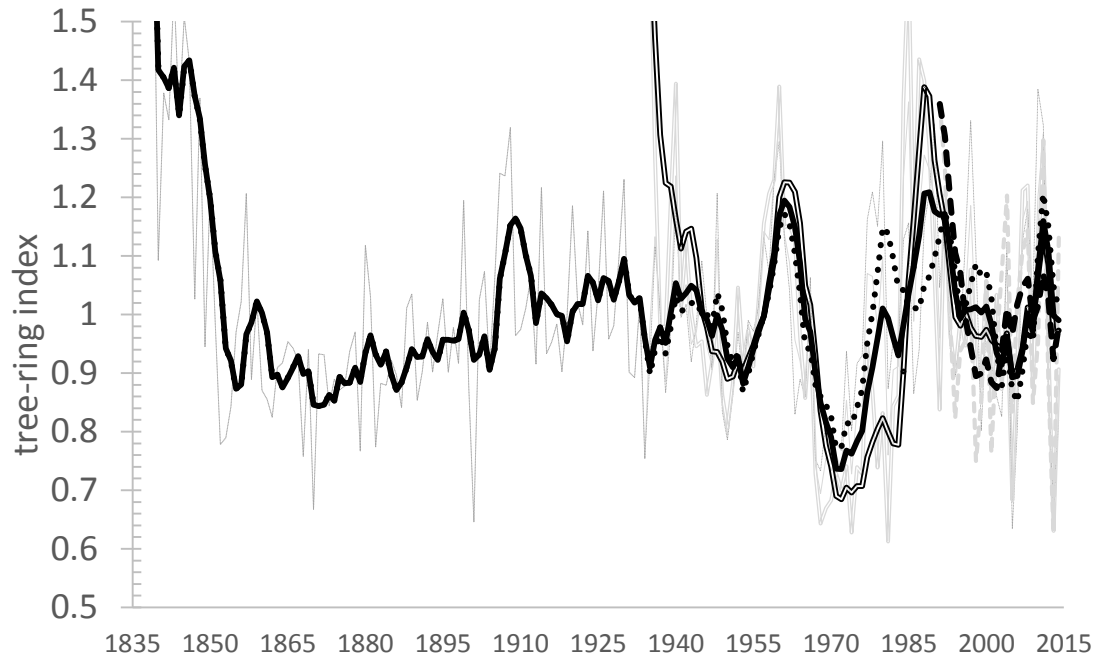
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29 **Figure 3.** Mean tree-ring index chronologies (grey line: raw, black line: 5-year smoother)  
30 for all cored trees (continuous), old trees only (dotted), medium trees (double), and young  
31 trees (dashed).

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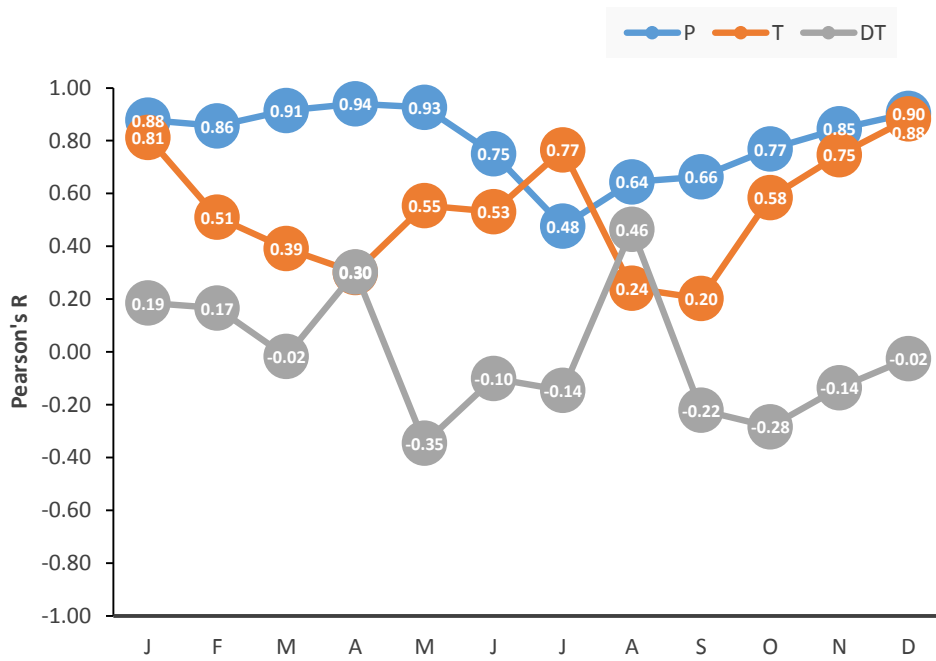
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43 **Figure 4.** Pearson's correlation between local and CRU monthly climate series for 1997-  
44 2014 in the study area.



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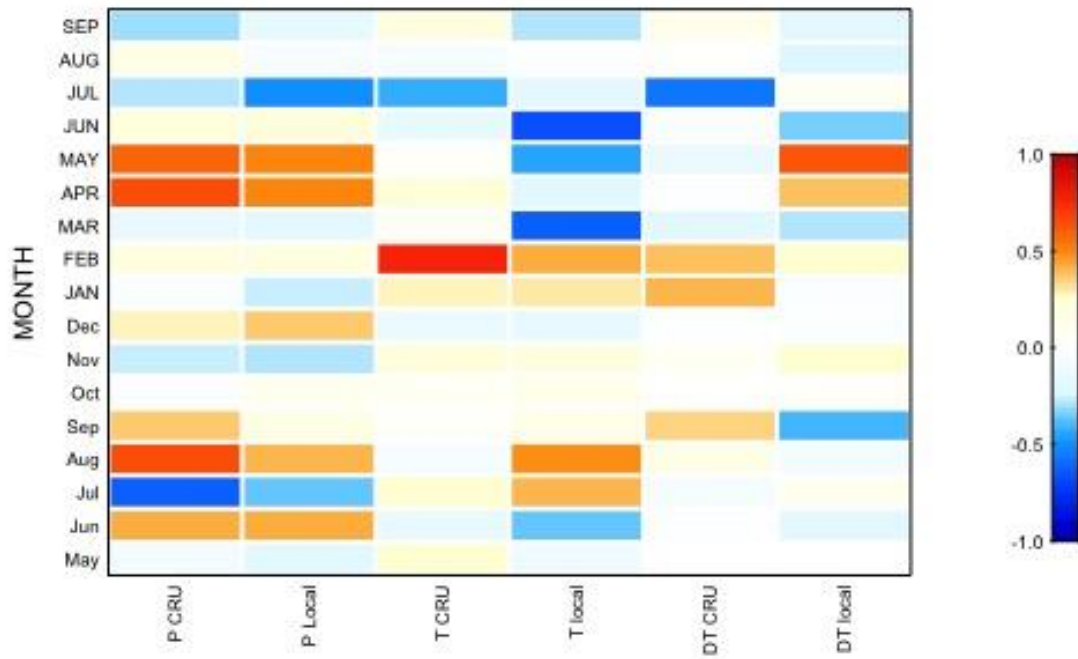
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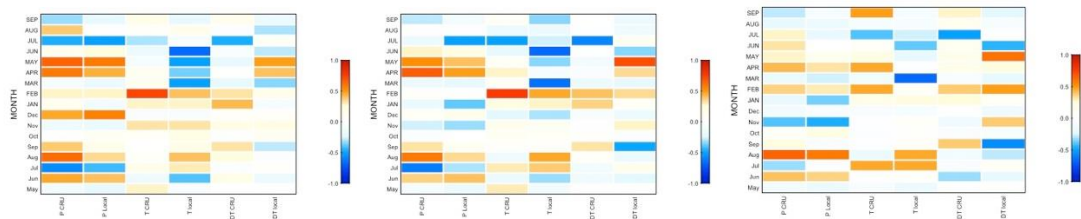
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58 **Figure 5.** Pearson's correlation between climate variables and BAI for all trees (above)  
59 and for old (left), medium (center) and young (right) tree chronologies (below).

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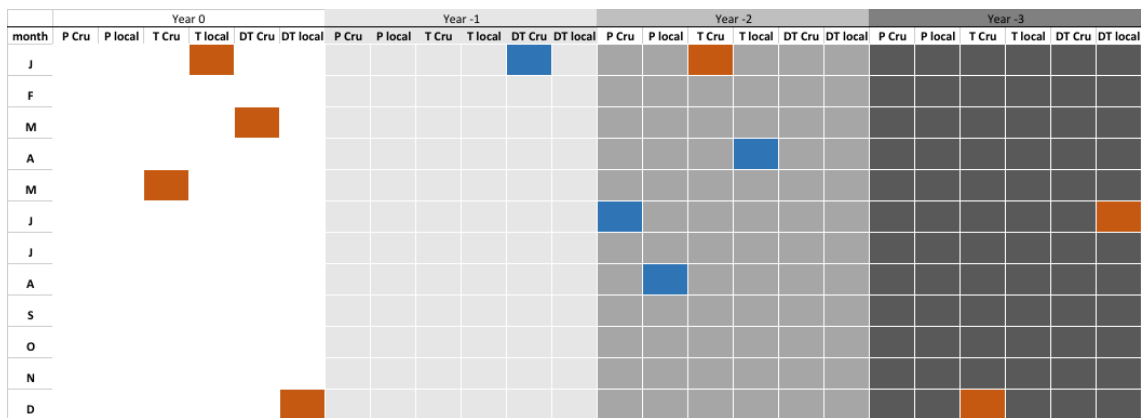
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70 **Figure 6.** Effect of climate on black pine fructification (non-masting vs. masting, red =  
 71 climate variables significantly higher in masting years, blue = significantly lower) (t-test,  
 72  $p < 0.05$ )

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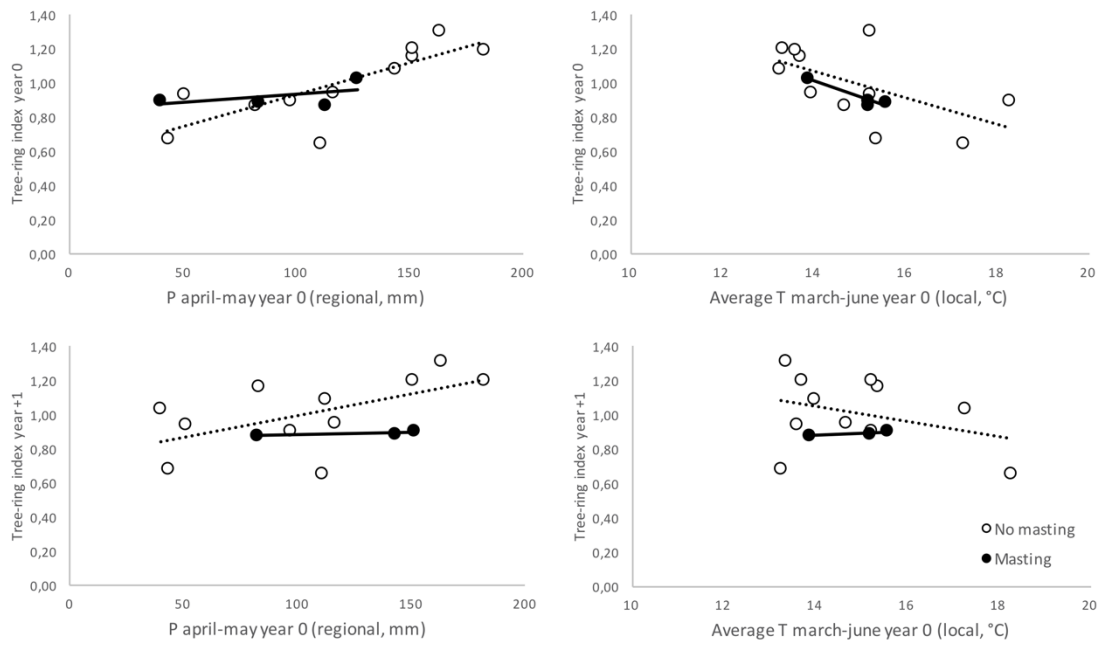
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89 **Figure 7.** Selected climate-growth relationships and linear trend in the study period  
90 (1997-2014) in masting (black circles, continuous line) vs. non-masting years (white  
91 circles, dotted line).

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1 **Tables**

2

3 **Table 1.** Geographical, topographical, edaphic, and structural characteristics (measured  
4 at 106 circular plots, mean±standar error) of the study site (source: Lucas-Borja, 2012;  
5 Candel-Perez, 2015).

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Elevation (m a.s.l.)	1186
Slope (%)	0.5
Aspect	Flat
Soil pH	6.8
Organic matter (%)	69.5
Total organic carbon (%)	6.2
P (mg kg <sup>-1</sup> )	27.6
Total N (%)	0.7
C/N	12.1
Sand (%)	70.0
Silt (%)	8.0
Clay (%)	22.0

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Mean dbh (cm)	22±6.2
Mean height (m)	13±5
Stand density (tree ha <sup>-1</sup> )	955±39
Canopy cover (%)	83±11%
Stand basal area (m <sup>2</sup> ha <sup>-1</sup> )	36±3.5

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19 **Table 2.** Mean growth features of 106 cored trees in the study site (average tree-ring  
20 index between 1997 and 2014). Different letters indicate significant differences  
21 determined by one-way ANOVA with Tukey's HSD post-hoc test ( $p < 0.05$ )

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<b>Variable</b>	<b>Young</b>	<b>Medium</b>	<b>Old</b>
dbh (cm)	8.0 <sup>a</sup>	22.5 <sup>b</sup>	41.2 <sup>c</sup>
Age at breast height in 2014 (years)	20.5 <sup>a</sup>	62.0 <sup>b</sup>	128.1 <sup>c</sup>
Mean tree-ring index 1997-2014	1.00 <sup>ab</sup>	1.12 <sup>a</sup>	0.94 <sup>b</sup>

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