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1 **Drought impacts on tree growth of two pine species along an altitudinal gradient**
2 **and their use as early-warning signals of potential shifts in tree species**
3 **distributions**

4

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19 **Abstract**

20 Mediterranean pine forests are at risk of experiencing a decline in tree growth in
21 response to climate warming if rising temperatures amplify drought stress. In mountain
22 areas, tree growth could be enhanced in temperature-limited high elevations, whilst it
23 might decline at water-constrained low elevations. Species differential responses could,
24 however, modulate the impact of drought on forests along altitudinal gradients. To test
25 for evidence of species differential drought impacts along an altitudinal gradient, we
26 studied the growth responses of two Iberian pine species (*Pinus sylvestris* and *Pinus*
27 *nigra*) subjected to Mediterranean conditions in Eastern Spain. We analysed the
28 stability of growth (basal area increment) responses to climate and drought during the
29 1950-2014 period by using resistance and resilience indices. *Pinus sylvestris* growth
30 was enhanced by warm spring temperatures, while *Pinus nigra* growth was improved by
31 a positive spring water balance. *Pinus sylvestris* growth decreased temporally at the
32 lower end of its altitudinal range, whereas *Pinus nigra* growth decreased at the upper
33 end. *Pinus sylvestris* exhibited low growth stability at its low-elevation limit. *Pinus*
34 *nigra* resistance also decreased along its altitudinal range, but this effect was
35 compensated by a high resilience. In mixed stands the results were contrasting with
36 *Pinus sylvestris* (at the lower altitudinal range) being more vulnerable to drought-
37 induced growth decline than *Pinus nigra* (at the upper altitudinal range). Under more
38 severe and frequent dry spells, *Pinus sylvestris* at low altitude may be highly vulnerable
39 to water shortage while *Pinus nigra* performs better. These growth responses are in line
40 with the expectation of a contraction in the realized niche of *Pinus sylvestris* with
41 extirpation of low-elevation stands if warmer and drier conditions continue. Moreover,
42 we show that analysing growth resilience in response to drought is a useful method to

43 anticipate likely changes in species dominance and thus to assist managers in designing
44 forest adaptation strategies.

45

46 **Key words:** basal area increment, dendroecology, drought stress, *Pinus nigra* subsp.
47 *salzmannii*, *Pinus sylvestris*, resilience.

48

49 **1. Introduction**

50 Global change is altering the world forest ecosystems at an unprecedented rate
51 (Sugden et al. 2008). Climate warming may result in negative impacts in drought-prone
52 forest ecosystems by diminishing several forest services as a result of increasing aridity
53 and water shortage (Allen et al., 2010; Lindner et al., 2010). Specifically, rising
54 temperatures could amplify drought frequency and severity leading to a decline of forest
55 growth and productivity in such drought-prone areas (Allen et al., 2015). Water
56 shortages are considered a major factor leading to increased forest dieback and tree
57 mortality (Galiano et al. 2010; Rigling et al. 2013), even leading to shifts in tree species
58 distribution (Allen and Breshears, 1998; Lenoir et al., 2008).

59 Altitudinal shifts of tree species are expected to occur in response to warmer and
60 drier conditions as a result of expansion at the uppermost edge and retraction at the
61 lowermost and driest edge of the species distribution due to changes in growth,
62 mortality and recruitment (Peñuelas and Boada, 2003; Peñuelas et al., 2007).
63 Nevertheless, there are also findings suggesting that rising CO₂ might compensate for
64 the negative effects of warming and drought by a fertilization effect translated into an
65 increase in water-use efficiency (Huang et al., 2007; Keenan et al., 2013; Madrigal-
66 González et al., 2015; Pretzsch et al., 2014). The impact of drought and warming on
67 forest structure and composition may depend upon species-specific responses, which

68 can vary significantly along environmental gradients, and biotic interactions such as
69 facilitation and competition (Pretzsch & Dieler 2011). Thus, analysing species-specific
70 growth responses to mean climate and extreme events across environmental gradients is
71 critical to properly assess forest vulnerability to climate change.

72 Tree growth has been widely used as an indicator of tree vitality, providing a
73 way to measure tree responses to environmental stresses (e.g. Dobbertin, 2005).
74 Additionally, tree-growth data can also be used to predict likelihood of drought-induced
75 death (Ogle et al., 2000; Pedersen, 1998). Therefore, while an enhancement of tree
76 growth at the upper altitudinal limit suggests an improvement of ecological conditions
77 and could favor an upward expansion, a reduced growth at the lowermost limit could be
78 indicative of a population decline and a subsequent retreat at the species dry distribution
79 limit (Jump et al., 2006; Matías and Jump, 2015). In this context, radial growth data
80 provides a unique opportunity to assess long-term growth-responses to climate along
81 altitudinal gradients and tree growth responses to past and current extreme drought
82 events.

83 Growth resilience, the capacity of an individual tree to restore growth level after
84 a climatic disturbance (e.g. an extreme drought), can influence long-term growth
85 responses and can modulate climate-induced species distribution under a scenario of
86 increasing aridity. Resistance, the capacity to endure growth levels during a climatic
87 disturbance, provides additional information in this respect (Lloret et al., 2011). For
88 instance, quantifying growth resilience and resistance in response to severe droughts
89 allows determining species- and site-specific vulnerability thresholds and detecting
90 those stands which show the best post-drought recovery (Gazol et al., 2017). Thus, the
91 analysis of growth resilience and resistance would help to reduce the uncertainty about
92 tree-growth responses to dry spells along altitudinal gradients (Kunstler et al., 2011).

93 The Mediterranean region is highly exposed to climate change (Nogués-Bravo et
94 al., 2008; Schröter et al., 2005). Specifically, increasing aridity can reduce tree growth
95 and alter species composition in forest ecosystems (Linares and Camarero, 2012;
96 Peñuelas et al., 2007; Ruiz-Labourdette et al., 2012; Sánchez-Salguero et al., 2015a). In
97 particular, Mediterranean Iberian mountain pine forests offer an ideal setting for
98 exploring species-specific growth responses and resilience to drought. These mountains
99 host mixed forests of Eurasian tree species such as boreal Scots pine (*Pinus sylvestris*)
100 and Mediterranean species such as black pine (*Pinus nigra* subsp. *salzmannii*), two
101 species with contrasting biogeographical origin. These two pine species tend to
102 segregate along environmental and altitudinal gradients in a predictable manner, with
103 Scots pine typically dominating in colder (e.g. higher altitude) and more humid
104 locations than black pine (Blanco et al., 1997). Scots pine has been identified among
105 one of the most drought vulnerable tree species in Europe since several drought-induced
106 dieback episodes have been described for this species (Eilmann and Rigling, 2012;
107 Herrero et al., 2013a; Martínez-Vilalta and Piñol, 2002). On the other hand, black pine
108 is considered more tolerant to drought stress along its elevation gradient because it
109 shows fewer signs of dieback (e.g. needle loss, growth reduction) than Scots pine
110 (Martín-Benito et al. 2013; Sánchez-Salguero et al. 2015a). Under warmer and more
111 arid climate scenarios, a change in dominance toward black pine is expected in those
112 locations where both species coexist (Herrero et al., 2013a, Herrero and Zamora, 2014;
113 Thiel et al., 2012).

114 In this study, we examined radial-growth responses of these two conifers to both
115 climatic variations and severe droughts of the late 20th century along an altitudinal
116 gradient in the Iberian system (Eastern Spain, Teruel). We evaluated climate-growth
117 relationships at three altitudinal positions: high-elevation (E_{High}), mid-elevation (E_{Mid})

118 and low-elevation (E_{Low}) sites for the two pine species. The specific objectives were: (i)
119 to determine the main climatic factors driving Scots pine and black pine growth, (ii) to
120 examine whether Scots pine and black pine growth trends and responses to climate
121 differ along the elevational gradient, and (iii) to assess interspecific differences in
122 growth stability following droughts, including resistance and resilience growth indices
123 as components of growth stability. Along an altitudinal gradient we expect growth rates
124 to be water limited and to decrease at lower altitudes, particularly in the case of Scots
125 pine, and to observe reduced growth stability at the species lower end of its distribution.

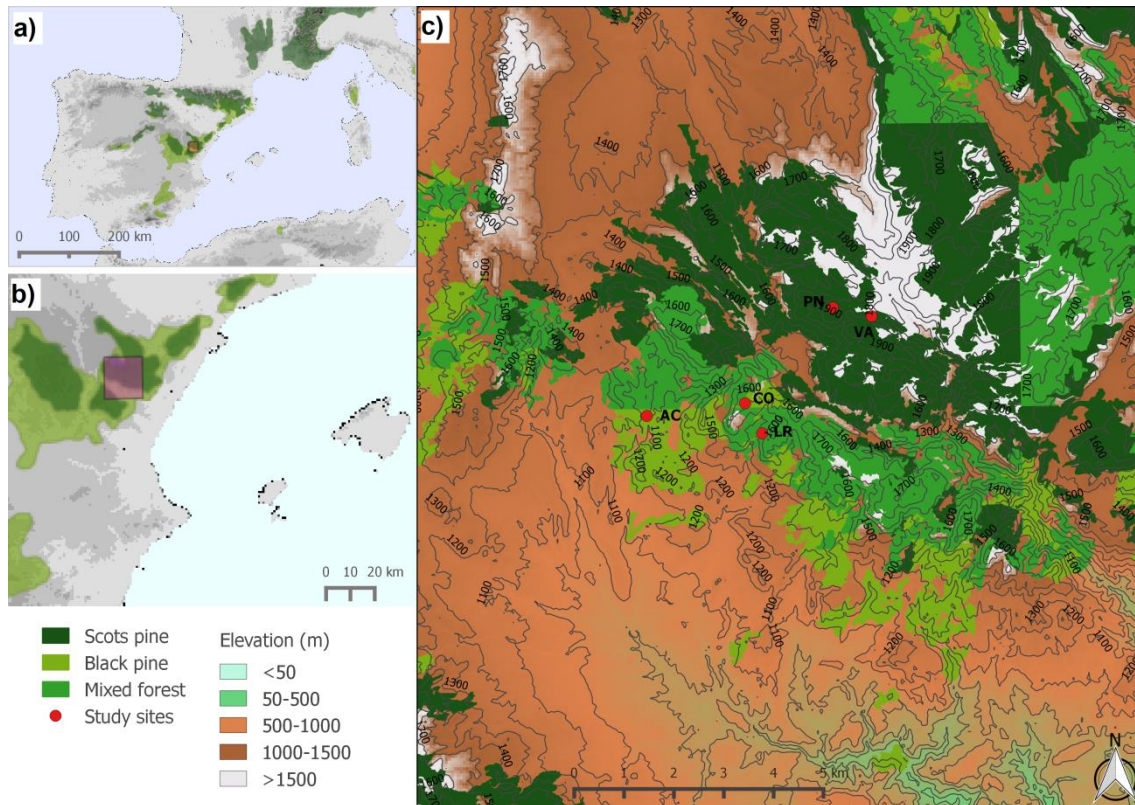
126

127 **2. Materials and methods**

128 ***2.1. Study area and species***

129 The study was carried out in the Gúdar range ($40^{\circ} 13' - 40^{\circ} 23' N$, $0^{\circ} 39' - 0^{\circ} 48'$
130 W, 1100-2020 m a.s.l.), within the southern Iberian Range (Teruel, Aragón, eastern
131 Spain). We selected five sites distributed along a wide (920 m) altitudinal gradient (Fig.
132 1, Table 1). We sampled three stands for each species at high, mid and low-elevation
133 sites (E_{High} , E_{Mid} , E_{Low} , respectively). In this manner, Scots pine and black pine were co-
134 occurring at their low and high-elevation site, respectively.

135



136

137 Figure 1. (a) Distribution of Scots pine and black pine forests in Spain and (b)
 138 geographical situation of the study area. (c) Location of the sampled sites in the Gúdar
 139 range (Teruel, Eastern Spain). The painted box (maps a and b) indicates the area of the
 140 detailed map (c). The mixed forest area represents the co-occurrence of Scots pine and
 141 black pine.

142

143 Table 1. Geographical and topographical characteristics of the Iberian pine forests
 144 sampled. Study sites are arranged from high to low elevation. Values are means \pm SD.

Species	Site (code)	Elevation (m a.s.l)	No. trees	DBH (cm)	Age at 1.3 m (years)	Basal area (m ² /ha)
Scots pine	Peñarroya (PN)	2020 (E _{High})	26	34.6 \pm 3.0	83 \pm 6	36.6
<i>Pinus sylvestris</i>	Valdelinares (VA)	1990 (E _{Mid})	23	39.0 \pm 3.3	96 \pm 7	29.7
	Las Roquetas (LR)	1600 (E _{Low})	22	35.6 \pm 1.5	116 \pm 11	38.0

Black pine	Las Roquetas (LR)	1600 (E _{High})	26	39.5 ± 1.9	134 ± 9	38.0
(<i>Pinus nigra</i> subsp. <i>salzmannii</i>)	Camino Olmedilla (CO)	1500 (E _{Mid})	26	43.1 ± 2.1	149 ± 3	9.5
	Alto de Cabra (AC)	1100 (E _{Low})	26	33.4 ± 1.1	107 ± 9	28.0

145

146 In Spain, the Scots pine (*Pinus sylvestris* L.) is distributed in cold mountains
147 areas due to its relatively high water requirements (Barbero et al. 1998). The Spanish
148 black pine (*Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco) occupies lower altitudes
149 across the Western Mediterranean Basin mountains, and is more tolerant to drought
150 (Herrero et al., 2013a; Sánchez-Salguero et al. 2012a). Both species co-occur in eastern
151 Spain close to the southernmost distribution limit of Scots pine and at the core of the
152 distribution range for black pine (Barbero et al. 1998).

153 In the highlands above 1600 m a.s.l., the dominant tree species is the Scots pine.
154 Other species of pines, such as mountain pine (*Pinus uncinata* Ram.) are present in the
155 forest above 1900 m a.s.l, frequently associated with savin juniper (*Juniperus sabina*
156 L.), and common juniper (*Juniperus communis* L.). Between 1100 and 1600 m a.s.l,
157 Scots pine is replaced by black pine and maritime pine (*Pinus pinaster* Ait.) coexisting
158 with holm oak (*Quercus ilex* L.) and Spanish juniper (*Juniperus thurifera* L.) in dry
159 sites, and Portuguese oak (*Quercus faginea* Lam.), in areas with higher soil moisture.
160 Below 1000 m a.s.l., Mediterranean pine species adapted to drought dominate, namely
161 maritime pine and Aleppo pine (*Pinus halepensis* Mill.), and are accompanied to
162 kermes oak (*Quercus coccifera* L.). In the study area, pine forests are composed of
163 natural stands and human activity has been practically nonexistent since the 1950's.

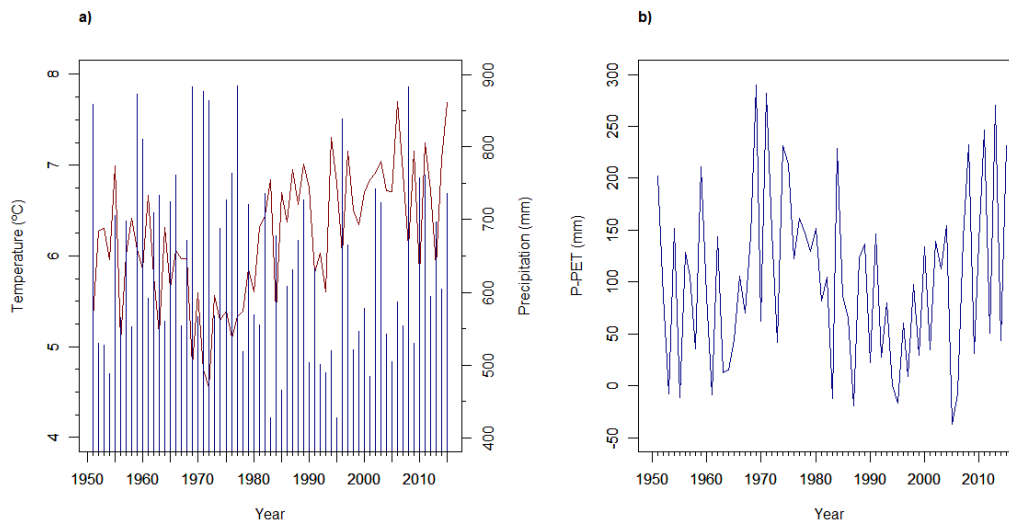
164 The climate in the study area is Mediterranean continental with a cold winter and
165 relatively low precipitation rates during the year. The annual average temperature is
166 around 4.5-7.7 °C and annual precipitation ranges from 425 to 885 mm (mean values for

167 the 1951–2014 period were obtained from several stations located at about 1050-1400
168 m, Fig. 2; see also Camarero et al. 2015b). The substrates in the study area are mainly
169 limestones.

170

171 *2.2. Climate data*

172 We obtained monthly climatic data (mean temperatures and total precipitation)
173 for the 1950–2014 period from E-OBS gridded dataset, which provided homogenized
174 and quality-controlled data at 0.25° spatial resolution (Haylock et al. 2008). The
175 selected grid was delimited by the following coordinates: 40.25-40.50° N, 0.75-1.00° W.
176 In order to assure the data quality, local climate information was obtained from
177 meteorological stations located at mid-elevation sites from 1050 to 1400 m in elevation
178 (see Camarero et al. 2015b). We corrected the temperature data considering the
179 environmental lapse rate of $-6.5^{\circ}\text{C km}^{-1}$, which refers to the actual change of mean
180 annual temperature with altitude, to take into account the elevation gradient (see also
181 Camarero et al. 2015b). For characterizing average water supply of the sampled stands,
182 we calculated the monthly water balance at each site as the difference between
183 precipitation and potential evapotranspiration (P-PET) following the Thornthwaite
184 (1948) method. During the 1950–2014 period no significant trend was found in annual
185 precipitation but mean temperatures significantly increased at a rate of $0.038^{\circ}\text{C yr}^{-1}$
186 (Fig. 2).



187

188 Figure 2. Climatic patterns and trends in the study area considering (a) mean annual
 189 temperature (line) vs. total precipitation (bars) and (b) spring water balance (P-PET,
 190 difference between precipitation and potential evapotranspiration). Data correspond to
 191 the 1950-2014 period and refer to a regional mean corresponding to mid-elevation sites
 192 (1500-1600 m a.s.l.).

193

194 **2.3. Dendrochronological methods and growth assessments**

195 Field sampling was done during winter 2014-2015. We randomly selected on
 196 average 25 dominant trees per site in 1-ha large sampling areas. We measured tree
 197 diameter at breast height or 1.3 m (DBH) of each tree using a girth tape. Two cores
 198 located perpendicular to the slope and in opposite directions were taken at 1.3 m from
 199 each tree using a Pressler increment borer. We also collected tree slices for some high-
 200 elevation Scots pine trees ($n = 15$) which were thrown down by a winter heavy snow
 201 load. The basal area at each site was estimated from two representative prism points
 202 using the Bitterlich (1984) method. In total, 149 trees were sampled; 71 Scots pines and
 203 78 black pines (Table 1). In order to minimize the impact of defoliation by the pine
 204 processionary moth (*Thaumetopoea pityocampa* Dennis and Schiff.) on black pine

205 growth we avoided recently defoliated sites following the information provided by
206 Sangüesa-Barreda et al. (2014).

207 The cores were prepared following standard dendrochronological methods
208 (Fritts 2001). Wood samples were air-dried, glued on wooden slides and polished on a
209 sanding machine until the tree-rings were clearly visible. Tree-ring widths were visually
210 cross-dated and measured to the nearest 0.01 mm using a binocular microscope and a
211 LINTAB measuring device (Rinntech, Heidelberg, Germany) linked to a computer.
212 Cross-dating of tree rings was checked using the program COFECHA (Holmes 1983).

213 To quantify growth, tree ring-width series were converted into basal area
214 increment (BAI) which provides a biologically meaningful variable showing growth
215 trends independently of tree age assuming stem growth is approximately concentric
216 (Biondi & Qeadan 2008). We used the following formula:

$$217 \quad \text{BAI} = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

218 where r_t and r_{t-1} are the stem radial increments at the end and the beginning of a given
219 annual ring increment corresponding to rings formed in t and $t-1$ years, respectively.

220

221 ***2.4. Drought events and growth stability***

222 To identify the main drought events affecting growth we identified the most
223 important reductions in BAI. We determined pointer years as those years in which most
224 series showed a pronounced BAI drop using the relative growth change method
225 (Schweingruber et al. 1990). Thus, a drought event was identified when there was an
226 impact on tree growth (Vicente-Serrano, 2010). This way, a negative pointer year was
227 considered when at least 60% of the BAI series of one species or 50% of the BAI series
228 of both species displayed an event year with a BAI decrease of at least 40% relative to
229 the average BAI in the 3 preceding years. The relative growth change method

230 characterized the 1967, 1979, 1994, 2005 and 2012 years as negative pointer years
231 (Supporting Information, Figure S1 (at the end of the document)).

232 To characterize growth stability as related to severe droughts along the
233 altitudinal gradient, we calculated resistance (R_t) and resilience (R_s) indices linked to
234 components of growth stability following Lloret et al. (2011). The indices were
235 calculated individually for each tree from its mean BAI series as follows:

236 Resistance, R_t $R_t = Dr/PreDr$ (2)

237 Resilience, R_s $R_s = PostDr/PreDr$ (3)

238 Resistance (R_t) is defined as the capacity to endure growth levels (BAI in this
239 case) during the drought period and represents the decrease from the pre-drought
240 (PreDr) to the drought (Dr) period. Resilience (R_s) quantifies the capacity to return to
241 the BAI level before the drought event and it is estimated as the ratio between the BAI
242 values of the post-drought (PostDr) and pre-drought (PreDr) periods (Lloret et al., 2011;
243 Pretzsch et al., 2013).

244 For analysing the growth response in the selected dry years, we calculated the
245 mean annual BAI in the 3 years before and after the drought period, except for 2012,
246 where we considered 2 years before and after the drought event (Supporting
247 Information, Figure S2). Other period lengths (2-5 years) yielded similar results to those
248 presented here. To calculate the pointer years and the resilience components we used the
249 *pointRes* package (van der Maaten-Theunissen and van der Maaten 2015).

250

251 **2.5. Data analyses**

252 To determine the main climatic drivers of tree growth, we first developed site
253 mean chronologies of basal area increment (BAI indexes), applying a cubic smoothing
254 spline fit with a 50% frequency cut off to all series and then fitting autoregressive

255 models for removing part of the first-order autocorrelation in the resulting values. This
256 procedure removes biological trends in growth and produces BAI indexes. BAI series
257 were detrended using the *dplR* software (Bunn et al., 2016). Then, we calculated
258 Pearson correlation coefficients between BAI indexes and monthly climate data (mean
259 temperature and water balance). Since radial growth of trees is usually also determined
260 by the climate of the year prior to ring formation (Fritts 2001), the temporal window of
261 growth–climate comparisons included from the previous up to the current September
262 (see Camarero et al. 2015b).

263 To evaluate long-term BAI trends and to compare whether trees growing along
264 the altitudinal gradient show different growth responses to water balance, we modeled
265 BAI using linear mixed-effects models for the two study species and considering the
266 1950-2014 period. We adjusted the following linear mixed-effects model:

$$267 \quad \text{BAI}_i = \alpha + \beta X_i + b_i Z_i + \varepsilon_i \quad (4)$$

268 where BAI_i represents the growth of tree i , and β is the vector of fixed effects (time,
269 water balance, elevation –high, middle and low elevation–, DBH and tree age), b_i is the
270 vector of random effects (tree identity), X_i and Z_i are fixed and random effects matrices,
271 and ε_i is the group error vector. Elevation was coded considering middle-elevation stand
272 as the reference group. We $\log(x+1)$ transformed BAI because it had a skewed
273 distribution. We considered seasonal water balance data as climatic predictors of BAI
274 following previous studies (Pasho et al. 2011). We selected water balance for previous
275 autumn (September to November) and spring (March to May) of the year of tree-ring
276 formation. We also included interactions between elevation and water balance as fixed
277 factors to assess if they affected BAI trends. All the continuous predictor variables were
278 standardized (i.e. the mean was subtracted from each value and divided by the standard
279 deviation), enabling the interactions to be tested and compared (Zuur et al. 2009).

280 Additionally, we evaluated the existence of multicollinearity among explanatory
281 variables by calculating the variance inflation factor (VIF), which was lower than two,
282 confirming no redundancy problems with the data.

283 To identify the best-supported model we constructed all possible combinations
284 of alternative models from the full model considering both the main effects and the pair-
285 wise interactions between the fixed effects. However, as we were interested in analysing
286 BAI trends, we retained time, DBH and tree age as fixed variables. Candidate models
287 were adjusted by the Maximum Likelihood method (ML). We used an information-
288 theoretic approach for multi-model selection based on minimizing the Akaike
289 Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson,
290 2002). Finally, parameter estimation of the selected model was obtained using the
291 restricted maximum likelihood (REML), which minimizes the likelihood of the
292 residuals from the fixed-effect portions of the model. Residuals of the models were
293 checked for normality and homoscedasticity. The percentages of variance explained by
294 fixed and random effects of the best model were obtained according to Nakagawa &
295 Schielzeth (2013).

296 To answer whether the tree species differ in growth stability components (R_t and
297 R_s) depending on site elevation, we fitted linear models using generalized least squares
298 (GLS), which extends the linear regression by modeling the heterogeneity with
299 covariates (Zuur et al. 2009). We analysed species-by-species the stability components
300 in each of the negative pointer years. We considered fixed hypothesis models for every
301 dry year analysed, and selected DBH, tree age, and elevation as covariates (quantitative
302 predictors). $\log(x+1)$ transformations of the resistance and resilience indexes were
303 calculated for ensuring normal distribution. The reference level for the categorical factor
304 elevation was again the middle-elevation. Additionally, we tested a model to study both

305 species together at the site where they co-occur. In this analysis, the black pine was the
306 reference level for the categorical factor species.

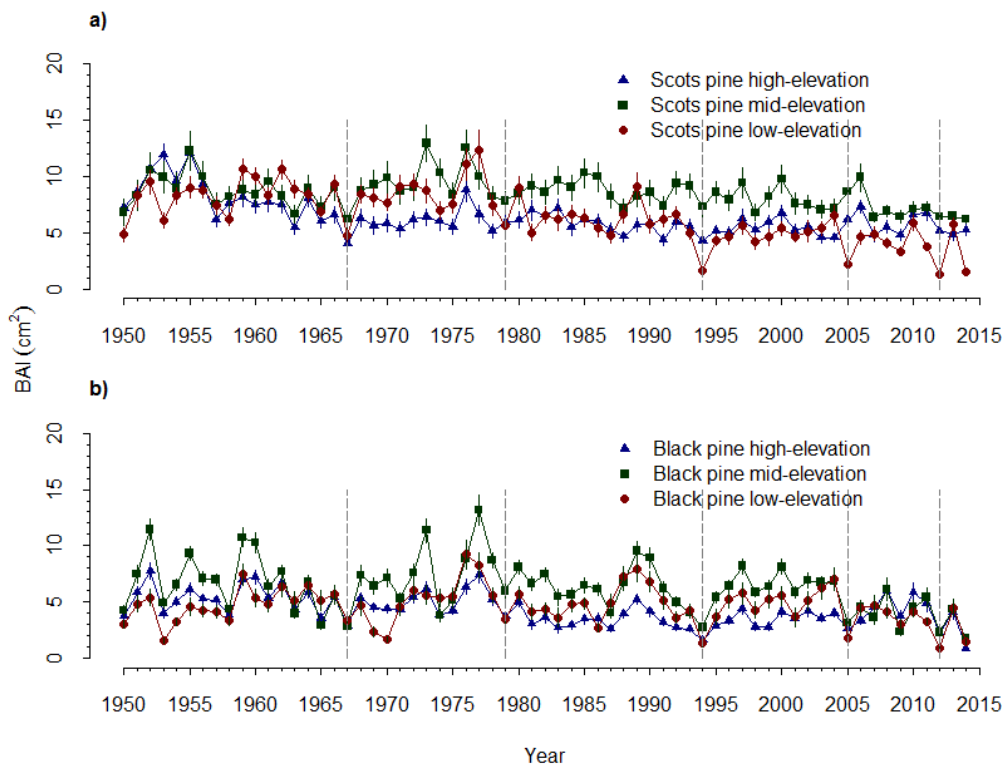
307 All statistical analyses were performed using the R statistical software (R
308 Development Core Team 2015). We fitted linear mixed-effects and generalized least
309 squares models using the *nlme* package (Pinheiro and Bates 2000). The best linear
310 mixed-effect model was selected with the package *MuMIn* (Barton 2015). Post-hoc
311 analyses based on Tukey contrasts allowed us to compare model results.

312

313 **3. Results**

314 ***3.1. Characteristics of sampled trees and BAI series***

315 Mean DBH of sampled trees ranged from 20.2 to 76.0 cm, and age at 1.3 m
316 varied from a minimum of 35 years (black pine) to a maximum of 237 years (Scots
317 pine). Over the 1950–2014 period, the mean BAI values for the low- mid- and high-
318 elevation stands of Scots pine were $6.63 \pm 2.36 \text{ cm}^2$, $8.19 \pm 2.14 \text{ cm}^2$ and 7.72 ± 1.98
319 cm^2 , respectively. For black pine, the mean BAI values for the low-, mid- and high-
320 elevation stands were $4.68 \pm 1.67 \text{ cm}^2$, $6.30 \pm 2.33 \text{ cm}^2$ and $5.19 \pm 1.71 \text{ cm}^2$,
321 respectively (Fig. 3).



322

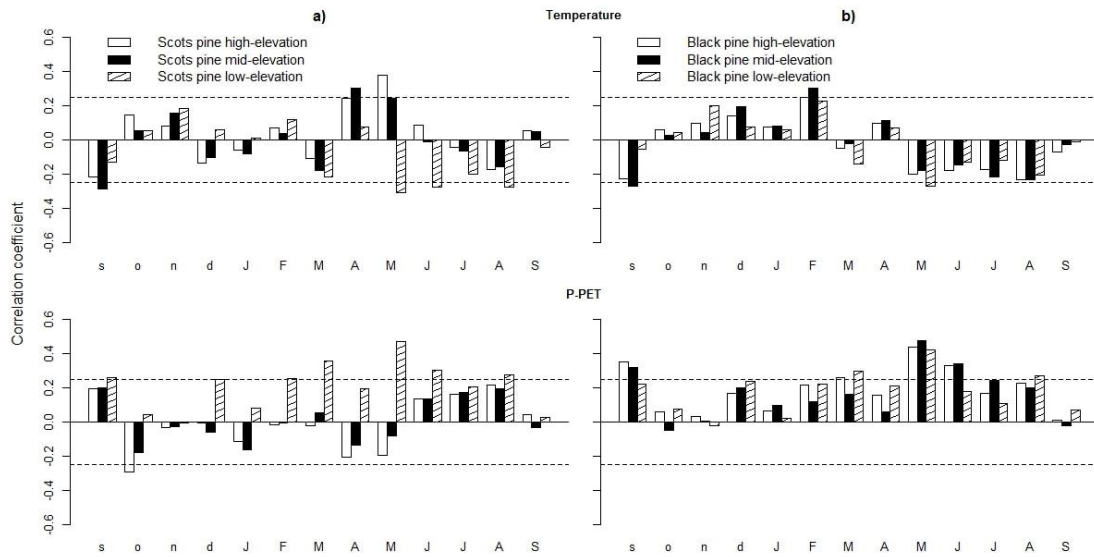
323 Figure 3. Basal area increment (BAI) of (a) Scots pine (n = 71) and (b) black pine (n =
 324 78) trees growing at different elevations for the 1950-2014 period. The vertical dashed
 325 lines indicate negative pointer years, calculated using the relative growth change
 326 method and defined when at least 60% of the tree-ring series of one species or 50% of
 327 the tree-ring series of both species show a growth decrease of at least 40%, relative to
 328 the average growth in the 3 preceding years. Values are means \pm SE.

329

330 3.2. Climate–growth associations

331 In Scots pine, the BAI index at mid- and high-elevation sites was positively
 332 associated with warm spring temperatures (April, May), while in low-elevation stands,
 333 positive associations were found with a positive spring water balance (Fig. 4). In black
 334 pine, the BAI index responded similarly to climatic variables, regardless of site
 335 elevation, showing significant positive correlations with warm February temperatures

336 and positive May water balance. The water balance of September prior to the growing
 337 season was positively correlated to the BAI index for both species in all sites. Mean
 338 monthly temperature for September of the previous year to ring formation was
 339 negatively associated to the BAI index of these pine species, but the effect was
 340 significant only for mid-elevation stands.



341
 342 Figure 4. Correlations (Pearson coefficients) obtained by relating radial growth (indexed
 343 basal area increment) of (a) Scots pine and (b) black pine sites located at three
 344 elevations and monthly climatic variables (mean temperature; P-PET, water balance)
 345 considering the 1950-2014 period. Months in lowercase letters correspond to the
 346 previous year, while those in uppercase letters correspond to the current year of tree-
 347 ring formation. The dashed horizontal lines indicate the $P < 0.05$ significance level.

348
 349 **3.3. Growth patterns and climatic factors**

350 In Scots pine, the most parsimonious BAI model was the full model and
 351 included all fixed factors (DBH, tree age, time, water balance and elevation), as well as
 352 the interactions between elevation and water balance, and elevation and time (Table 2).

353 The model showed the positive effect of DBH on BAI to be much more important than
354 the negative effect of tree age. The percentage of BAI variance explained by both the
355 fixed and random effects was 72% (conditional pseudo-R²) and the fixed effects
356 explained 53% of variance (marginal pseudo-R²). Predicted BAI tended to decrease
357 significantly with time at the low-elevation stand. Scots pine growing at the low-
358 elevation site was predicted to present significantly higher BAI values than at mid and
359 high elevation in response to increasing seasonal water balance, suggesting an increased
360 responsiveness of BAI to water deficit at the low-elevation limit.

361 In black pine, the most parsimonious BAI model included the same fixed factors
362 as in Scots pine except for the interaction between elevation and water balance for
363 previous autumn (Table 2). The model showed a significant positive effect of DBH and
364 seasonal water balance on BAI, while tree age was negatively related to BAI. The
365 percentage of BAI variance explained by both the fixed and random effects was 61%,
366 while the fixed effects explained 30% of variance. Predicted BAI indicated a significant
367 decrease in the high-elevation stand. Black pine BAI at the low-elevation site was also
368 predicted to be enhanced by a higher spring water balance.

369

370 Table 2. Statistics for the best linear mixed-effects models of basal area increment for
371 Scots pine and black pine, considering the 1951–2014 period. The table shows t values
372 and the last three lines show the Z value for multiple comparisons based on Tukey
373 Contrasts. Values with asterisk are significant ($P < 0.05$). Abbreviations: DBH:
374 diameter at breast height; $PPET_{AutPre}$: water balance for the previous autumn; $PPET_{Spr}$:
375 water balance for the spring; E_{High} : High-elevation stand; E_{Mid} : Mid-elevation stand;
376 E_{Low} : Low-elevation stand. The reference level for elevation is the mid-elevation stand

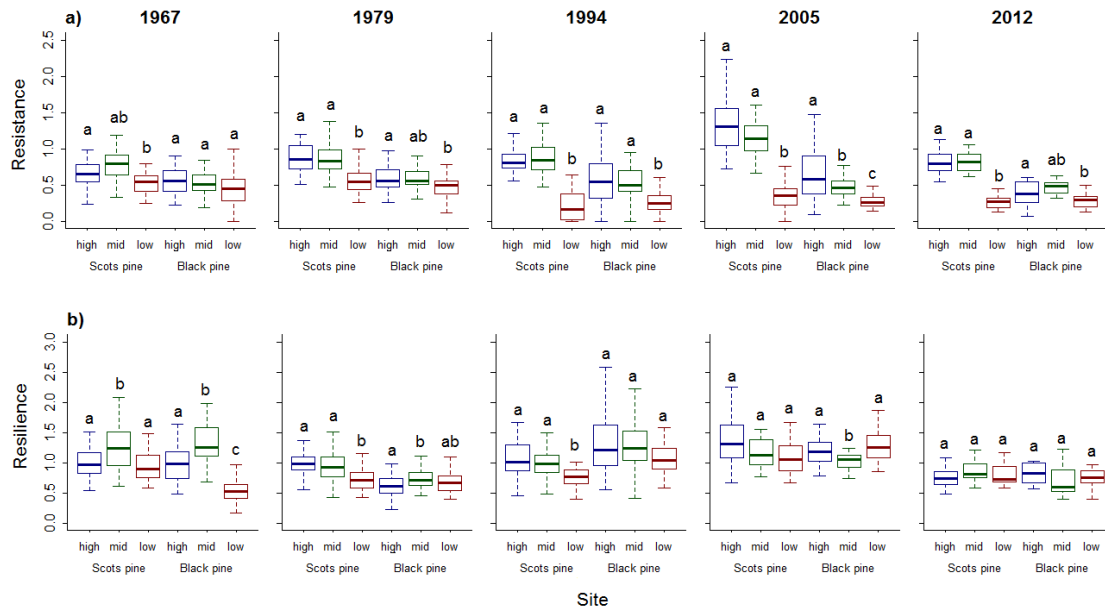
377 (E_{Mid}). The standard deviation of the random effect was 0.298 (residual: 0.363) for
 378 Scots pine and 0.354 (residual: 0.392) for black pine.

	Scots pine	Black pine
t values		
Intercept	28.040*	23.221*
DBH	12.662*	6.289*
Age	-3.739*	-4.035*
Year	1.923	-4.015*
PPET _{Spr}	1.918	10.660*
PPET _{AutPre}	-3.091*	18.987*
E_{High}	0.821	-0.990
E_{Low}	1.379	-1.226
Year x E_{High}	-0.617	-3.437*
Year x E_{Low}	-7.945*	2.258*
PPET _{Spr} x E_{High}	-1.550	1.280
PPET _{Spr} x E_{Low}	16.952 *	4.859*
PPET _{AutPre} x E_{High}	-1.479	-
PPET _{AutPre} x E_{Low}	8.712*	-
Z values		
E_{High} vs. E_{Mid}	0.821	-0.990
E_{Low} vs. E_{Mid}	1.379	-1.226
E_{Low} vs. E_{High}	0.599	-0.371

379

380 ***3.4. Growth stability components in response to drought***

381 Growth stability components varied between species, but also at all elevations
 382 and drought events. Resistance indices clearly revealed a stronger growth decline at
 383 lower elevation for both pine species, reaching values around 80% for Scots pine and
 384 75% for black pine. Meanwhile, in the Scots pine at high- and mid-elevation sites
 385 growth decreased less than 30%. Resilience values revealed growth levels rather similar
 386 to those 3 years before a drought at the high-elevation sites, but this did not occur at
 387 lower elevations (Fig. 5). Nevertheless, growth resilience for the 1994 and 2005
 388 droughts presented average values along the gradient, which means similar performance
 389 after and before these droughts. In 2012, growth displayed lower resilience values along
 390 the entire gradient.



391

392 Figure 5. Box plots showing the (a) resistance and (b) resilience indices
 393 calculated for the following negative pointer years 1967, 1979, 1994, 2005 and 2012
 394 corresponding to severe droughts during the 1950-2014 period. The letters indicate
 395 significant ($P < 0.05$) differences in growth stability among elevations for each species.

396

397 Tree age and DBH covariates did not show a general pattern in their effects on
 398 growth stability components (R_t and R_s), and only revealed significant differences in
 399 the 1967, 1979 and 2012 droughts (Table 3). Scots pine growing at low elevation was
 400 significantly less resistant than at mid- and high-elevation sites for all droughts, but less
 401 resilient for the first three drought events (1967, 1979 and 1994). Black pine growth
 402 was also less resistant at low-elevation for most of the years analysed. However, growth
 403 resilience did not show a clear sign during the drought events for the different elevation
 404 sites. For instance, in 1967 high and low-elevation sites were less resilient than the mid-
 405 elevation sites, while a reverse pattern was found in 2005 (Table 3).

406 Growth stability also differed among the dry years at sites where pine species
407 were co-occurring (Table 4). Generally, black pine was more resistant and resilient to
408 drought than Scots pine, although results were not significant for all drought events.

409 Table 3. Results of the generalized least squares models of growth stability components for Scots pine and black pine and the negative pointer
 410 years as a function of individual characteristics (DBH and tree age), considering the effect of site elevation (E_{High}: High-elevation stand; E_{Low}:
 411 Low-elevation stand; and E_{Mid}: Mid-elevation stand). The table shows the t and Z statistics for multiple comparisons based on Tukey contrasts.
 412 Values with asterisk are significant (P < 0.05).

413

			Scots pine					Black pine				
	Stability components		1967	1979	1994	2005	2012	1967	1979	1994	2005	2012
Resistance	<i>t</i> values	Intercept	8.903*	13.928*	10.455*	14.107*	7.905*	5.320*	7.206*	1.430	4.367*	2.759*
		Age	-1.652	2.162*	1.203	-0.706	0.577	-4.482*	-0.079	0.402	-0.716	-0.794
		DBH	0.779	-3.383*	0.137	0.970	0.098	4.020*	0.977	1.801	0.072	0.628
		E _{High}	-1.605	-0.838	0.015	1.489	0.436	1.153	-0.425	1.465	2.377*	-1.033
		E _{Low}	-3.183*	-6.567*	-12.071*	-13.695*	-7.848*	-1.175	-2.519*	-2.109*	-3.476*	-2.354*
	Z values	E _{High} vs. E _{Mid}	-1.605	-0.838	0.015	1.489	0.436	1.153	-0.425	1.465	2.377*	-1.033
		E _{Low} vs. E _{Mid}	-3.183*	-6.567*	-12.071*	-13.695*	-7.848*	-1.175	-2.519*	-2.109*	-3.476*	-2.354*
		E _{Low} vs. E _{High}	-1.579	-5.768*	-12.180*	-15.217*	-9.187*	-2.323	-2.277	-3.696*	-6.055*	-1.458
Resilience	<i>t</i> values	Intercept	7.849*	14.365*	14.662*	6.863*	10.292*	5.781*	7.013*	7.084*	5.834*	2.296*
		Age	-0.439	0.696	-1.406	0.982	1.394	0.350	-0.357	-1.742	0.967	-1.272
		DBH	0.714	-2.489*	-1.527	-1.138	-3.624*	2.716*	1.862	0.839	0.663	0.801
		E _{High}	-2.021*	-0.520	0.715	1.656	-0.333	-2.899*	-2.376*	-0.309	2.379*	0.415
		E _{Low}	-2.448*	-4.723*	-2.737*	0.191	1.267	-7.433*	-0.654	-1.908	3.162*	0.509
	Z values	E _{High} vs. E _{Mid}	-2.021*	-0.520	0.715	1.656	-0.333	-2.899*	-2.376*	-0.309	2.379*	0.415
		E _{Low} vs. E _{Mid}	-2.448*	-4.723*	-2.737*	0.191	1.267	-7.433*	-0.654	-1.908	3.162*	0.509
		E _{Low} vs. E _{High}	-0.444	-4.254*	-3.437*	-1.660	1.812	-5.160*	1.491	-1.791	1.171	-0.024

414

415

416 Table 4. Results of the generalized least squares model of the growth stability components for Scots pine and black pine at the mixed stand
 417 (elevation 1600 m) and the negative pointer years as a function of individual characteristics (DBH and tree age). Reference level for factor
 418 species is black pine. Values with asterisk are significant ($P < 0.05$).

Resistance	1967	1979	1994	2005	2012
Intercept	4.271*	4.065*	0.330	2.229*	1.710
Age	-1.767	0.936	1.062	-1.085	-0.482
DBH	2.060*	1.567	2.964*	2.828*	0.258
Scots pine vs. black pine	0.004	0.501	-4.560*	-4.069*	1.558
Resilience					
Intercept	4.123*	5.848*	6.674*	4.318*	4.234*
Age	0.176	0.869	-0.669	0.548	2.879*
DBH	2.063*	0.445	0.135	0.504	-2.397*
Scots pine vs. black pine	0.304	2.618*	-4.593*	-0.805	0.456

419 **4. Discussion**

420 Mid-century pine growth responses to climatic conditions and drought varied
421 along the altitudinal gradient studied in the Eastern Iberian Peninsula. While in the
422 upper elevations low temperature was the main limiting factor for tree growth, trees in
423 the lower sites were more sensitive to water shortage and drought. Drought impacted
424 Scots pine growth and stability mainly at the lowermost distribution limit of the species.
425 Black pine growth resistance decreased also at low-elevation but growth decline was
426 more evident near the uppermost distribution limit of the species (high-elevation site).

427

428 ***4.1. Climate-growth relationships along the elevation gradient***

429 Temperature has increased in the study area during the second half of the
430 twentieth century (Camarero et al., 2015b) as has been observed in other Mediterranean
431 mountains (García-Ruiz et al. 2011), affecting growth patterns of Scots pine and black
432 pine. Rising spring temperatures boosted Scots pine growth at the highest elevations,
433 possibly because warm temperatures are a triggering factor for growth onset at these
434 sites and growing season becomes longer (Camarero et al., 2010; Herguido et al., 2016).
435 However, at lower altitudes, warmer temperatures exacerbated negative drought impacts
436 on growth of Scots pine and black pine probably by reducing soil moisture and
437 enhancing evapotranspiration rates (Camarero et al., 2015a; Granda et al., 2013;
438 Herguido et al., 2016). Temperature of the prior September had a negative impact on
439 both species growth (Fig. 4) as reported in previous studies and this may be a
440 consequence of prolonged summer drought which negatively impacts late-summer
441 photosynthesis and carbohydrate storage (Andreu et al., 2007; Herrero et al., 2013b;
442 Martín-Benito et al., 2010). Dry conditions during current spring and the previous
443 autumn have also been shown to strongly reduce tree growth in other drought-prone

444 areas by directly reducing radial-growth rates (Eilmann et al., 2011; Lévesque et al.,
445 2014).

446

447 ***4.2. Growth patterns across species and sites***

448 The decline in basal area increment was much more evident at the lower sites of
449 the altitudinal gradient than in the other sites. While Scots pine growth decreased at the
450 low-end of its altitudinal range in response to drought as has been detected in other
451 areas (Sánchez-Salguero et al. 2015a), we did not observe such a response at mid- and
452 high-elevation sites. This is in agreement with the idea that upper distribution limits in
453 mountain pines is set by tolerance to low temperatures (Körner et al., 2016; Ruiz-Benito
454 et al., 2012) and thus warmer temperature may increase growth rates wherever water
455 shortage does not override this temperature effect (Scholze et al., 2006; Wilmking et al.,
456 2004). A growth enhancement may also be connected with CO₂ fertilization and warmer
457 temperatures in areas where growth was limited by low temperatures (Keenan et al.,
458 2013; Madrigal-González et al., 2015). However, this was not observed in the study
459 area according to Camarero et al. (2015b).

460 Contrary to our expectations, black pine showed higher vulnerability to drought
461 and exhibited a more pronounced BAI decline in the upper end of its altitudinal range,
462 while BAI at the low-elevation site remained stable or even increased. These findings
463 seem contrary to the posed hypothesis of warming-induced growth decrease due to
464 amplified drought stress. However, similar results were found by Herguido et al. (2016)
465 studying black pine in Central Spain mountains, and attributed to poorer soils and
466 steeper slopes at high elevation sites. At high altitudes, black pine tends to be replaced
467 by Scots pine, probably because of a greater tolerance to low temperatures of the latter
468 species which would outcompete black pine in cold and wet sites (Barbero et al., 1998).

469 Thus, even though average temperatures have increased over the second half of the
470 twentieth century, the upper distribution of black pine growth might be set by low
471 temperatures or by interspecific competition (i.e. with Scots pine).

472 Growth responses to climate may also be modulated by local factors, such as site
473 composition and competition (Rigling et al. 2013; Sánchez-Salguero et al. 2015b). In
474 our research area, black pine at high-elevation forms mixed stands with Scots pine (low-
475 elevation stand) and both conifers growth tends to show a decline in BAI where they co-
476 occur. Furthermore, basal area is higher in this stand than in the rest of the study area.
477 Competition for water and nutrients among these two species may play an important
478 role for drought-related impacts at that altitude, as it has been reported in other studies
479 (Linares et al. 2009; Ruiz-Benito et al. 2013). Lastly, as expected, tree size influenced
480 growth responses in a positive way (Gómez-Aparicio et al., 2011; Granda et al., 2013).

481

482 ***4.3. Response to extreme drought events***

483 Our findings confirm that severe droughts negatively impacted tree growth, but
484 pine species were not equally affected along its altitudinal range. There was also
485 variability in the length and severity of growth suppression periods. A severe and long-
486 lasting drought characterized the 1994-1995 episode, while 2005 and 2012 droughts
487 were more intense but corresponded to short dry spells. The fact that tree age did not
488 show consistent effects overall on tree growth stability components may be explained
489 because our sample only considered mature tree individuals but no other age classes
490 (Pretzsch et al., 2013).

491 Scots pine presented both the lowest growth rates and growth stability
492 components -resistance and resilience indices- at the lower end of its altitudinal range.
493 This result agrees with the hypothesis of drier conditions and higher vulnerability to

494 drought for low elevation Scots pine stands, which showed dieback episodes in nearby
495 study areas (Sánchez-Salguero et al. 2012b; Camarero et al. 2015a). Black pine showed
496 the sharpest growth decline during dry spells along its distribution range. At the low-
497 elevation site, black pine growth was also less resistant to drought (see also Herrero and
498 Zamora 2014). These findings seem to be contradictory with our previous result
499 showing a pronounced black pine growth decline at its high-elevation site. This pointed
500 out the different growth responses to climate and drought stress depending on the time
501 scale. Analysing short-term changes triggered by extreme events such as dry spells
502 could allow assessing the species drought tolerance in a more realistic way than
503 considering average growth values, whereas long-term growth trends would allow better
504 characterizing responses to lasting processes such as climate warming (Eilmann and
505 Rigling, 2012). Moreover, species growth stability depends on both resistance and
506 resilience growth indices as low resistance values can be compensated by a higher
507 resilience. Growth rates for the two species recovered three years after the dry spells,
508 particularly for the 1994, 2005 and 2012 droughts. These results agree with other
509 studies on black pine (Granda et al., 2013; Martín-Benito et al., 2008) and Scots pine
510 (Gea-Izquierdo et al., 2014) which found a recovery two years after the drought episode.

511 In the area where both species form mixed forests (lowest and highest altitude
512 for Scots and black pine respectively), black pine was more resistant and resilient to
513 drought, exhibiting a higher growth plasticity than Scots pine (Eilmann and Rigling,
514 2012). Other studies have pointed higher vulnerability to drought for Scots pine than for
515 black pine in stands where both conifers co-occur (Herrero and Zamora, 2014;
516 Martínez-Vilalta and Piñol, 2002) or have reported drought-induced dieback and growth
517 decline in Scots pine populations subjected to persistent drought stress (Bigler et al.,
518 2006; Galiano et al., 2010).

519

520 **5. Conclusions and management implications**

521 Shifts in species dominance may be detected focusing on mortality and
522 regeneration rates (Ruiz-Labourdette et al., 2012). Nonetheless, here we show that tree-
523 ring data analyses may be adequate to detect early-warning signals of likely shifts in
524 species distributions along an altitudinal gradient (Adams and Kolb, 2005; Eilmann and
525 Rigling, 2012; Weber et al., 2007). Species turnover is a slow demographic process that
526 can take decades and it involves a series of demographic stages -from recruitment to
527 mortality- which are difficult to monitor over time. Stand past growth responses to
528 extreme climate events - such as drought- can provide forest managers with critical
529 information on population dynamics that can help them in the decision process (e.g.
530 adaptation measures).

531 Our study constitutes one of the few attempts to gain knowledge about
532 differential species responses to extreme droughts along their altitudinal distribution
533 using growth stability components such resilience. The low-elevation Scots pine
534 populations showed the lowest resilience in response to drought. Black pine had less
535 growth resistance to drought at their low-elevation limit, although a high resilience
536 allowed recovering previous growth levels after drought. In mixed mid-elevation stands,
537 black pine was more resistant and resilient to drought than Scots pine. Low-elevation
538 Scots pine stands seem those most vulnerable to drought. Analyses of growth resilience
539 could imply a range contraction of lowermost Scots pine populations under the
540 forecasted aridification trends. This information is crucial to validate models of climate
541 change predictions –including temporal scales of likely extirpation processes at the rear
542 edge and to advance proper management measures.

543 In order to better assess ecosystem vulnerability to extreme climatic changes
544 other factors need to be considered such as responses at different demographic stages
545 from reproduction to mortality as well as species interactions. Also functional studies,
546 from carbohydrate depletion to xylem acclimation, aiming to understand mechanisms
547 underlying growth resilience to recurrent droughts, may be needed to understand
548 resilience thresholds in response to climate change.

549

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563

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Supporting Information

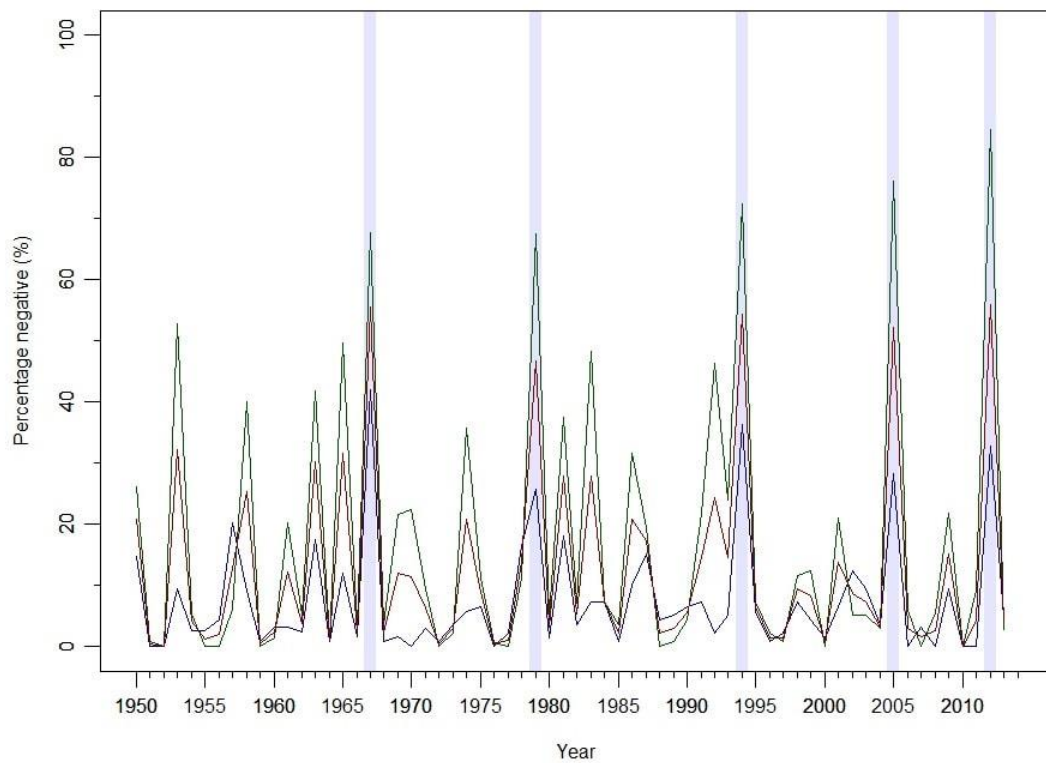
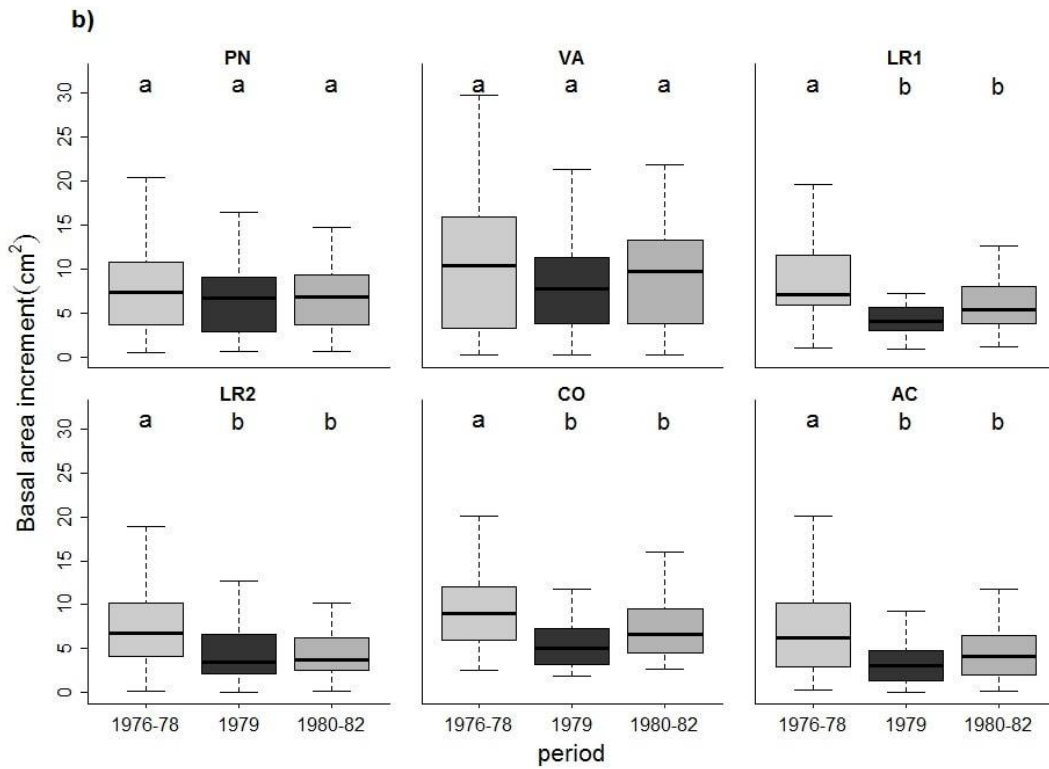
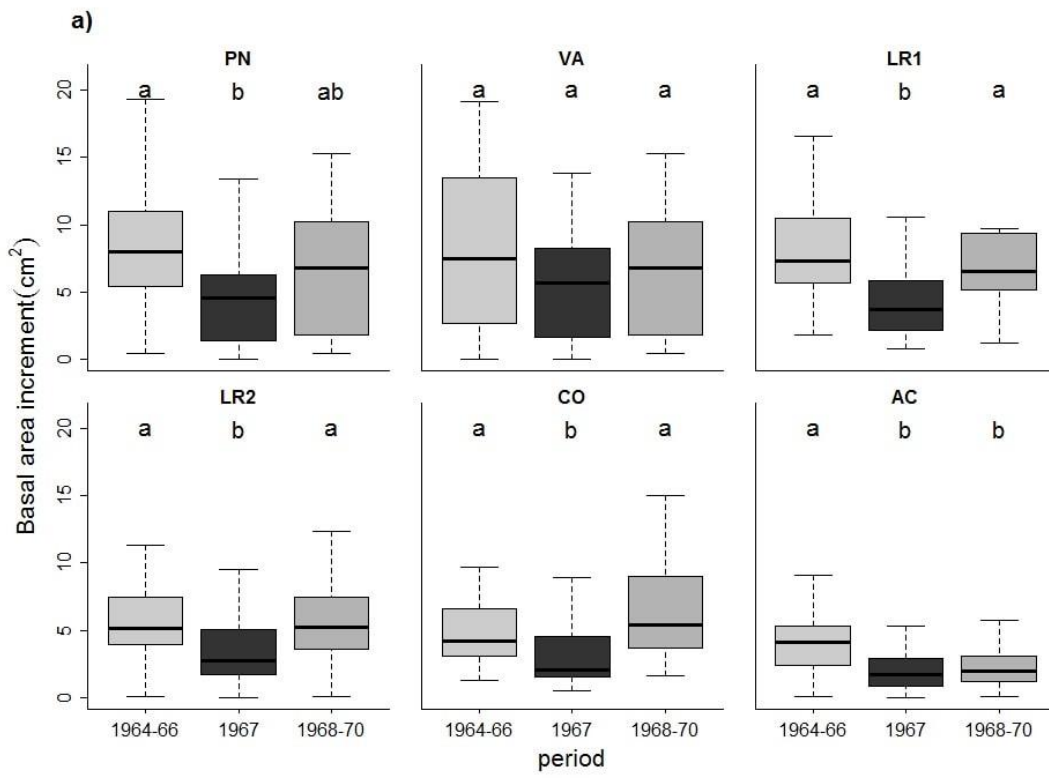
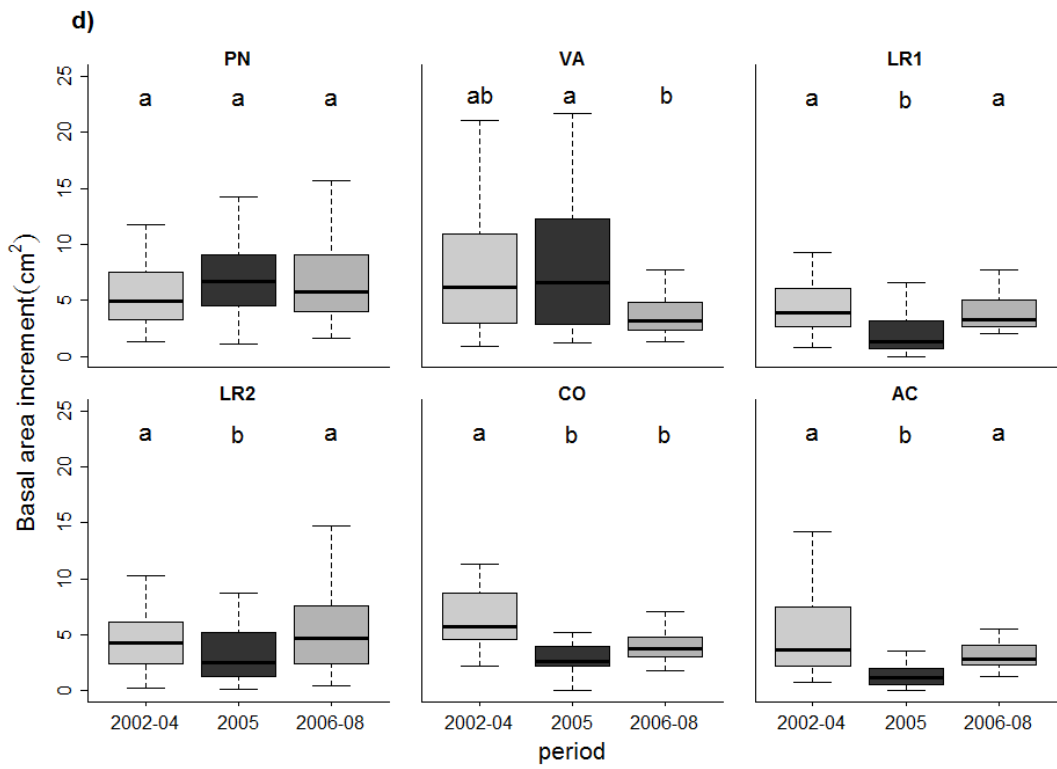
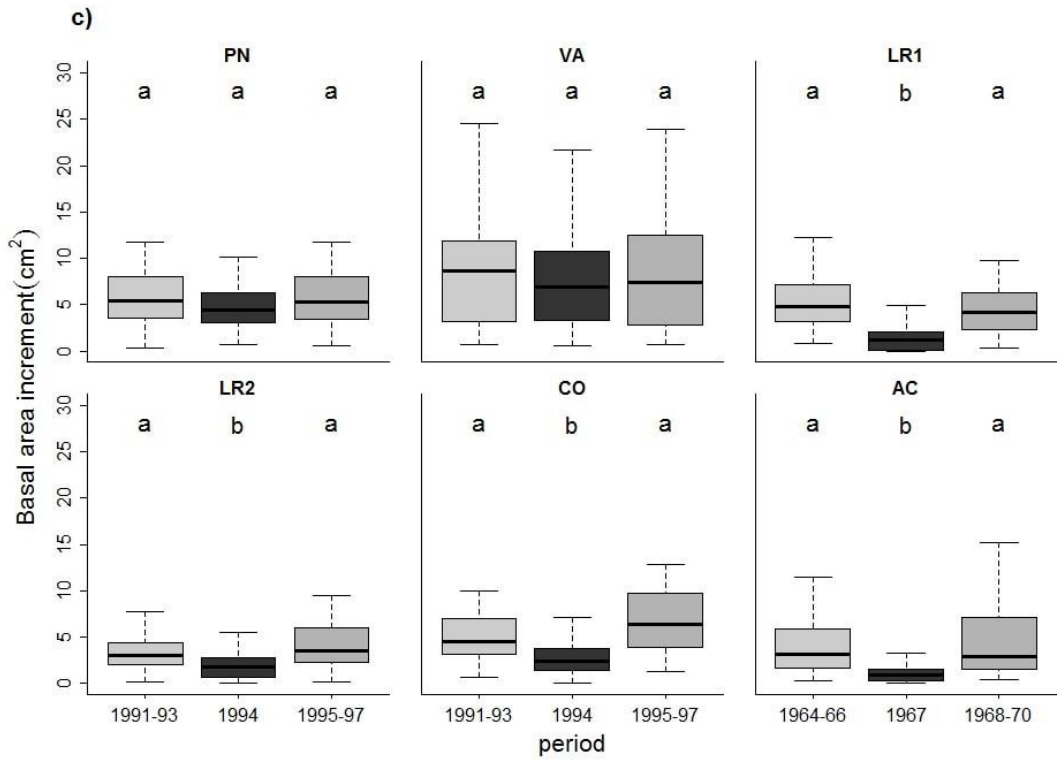


Figure S1. Percentage of trees showing a negative event year during the 1950-2014 period. The blue line refers to Scots pine (*Pinus sylvestris*) sites, and the green line indicates black pine (*Pinus nigra*) sites. The average percentage of both species is represented by the red line. The selected drought years (1967, 1979, 1994, 2005 and 2012) were those which at least 50% of the BAI series of both species and 60% of one species displayed an event year with a BAI decrease of at least 40%, relative to the average BAI in the 3 preceding years.





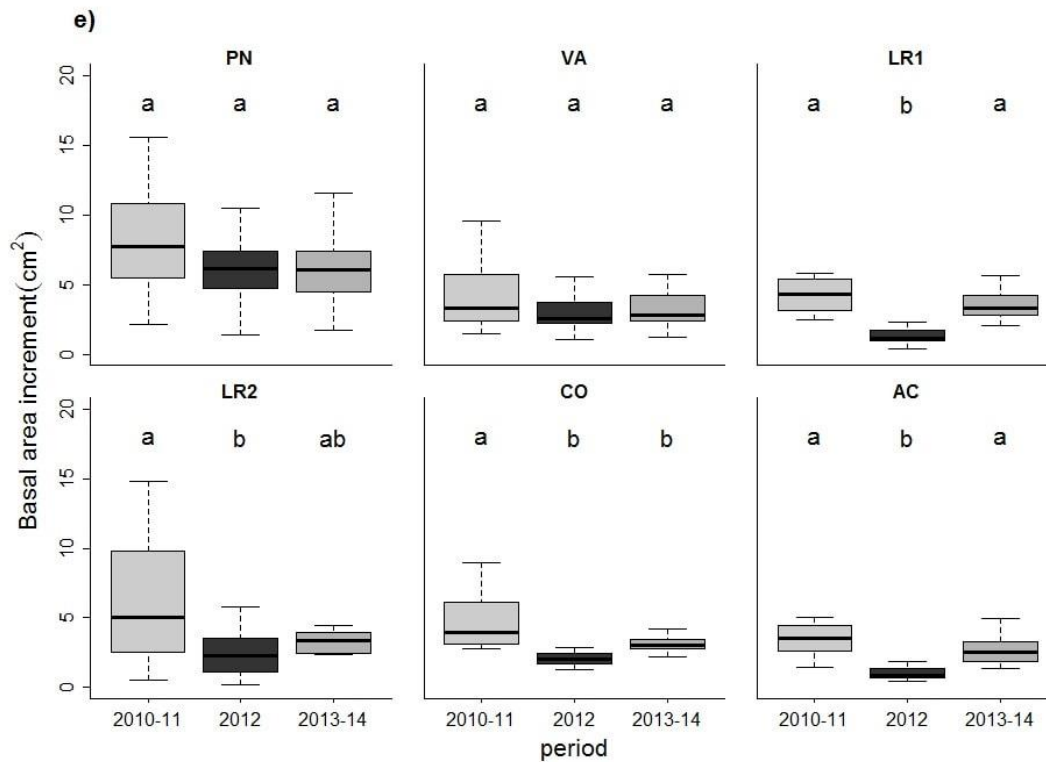


Figure S2. Basal area increment (BAI) measured during, before and after the 1967 (a), 1979 (b), 1994 (c), 2005 (d) and 2012 (e) droughts. For each site, the graph shows the average BAI in the period three years before (light grey), during (black) and three years after (grey) the drought, except for 2012, where two years before and after the drought are presented. The letters indicate significant ($P < 0.05$) differences in BAI between the three periods according to one-way ANOVAs.