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2 **depend on pre-drought growth conditions**

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4 **Running title:** Growth predisposition modifies drought impact

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50 Abstract

51 Global climate change is expected to further raise the frequency and severity of
52 extreme events, such as droughts. The effects of extreme droughts on trees are difficult to
53 disentangle given the inherent complexity of drought events (frequency, severity, duration
54 and timing during the growing season). Besides, drought effects might be modulated by trees'
55 phenotypic variability, which is, in turn, affected by long-term local selective pressures and
56 management legacies. Here, we investigated the magnitude and the temporal changes of tree-
57 level resilience (i.e., resistance, recovery, and resilience) to extreme droughts. Moreover, we
58 assessed the tree-, site-, and drought-related factors and their interactions driving the tree-
59 level resilience to extreme droughts. We used a tree-ring network of the widely distributed
60 Scots pine (*Pinus sylvestris*) along a 2800 km latitudinal gradient from southern Spain to
61 northern Germany. We found that the resilience to extreme drought decreased in mid-
62 elevation and low productivity sites from 1980-1999 to 2000-2011 likely due to more
63 frequent and severe droughts in the later period. Our study showed that the impact of drought
64 on tree-level resilience was not dependent on its latitudinal location, but rather on the type of
65 sites trees were growing at and on their growth performances (i.e., magnitude and variability
66 of growth) during the pre-drought period. We found significant interactive effects between
67 drought duration and tree growth prior to drought, suggesting that Scots pine trees with
68 higher magnitude and variability of growth in the long term are more vulnerable to long and
69 severe droughts. Moreover, our results indicate that Scots pine trees that experienced more
70 frequent droughts over the long-term were less resistant to extreme droughts. We therefore
71 conclude that the physiological resilience to extreme droughts might be constrained by their
72 growth prior to drought, and that more frequent and longer drought periods may overstrain
73 their potential for acclimation.

74 **Keywords:** Acclimation; latitudinal gradient; *Pinus sylvestris*; predisposition; tree rings

75 **Introduction**

76 Climate change effects are broadly characterized by elevated temperature, changed
77 precipitation regimes, and increased inter-annual variability, often resulting in more frequent
78 and intense climate extremes such as severe droughts (Dai, 2012; Spinoni *et al.*, 2018). The
79 increased frequency and severity of droughts can significantly impact tree growth by
80 reducing their photosynthetic activity (Flexas & Medrano, 2002; Reddy *et al.*, 2004) and
81 altering their cambial activity (Gruber *et al.*, 2010). In addition, severe drought events have
82 been associated to forest decline either through direct abiotic effects leading to hydraulic
83 failure and/or carbon starvation (Adams *et al.*, 2017; Choat *et al.*, 2018; McDowell *et al.*,
84 2008) or mediated by biotic factors, such as insects (Rouault *et al.*, 2006), fungi (Giordano *et*
85 *al.*, 2009), and mistletoes (Rigling *et al.*, 2010). These effects may ultimately induce shifts in
86 forest composition (Buras & Menzel, 2019; Walther *et al.*, 2002) and reduction in forest
87 productivity (Ciais *et al.*, 2005).

88 Growing recognition of the impacts of extreme droughts on forest ecosystems has
89 spurred on a number of long-term experiments and observational studies (e.g., Breshears *et*
90 *al.*, 2005; Jentsch *et al.*, 2011; Seidel *et al.*, 2019). The results of these studies revealed a
91 large variability in pattern and magnitude of responses to extreme droughts (McDowell *et al.*,
92 2008; Smith, 2011), because phenotypic acclimation to such extreme events may depend on a
93 multitude of factors and their interactions, including drought characteristics (Anderegg *et al.*,
94 2015; Gazol *et al.*, 2018), drought history of the growing environment (Vicente-Serrano *et*
95 *al.*, 2013), species-specific functional traits and life-history strategies (Anderegg *et al.*, 2016;
96 Greenwood *et al.*, 2017; Lévesque *et al.*, 2013), provenance (Sánchez-Salguero *et al.*, 2018;
97 Seidel *et al.*, 2016), tree size and age (Granda *et al.*, 2018; Magnani *et al.*, 2000; Serra-
98 Maluquer *et al.*, 2018), tree-to-tree competition (Linares *et al.*, 2010), nutrient imbalances

99 (Hevia *et al.*, 2019), nutrient availability (Gessler *et al.*, 2017), species composition and
100 stocking of the forest stand (Bottero *et al.*, 2017; Forrester *et al.*, 2016; Grossiord *et al.*,
101 2014), trees neighbourhood composition (Grossiord, 2019), micro-climatic conditions related
102 to forest edge and interior (Buras *et al.*, 2018), and growth trends prior to drought (Zang *et al.*,
103 2014). On the longer term, acclimation is often complemented by evolutionary genotypic
104 adaptation (Bose *et al.*, 2020; Hamrick, 2004; Sánchez-Salguero *et al.*, 2018) leading to
105 differentiation of populations and ecotypes with varying adaptive capacities to drought, often
106 observed for marginal populations at dry species range margins (Bolte *et al.*, 2016; Hampe &
107 Petit, 2005).

108 Moreover, the effects of past drought and growing conditions (legacy effects), can
109 remain for several years and modify the tree growth and physiological responses to the
110 current drought (Anderegg *et al.*, 2015; Kannenberg *et al.*, 2019; Seidel *et al.*, 2019). An
111 important question in the debate on drought and acclimation is whether individuals will be
112 able to acclimate fast enough to cope with increased frequency and severity of droughts (Dai,
113 2012; Szejner *et al.*, 2019). It is therefore important to understand how tree growth responses
114 to extreme droughts vary across sites with different productivity (Valladares *et al.*, 2007;
115 Valladares *et al.*, 2014), since site productivity can modify trees phenotypic strategies such as
116 tree height, root to shoot ratio, and crown development for efficient conservation and
117 utilization of water (Vanninen & Mäkelä, 2005). For example, tree height which is commonly
118 used as an indicator of site productivity (e.g., Westoby *et al.*, 2002) was reported to be the
119 strongest predictor of tree mortality in southwestern USA where 1.8 million trees were
120 studied (Stovall *et al.*, 2019).

121 Several recent studies conducted in southern and central Europe have reported
122 drought-induced dieback of Scots pine (Buras *et al.*, 2018; Camarero *et al.*, 2015b; Etzold *et al.*,
123 2019; Galiano *et al.*, 2010; Hereş *et al.*, 2012; Sánchez-Salguero *et al.*, 2012) causing a

124 shift towards the dominance of oak (*Quercus* spp) species (Carnicer *et al.*, 2014; Galiano et
125 al., 2010; Rigling *et al.*, 2013). Although the impact of various tree- and site-level factors on
126 tree growth during drought has been studied from local to global scales (e.g., Anderegg et al.,
127 2015; Buras et al., 2018; Gazol et al., 2018; Zang *et al.*, 2014), their interactive effects are
128 still not clearly understood (Maes *et al.*, 2019). For example, some large-scale studies found a
129 low to moderate influence of drought severity on tree growth response (e.g., Gazol *et al.*,
130 2017; Sánchez-Salguero et al., 2018), possibly because they did not consider interactive
131 effects between drought characteristics and long-term tree growth performances. In addition,
132 large-scale studies often characterize drought according to a pre-defined meteorological
133 season (e.g., drought in spring-summer) irrespective of local site conditions, soil moisture
134 content, and geographic location (e.g., Bottero et al., 2017; Gao *et al.*, 2018; Gazol et al.,
135 2018). As a consequence, site-specific climate-growth signals might be overlooked if a
136 particular studied season is not the most relevant period for tree radial growth (Pasho *et al.*,
137 2011; Sánchez-Salguero *et al.*, 2015).

138 Here we combined Scots pine tree-ring width data from 30 sites into a network to
139 determine how growth responses to extreme drought varied along a latitudinal gradient across
140 Europe stretching from southern Spain to northern Germany. Tree growth response was
141 assessed to retrospectively quantify short- and long-term drought effects on growth for
142 numerous individuals, sites, and species at annual resolution. Tree growth resilience was
143 defined as the capacity of a tree to reach growth rates similar to those prior to a given drought
144 event. Thus, resilience encompasses the capacity to buffer the impact of a disturbance
145 (resistance), as well as the ability to return to pre-disturbance growth levels (recovery) (Lloret
146 *et al.*, 2011). Specifically, we asked four research questions: (i) How does the impact of the
147 climatic water balance (i.e., precipitation minus potential evapotranspiration) of different
148 seasons on tree growth vary along a latitudinal gradient? (ii) How do radial growth rates of

149 Scots pine during drought and non-drought years vary across sites? (iii) Has tree growth
150 resilience to extreme drought changed over the past decades due to an increased frequency
151 and severity of droughts (Serra-Maluquer et al., 2018; Szejner et al., 2019)? (iv) How do
152 drought characteristics, site conditions, and tree growth related variables modulate the tree
153 growth resilience to extreme drought events? For this last research question, we considered a
154 list of biological hypotheses based on a literature review (see Table S1: e.g., Gazol et al.,
155 2017; Gazol et al., 2018; Sánchez-Salguero et al., 2018; Vitali et al., 2017; Zang et al., 2014).

156 **Materials and Methods**

157 **Study sites and tree-ring data**

158 We compiled tree-ring width data of Scots pine from 30 sites (Table S2) along an
159 approximately 2800 km long latitudinal gradient from southern Spain (Baza; 37.2° N, 4.0°
160 W) to north-eastern Germany (Torgelow; 53.6 °N, 14° E) (Fig 1). To avoid age-related
161 growth effects only trees older than 30 years at the time of examined drought were selected,
162 resulting in 615 adult Scots pine trees (6 to 60 trees per site). From each tree, two to four tree
163 ring width series were included, measured from increment-cores extracted at breast height
164 (1.3 m height) and cross-dated following standard dendrochronological procedures (Grissino-
165 Mayer, 2001).

166 Considering the large differences in productivity among study sites along this long
167 gradient, the sites were grouped using a hierarchical cluster analysis (Kaufman & Rousseeuw,
168 1990). The classification was based on site productivity index (i.e., dominant tree height at 50
169 years of stand age) and site elevation. Dominant tree height has been commonly used as an
170 indicator of site productivity (e.g., Bugmann, 1996; Diéguez-Aranda *et al.*, 2005a; Westoby
171 *et al.*, 2002) including Scots pine sites (e.g., Diéguez-Aranda *et al.*, 2005b; Hökkä &
172 Ojansuu, 2004; Mäkinen *et al.*, 2017; Palahí *et al.*, 2004). The hierarchical clustering was
173 done using the *hclust* function and *ward.D* method in R (R Development Core Team, 2018).

174 Based on the hierarchical cluster analysis (Fig S1), three groups (i.e., site types) were
175 characterized as (1) high- elevation sites (1865-2011 m a.s.l.) with low productivity (6.0-14.0
176 m in stand dominant tree height) referred as “HELP”, (2) mid-elevation sites (600-1450 m
177 a.s.l.) with low productivity (7.5-11.0 m in stand dominant tree height) referred as “MELP”,
178 and (3) low-elevation sites (33-326 m a.s.l.) with high productivity (15-23.7 m in stand
179 dominant tree height) referred as “LEHP” (Fig S1).

180 **Analytical approaches**

181 Addressing our four research questions, the analytical approach involved two steps:
182 data preparation and data analysis. The data preparation step embodied four sub-steps, (i)
183 quantification of tree-ring width indices, (ii) quantification of drought indices, (iii)
184 identification of drought, pre-drought, and post-drought periods (i.e., years), and (iv)
185 quantification of tree growth resilience indices. The data analysis step embodied four steps,
186 i.e., one for each research question.

187 **Quantification of tree-ring width indices**

188 We aimed at quantifying growth responses to extreme drought events over the recent
189 50 years period roughly from year 1960 to year 2011. However, our studied trees largely
190 differed in age across sites (Table S2). Hence, ring width data were transformed into
191 dimensionless ring width indices (RWI) with both age-related growth trends and lower-
192 frequency variation removed from the time series (Cook & Kairiukstis, 1990). For this, ring
193 width data were detrended by fitting a negative exponential curve or using a 30 year cubic
194 spline with a 50% frequency cut-off (Cook & Kairiukstis, 1990). In addition to these
195 detrending methods, we also converted the raw ring width data into basal area increment (cm²
196 per year) (Biondi & Quedan, 2008) using the *dplR* package in R (Bunn *et al.*, 2018). We
197 assessed the suitability of these approaches to disentangle the drought effects on tree growth
198 by computing the correlation coefficient with the drought indices (*cf.* next section) and by

199 characterizing the trend over a 50-year period (Table S3 and Fig S2). The results showed that
200 the negative exponential detrending method performed best among the used approaches in
201 terms of the magnitude of correlation with the drought and of capturing the long-term trends
202 (Table S3 and Fig S2). We thus used the detrended negative exponential RWI (hereafter
203 referred to as RWI) for the analysis.

204 To build the site-level tree-ring chronology, we averaged the detrended individual
205 RWI series with a Tukey's biweight robust mean (Cook & Kairiukstis, 1990; Fritts, 2001).
206 The RWI and average tree-level chronology were calculated using the *detrend* and *chron*
207 functions, respectively, available from the *dplR* R package (Bunn et al., 2018; R
208 Development Core Team, 2018).

209 **Quantification of drought indices**

210 Monthly mean temperature (°C) and total precipitation (mm) data were obtained for
211 each site from different climate data sources (Table S4). To compute the correlation
212 coefficient between drought indices and the RWI, we considered a 50-year period for all
213 sites. However, the range of years for the 50-year period varied across sites due to differences
214 in timing of data collection.

215 For drought index, we initially considered the De Martonne Index (De Martonne,
216 1926), the Standardized Precipitation Index (McKee *et al.*, 1993), and the Standardized
217 Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano *et al.*, 2010). The SPEI had a
218 stronger correlation with RWI than the other indices examined for most of the sites (see
219 Table S5). Hence, SPEI was used for defining the drought and non-drought years.

220 The SPEI is a unitless drought index, which takes into account both precipitation and
221 potential evapotranspiration effects in the calculation of the climatic water balance (CWB),
222 and is commonly used in the literature for identifying and characterizing drought and non-
223 drought years (e.g., Bottero et al., 2017; Gazol et al., 2018). The potential evapotranspiration

224 was calculated using the *Thornthwaite* function of the R package SPEI (Begueria & Vicente-
225 Serrano, 2013). The SPEI was then calculated from CWB using the *spei* function of the R
226 package SPEI (Begueria & Vicente-Serrano, 2013). For each site, we calculated SPEI of
227 various timescales i.e., integrated over 1 to 15 months in order to represent different lengths
228 of the growing season or at least different growth sensitive periods within the current and the
229 previous growing season. We assessed the Pearson correlation between RWI (ring width
230 index) and SPEIs (i.e. the different time intervals) for identifying the most relevant SPEI (i.e.,
231 most sensitive time interval) for each site to define the drought and non-drought years (see
232 Table S6). The resulting SPEIs (i.e., those best correlated with RWI) are presented in the
233 Table S7.

234 For identifying the extreme drought year of a site, we selected the year with the
235 lowest SPEI value. For each site, we first selected the extreme drought years for the period of
236 1980-2011. We then selected the extreme drought year for the period of 1980-1999 and for
237 the period of 2000-2011.

238 **Identification of drought, pre-drought, and post-drought periods**

239 We characterized drought periods by single or multiple years based on $\text{SPEI} \leq -1.00$
240 and pre-drought or post-drought periods (i.e., without drought) based on $\text{SPEI} \geq -0.99$. We
241 limited the pre-drought and post-drought periods to a maximum of three years, but for
242 drought periods we considered all consecutive years with $\text{SPEI} \leq -1.00$ (see Table S6). We
243 identified the most extreme droughts during 1980-1999, and during 2000-2011 for all study
244 sites (see Table S6) for comparing the tree growth responses to extreme droughts during the
245 recent decade (2000-2011) with the previous two decades (1980-1999). Since many sites had
246 no drought during 1990-1999, we decided to enlarge the earlier period back until 1980.

247 **Tree growth resilience indices**

248 For tree growth resilience, we computed three resilience indices as suggested by
249 Lloret et al. (2011): resistance, recovery, and resilience. The resistance quantifies the ratio
250 between growth during a drought period and growth during the preceding non-drought
251 period, representing thus the capacity of the trees to buffer the stress and maintain growth
252 during drought. The recovery quantifies the growth reaction following the drought period and
253 is defined by the ratio between growth during the post-drought period and growth during the
254 drought period. The resilience quantifies the ratio between growth during the post-drought
255 period and growth during the pre-drought period, which represents the capacity of trees to
256 recover and regain the growth of the pre-drought period. We quantified resistance, recovery,
257 and resilience for all trees of all sites during the most extreme droughts in 1980-1999 and in
258 2000-2011 (see Table S6).

259 **Research question 1: Impact of seasonal drought (SPEI) on tree growth**

260 Based on the results of preliminary analysis (i.e., correlation between RWI and
261 different SPEIs), we identified the eight best correlated SPEIs for understanding the
262 magnitude (i.e., degree of correlation) and pattern (i.e., type of correlation) of influences of
263 drought on RWI, and how that magnitude and pattern of correlation varied across the
264 latitudinal gradient examined in this study. The selected SPEI timescales were August-15
265 (i.e., from previous June to current August), May-12 (i.e., from previous June to current
266 May), May-9 (i.e., from previous September to current May), May-6 (i.e., from previous
267 December to current May), May-3 (i.e., spring, from current March to current May), August-
268 6 (i.e., summer, from current March to current August), August-3 (i.e., from current June to
269 current August), and November-6 (i.e., from current June to current November).

270 **Research question 2: Tree growth rate in drought and non-drought years**

271 For understanding the absolute tree radial growth performances during drought and
272 non-drought years, we modelled absolute tree radial growth (non-detrended tree ring width)

273 as a function of site types (three levels: LEHP, MELP, and HELP), drought status (two
274 levels: drought years and non-drought years), and the interaction between site types and
275 drought status. For understanding the potential role of tree age on absolute tree radial growth,
276 we considered tree age as a covariate in this analysis.

277 **Research question 3: Temporal change in tree growth resilience to extreme droughts**

278 We modelled resistance, recovery, and resilience as a function of time period (two
279 levels: 1980-1999 and 2000-2011), site types (three levels: LEHP, MELP, and HELP), and
280 the interaction between time period and site types.

281 **Research question 4: Factors affecting tree growth resilience to extreme drought**

282 For this research question, we selected the most extreme drought during the entire
283 study period 1980-2011 and used the corresponding resistance, recovery and resilience
284 indices as response variables in a mixed-effects model (*cf.* next section). We considered
285 several tree-, site-, and drought-level explanatory variables and various two-way interaction
286 terms (see Table S1). The variables included tree size (i.e., tree diameter at breast height
287 (DBH) inside bark at the drought year), tree growth and tree growth variability prior to
288 drought representing the average and standard deviation of RWI, respectively of 10
289 consecutive years prior to the extreme drought excluding the years considered as pre-drought
290 period for quantifying the three resilience indices, site types, elevation, latitude, drought
291 severity (measured by the average SPEI during the drought period), drought duration
292 (measured by the length of the drought period in years), and drought frequency (measured by
293 the number of drought years ($\text{SPEI} \leq -1.00$) within 10 years preceding the maximum drought
294 period).

295 **Statistical analyses**

296 We used a linear mixed-effect modelling approach for research question 2, 3, and 4 in
297 which our variables of interest were considered as fixed effects and trees nested within sites

298 were considered as random effects. The modelling was performed using the function *lme* of
299 the R package *nlme* (Pinheiro *et al.*, 2014; Pinheiro & Bates, 2000). The response variables
300 were log-transformed to normalize residuals and homogenize variances and we checked the
301 assumptions of normality of the residuals and homogeneity of the variances. Preliminary
302 analysis indicated that an additional error structure to account for plot spatial autocorrelation
303 did not improve model performance and thus was not incorporated into the final model. We
304 also assessed potential multicollinearity among explanatory variables using the Variance
305 Inflation Factor (VIF) and discarded variables when $VIF > 2.0$. The VIF was calculated using
306 the function *vif* of the R package *car* (Fox & Weisberg, 2011). The post hoc Tukey multiple
307 comparison test was performed to detect the statistical differences (Hothorn *et al.*, 2008).

308 For research question 4, we used the information-theoretic approach (Burnham &
309 Anderson, 2002; Johnson & Omland, 2004), which provides a measure of strength for each
310 candidate model that represents a plausible hypothesis relative to the entire set of candidate
311 models considered (Mazerolle, 2006). In the context of our research question (i.e., what are
312 the factors driving the tree growth resilience to extreme drought?), we considered 16
313 hypotheses (i.e., candidate models) (Table S1), which were developed based on the current
314 understanding resulted from different studies that examined tree growth resilience to extreme
315 droughts. Model selection was performed using the *AICcmodavg* package of R (Mazerolle,
316 2011). Candidate models were compared using Akaike's Information Criterion corrected for
317 small sample sizes (AICc). Akaike weights were computed to assess the support for each
318 model. We used multi-model inference to compute the model-averaged estimates of the
319 explanatory variables and their 95% confidence intervals (Burnham & Anderson, 2002). A
320 confidence interval excluding 0 indicated that the corresponding explanatory variable had an
321 effect on the response variable (Burnham & Anderson, 2002; Mazerolle, 2006). In addition to
322 our candidate models we also considered a null model and a full model. The coefficient of

323 variation (R^2) for fixed and random effects were calculated using the function
324 *r.squaredGLMM* of the MuMIn package in R (Bartoń, 2013).

325 **Results**

326 **Impact of seasonal drought (SPEI) on tree growth**

327 Our results showed significant differences in the response of tree growth to the
328 different time periods of SPEI. The current year summer to autumn (June-November) SPEI
329 significantly controlled tree growth at LEHP sites of northern Germany (Fig. 2), while tree
330 growth at MELP sites was driven by SPEI of spring (March-May), summer (June-August),
331 and spring and summer combined. Tree growth in HELP sites was either non-related or
332 negatively correlated with different time periods of the SPEI (Fig. 2; Table S3). Overall, the
333 magnitude of correlation between RWI and different SPEIs was higher for MELP than the
334 two other site types (Table S3). Three sites of HELP site type had a negative correlation with
335 SPEIs while one site of HELP site type was not significantly correlated with any SPEI
336 considered in our analysis (Table S3).

337 **Tree growth rate in drought and non-drought years**

338 In drought and non-drought years, tree radial growth was higher at LEHP than at
339 HELP and at MELP sites (Fig. 3). The MELP sites had significantly lower tree radial growth
340 in drought years than in non-drought years (Table S8 and Fig. 3). Contrary to MELP, tree
341 growth was not significantly different between drought and non-drought years at LEHP and
342 at HELP sites (Table S8 and Fig. 3). Tree age was negatively associated with the radial
343 growth ($p < 0.0001$) irrespective of site types (Table S8).

344 **Temporal change in tree growth resilience to extreme droughts**

345 Tree growth resistance to extreme drought for all site types (i.e., HELP, LEHP, and
346 MELP) did not change over the two periods (i.e., 1980-1999 and 2000-2011) (Fig. 4A).

347 Nevertheless, resistance was higher at HELP than at LEHP, and higher in the latter compared
348 to MELP, irrespective of the period (Table S9 and Fig. 4A).

349 Tree growth recovery changed significantly over the two periods for all site types,
350 where recovery decreased from 1980-1999 to 2000-2011 at MELP and HELP sites, while
351 increased from 1980-1999 to 2000-2011 at LEHP sites (Table S9 and Fig. 4B). In 1980-1999,
352 recovery was significantly higher at MELP compared to the two other site types irrespective
353 of period (Table S9 and Fig. 4B).

354 Tree growth resilience changed significantly over the two periods for LEHP and
355 MELP sites, but not for HELP sites. Resilience decreased from 1980-1999 to 2000-2011 at
356 MELP sites, while it increased from 1980-1999 to 2000-2011 at LEHP sites (Table S9 and
357 Fig. 4C).

358 **Factors affecting tree growth resilience to extreme drought**

359 The model that included additive and interaction effects of all variables considered in
360 the analysis had full support of Akaike weight for resistance (Table 1). A lower resistance
361 was associated with higher pre-drought growth rate (Table 2). In addition, a lower resistance
362 was associated with greater drought frequency, and with longer drought but depending upon
363 pre-drought growth rate (Table 2). Resistance was higher at HELP and LEHP sites than at
364 MELP sites (Table 2 and Fig. 5A).

365 The model that included drought severity and site types, and the interaction between
366 the two variables had the highest support of Akaike weight for recovery (0.74; Table 1).
367 Recovery was lower at HELP and LEHP sites than at MELP sites (Table 2 and Fig. 5B). In
368 addition, the recovery was higher where trees experienced a higher frequency of droughts
369 (Table 2).

370 The model that included pre-drought growth rate and drought duration, and the
371 interaction between the two variables had the highest support of Akaike weight for resilience

372 (Table 1). Resilience was negatively associated with pre-drought growth rate and pre-drought
373 growth variability and there was no difference across the three site types (Table 2 and Fig.
374 5C).

375 **Discussion**

376 Using tree ring width data from 30 sites along a 2800 km latitudinal gradient across
377 Europe we analysed whether tree growth resilience to extreme drought depended on the
378 geographical location of the tree (Isaac-Renton *et al.*, 2018) and if resilience to extreme
379 drought decreased over time due to more frequent drought events in recent years (Serra-
380 Maluquer *et al.*, 2018; Spinoni *et al.*, 2014). We examined these questions on Scots pine, one
381 of the most widely distributed tree species in the world which is also considered vulnerable to
382 extreme drought conditions (Camarero *et al.*, 2015b; Galiano *et al.*, 2010; Matías *et al.*, 2017;
383 Rigling *et al.*, 2013). Our study shows that tree-level resilience to drought was not dependent
384 on the latitudinal location, but rather on the type of site they were growing at and their growth
385 performance (i.e., magnitude and variability of growth) during the pre-drought period. Our
386 results indicate that trees with higher magnitude and variability in growth are more
387 vulnerable to long and severe droughts. In addition, we found that tree growth resilience to
388 extreme drought was lower during 2000-2011 than during 1980-1999 at mid-elevation and
389 lower productivity sites. These results may indicate that more frequent drought events that
390 occurred in 2000-2011 than in earlier period make Scots pine trees more vulnerable to
391 extreme droughts. However, we found high variability in tree-level responses (Fig. 5) as
392 detected by previous studies (e.g., Gazol *et al.*, 2018; Maes *et al.*, 2019). This high tree-level
393 variability (Fig 5) and low marginal R^2 values (Table 2) may indicate that combining tree
394 information from different sites without direct measurements of local site-related factors
395 (e.g., soil water content, nutrient availability, stand stocking, and rooting depth) compromises

396 the predictive power of the models (DeSoto *et al.*, 2020; Gazol *et al.*, 2018; Grossiord *et al.*,
397 2014).

398 **Impact of seasonal drought on tree growth**

399 Our results reveal important seasonal differences across lower and higher productivity
400 sites in terms of SPEI-RWI correlations. Scots pine trees growing at mid-elevation lower
401 productivity (MELP) sites showed a greater sensitivity to spring-summer SPEI while trees
402 growing at low-elevation higher productivity (LEHP) sites of northern Germany were more
403 sensitive to summer-autumn SPEI (Fig. 2). This is consistent with results from Pasho *et al.*
404 (2011), who studied eight tree species including Scots pine for the period of 1950-2005 using
405 the Standardized Precipitation Index at timescales from 1 to 48 months. Our results showed
406 that Scots pine trees growing in MELP are more sensitive to drought (measured by SPEI)
407 than trees growing in LEHP and HELP sites (Fig. 3 and Table S3), which is consistent with
408 the findings of other studies on Scots pine (Lévesque *et al.*, 2014; Pasho *et al.*, 2011;
409 Sánchez-Salguero *et al.*, 2015). Trees at MELP sites are likely to grow under water limitation
410 during extended periods of the year, and changes in precipitation or evaporative demand
411 during these periods will directly affect the water availability of the trees and thus their
412 physiological responses, resulting in lower growth (Cabon *et al.*, 2020). A tree at a less dry
413 site in contrast is growing mostly without water limitations. During such periods with plenty
414 of water supply there will be no strong direct effect of precipitation (and at least within a
415 certain range of evaporative demand) on tree physiology and on growth (Martínez-Vilalta *et*
416 *al.*, 2009; Sterck *et al.*, 2008). Thus, it is reasonable to consider that the climatic control of
417 tree growth is stronger at MELP which are relatively drier than LEHP sites (Table S2).
418 However, we need to improve our understanding on local drought characteristics because the
419 climatic water balance and SPEI do not consider the soil water holding capacity and the depth

420 of water table which are important parameters for estimating the soil water available for trees
421 (Zang *et al.*, 2019).

422 **Tree growth rate in drought and non-drought years**

423 We found higher annual growth among trees at lower-elevation sites than trees at
424 higher-elevation sites (Fig. 3). Trees at low-elevation sites were relatively younger than trees
425 at high-elevation sites and thus more likely in their full growth ontogenetic stage. However,
426 Scots pine trees at high-elevation sites had no growth difference between our selected
427 drought and non-drought years (Fig. 3) irrespective of the fact that they experienced similar
428 drought severity and frequency as the two other site types in terms of SPEI (Fig. 6).
429 Therefore, tree growth at high-elevation Scots pine forests is probably controlled by other
430 factors than changes in water availability during drought (Carrer *et al.*, 2007; Cudlín *et al.*,
431 2017). In our dataset, three out of six high-elevation sites had negative correlation with SPEI
432 (Table S3) indicating that tree radial growth at high-elevation sites examined in our study was
433 more related to other factors such as ontogeny and temperature (Camarero *et al.*, 2015a;
434 Körner, 2003) than to water availability (Hagedorn *et al.*, 2014). Our high-elevation site type
435 has three sites with trees that were older than 150 years during our selected drought period
436 and older than the trees at any other site examined in our analysis. Besides, the mean annual
437 temperature at four out of six high-elevation sites was <7.0 °C which is almost 2 °C cooler
438 than at any other site examined in our analysis. Trees in our high-elevation sites are perhaps
439 well adapted to such low mean annual temperature and thus short growing season, confirming
440 the findings of other studies conducted in southern Europe (Peñuelas *et al.*, 2008) and in
441 southwestern United States (Adams & Kolb, 2004). It is also important to mention that our
442 drought intensity index may not fully capture the absolute water balance differences between
443 drought and non-drought years because of the elevational differences between the sites and

444 climate stations (Table S4), which may partly explain the lack of growth differences between
445 drought and non-drought years for our high-elevation sites.

446 **Temporal change in tree growth resilience to extreme droughts**

447 Although Scots pine is a relatively drought-tolerant species, our results showed a
448 decreased growth recovery and resilience to extreme drought at mid-elevation and lower
449 productivity sites. This is largely consistent with the patterns reported by Serra-Maluquer et
450 al. (2018) in three pine species (including Scots pine) growing in NE Spain. In our case, this
451 result likely reflects the higher frequency and severity of droughts events prior to the extreme
452 drought occurring in 2000-2011 than prior to the extreme drought occurring in 1980-1999
453 (Fig. 6). Moreover, trees became older and larger over time. A larger tree carries higher non-
454 photosynthetic biomass, which requires a greater investment for defence and maintenance
455 (Ryan & Yoder, 1997; Scholz *et al.*, 2011) and increasing tree height may increase hydraulic
456 constraints and xylem cavitation risks under drought (Olson *et al.*, 2018). This reduced tree
457 resilience over time may challenge the physiological potential for acclimation to more
458 intensive and frequent drought events that we expect in the future (Dai, 2012). The decreased
459 tree growth resilience at MELP sites may indicate that drought hardening (i.e., physiological
460 processes by which a tree becomes more acclimate to drought conditions) (Villar-Salvador *et*
461 *al.*, 2013) is not very important and does not allow trees to acclimate to frequent and
462 prolonged drought events irrespective of their drought experiences.

463 In contrast to MELP sites, tree growth recovery and resilience to extreme droughts
464 increased at LEHP sites during the recent period (i.e., 2000-2011) compared to the previous
465 period (i.e., 1980-1999). Although drought severity and drought frequency did not change
466 significantly at LEHP sites over these two periods (Fig 6), the duration of the extreme
467 drought was longer in 1980-1999 than in 2000-2011. For example, seven sites of the LEHP

468 site type experienced a two-year long drought during 1980-1999, while none of the droughts
469 occurring during 2000-2011 was longer than one year at that site type (Table S6).

470 **Factors affecting tree growth resilience to extreme drought**

471 Several studies conducted at local to global scales provided understanding on tree,
472 site, and drought related variables influencing tree-level resilience to extreme drought (e.g.,
473 Gao et al., 2018; Gazol et al., 2017; Gazol et al., 2018; Sánchez-Salguero et al., 2018; Taeger
474 *et al.*, 2013; Vitali *et al.*, 2017; Zang et al., 2014). To our knowledge, however, none of these
475 studies compared explicitly the model performances with and without interaction effects
476 among all these variables.

477 Our results showed that the top-ranked model (according to Akaike weights) for all
478 the three resilience indices (resistance, recovery, and resilience) included interaction effects
479 between tree and drought-related variables (Table 1). This means that the impact of drought
480 on tree-level resilience is not independent, but rather dependent on how the trees were
481 growing (i.e., magnitude and variability of growth) during the pre-drought period and on the
482 type of site they were growing at. In addition to drought severity, which was usually found to
483 significantly affect tree-level resilience at various spatial scales variables (Gazol et al., 2017;
484 Gazol et al., 2018; Zang et al., 2014), we also considered drought duration and drought
485 frequency as explanatory variables as suggested by Gao et al., (2018). We indeed found a
486 significant negative effect of drought frequency on tree resistance (Table 2), suggesting that
487 trees that experienced more frequent droughts were less resistant to extreme droughts.
488 Therefore, trees that display higher variability in growth are not only sensitive to extreme
489 drought but also to frequent drought occurrence as e.g. shown by Seidel et al. (2016) for
490 different Scots pine provenances. Higher above-ground biomass growth can be related to
491 lower or at least non-proportional biomass allocation to roots (Gessler et al., 2017) and might
492 consequently increase tree-level sensitivity to upcoming drought periods (Martínez-Vilalta *et*

493 *al.*, 2012). Long or repeated droughts may reduce the number of living branches and, because
494 of needle multi-year life-span, the leaf area per branch (Galiano *et al.*, 2011; Vennetier *et al.*,
495 2013). This holds back short-term tree leaf area recovery and may drive tree growth to very
496 low levels during and after drought. Although a reduced leaf area limits water stress during
497 and after droughts and may favour resilience, it also hampers carbohydrate reserves build-up
498 and may lead to carbon starvation. Accordingly, higher growth variability may be related to a
499 higher vulnerability to the upcoming stresses (Cailleret *et al.*, 2019; DeSoto *et al.*, 2020;
500 McDowell *et al.*, 2008; Ogle *et al.*, 2000). For instance, Ogle *et al.*, (2000) noticed a 1.5 times
501 higher growth variability in dead pinyon pine trees relative to surviving ones in drought years
502 preceding mortality across forests of southwestern USA.

503 Although the pre-drought growth of Scots pine had a strong relationship with
504 resistance, it had no-relationship with recovery. This lack of relationship between pre-drought
505 growth and recovery resulted in a relatively weak relationship (although statistically
506 significant) between pre-drought growth and resilience (Fig 5), because the resilience is
507 mathematically related to both resistance and recovery (Lloret *et al.*, 2011), and in the context
508 of our study, recovery was more closely related to resilience than the relationship between
509 resistance and resilience (Fig S3). Scots pine trees growing at MELP sites displayed lower
510 resistance but higher recovery than trees growing at LEHP and HELP sites (Table 2 and Fig.
511 5), suggesting different growth strategies exercised by trees from different sites to cope with
512 drought (Sánchez-Salguero *et al.*, 2018). However, resistance and recovery are relative
513 indices and do not allow comparison across trees in terms of their absolute growth
514 performances. Although resistance and recovery hold a negative mathematical relationship
515 (Lloret *et al.*, 2011), they provide useful insights on disentangling trees that tried to remain
516 firm during drought years (i.e., higher resistance and lower recovery) from trees that tried to
517 conform drought impact (i.e., lower resistance and higher recovery) (Gazol *et al.*, 2017a).

518 These two different strategies to extreme droughts by trees from high-productivity and low-
519 productivity sites are also reported by other local (Vitali et al., 2017; Zang et al., 2014) and
520 global scale studies (Gazol et al., 2017). For instance, a multi-species comparison across
521 Spain found higher resistance for species dominating mesic sites than for species from more
522 xeric sites, which presented a higher recovery (Gazol et al., 2018). At our LEHP, Scots pine
523 trees were on average taller and larger than MELP sites (Table S2). These larger trees in
524 mesic sites most likely developed larger crowns, which might be able to still provide
525 sufficient photosynthates to sustain growth during the drought period. Alternatively, these
526 larger trees had sufficient reserves to compensate for the drought-induced reduction in
527 photosynthesis. Both mechanisms would result in a higher resistance compared to trees in
528 lower productivity sites (Martínez-Vilalta et al., 2009). However, taller trees associated with
529 larger crowns and concomitantly greater water demand can be more vulnerable to drought
530 induced hydraulic failure (McDowell et al., 2008; Olson et al., 2018) and the required post-
531 drought investment of assimilates for restoring their hydraulic system could slow down their
532 recovery process (Brodribb *et al.*, 2010).

533 In this analysis, we considered tree, site, and drought level variables and their
534 interactions, but available data did not allow to quantify the effects of forest stand-level
535 variables including tree-to-tree competition (Serra-Maluquer et al., 2018), site conditions
536 including soil and topography (Venetier *et al.*, 2018; Zalloni *et al.*, 2019), species mixtures
537 (Pretzsch *et al.*, 2013), trees neighbourhood composition (Grossiord, 2019), and stand
538 stocking (Bottero et al., 2017; D'Amato *et al.*, 2013), which will be the subject of subsequent
539 analyses. Moreover, we did not include possible sub-species variation due to local
540 evolutionary adaptation induced by drought-related selection (Hampe and Petit 2005). We
541 detected large tree-level variability within and across sites, and a larger proportion of the
542 variance of our models was explained by the random effects (i.e., trees nested within sites)

543 than by the fixed effect variables (Table 1). Therefore, these points need to be considered
544 when interpreting our results.

545 To conclude, we show that tree radial growth responses of Scots pine to extreme
546 drought depend on site condition, tree growth prior to drought, and the number of droughts
547 that a tree experienced within the 10 years before the selected drought. Our study identified a
548 reduced tree growth resilience to extreme drought in Scots pine trees growing at mid-
549 elevation and low productivity sites likely driven by the more frequent and severe drought
550 events that occurred at those sites in recent years. We show that the assessment of tree growth
551 responses in terms of resistance, recovery, and resilience to extreme drought using radial
552 growth data is challenging along large ecological and biogeographical gradients, since a
553 multitude of location-specific tree-, site-, and drought-related factors and their interactions
554 drive tree growth performances.

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578 **Conflict of Interest**

579 None is declared.

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949 Table 1. Results of the best models explaining tree growth resistance, recovery and resilience of Scots pine trees along the studied gradient. From the 16 tested models, only the three with the highest Akaike’s
950 Information Criterion (AIC) weight are presented.

| 951 952 | Models | Hypotheses | References | AICc | Δ AICc | AICc weight | R² (Fixed) | R² (Fixed and random) |
|------------|------------------------|--|--------------------------------|-------------|---------------|--------------------|------------------------------|---|
| 953 954 | | | | | | | | |
| 955 | Resistance (RT) | Tree resistance to drought is affected by | | | | | | |
| 956 | RT~all variables | Full model | | 117.9 | 0.0 | 1.00 | 0.33 | 0.49 |
| 957 | RT~D_INT*PGR+ | the intensity of the drought, but depending upon the growth prior to drought | Adapted from Gazol et al., | 130.4 | 12.5 | 0.00 | 0.22 | 0.46 |
| 958 | D_INT*ST | and site types | (2018) | | | | | |
| 959 | RT~D_FRE*PGR | the frequency of the drought, but depending upon the growth prior to drought | Adapted from Gao et al., | 130.5 | 12.6 | 0.00 | 0.14 | 0.47 |
| 960 | | | (2018) | | | | | |
| 961 | | | | | | | | |
| 962 | Recovery (RC) | Tree recovery after drought | | | | | | |
| 963 | RC~D_INT*ST | is affected by the intensity of the drought, but depending upon the site types | Adapted from Gazol et al., | 301.9 | 0.0 | 0.74 | 0.16 | 0.36 |
| 964 | | | (2018) | | | | | |
| 965 | RC~ST | decreased with site types | Sánchez-Salguero et al., 2018 | 307.0 | 5.1 | 0.06 | 0.07 | 0.37 |
| 966 | RC~D_INT+ D_FRE+ | is affected combinedly by intensity of drought, duration of drought, and | Gao et al., 2018 | 308.4 | 6.5 | 0.03 | 0.08 | 0.37 |
| 967 | D_DUR | frequency of drought | | | | | | |
| 968 | | | | | | | | |
| 969 | Resilience (RS) | Tree resilience to drought is | | | | | | |
| 970 | RS~ D_DUR*PGR | affected by the duration of the drought, but depending upon the growth prior | Adapted from Taeger et al., | 342.4 | 0.0 | 0.45 | 0.03 | 0.35 |
| 971 | | to drought | (2013) | | | | | |
| 972 | RS~PGR | negatively associated with the growth prior to drought | Zang et al., 2014; Ruijven and | 344.3 | 1.9 | 0.17 | 0.02 | 0.35 |
| 973 | | | Berendse 2010 | | | | | |
| 974 | RS~D_FRE*PGR | affected by the frequency of the drought, but depending upon the growth prior | Adapted from Gao et al., | 344.6 | 2.2 | 0.15 | 0.02 | 0.36 |
| 975 | | to drought | (2018) | | | | | |

976 Note. PGR=average tree growth (ring width indices) prior to drought, ST= site type (LEHP (low-elevation and higher productivity), MELP (mid-elevation and lower productivity), and HELP (high-elevation and lower
977 productivity)), D_FRE= number of drought years within the past 10 years from the studied drought, D_INT= intensity of drought, and D_DUR= duration of drought, *indicates an interaction term and +indicates an
978 additive term, PGR was quantified from tree growth performances during the 10 consecutive years prior to drought excluding the years considered as pre-drought period quantifying the three indices (i.e., resistance,
979 recovery, and resilience).

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981 Table 2. Log-transformed estimates of predictor variables and 95% confidence intervals (CI) based on model averaging for the three response variables resistance, recovery, and resilience. Only predictor variables that
 982 had a strong effect (i.e., a 95 % confidence interval excluding 0) are presented.

| Parameters | Types of effect | Estimate (β) | Lower 95% CI | Upper 95% CI |
|---|-----------------|----------------------|--------------|--------------|
| Resistance | | | | |
| Pre-drought growth | Additive | -0.13 | -0.22 | -0.04 |
| High-elevation and lower productivity vs mid-elevation lower productivity | Additive | 0.31 | 0.09 | 0.52 |
| Low-elevation higher productivity vs mid-elevation lower productivity | Additive | 0.19 | 0.02 | 0.36 |
| Drought intensity*Pre-drought growth | Interaction | 0.005 | 0.002 | 0.008 |
| Drought duration*Pre-drought growth | Interaction | -0.22 | -0.35 | -0.09 |
| Drought frequency | Additive | -0.13 | -0.20 | -0.06 |
| Recovery | | | | |
| High-elevation and lower productivity vs mid-elevation lower productivity | Additive | -0.23 | -0.45 | -0.02 |
| Low-elevation higher productivity vs mid-elevation lower productivity | Additive | -0.16 | -0.34 | -0.01 |
| Drought frequency | Additive | 0.08 | 0.01 | 0.16 |
| Resilience | | | | |
| Pre-drought growth | Additive | -0.18 | -0.28 | -0.07 |
| Pre-drought growth variability | Additive | -0.22 | -0.43 | -0.01 |

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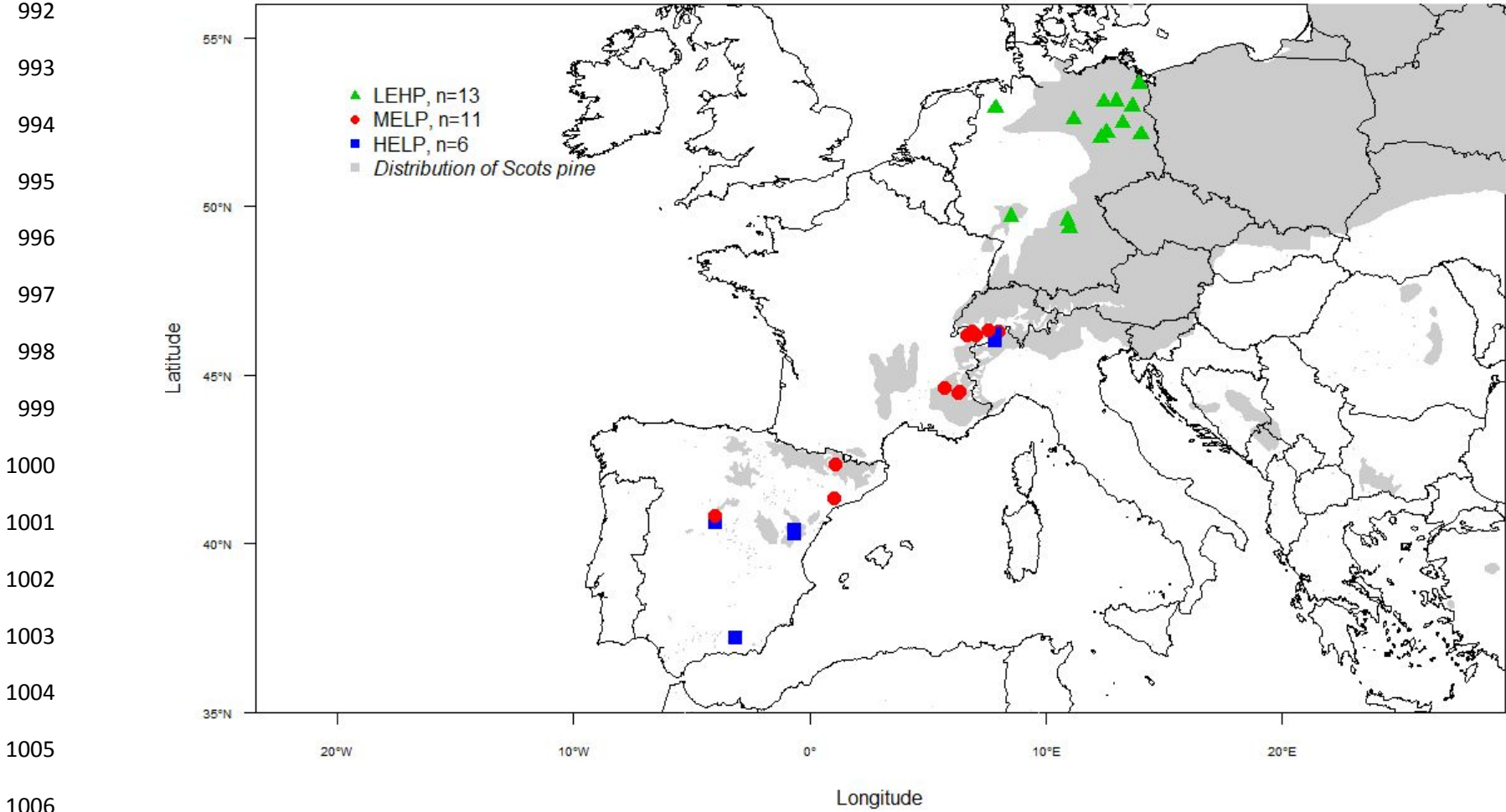
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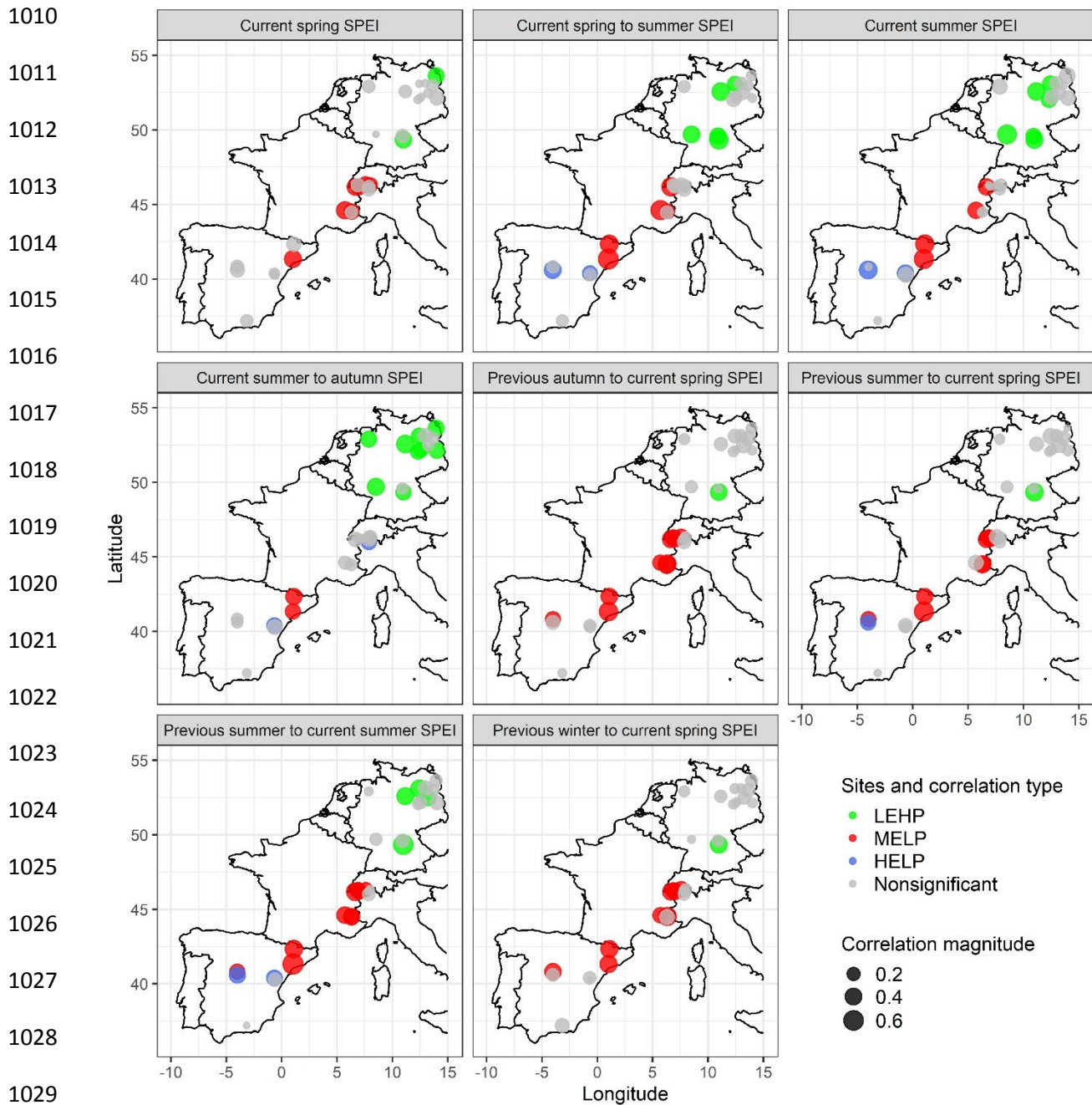
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1007 Figure 1. Location of the 30 Scots pine study sites distributed along a latitudinal gradient that ranged from southern Spain to northern Germany. Where, LEHP: low-elevation
 1008 sites with high productivity, MELP: mid-elevation sites with low productivity, and HELP: high-elevation sites with low productivity. The grey shade used as a background
 1009 within the map represents the natural distribution of Scots pine adapted from Mátyás *et al.* (2004).



1030 Figure 2. Seasonal correlations between Scots pine tree-ring width indices and the Standardized Precipitation-
 1031 Evapotranspiration Index (SPEI) for the period of approximately 1960-2011 across the latitudinal gradient. Only
 1032 the seasons that exhibited the strongest effect on tree-ring width indices are plotted (see materials and methods).
 1033 Note. 'previous' refers to the year previous to tree ring formation, while 'current' refers to the current year of
 1034 ring formation, summer: June, July, and August, spring: March, April, and May, autumn: September, October,
 1035 and November. LEHP: low-elevation sites with high productivity; MELP: mid-elevation sites with low
 1036 productivity; and HELP: high-elevation sites with low productivity. Pearson's product-moment correlation with
 a threshold <0.05 was used for statistical significance. Correlation magnitude: the larger the circles, the stronger
 the correlations. See Table S7 for correlation scores that displayed in this figure.

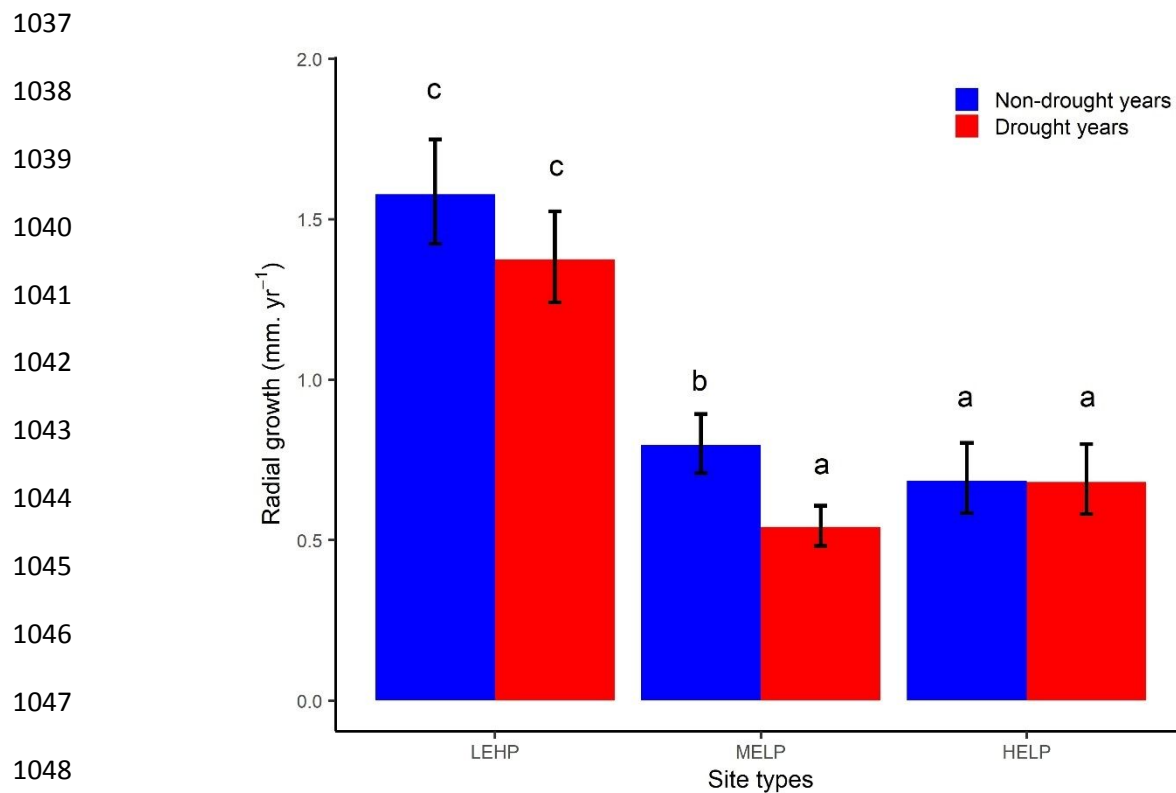


Figure 3. Mean annual radial growth in drought and non-drought years for the period of approximately 1980-2011 across the three site types (i.e., LEHP: low-elevation sites with high productivity; MELP: mid-elevation sites with low productivity; and HELP: high-elevation sites with low productivity). The error bars represent the mean \pm standard error (n=615). The letters on top of the bars show the results (a < b < c) of the post hoc Tukey multiple comparison test with a threshold < 0.05 for statistical significance indicating the differences among the three site types and between non-drought years and drought years within each site type.

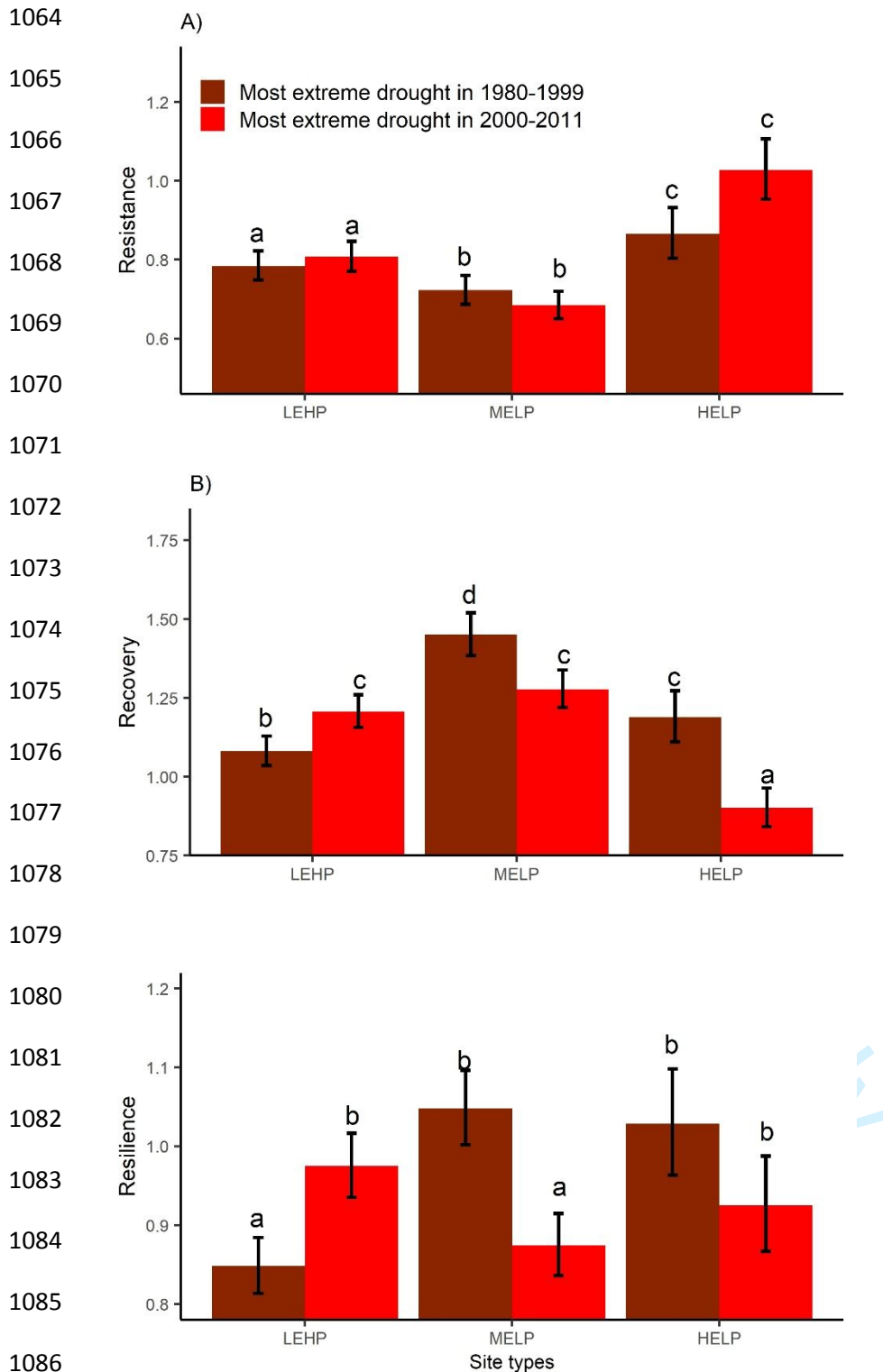
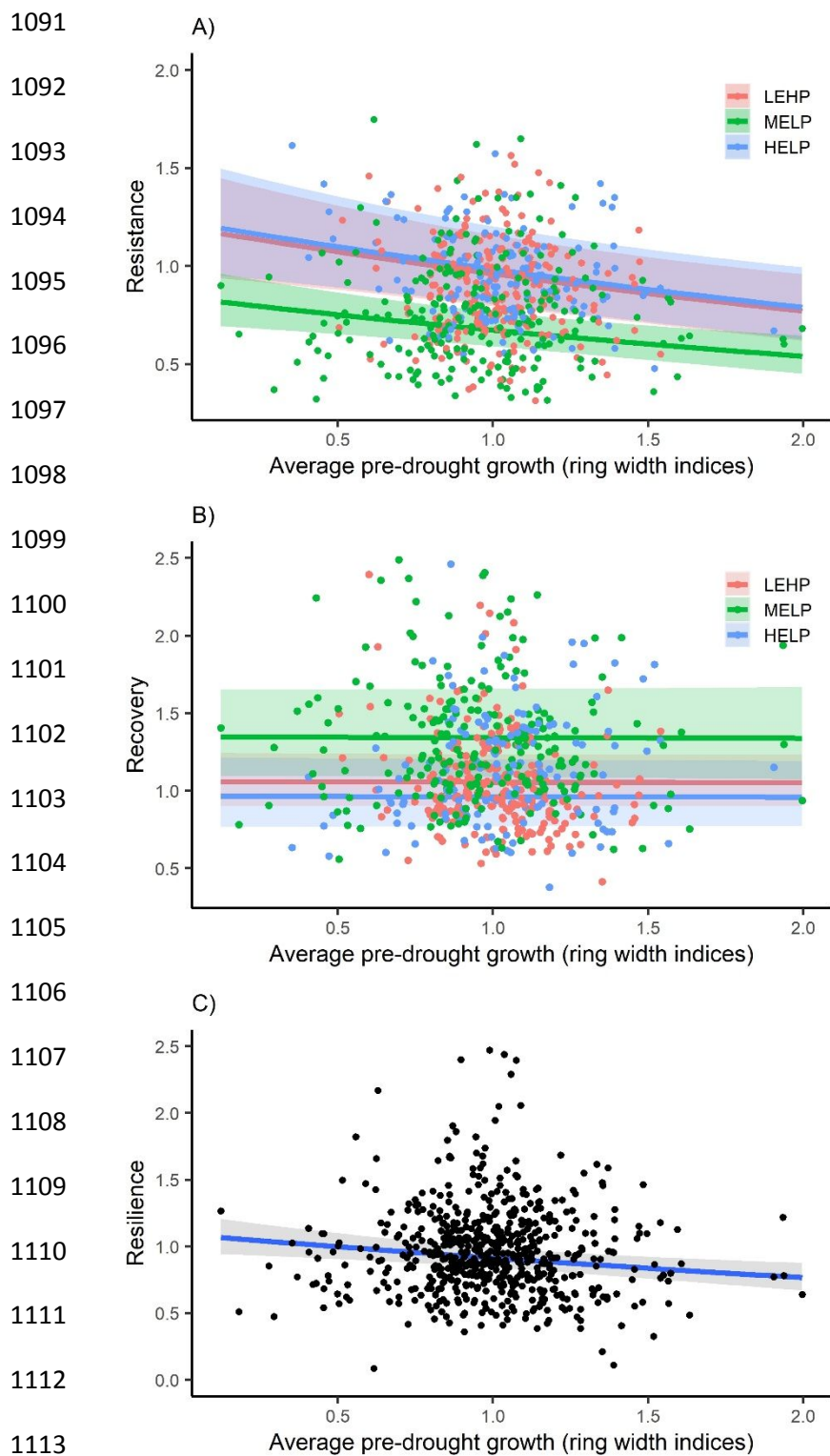


Figure 4. Tree-level resistance (A), recovery (B), and resilience (C) to the most extreme drought during 1980-1999 and during 2000-2011 for three site types. The error bars represent the mean \pm standard error (n=615). The letters on top of the bars show the results (a < b < c) of the post hoc Tukey multiple comparison test with a threshold < 0.05 for statistical significance indicating the differences among the three site types and between the two periods within each site type. LEHP: low- elevation sites with high productivity, MELP: mid- elevation sites with low productivity, and HELP: high-elevation sites with low productivity.



1114 Figure 5. Tree growth resistance, recovery, and resilience to the most extreme drought during 1980-2011 with
 1115 95% confidence intervals. Note. Average pre-drought growth (ring width indices) were quantified from tree
 1116 growth performances during the 10 consecutive years prior to drought excluding the years considered as pre-
 1117 drought period for quantifying the three indices (resistance, recovery, and resilience). LEHP: low-elevation sites
 with high productivity, MELP: mid-elevation sites with low productivity, and HELP: high-elevation sites with
 low productivity. See statistics for the fitted line in Table 1.

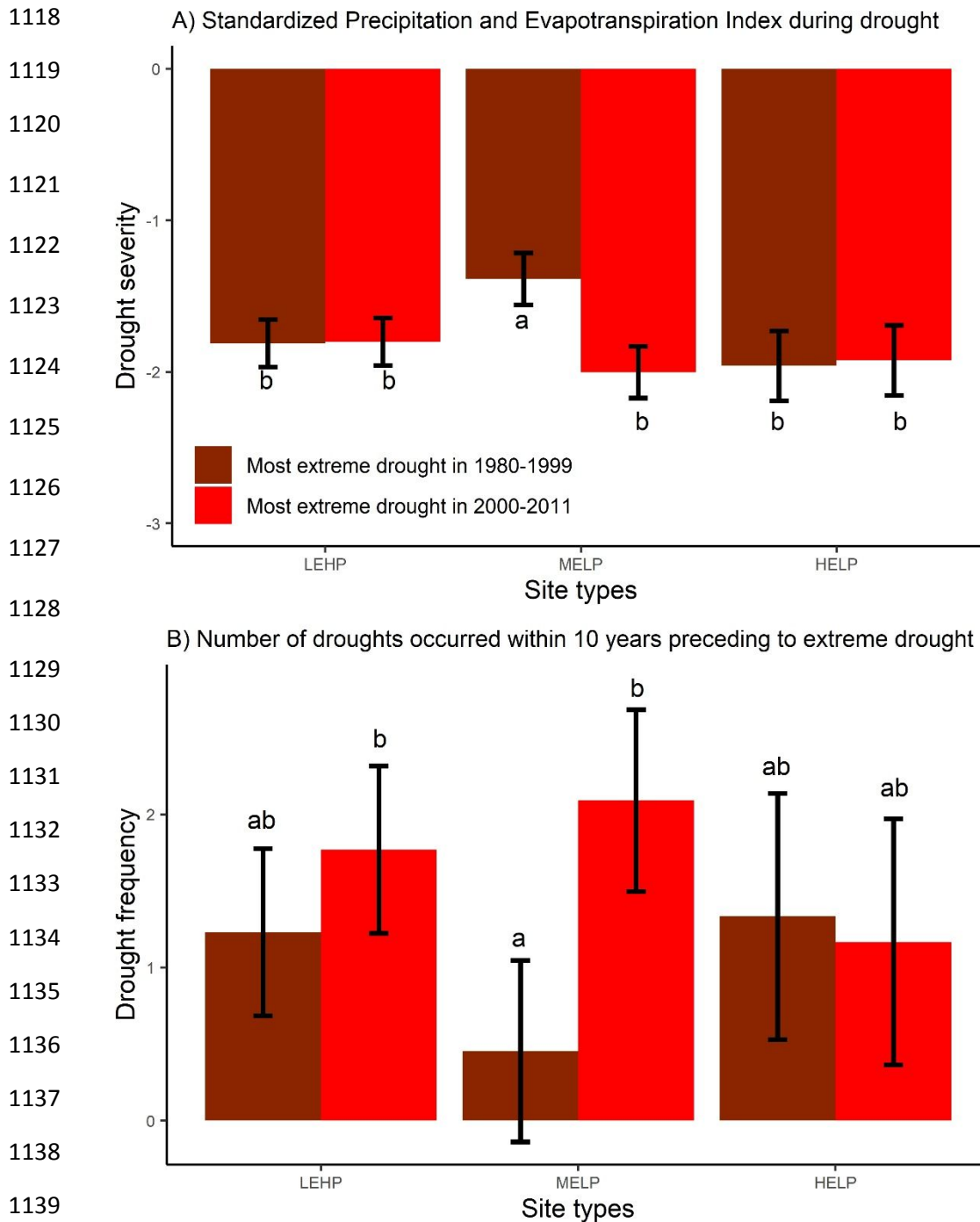


Figure 6. Drought severity (Standardized Precipitation and Evapotranspiration Index) and drought frequency (number of droughts occurred within 10 years preceding to extreme drought) over the two periods across the three site types. The error bars represent the mean \pm standard error ($n=30$). The letters on top of the bars show the results of the post hoc Tukey multiple comparison test with a threshold <0.05 for statistical significance. LEHP: low-elevation sites with high productivity, MELP: mid-elevation sites with low productivity, and HELP: high-elevation sites with low productivity.