

1 Impacts of recurrent dry and wet years alter long-term tree growth 2 trajectories

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22

23 *Abstract*

24

25 1. Climate extremes, such as abnormally dry and wet conditions, generate abrupt shifts in
26 tree growth, a situation which is expected to increase under predicted climate conditions.

27 Thus, it is crucial to understand factors determining short- and long-term tree
28 performance in response to higher frequency and intensity of climate extremes.

29 2. We evaluated how three successive droughts and wet years influenced short- and long -
30 term growth of six dominant Iberian tree species. Within species variation in growth
31 response to repeated dry and wet years was evaluated as a function of individual traits
32 related to resource and water use (diameter at breast height (DBH), wood density (WD)
33 and specific leaf area (SLA)) and tree-to-tree competition across climatically contrasted
34 populations. Furthermore, we assessed how short-term accumulated impacts of the
35 repeated dry and wet years influenced long-term growth performance.

36 3. All species showed strong short-term growth decreases and enhancements due to repeated
37 dry and wet years. However, patterns of accumulated growth decreases (AcGD) and
38 enhancements (AcGE) across climatically contrasting populations were species-specific.
39 Furthermore, individual trait data were weakly associated to either AcGD or AcGE and
40 the few relevant associations were found for conifers. Intraspecific variations in tree
41 growth responses to repeated climates extremes were large, and not explained by
42 intraspecific variability in SLA and WD. Accumulated impacts of repeated dry and wet
43 years were related to long-term growth trends, showing how the recurrence of climate
44 extremes can determine growth trajectories. The relationships of AcGD and AcGE with
45 long-term growth trends were more common in conifers species.

46 4. “Synthesis”. Repeated climate extremes do not only cause short-term growth reductions
47 and enhancements, but also determine long-term tree growth trajectories. This result
48 shows how repeated droughts can lead to growth decline. Conifers were more susceptible
49 to the accumulated effects of extreme weather events indicating that in the future, more

50 intense and frequent climate extremes will alter growth performance in forests dominated
51 by these species.

52

53 **Keywords:** Dendroecology, drought, forest, functional traits, growth, Iberian Peninsula,
54 wetness.

55 ***Introduction***

56 Climate models forecast an increase in the frequency and intensity of climate extremes such as
57 abnormally dry and wet years (IPCC 2014). Forest vulnerability to drought has been highlighted
58 worldwide (Allen et al., 2010), but the consequences of increasing drought frequency for forest
59 long-term growth dynamics are poorly understood. Most forest responses to drought are studied
60 at short-time interannual scales (Lloret, Keeling & Sala, 2011; Gazol, Camarero, Anderegg &
61 Vicente-Serrano, 2017), and miss the long-term perspective (e.g. decades) needed to understand
62 how forest will respond to climate change (Camarero, Gazol, Sangüesa-Barreda, Oliva & Vicente-
63 Serrano, 2015; Camarero et al., 2018; Peltier & Ogle, 2019). Extreme wet years also influence
64 growth, and their occurrence between dry years could mitigate the damage caused by droughts
65 (Jiang et al., 2019). However, the importance of wet years has received relatively little attention
66 and our ability to quantify their lasting impact is still limited. Thus, a better understanding of the
67 long-term impact on tree growth caused by repeated dry and wet years should improve our
68 capacity to predict forest vulnerability to climate projections.

69 Tree rings archive past climate influence on tree performance (Fritts, 1976) which makes radial
70 growth a good proxy to study tree responses to climate change (Marchand et al., 2019). For
71 instance, evaluation of tree-ring growth during and after extreme weather events allows us to
72 examine the stability of forest productivity and tree growth across different spatial and temporal
73 scales (Lloret et al., 2011; Gazol et al., 2017a; Cavin & Jump, 2017; Sánchez-Salguero et al.,
74 2017a, 2018; Gazol et al., 2018). Furthermore, impacts of drought on tree growth can last for
75 years, resulting in the so called “legacy effects” (Cavin, Mountford, Peterken & Jump, 2013;
76 Anderegg et al., 2015, Peltier, Fell & Ogle, 2016; Kannenberg et al., 2019; Gazol et al., 2020).
77 These legacy effects increase as drought episodes become longer and occur closer in time (Peltier
78 & Ogle, 2019). Moreover, high drought impacts on growth might lead to lower growth resilience
79 to the next drought period (Vilà-Cabrera & Jump, 2019). However, Jiang et al., (2019) suggested
80 that growth responses to extreme wet years might compensate for drought legacy effects.
81 Therefore, repeated wet periods between droughts might buffer trees from pervasive growth

82 reductions caused by drought (Matías, González-Díaz & Jump, 2014). Nevertheless, enhanced
83 growth on mesic sites or during periods of resource surplus (i.e. extreme wetness, competition
84 release) might result in a structural overshoot leading to a higher predisposition to damage during
85 periods of water scarcity (Jump et al., 2017). These potentially conflicting responses raise the
86 question of how the recurrence of dry and wet periods determines growth performance across
87 long time scales, i.e. to what extent repeated dry and wet years impact growth.

88 Tree growth response to drought varies across a species geographic range (Cavin & Jump, 2017;
89 Sánchez-Salguero et al., 2018; Vilà-Cabrera & Jump 2019; Sánchez-Salguero et al., 2017a; Gazol,
90 Rivas, Gutierrez & Camarero, 2017b). However, patterns of growth resistance to drought across
91 species biogeographical gradients are not yet clear. While some studies point to higher
92 vulnerability to drought of rear-edge (equatorward) tree populations, particularly in xeric sites
93 (Sánchez-Salguero et al., 2017b; Anderegg, Anderegg, Kerr & Trugman, 2019), others found that
94 core populations are more affected than expected (Cavin & Jump, 2017; Lloret & Kitzberger,
95 2018). One explanation to these disparate results may be that in some rear edges, microclimatic
96 refugia allow some populations to avoid droughts, promoting patchy effects across the
97 distribution range limit rather than a widespread growth decline (Vilà-Cabrera, Premoli & Jump,
98 2019; Oldfather, Kilng, Sheth, Emery & Ackerley, 2019).

99 Intraspecific responses to extreme climate events may vary based on individual characteristics
100 such as tree size, competition pressure and functional trait variability. For instance, big and/or
101 low competitive trees are prone to drought damage (Nepstad, Tohver, Ray, Moutinho & Cardinot,
102 2007). Functional traits such as wood density (WD) and specific leaf area (SLA) have been used
103 to describe plant strategies related to resource acquisition gradients (Wright et al., 2004; Chave et
104 al., 2009; Reich, 2014). These traits have been linked, although weakly, to demography (mortality
105 and growth rates) across species (Martínez-Vilalta, Mencuccini, Vayreda & Retana, 2010;
106 Greenwood et al., 2017). However, intraspecific trait variation of functional traits such as SLA
107 and WD is high for some species (Fajardo & Piper, 2011). Whether this intraspecific trait
108 variability is related tree radial growth performance during dry and wet years is unclear.

109 Here we evaluate the impact of repeated dry and wet years on tree growth and their relationship
110 with individual functional traits and competitive tree-to-tree interactions. Subsequently, we
111 explore whether such impacts determine long-term growth trends. To this end, we studied growth
112 dynamics in six tree species dominant in Iberian forests across a 26-year period. We selected
113 species growing in contrasting climatic regions, including Eurosiberian (*Pinus sylvestris* L., *Abies*
114 *alba* Mill.) and Mediterranean species (*Pinus halepensis* Mill., *Pinus nigra* Arn., *Quercus faginea*
115 Lam., and *Quercus ilex* L.). Specifically, we aim to answer the following questions: (i)- Is there
116 a geographical variation in the growth response to repeated dry and wet years? (ii)- do individual
117 functional traits and competitive interactions between neighbour trees influence growth responses
118 to repeated dry and wet years? and (iii)- do short-term growth responses to repeated dry and wet
119 years influence individual growth trends in the long-term? We hypothesize that the impacts of
120 repeated dry and wet years on growth are more prevalent on tree populations located in dry sites
121 (xeric rear edges; cf. Anderegg et al., 2019). Furthermore, we expect that drought year impacts
122 will be more prevalent in trees with strong competitive pressure (Bottero et al., 2017). We also
123 expect relationships of WD and SLA with drought resistance at intraspecific level to follow
124 patterns observed at interspecific level (Greenwood et al., 2017). Finally, we expect that the short-
125 term growth impacts of repeated dry and wet years will strongly determine growth trajectories
126 across the studied period (see Fig. 1).

127

128 ***Material and methods***

129 ***Species and study sites***

130 We studied six tree species, four gymnosperms of the *Pinaceae* family (*Abies alba* Mill., *Pinus*
131 *syvestris* L., *Pinus nigra* Arn., *Pinus halepensis* Mill.) and two angiosperms of the *Fagaceae*
132 family (*Quercus faginea* Lam. and *Quercus ilex* L.). *A. alba* is a montane or subalpine fir widely
133 distributed across Europe, and it reaches its southwestern distribution limit in the Iberian
134 Peninsula, forming abundant populations in the Pyrenees and isolated stands in the Pre-Pyrenees
135 (Supplementary Materials, Fig. S1a). *P. sylvestris*, has a Eurosiberian distribution that reaches its

136 southern distribution at the Iberian Peninsula (Supplementary Materials, Fig. S1b). *P. nigra* is a
137 pine present across the Mediterranean Basin and Central Europe (Supplementary Materials, Fig.
138 S1c). *P. halepensis* is a drought-tolerant species distributed across the Mediterranean Basin with
139 its biggest populations located in the Iberian Peninsula (Supplementary Materials, Fig. S2d). *Q.*
140 *ilex* is an evergreen oak mainly distributed across the Western Mediterranean Basin
141 (Supplementary Materials, Fig. S2f). *Q. faginea* is a deciduous Mediterranean oak present in the
142 north of Africa and the Iberian Peninsula (Supplementary Materials, Fig. S2e). In Spain, this
143 species forms abundant hybrid populations with *Quercus humilis* Mill., resulting in *Quercus x*
144 *cerrioides*, which does not have clear morphological differentiation from the parental species (See
145 Supplementary Materials). In recognition of the complex taxonomy of these oaks, we take a
146 conservative approach to sampled *Q. faginea* and refer to it here as *Q. faginea/Q. humilis*.

147 We sampled three populations across the distribution area of each species in the Iberian Peninsula
148 (Supplementary Materials, Fig. S1). We selected populations subjected to contrasting climatic
149 conditions for each species and classified them as dry, intermediate and wet sites. A precipitation
150 gradient between the dry and wet site was present for all species, albeit the range of precipitation
151 between dry and wet sites varied across species (Supplementary Materials, Fig. S2). For *Q. ilex*
152 and *Q. faginea/Q. humilis* wet and intermediate sites precipitation difference was only 35 mm;
153 however, the wet Collserola coastal site presented mild temperatures conditions (Table 1).
154 Detailed information of each sampled population can be found in Table 1. In the case of *Q. ilex*
155 and *Q. faginea/Q. humilis*, we sampled three sites where both taxa coexisted. For conifers, species
156 composition of the sampled stands ranged from coexistence with several species (both conifers
157 and deciduous) to pure stands (Supplementary Materials, Table S1).

158 At each site, we randomly selected between 21 and 31 adult, healthy and non suppressed
159 individuals and obtained increment cores, functional traits and neighbourhood measures at the
160 individual level as described below.

161 ***Individual tree level measures***

162 To characterize each individual tree, we measured structural and functional variables. For each
163 tree, we measured the four closest neighbours at each cardinal point. Diameter at Breast Height
164 (DBH), distance and species identity of each neighbour were recorded (Table 1). Then, the
165 following competition index (CI) was calculated to assess potential effects of each neighbour
166 depending on its size and distance to focal tree (Forrester, Kohnle, Albrecht & Bauhus, 2013):

$$167 \quad CI = \sum_i^n \frac{DBH_i}{Distance_{i-j}} \quad (1)$$

168 Where i is the neighbour tree and $Distance_{i-j}$ is the distance between the neighbour (i) and focal
169 tree (j).

170 Furthermore, we measured wood density (WD) and specific leaf area (SLA) for each focal
171 individual (Cornelissen et al., 2003; Supplementary Materials, Fig. S3). To quantify WD, we
172 extracted one wood sample (5 cm long) at 1.3 m using 12- and 5-mm increment borers for pine
173 and oak species, respectively. We measured wood samples fresh volume following the volume
174 replacement method. We oven dried the samples at 100 °C for 48 hours before weighting them at
175 0.01g precision. We divided the fresh volume by the dry weight what gave us WD. To quantify
176 SLA, we collected two sun-exposed branches per individual. Once in the laboratory, we separated
177 between 5 and 10 leaves per branch. We measured leaf area in a scanner (Epson Expression
178 10000XL) using the ImageJ software (Schneider, Rasband & Elicieri, 2012). Then, we oven dried
179 leaves at 100 °C for 48 hours and weighted them at 0.01g precision. Finally, we calculated SLA
180 as the fresh leaf area divided by the dry leaf weight.

181 ***Tree-ring width data***

182 We cored each focal tree at 1.3 m height using 5-mm borers. Once in the laboratory, we air dried
183 and mounted the cores on wood supports and sanded them with progressively finer grits until tree
184 rings were clearly recognisable. We performed visual cross dating and measured tree-ring width
185 at 0.01 mm resolution using a LINTAB-TSAP™ measuring device (Rinntech, Heidelberg,
186 Germany). We checked the visual cross-dating reliability using the COFECHA software (Holmes,
187 1983). Due to non-reliable cross-dating, we excluded 16 *Q. ilex* and 4 *Q. faginea/Q. humilis* trees

188 from the following analyses. Common dendrochronological statistics were calculated
 189 (Supplementary Materials, Table S2). We transformed tree-ring widths to basal area increment
 190 (BAI) to account for geometrical effects of stem enlargement on growth (Biondi & Qeadan,
 191 2008). We calculated BAI using the *bai.out* function of the *dplR* package (Bunn et al., 2018).
 192 Furthermore, we standardized BAI as follows: $BAI/\text{mean}(BAI_{\text{site}})$, where $\text{mean}(BAI_{\text{site}})$ is the
 193 mean BAI in each site. This standardization allowed us to eliminate differences in BAI level
 194 between sites.

195 We calculated relative growth decreases (RGD) for drought episodes as the inverse of the ratio of
 196 BAI during the drought year (BAI_{drought}) by the mean BAI of the four preceding years ($BAI_{\text{pre-}}$
 197 *drought*):

$$198 \quad RGD = 1/(BAI_{\text{drought}}/BAI_{\text{pre-drought}}) \quad (2)$$

199 Note, that this is the inverse of the resistance index defined by Lloret et al., (2011). Then, we
 200 computed the accumulated growth decrease (AcGD) of all the studied droughts as the sum of the
 201 RGD of each drought period:

$$202 \quad AcGD = RGD_1 + \dots + RGD_n \quad (3)$$

203
 204 AcGD quantifies the drought impact on tree growth across longer periods of time by reflecting
 205 cumulative RGD effects. Furthermore, we also calculated the relative growth enhancement (RGE)
 206 for the wet years as the ratio of BAI during the wet (BAI_{wet}) and the mean BAI values of the four
 207 years preceding the wet year ($BAI_{\text{pre-wet}}$):

$$208 \quad RGE = BAI_{\text{wet}}/BAI_{\text{pre-wet}} \quad (4)$$

209 The accumulated growth enhancement (AcGE) of the recurrent wet years was then calculated as
 210 the sum of the RGE of each wet period:

$$211 \quad AcGE = RGE_1 + \dots + RGE_n \quad (5)$$

212 RGE can be interpreted as a measure of tree capacity to grow when resources are available (in
213 this case high water availability). Both, AcGD and AcGE were calculated at individual tree level.
214 In cases when RGD or RGE for a single event were lower than 1 (i.e. no decrease/increase of
215 growth), we set the value to 0 to account for the lack of response of the tree to that event
216 (Supplementary Materials, Fig. S4). We also calculated AcGD and AcGE using different
217 reference periods (from 1 to 7 years). This was done to evaluate the influence of the reference
218 period in the calculation of RGD and RGE and thus on further results.

219 *Selection of dry and wet years*

220 To evaluate the effect of recurrent droughts on tree growth performance we focused on the period
221 from 1990 to 2016. We downloaded series of the Standardized Precipitation Evapotranspiration
222 Index (hereafter SPEI) at 1.1-km² resolution (Vicente-Serrano et al., 2017) for each studied site.
223 The SPEI reflects the cumulative drought stress experienced by vegetation as it is calculated as a
224 function of temperature and precipitation data (Vicente-Serrano, Begueria & López-Moreno,
225 2010). We selected three common droughts (1994-1995, 2005 and 2012) for all sites. To select
226 these common years, we used the following criterion: in all sites, SPEI had to be below the lower
227 30% values of the 1990-2016 period for at least one of both, September 6-month scale or
228 September 12-month scale. To select wet years, we used the following criterion: in all sites SPEI
229 had to be above the higher 30% values of 1990-2016 period for at least one of both, September 6
230 or September 12-month resolution. The years 1997, 2008 and 2013 were selected as wet years.
231 More detailed information on methods for selection of dry and wet years can be found in
232 Supplementary Materials.

233

234 *Statistical analyses*

235 To evaluate the effects of recurrent dry and wet years on tree growth performance during the
236 1990-2016 period we used the following analyses. First, to evaluate tree structural and functional
237 characteristics and site effects on growth response to repeated dry and wet years we fitted a set of

238 species-specific generalized linear models. For each species, AcGD and AcGE were modelled as
239 function of site, DBH, CI, SLA and WD (all variables were log transformed prior to the analyses)
240 using the following formulae:

$$241 \quad AcGD = \beta_0 + \beta_1 * site + \beta_2 * \log(DBH) + \beta_3 * \log(CI) + \beta_4 * \log(SLA) + \beta_5 * \log(WD) + \varepsilon \quad (6)$$

$$242 \quad AcGE = \beta_0 + \beta_1 * site + \beta_2 * \log(DBH) + \beta_3 * \log(CI) + \beta_4 * \log(SLA) + \beta_5 * \log(WD) + \varepsilon \quad (7)$$

243 Where β_0 represents the overall intercept and β_1 to β_5 the parameters adjusting each predictor
244 variable and ε the error term.

245 Then, to evaluate the effect of recurrent dry and wet years on growth performance across longer
246 period we used linear mixed-effect models. Log-transformed BAI for the 1990-2016 was
247 modelled as a function of calendar year, AcGD, AcGE (as proxies of cumulative dry and wet year
248 impact) and the interaction of calendar year with AcGD and AcGE.

$$249 \quad \log(BAI_i) = \beta_0 + \alpha_{0i} + \beta_1 * Year_i + \beta_2 * AcGD_i + \beta_3 * AcGE_i + \beta_4 * (Year_i * AcGD_i) + \beta_5 * (Year_i * \\ 250 \quad \quad \quad AcGE_i) + \varepsilon_i \quad (8)$$

251 Where i represents individual tree identity, β_0 the overall intercept and β_1 to β_5 the parameters
252 adjusting fixed effects, α_0 the random effects on the intercept associated with tree. An error term ε_i
253 with a first-order temporal autocorrelation [AR(1)] was also included in the model. Log
254 transformation was applied to standardized BAI to achieve a normal distribution. The inclusion
255 of the factor “Year” allows to determine growth trajectories across the studied period. The
256 inclusion of AcGD and AcGE was used to detect the cumulative effects of recurrent dry and wet
257 years on tree growth trajectories (interaction Year * AcGD/AcGE). We applied this model to each
258 species (6 species) and at population level (18 models, one per species and site). Mixed models
259 were fitted using the package *nlme* (Pinheiro et al., 2019). Finally, the marginal R^2 (R^2_m , variance
260 explained by fixed effects) and conditional R^2 (R^2_c , variance explained by fixed and random
261 effects) were calculated following Nakagawa et al., (2017). Furthermore, we evaluated the fit of
262 the models by graphical inspection of the residuals and the fitted values. We performed all
263 analyses in R environment (R Project Team, 2018).

264 All models presented here use a reference period of 4 years to calculate AcGD and AcGE, results
265 using other reference period (from 1 to 7 years) are presented in the Supplementary Materials,
266 Figs. S5 and S6. To perform the abovementioned analyses some trees had to be discarded due to
267 their young age (5 *Q. ilex*; 7 *Q. faginea/Q. humilis*; 13 *P.halpensis*; 3 *P. nigra*; 13 *P. sylvestris* and
268 9 *A. alba*) which left us with a total sample of 468 trees (71 *Q. ilex*, 79 *Q. faginea/Q. humilis*, 77
269 *P. halpensis*, 87 *P. nigra*, 77 *P. sylvestris* and 77 *A. alba*).

270

271 **Results**

272 **Growth impacts**

273 Accumulated growth decreases (AcGD) and enhancements (AcGE) due to recurrent dry and wet
274 years, occurred for all tree species (Fig. 2). Site differences in AcGD and AcGE were evident in
275 all species except AcGE in *P. nigra* (Table 2, Fig. 2). However, AcGD/AcGE differences across
276 populations with contrasting climate conditions were species-specific (Fig. 2). The impact of
277 recurrent dry years on growth was higher in dry populations of *P. sylvestris* and *P. halepensis*,
278 the intermediate population of *P. nigra*, the wet population of *Q. ilex*, both dry and wet
279 populations of *Q. faginea/Q. humilis*, and intermediate population of *A. alba* (Fig. 2). The impact
280 of recurrent wet years on growth was also species specific. For example, *Q. ilex* presented the
281 higher growth enhancement in intermediate sites (Fig. 2) whilst this was observed for *P. sylvestris*,
282 *Q. faginea/Q. humilis* and *A. alba* on the dry site and *P. halepensis* at both dry and intermediate
283 sites (Fig. 2).

284 The influence of functional traits and competition on AcGD and AcGE was weak and
285 species-specific (Table 2). Conifer species were affected by structural and functional variables
286 (Table 2.). AcGD of *P. nigra* was higher in big trees suffering high competition (Table 2). AcGE
287 of *A. alba* was negatively related to CI and DBH (Table 2). AcGE of *P. sylvestris* and *A. alba* was
288 higher in trees with low SLA. AcGD of *A. alba* was higher in trees with high SLA.

289

290 ***AcGD, AcGE and growth trends***

291 Successive dry and wet years determined growth trends across the study period (Fig. 3a, b). In all
292 species but *Q. ilex*, trees suffering higher cumulative drought impact (i.e. higher AcGD) showed
293 more negative growth trends (negative significant interaction year * AcGD, Table 3, Fig. 3a). In
294 all species, trees that grew more during wet years presented the most positive growth trends
295 (positive significant interaction year * AcGE, Table 3, Fig. 3b). For *P. halepensis* and *P.*
296 *sylvestris*, the AcGD-growth trend relationship was influenced by the dry population showing
297 extreme growth reductions (Fig. 2) while, for the other species, populations with higher AcGD
298 did not present the more negative growth trends (Fig. 2).

299 Differences in AcGD and AcGE also resulted in different growth trends at the within-
300 population (Table 3, Fig. 4). Recurrent dry years resulted in negative growth trends (significant
301 negative year * AcGD interaction; Table 3, Fig 4) in all conifer populations except at the dry site
302 of *P. sylvestris* (Table 3, Fig. 4). The effect of successive wet years on growth trends was present
303 (significant year * AcGE interaction; Table 3) in two or more populations of all species (Table 3,
304 Fig. 4).

305

306 ***Discussion***

307 Our results show how successive extreme dry and wet conditions strongly influence tree growth.
308 Widespread accumulated growth decreases (AcGD) and enhancements (AcGE) after three
309 successive dry and wet years were present for all species. These AcGD and AcGE were related
310 to long term growth trajectories (Fig. 1). As a consequence, the three drought and wet years
311 studied determined the trajectory of tree performance throughout the 1990-2016 period. This
312 pattern was more prevalent for conifers, although with variation between and within populations
313 (Fig. 2, 3 and 4).

314 ***Geographical variation of AcGD and AcGE***

315 Geographical variation in growth responses to extreme weather events depends on several factors,
316 which result in species-specific responses across the studied climatic and biogeographic gradients.
317 First, topographical complexity generates microclimatic conditions that can decouple tree
318 response and macroclimatic weather events (Adams, Barnard & Loomis, 2014). Non-climatic
319 environmental conditions (e.g. soil texture and nutrients) may exacerbate this disparity between
320 macroclimatic conditions and growth response to dry and wet years (Lévesque, Walthert &
321 Weber, 2016). For instance, here we only found two species, *P. sylvestris* and *P. halepensis* that
322 presented higher AcGD on the dry sites (Fig. 2). Besides, differences in biotic conditions and
323 species-specific traits can result in different performance across species growing under the same
324 regional climate conditions (Battipaglia, Saurer, Cherubini, Siegwolf & Cortufo, 2009; Friedrichs
325 et al., 2009). For example, different growth phenology may result in contrasted responses during
326 dry and wet years. In this sense, *Q. ilex* and *Q. faginea/Q. humilis* coexist in the same sites but
327 showed different responses to repeated dry years in the dry site and to repeated wet years in all
328 sites (Fig. 2). *Q. ilex* is able to grow in early-summer and fall, whereas most of the *Q.*
329 *faginea/Q.humilis* radial growth occurs in spring and summer (Montserrat-Martí et al., 2009)
330 suggesting higher drought vulnerability to summer water shortage in the latter. Furthermore,
331 different strategies related to water use result in different responses to drought under the same
332 conditions (Anderegg & HilleRisLambers, 2016). In this study, *P. halepensis* populations which
333 were sampled in the same or nearby *Q. ilex* and *Q. faginea/Q. humilis* sites presented different
334 responses to repeated dry and wet years which could be explained by differences in water use
335 (Fig. 2). Therefore, site, population and even tree specific characteristics (i.e, population density,
336 age, community compositions...) can be related to different response to dry and wet years,
337 exacerbating or mitigating predictions solely made by macroclimatic conditions. Furthermore,
338 precipitation variability between dry and wet sites differed across tree species, which may
339 contribute to the lack of common geographical pattern of AcGD/AcGE across species. This
340 suggests that wider gradients across the species distribution range should be used.

341

342 ***Effects of structural and functional characteristics on AcGD and AcGE***

343 Empirical evidence indicates that the occurrence of drought years strongly reduces radial growth
344 (Zang, Hartl-Meier, Dittmar, Rothe & Menzel, 2014; Martínez-Vilalta, López, Loepfe & Lloret,
345 2012; Gazol et al., 2017a; Cavin & Jump, 2017; Serra-Maluquer, Mencuccini & Martínez-Vilalta,
346 2018; Kannenberg et al., 2019). However, which individual traits and stand-level abiotic and
347 biotic factors are related to these growth reductions is less clear (Kannenberg, Schwalm &
348 Anderegg 2020). We found weak, species-specific relationships between functional traits (SLA)
349 and competition intensity and/or tree dominance (competition index and tree size) with AcGD
350 and AcGE of successive dry and wet years. Our expectations based on tree size and competition
351 (higher response to water scarcity in bigger trees and higher growth reductions but lower
352 enhancements under highly competitive pressure) were only found on AcGD for *P. nigra* and
353 AcGE for *A. alba* (Table 2). High resource acquisitive strategies (high SLA, low WD) were only
354 related to AcGD and AcGE in two species (*P. sylvestris* and *A. alba*). However, only the patterns
355 observed for *A. alba* supported the idea that more resource acquisitive strategy (high SLA) would
356 lead to higher drought damage (Table 2, Greenwood et al., 2017). Recent studies suggest that
357 functional traits have low potential to predict variability in resource use strategy at the within-
358 species scale (Anderegg et al., 2018; Rosas et al., 2019). For instance, Fajardo (2016, 2019) found
359 no relationship between WD and growth rates or competition ability in *Nothofagus pumilio*. Our
360 results agree with these studies, and indicate that variability of WD and SLA are poorly related
361 to growth responses to extreme events at the intraspecific level, although they can determine to
362 some degree growth seasonality (Camarero, 2019). It is also possible that the absence of
363 relationships between CI, tree size and the measured functional traits with AcGD and AcGE are
364 due to differences in the temporal resolution of the data. We evaluate present information (CI and
365 traits) and changes in this data through the study period (i.e. differences in stand structure) may
366 influence lack of patterns in our results. Furthermore, hydraulic traits may be more informative
367 than WD or SLA, however, such data is difficult to obtain in a sample size as ours, but further
368 research is needed in this direction (Hartmann et al., 2018).

369 When within-species results are compared across species, the relationships of AcGD and AcGE
370 with structural and functional variables are only present in gymnosperms (Table 2). Hence, our
371 expectations of the relationships between growth responses to extreme events and structural and
372 functional characteristics were only present in conifers. In the Iberian Peninsula variability in tree
373 growth response to drought (Gazol et al., 2018), growth responses to climate and competition
374 (Gómez-Aparicio, García-Valdés, Ruiz-Benito & Zavala, 2011) and functional traits (Poorter,
375 Lianes, Moreno de las Heras & Zavala, 2012; Carnicer, Barbeta, Sperlich, Coll, & Peñuelas, 2013;
376 Vilà-Cabrera, Martínez-Vilalta & Retana, 2015) reflect differences between *Pinaceae* and
377 *Fagaceae* species, mainly pine and oaks. As a result, differences in the incidence of structural and
378 functional variables on growth response to extreme events between these groups was expectable.

379 ***Relationships between AcGD, AcGE and growth trends***

380 Extreme weather impacts on tree growth can last for several years causing legacies (Anderegg et
381 al., 2015, Jiang et al., 2019), and if they occur several times, their effects might accumulate
382 affecting long-term tree performance. For instance, Peltier & Ogle (2019) showed how successive
383 droughts resulted in larger legacy effects on tree-ring growth of *Pinus ponderosa* than a single
384 drought. Our results agree with this previous evidence, i.e. accumulated growth reductions of
385 successive droughts resulted in negative long-term growth trends (Figs. 3 and 4). The fact that
386 successive droughts ended up reducing the growth trends of populations with overall positive,
387 negative, and neutral growth (Figs. 2 and 4) indicates that recurrent drought impacts affect tree
388 performance independently of the mean population growth trends. This finding suggests
389 widespread vulnerability to growth decline, which has been identified as an indicator of reduced
390 health and increased probability of tree death (Camarero et al., 2015; Cailleret et al., 2017).
391 Furthermore, the accumulated effects of repeated droughts could also generate a decrease in
392 growth resistance across time, a pattern already seen in some pine species in the studied area
393 (Serra-Maluquer et al., 2018, Gazol et al., 2018). Moreover, repeated wet years may result in
394 positive or stable growth trends (Figs. 2 and 3), which in fact could potentially reverse negative
395 trends caused by repeated dry years (Jiang et al., 2019). However, caution must be taken as growth

396 enhancement due to water surplus may be overestimated due to competition releases after
397 drought-induced tree death, a process observed in the study area (Galiano, Martínez-Vilalta &
398 Lloret ,2010; Camarero et al., 2015). Finally, the effects of repeated dry and wet years on growth
399 trends were predominant in conifers, which is in accordance with studies reporting higher legacy
400 effects in these species compared to angiosperms (e.g. oaks) after both dry and wet years
401 (Anderegg et al., 2015; Jiang et al., 2019).

402 Low growth rates and declining growth trends are observed in dead individuals when comparing
403 them to living conspecifics in the same populations (Hereş et al., 2012, Camarero et al., 2015,
404 Cailleret et al., 2017). Recently, De Soto et al., (2020) reported that dead trees presented lower
405 resilience (short-term impact) to past drought events than their surviving neighbours. Here we
406 show that these two growth responses potentially leading to tree death, i.e. short-term growth
407 reductions and long-term negative growth trends, are related and that the accumulation of
408 successive droughts impacts may increase the declining growth trends.

409 Climate projections indicate that the frequency and intensity of extreme climate events will
410 increase. These will cause higher impacts on tree growth and as a consequence determine their
411 future growth trajectories. If the frequency and severity of extreme drought events increase, their
412 accumulated impacts will be higher, which will lead to increasingly widespread growth decline,
413 dieback and, potentially, tree death. The intraspecific growth and trait variability presented here
414 suggests that, to accurately predict when and where the effects of successive extremes climate
415 events will be more pervasive, better knowledge on which site and individual characteristics
416 prevent drought vulnerability is needed.

417

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431

432 ***Author's contribution***

433 XSM, EG, JJC and AG designed the study. XSM, EG, JJC, AG, RSS, GSB and JBI collected and
434 processed the data. XSM, AVC & ASJ analysed and interpreted the data. XSM lead the writing
435 of the manuscript with significant contributions of all authors.

436 ***Data availability***

437 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dfn2z350f>
438 (Serra-Maluquer et al., 2020)

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668 **Tables**

669 **Table 1.** Description of the sampled sites. Coordinates, altitude, mean annual temperature (MAT),
670 mean maximum (MAT_{max}) and minimum (MAT_{min}) temperatures, and mean annual
671 precipitation (MAP) are given. Temperature and precipitation data were extracted from the
672 Climatic Atlas of the Iberian Peninsula (Ninyerola, Pons & Roure 2005). Position in the sampled
673 climatic gradient is indicated by the site type variable as WET, INT (intermediate) and DRY.
674 Name of the sampled localities are given as sites. Tree data variables are presented as means ±
675 SE (standard error).

676 **Table 2.** Results of the generalized linear models evaluating intraspecific effects of site, diameter
677 at breast height (DBH), competition Index (CI), Specific leaf area (SLA) and wood density (WD)
678 on accumulated growth decreases (AcGD) and accumulated growth enhancements (AcGE)
679 caused by recurrent dry and wet years, respectively. One model per species is presented. For site,
680 results of post-hoc analyses between the different sites are reported, + means that at least two
681 sampled sites differ in values of AcGE or AcGD. For continuous variables, variable estimates are
682 reported once effects are significant ($p < 0.05$). ns indicates non-significant effect. Significance
683 levels: *, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$. + indicate differences among site levels.

684 **Table 3.** Mixed models of intraspecific (All) and intra-population (Dry, Int, Wet) effects of
685 accumulated growth decreases (AcGD) and enhancements (AcGE), year and year*AcGD/AcGE
686 interaction on log-transformed basal area increment (BAI). Estimates are given for significant or
687 marginally significant variables. Marginal (R^2_m) and conditional R^2 (R^2_c) values for each model
688 are also given. Significant levels: +, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

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Species	Site	Site type	Coordinates	Altitude (m a.s.l.)	MAT (C°) (MATmin-MATmax)	MAP (mm)	Mean ± SE DBH (cm)	Mean ± SE neighbour DBH (cm)	Mean ± SE neighbour distance (m)
<i>Quercus ilex</i>									
	Alcubierre	DRY	41° 48' 17'' N 0° 30' 37'' W	635	13 (6-19)	405	15.4 ± 1	15.5 ± 0.5	5.3 ± 0.2
	Sansoain	INT	42° 33' 15'' N 1° 35' 22'' W	742	11 (6-17)	657	14.3 ± 0.8	13.5 ± 0.6	3.1 ± 0.2
	Collserola	WET	41° 25' 34'' N 2° 4' 17'' E	300	15 (10-19)	692	18 ± 0.9	18.9 ± 0.8	4.8 ± 0.2
<i>Quercus faginea/humilis</i>									
	Alcubierre	DRY	41° 48' 17'' N 0° 30' 37'' W	635	13.0 (6-19)	405	18.5 ± 1.2	15.4 ± 0.5	4.6 ± 0.2
	Sansoain	INT	42° 33' 15'' N 1° 35' 22'' W	742	11 (6-17)	657	16.5 ± 0.9	13.2 ± 0.5	3.9 ± 0.2
	Collserola	WET	41° 25' 34'' N 2° 4' 17'' E	300	15 (10-19)	692	18.5 ± 1.2	19.3 ± 0.8	4.7 ± 0.1
<i>Pinus halepensis</i>									
	Peñaflor	DRY	41° 47' 11'' N 0° 43' 21'' W	284	14 (8-21)	403	33.9 ± 1.5	13.3 ± 0.9	5.4 ± 0.2
	Carcastillo	INT	42° 21' 26'' N 1° 26' 51'' W	374	13 (7-19)	480	35.7 ± 1.1	32 ± 1.2	6.4 ± 0.2
	Collserola	WET	41° 25' 34'' N 2° 4' 17'' E	300	15 (10-19)	692	34.8 ± 1.5	18.6 ± 0.9	4.2 ± 0.2
<i>Pinus nigra</i>									
	Sierra María	DRY	37° 40' 52'' N 2° 13' 19'' W	1421	12 (5-18)	446	25.3 ± 1.1	15 ± 0.7	5.2 ± 0.3
	Corbalán	INT	40° 25' 06'' N 0° 59' 13'' W	1400	11 (5-17)	483	22.15 ± 1.1	16 ± 0.7	3.1 ± 0.1
	Villalangua	WET	42° 25' 06'' N 0° 48' 18'' W	700	12 (6-18)	806	28.4 ± 1.9	20.3 ± 0.8	5.2 ± 0.2
<i>Pinus sylvestris</i>									
	Corbalán	DRY	40° 25' 06'' N 0° 59' 13'' W	1202	11 (5-17)	483	26.2 ± 1.5	22 ± 0.9	3 ± 0.1
	Pico del Águila	INT	42° 18' 19'' N 0° 24' 18'' W	1434	9 (3-15)	811	34.2 ± 2.8	33.7 ± 1.6	6.8 ± 0.3
	Las Eras	WET	42° 52' 42'' N 0° 48' 17'' W	1299	8 (2-14)	1527	39.7 ± 3.6	33.4 ± 1.6	5.5 ± 0.3
<i>Abies alba</i>									
	La Betosa	DRY	42° 18' 02'' N 0° 11' 56'' W	1399	8 (1-14)	1022	32.9 ± 3.1	23.9 ± 1.1	5.3 ± 0.2
	Paco Ezpela	INT	42° 45' 05'' N 0° 50' 33'' W	1152	9 (3-15)	1240	30.8 ± 2.1	23.9 ± 1	3.3 ± 0.1
	Las Eras	WET	42° 52' 42'' N 0° 48' 17'' W	1299	8 (2-14)	1527	32.7 ± 2.8	28.6 ± 0.9	3.9 ± 0.1

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Table 2.

Species	Variable	Site	DBH	CI	SLA	WD
<i>Quercus ilex</i>	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	ns	ns
<i>Quercus faginea/humilis</i>	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	ns	ns
<i>Pinus halepensis</i>	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	ns	ns
<i>Pinus nigra</i>	AcGD	+	0.27*	0.22**	ns	ns
	AcGE	ns	ns	ns	ns	ns
<i>Pinus sylvestris</i>	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	-1.56*	ns
<i>Abies alba</i>	AcGD	+	ns	ns	1.52*	ns
	AcGE	+	-0.56*	-0.46*	-2.57***	ns

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Species	Site	Year	AcGD	AcGE	Year*AcGD	Year * AcGE	R ² m	R ² c
<i>Quercus ilex</i>	All	-0.010*		-16.06***		0.008***	0.03	0.41
	Dry	-					0.009	0.48
	Int			-18.833***		0.009***	0.10	0.47
	Wet		7.655*	-14.003**	-0.003**	0.006**	0.06	0.38
<i>Quercus faginea/humilis</i>	All	0.010**	3.086*	-3.151*	-0.002*	0.002*	0.03	0.64
	Dry		9.839*	-8.364*	-0.005*	0.004**	0.05	0.74
	Int	-0.013+		-18.284**	-	0.009**	0.05	0.70
	Wet	-					0.16	0.54
<i>Pinus halepensis</i>	All	0.028***	17.500***	-9.050***	-0.009***	0.005***	0.09	0.52
	Dry	-0.064***	11.397***	-35.537***	-0.006***	0.018***	0.25	0.59
	Int		14.060***	-16.830***	-0.007***	0.008***	0.04	0.48
	Wet	0.026**	12.179**	-9.363*	-0.006***	0.005**	0.02	0.58
<i>Pinus nigra</i>	All	-0.040***	6.612***	-25.558***	-0.003***	0.013***	0.11	0.57
	Dry	-0.039**	16.635***	-36.768***	-0.008***	0.019***	0.38	0.65
	Int		5.046**	-11.849*	-0.003**	0.006*	0.07	0.47
	Wet		23.692***	-15.310***	-0.012***	0.008***	0.14	0.77
<i>Pinus sylvestris</i>	All	-0.026***	5.274***	-21.040***	-0.003***	0.011***	0.08	0.60
	Dry	-0.025*					0.12	0.54
	Int		14.633***	-15.337***	-0.007***	0.008***	0.03	0.66
	Wet	-0.073***	16.226***	-70.961***	-0.008***	0.036***	0.41	0.81
<i>Abies alba</i>	All		21.045***	-33.614***	-0.011***	0.017***	0.12	0.79
	Dry	0.009*	30.595***	-31.928***	-0.015***	0.016***	0.24	0.92
	Int		10.197+	-34.479***	-0.005+	0.017***	0.13	0.69
	Wet	0.016*	31.043**	-24.798***	-0.016***	0.012***	0.16	0.82

718 **Figure 1.** Theoretical effects of consecutive dry and wet years on radial growth trends. Two
719 successive dry and wet years (vertical red and blue rectangles, respectively) cause low and high
720 growth (red and blue arrows respectively). The magnitude of these low and high growth years
721 (AcGD, accumulated growth decreases; AcGE, and accumulated growth enhancements) could
722 end up determining the overall tree performance within a specific period (i. e. different growth
723 trends, represented by grey dashed lines).

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725 **Figure 2.** Growth trajectories represented as linear regressions of log-transformed Standardized
726 Basal Area Increment (BAI) against calendar year (from 1990 to 2016) for each studied tree
727 population. Boxplots of accumulated growth decreases (AcGD) and accumulated growth
728 enhancements (AcGE) are shown for each population. Colour defines population classification
729 being red, dry populations (DRY), green, intermediate populations (INT), and blue, wet
730 populations (WET). In the boxplots, different letters indicate significant ($p < 0.05$) differences in
731 AcGD or AcGE between populations following post hoc tests of the generalized linear models
732 (Table 2.)

733

734 **Figure 3.** Changes in growth trends during 1990-2016 period depending on (a) accumulated
735 growth decrease (AcGD) and (b) accumulated growth enhancement (AcGE) at intraspecific level.
736 Individual trees irrespective of their population are classified in three categories depending on the
737 intensity of AcGD or AcGE: L, low AcGD and AcGE = 1 – 32%, I, intermediate AcGD and
738 AcGE = 33 - 65%; H, high AcGD and AcGE = 66-100%. Significance levels (p) from the
739 interaction term of Year * AcGD/AcGE in the intraspecific models are given (Table 3). ns = non-
740 significant.

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742 **Figure 4.** Changes in growth trends during 1990-2016 period depending on (a) accumulated
743 growth decrease (AcGD) (b) accumulated growth enhancement (AcGE) at intra-population level.
744 Individual trees within populations are classified in three categories depending on the intensity of
745 AcGD or AcGE: L, low AcGD and AcGE = 1 – 32%, I, intermediate AcGD and AcGE = 33 -

746 65%; H, high AcGD and AcGE = 66-100%. Significance (*p*) levels from the interaction term of
747 Year * AcGD/AcGE in the intra-population models are given (Table 3). ns = non-significant.
748 Colour defines population classification being red, dry populations (DRY), green, intermediate
749 populations (INT), and blue, wet populations (WET).

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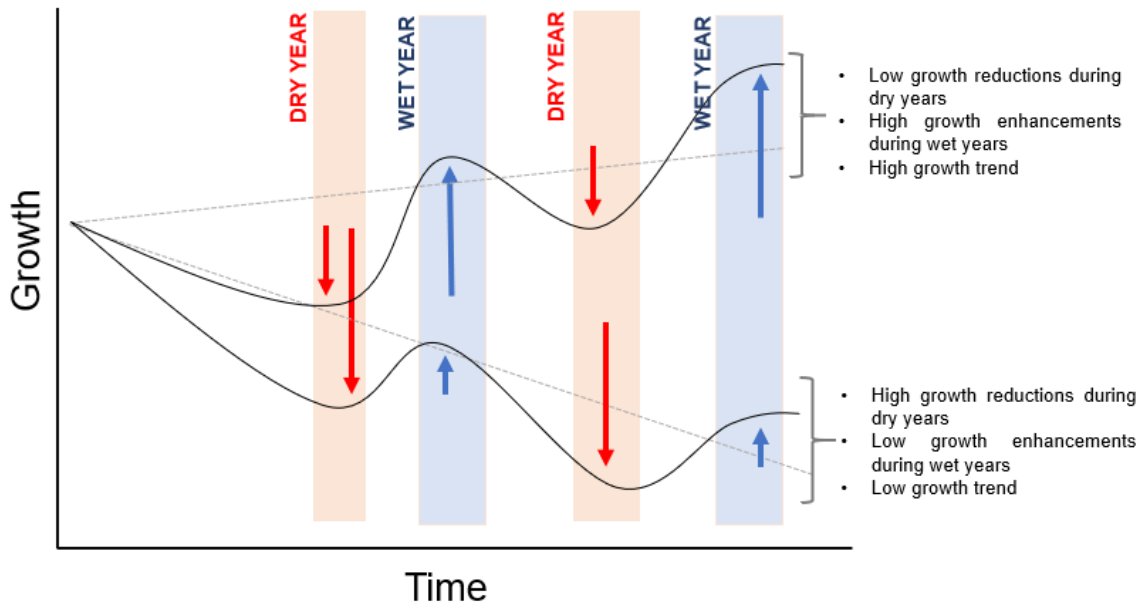
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780 **Figure 1**

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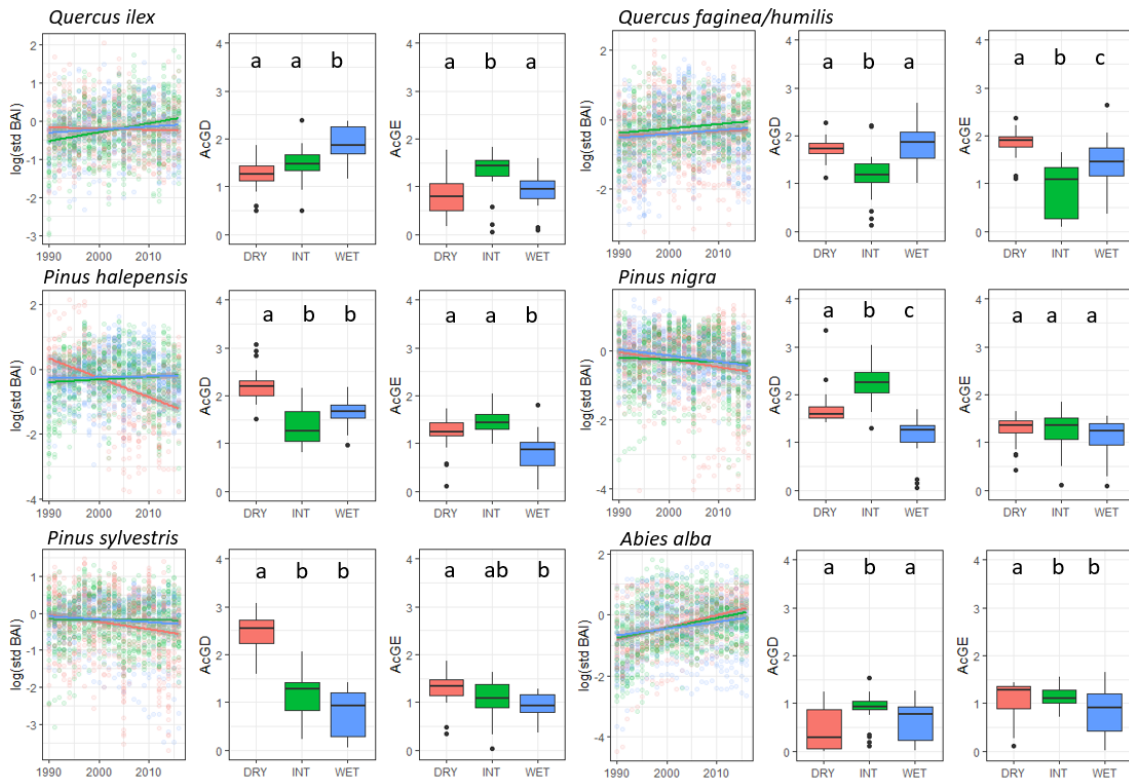
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786 **Figure 2**



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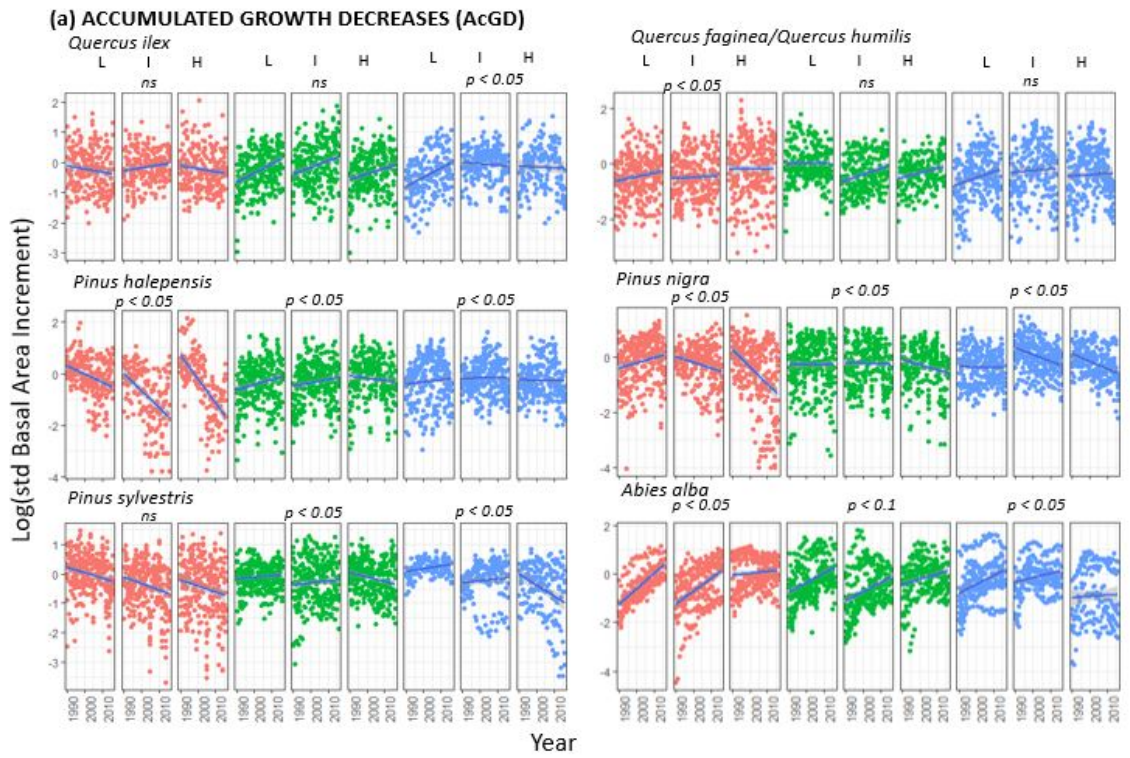
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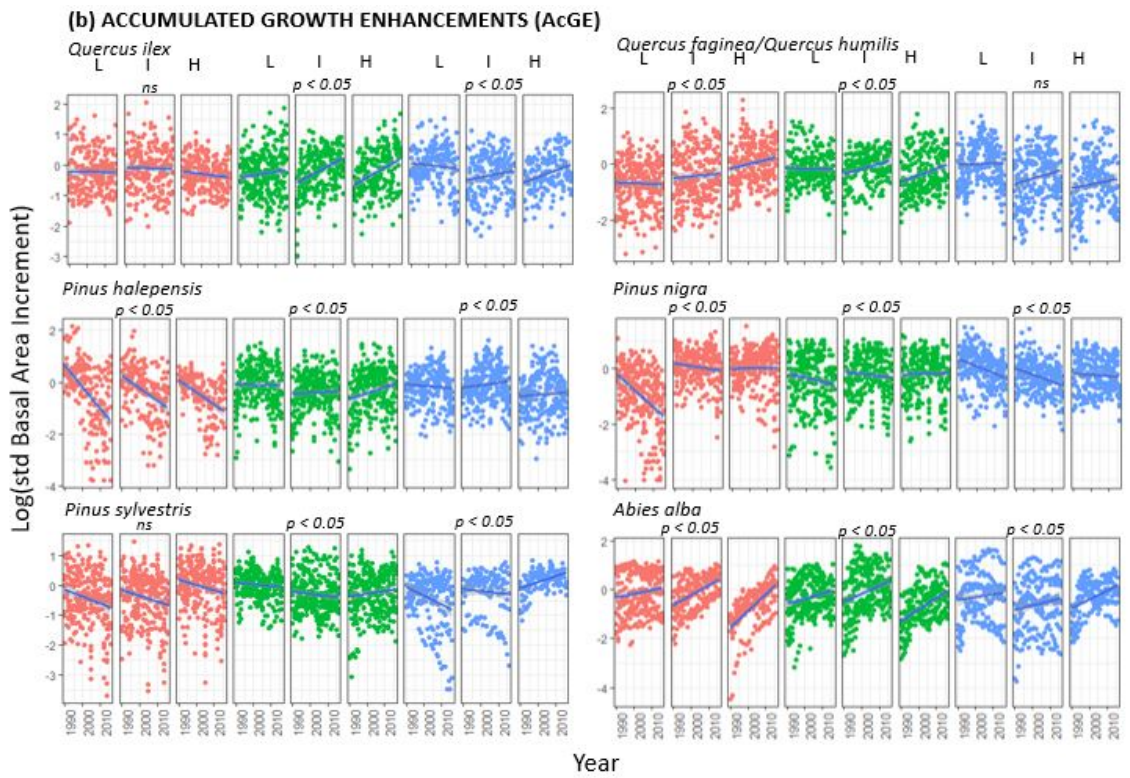
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Figure 4

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