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(Article begins on next page)

1 **Thinning improves growth and resilience after severe droughts in *Quercus***
2 ***subpyrenaica* coppice forests in the Spanish Pre-Pyrenees**

3

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12 **Abstract**

13 During the past years, growth and productivity of different oak species have been constrained by
14 water shortage in seasonally dry regions such as the Mediterranean Basin. Thinning could improve
15 oak radial growth in these drought-prone regions through the reduction of tree competition for soil
16 water in summer. However, we still lack adequate, long-term assessments on how lasting are thinning
17 treatments effects and to what extent they contribute to oak growth recovery after drought. Here we
18 aim: (i) to study the radial growth sensitivity to drought of *Quercus subpyrenaica* in the Spanish Pre-
19 Pyrenees, and (ii) to verify if thinning represents a suitable option to enhance growth resistance to
20 drought and post-drought growth recovery. We analysed basal area increment (BAI) trends in the
21 period 1960-2020 of formerly coppiced oak stands thinned in 1984 and compared them with
22 unthinned plots and also with coexisting Scots pine (*Pinus sylvestris*) growing in thinned plots. We
23 used the Standardized Precipitation Evapotranspiration Index (SPEI) to estimate the severity of
24 droughts and we also assessed climate-growth relationships. Oaks in thinned plots showed higher
25 BAI (369 mm²) than those in unthinned plots (221 mm²). Growth rates remained higher in thinned
26 than in unthinned plots also under severe drought stress. A severe summer drought in 1986 caused
27 abrupt BAI reductions in both oaks (- 40.5%) and pines (- 40.1%). The positive effect of thinning on
28 growth lasted for over 20 years and slightly declined as canopies closed. In the thinned plots, trees
29 with smaller diameter showed the greatest growth release. Oaks in unthinned plots and Scots pine
30 were more sensitive to short-term droughts in terms of growth reduction than oaks in thinned plots,
31 while long term droughts have similar effects on oaks from both thinned and unthinned plots. Oaks
32 were resilient to drought, showing recovery periods lasting from 1 to 2 years in both thinned and
33 unthinned plots. However, intense and prolonged droughts could strongly reverse the expected
34 growth enhancement of thinned plots, and a greater frequency of droughts would limit coppice growth
35 and productivity thus lengthening the rotation periods.

36 **Key words:** Mediterranean oaks, dendroecology, SPEI, release, resilience.

1. Introduction

Under a climate warming scenario, there is a greater likelihood of air temperatures and evapotranspiration rate exceeding the optimum range for many tree species, leading to range contractions in drought-prone regions (Thuiller 2004, Wang et al. 2018). In seasonally dry Mediterranean regions, models predict greater susceptibility to climate warming and drought for winter deciduous, ring-porous oaks, often dominant in mesic sites (Benito Garzón et al. 2008, de Dios et al. 2009, Acácio et al. 2017, Vila-Viçosa et al. 2020). However, we lack field data to test these predictions and to assess the sensitivity to drought of oaks given their ecological and socio-economic relevance in Mediterranean regions.

In recent years, dieback and mortality related to drought events have been reported in southern European deciduous oak forests, mainly in Spain and Italy (Amorini et al. 1996, Camarero et al. 2016, Colangelo et al. 2017, Gentilesca et al. 2017, Lloret et al. 2022). Under drought stress, deciduous, ring-porous oaks may osmotically adjust their tissues to continue to draw water into the leaves and keep high photosynthesis rates (anisohydry), increasing the risk of damage due to hydraulic failure since most of the stem conductivity depends on vessels located in the last-formed ring (Novick et al. 2022, Kaproth and Cavender-Bares 2016). In these species, stem radial increment is reduced in drought years, as well as mean lumen area of earlywood vessels thus decreasing hydraulic conductivity (Eilmann et al. 2006).

The effects of drought events on trees and forests can be assessed through the analysis of resilience components, and tree-ring data constitute one of the main valuable proxies for this purpose (Lloret et al. 2011). Resilience is defined as the capacity of ecosystems, communities, or individuals to recover after disturbance and regain its pre-disturbance structure and function (Scheffer et al. 2001, Folke et al. 2004). Several dendroecological studies have shown how drought severity is the major factor influencing radial growth resilience to drought (e.g., Gazol et al. 2018). How oaks respond to climate (drought) also depend on both, external and internal constraints. For example, site characteristics may modify soil water availability resulting in a persisting environmental constraint for tree growth, as demonstrated in *Quercus pubescens* Willd on limestone bedrock (Vodnik et al. 2019). In addition, the risk of drought-induced dieback may be size-dependent, with canopy defoliation and mortality risk increasing with decreasing height and radial growth rate as found in *Quercus faginea* Lam. (Camarero et al. 2016). Drought-induced dieback leads to cascading effects on oak forests and associated species because it not only reduces tree growth but vitality since it may also increase tree vulnerability to biotic stressors such as insect defoliators and fungal pathogens (Wargo 1996; Thomas et al. 2002; Canelo et al. 2021).

70 In Spain, winter-deciduous oaks such as *Q. faginea*, *Q. pubescens* and *Quercus pyrenaica* Willd.
71 dominate many formerly coppiced forests, which comprise about 20% of the total forest area (Serrada
72 et al. 1992, Cañellas et al. 2004). In the past, these oak coppices played relevant socio-economic roles
73 in Mediterranean countries, primarily providing firewood and charcoal but also ensuring grazing for
74 livestock in wood-pasture mixed systems. However, the withdrawal of these traditional uses and of
75 regular coppicing has reduced stem radial growth rate making these overaged stands prone to drought-
76 induced dieback (Corcuera et al. 2006). The management of such coppice forests is a key forestry
77 issue, especially in the Mediterranean countries where scenarios of warmer and drier climate
78 conditions are forecasted (Vila-Viçosa et al. 2020).

79 Thinning could reduce the impact of drought in coppiced forests that enter the stem exclusion
80 stage, reducing intra- and inter-species competition between trees for water (Cabon et al. 2018;
81 Gavinet et al. 2020). Canopy openings following thinning improve light conditions and enhance
82 coppice above-ground growth with an abrupt increase in tree growth (Müllerová et al. 2016; Hepner
83 et al. 2020). Furthermore, comparing growth responses to climate variability between thinned and
84 unthinned stands would provide a reliable assessment on post-thinning resilience to drought.
85 However, we still lack suitable assessments of post-drought growth responses after thinning and
86 drought to discern if post-thinning growth enhancement is transitory and linked to drought alleviation.

87 In this work we aimed: (i) to evaluate the effects of thinning on radial growth in treated and
88 untreated *Q. subpyrenaica* formerly coppiced stands; and (ii) to assess if thinning can enhance
89 growth and improve resilience by alleviating drought stress. Our hypothesis is that thinning can
90 increase resistance to drought impact and improve resilience (post-drought recovery) of trees to
91 severe water deficit by reducing tree-to-tree competition for soil water and light. We compared oak
92 growth responses to thinning and drought and used as reference Scots pine (*Pinus sylvestris* L) trees
93 inhabiting thinned and unthinned stands.

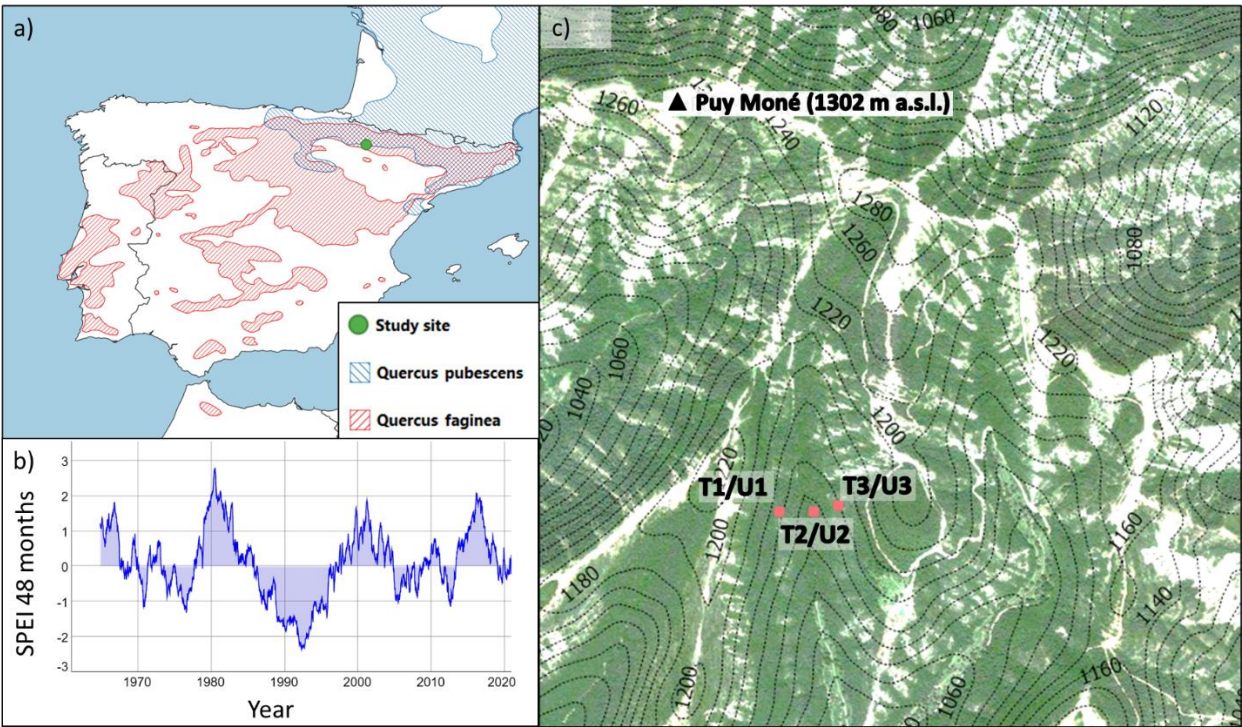
94 **2. Material and methods**

95 **2.1 Study area and species**

96 In North-eastern Spain, *Q. pubescens* and *Q. faginea* form a major biogeographic transition between
97 the northern Eurosiberian and southern Mediterranean regions subjected to seasonal summer drought
98 (Loidi and Herrera 1990). *Q. pubescens* is a sub-Mediterranean species present in sites with summer
99 precipitation higher than 150 mm and altitude range between 400 and 1500 m (Ruiz de la Torre and
100 Ceballos 1979). *Q. faginea* is a Mediterranean oak restricted to Morocco and Iberian Peninsula,
101 mostly in sites with basic soils, summer precipitation higher than 100 mm and altitudes between 600-
102 1200 m a.s.l. (Ruiz de la Torre and Ceballos 1979). The contact areas between both species allowed
103 their mixing and the resulting hybrid was named *Quercus subpyrenaica* E.H. del Villar (Amaral

104 Franco 1990), which may be also regarded as a *Q. pubescens* subspecies (Govaerts and Frodin 1998).
 105 Currently, *Q. subpyrenaica* populations are mainly found in the Central and Western Spanish Pre-
 106 Pyrenees, where usually form mixed forests with Scots pine.

107 The study site is located in one of these Spanish Pre-Pyrenean ranges (Sierra de Luesia-Sto.
 108 Domingo) near the “Puy Moné” peak (1302 m a.s.l.), Aragón region (**Fig. 1a**). The main forest type
 109 is a *Q. subpyrenaica* (*Qs*) mixed forest, whit *Acer campestre* L., *Acer opalus* Mill., *Pinus sylvestris*
 110 L. and *Fagus sylvatica* L. in the most mesic sites (valley bottoms, N-oriented slopes) and *Arbutus*
 111 *unedo* L. in warm-dry sites (S-oriented slopes). Other less abundant woody species are among trees
 112 *Ilex aquifolium* L., *Crataegus monogyna* Jacq., *Sorbus torminalis* L., among shrubs *Buxus*
 113 *sempervirens* L. and *Juniperus communis* L., and the vine *Amelanchier ovalis* Medik. Bioclimate in
 114 this region is temperate oceanic (Sub-Mediterranean variant). The mean annual temperature is 10.4
 115 °C whereas mean annual precipitation is 795 mm, with a mean annual water balance of -16 mm
 116 (Spanish Meteorological Agency AEMET, period 1961-2020 period). Weekly values of the
 117 Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2017), calculated
 118 on 48-month long scales, were high in 1978–1985 and low in 1985–1996 indicating wet and dry
 119 conditions, respectively (**Fig. 1b**).



120
 121 **Figure 1.** (a) Location of the study site and distribution range of *Q. pubescens* and *Q. faginea* in the Iberian
 122 Peninsula (Caudullo et al. 2017). (b) SPEI calculated on 48-month scale in study site area (Vicente-Serrano et
 123 al. 2017). (c) Location of sampled plots: east-facing side (T1/U1), valley floor (T2/U2) and west-facing side
 124 (T3/U3).

125 2.2 Field sampling

126 Thinning was carried out in 1984 on three squared plots of 100 m² in *Q. subpyrenaica* coppice stands.
127 The basal area percentage removed in the thinning was 50%, corresponding to about 20-30 m² ha⁻¹.
128 The three thinned plots have different topographic features within the study area slope (SE and SW
129 aspects, valley floor). In each thinned plot (T1, T2 and T3) structural parameters (dbh, diameter at
130 breast height; height) were measured, and tree increment cores were collected. Cores and
131 measurements were also collected in nearby unthinned plots (U1, U2, U3) of the same size and with
132 similar topographic features than T1, T2 and T3, respectively. Sampling with the same protocol was
133 repeated at all plots in 2003/2004 and 2021, except for the T3 plot which was surveyed only in 2003.

134 For each plot and woody species, we calculated mean dbh and height, tree density and total basal
135 area (**Table 1**). We also calculated species richness (S) and species diversity (Shannon H' index)
136 considering all woody plant species sampled within each plot.

137 2.3 Tree-ring data processing

138 All *Q. subpyrenaica* trees inside each plot were cored using a 0.5-mm increment borer (Haglof,
139 Sweden). For each tree, 2 cores were extracted at breast height (1.3 m) from the thickest stems of
140 each multi-stemmed individual. Additional cores were also collected from *P. sylvestris* trees located
141 in T1. In total, we sampled 145 oaks (71 trees in thinned plots and 74 trees in unthinned plots) and
142 12 pines. We considered the Scots pine series because pines were present in formerly thinned plots
143 and could be used as a reference growth data to detect post-thinning growth enhancements.

144 We mounted all cores on wooden supports after air drying and polished them with progressively
145 finer sandpapers. We visually cross-dated each core and then measured ring widths using a semi-
146 automatic system (LINTAB-TSAP, Rinntech, Germany) at 0.01 mm accuracy. We used the
147 COFECHA software to check the visual cross-dating (Holmes 1983). Next, tree-ring width series
148 measured from the same tree were transformed into basal area increment (BAI) series and averaged
149 for each tree using the *bai.in* function contained in *dplR* package (Bunn 2008) of R software (R
150 Development Core Team, 2020).

151 2.4 Growth release detection

152 To detect potential growth releases following the 1984 thinning, BAI series were analysed. The
153 95% confidence interval of mean BAI series in thinned and unthinned plots was calculated using
154 1000 bootstrap resampling. Growth release following canopy opening in 1984 was estimated by
155 calculating the percentage of BAI change (BC). For each individual tree, the BC was calculated
156 comparing mean BAI values in the 1981–1984 and 1985–1988 periods using the equation [1] where

M1 is the 4-year mean BAI including the thinning year (period 1981–1984) and M2 is the following 4-year mean (1985–1988 period).

$$BC = [(M2-M1) / M1] \times 100 \quad [1]$$

This approach is similar to the growth averaging method (Nowacki and Abrams 1997) based on comparing running 10-year ring-width means and used to detect growth releases or suppressions.

Table 1. Topographic and structural characteristics of thinned (T1, T2 and T3) and unthinned (U1, U2 and U3) sampled plots. Woody species abbreviations: *Ac*, *Acer campestre*; *Ao*, *Acer opalus*; *Au*, *Arbutus unedo*; *Av*, *Amelanchier ovalis*; *Bs*, *Buxus sempervirens*; *Cm*, *Crataegus monogyna*; *Ia*, *Ilex aquifolium*; *Jc*, *Juniperus communis*; *Ps*, *Pinus sylvestris*; *Qi*, *Quercus ilex*; *Qs*, *Quercus subpyrenaica*. Variables' abbreviations: S, species richness; H', diversity.

Plot	Elevation (m a.s.l.)	Slope (°)	Aspect	Density (No. stems ha ⁻¹)	Qs density (No. stems ha ⁻¹)	Total basal area (m ² ha ⁻¹)	Qs basal area (m ² ha ⁻¹)	Qs mean diameter (cm)	Qs domin ant height (m)	Woody species	S	H'
T1	1150	25	SE	3200	1800	44.35	41.74	17.2	13.5	Qs, Bs, Av, St, Ia, Ac, Ps	7	1.33
T2	1110	6	S	5900	1500	91.19	63.47	23.2	21.5	Qs, Bs, Ao, Ia, Fs	5	1.29
T3	1140	20	SW	2800	1500	21.75	14.31	11.0	14.0	Qs, Qi, Au, Cm	4	1.44
U1	1150	25	SE	7300	4400	56.92	53.45	12.4	11.0	Qs, Bs, Jc, Cm, Ia	5	0.82
U2	1110	6	S	6900	3200	52.78	48.15	13.8	12.0	Qs, Bs, Jc, Ps	4	0.87
U3	1140	20	SW	5900	3300	31.76	22.78	9.4	11.5	Qs, Qi, Au, Cm	4	1.6

167

168

169 2.5 Growth responses to drought

170 To analyse growth responses to drought we compared detrended BAI series and the SPEI drought
 171 index. First, the BAI series were detrended by fitting cubic spline functions to remove the age-, size-
 172 and disturbance-related trends and to emphasize the high-frequency growth variability (Cook et al.
 173 1990). We set the smoothing spline rigidity at 10 years and its wavelength cut-off value at 50%. We
 174 detrended all measured series dividing observed by fitted values to obtain dimensionless BAI indices.
 175 Three mean site chronologies were developed with a minimum sample depth of 10 series: (i) a *Q.*
 176 *subpyrenaica* chronology in thinned plots, (ii) a *Q. subpyrenaica* chronology in unthinned plots, and

177 (iii) a *P. sylvestris* chronology. Mean standard chronologies were obtained averaging individual BAI
178 indexed series using a bi-weight robust method (Fritts 1976).

179 For climate-growth analyses we used mean standard chronologies and monthly SPEI indices
180 calculated on 1-, 3-, 6- and 9-months. SPEI data correspond to the 1.1-km² gridded SPEI dataset for
181 Spain (Vicente-Serrano et al. 2017). Correlation values were calculated between monthly SPEI and
182 indexed BAI for all the months of the vegetative period, April to November, in the post-thinning,
183 common period 1984–2020. The stability of the strongest climate signals detected in this analysis
184 was assessed by calculating moving response coefficients using 30-year moving windows and a 1-
185 year offset. Function parameters were bootstrapped to calculate their significance and confidence
186 intervals. This analysis was done using the treeclim R package (Zang and Biondi 2015).

187 Finally, potential severe drought events were detected based on a SPEI threshold of -1.28 (Agnew,
188 2000). For these years (1967, 1986, 1989, 1995 and 2012) the Lloret resilience components (Lloret
189 et al. 2011), i.e. resistance (R_t), recovery (R_c), resilience (R_s) and relative resilience (RRs) indices,
190 and the growth recovery time (GRT, Thurm et al. 2016) were calculated on individual detrended BAI
191 series using the “*res.comp*” function in “*pointRes*” R package (van der Maaten-Theunissen et al. 2015).
192 We considered 4 years of pre- and post-disturbance for calculating resilience components and
193 considered the maximum length of the recovery period equal to 10 years.

194 **2.6 Variability of resilience components**

195 Components of oak trees resilience (R_t , R_c , R_s and RRs) relative to drought events were used as
196 response variables for each Generalized Linear Mixed-Effects (GLME) model applied, using the
197 following predictors as fixed effects: (i) tree age, (ii) tree dbh, (iii) mean ring-width increment (RW),
198 (iv) mean sensitivity (MS), a measure of the relative change in width between consecutive rings (Fritts
199 1976), and (v) individual climate-growth correlation values (CorrSPEI). Treatment (unthinned
200 /thinned) was used as dummy variable to search for response differences. Then, separate models for
201 thinned and unthinned plots were fitted. Parameters (i), (ii), (iii) and (iv) refer to reconstructed values
202 at the date of each drought events, based on ring-width measurements. MS was calculated using
203 “*sensI*” function of the “*dplR*” R package (Bunn 2008). CorrSPEI is to the correlation value between
204 each tree indexed BAI series and the SPEI within the common period 1984–2002 using the Pearson’s
205 coefficient. This 19-year interval follows the thinning and was selected to include most of the BAI
206 series from trees sampled in 2003. To avoid multicollinearity between predictors, we considered only
207 a specific period for the SPEI computation, choosing the months that returned greater significance
208 based on the results of the previous analysis (chapter 2.5). The Variance Inflation Factor (VIF) was
209 used to detect multicollinearity among predictors considering a threshold of $VIF > 5$ for presence of
210 multicollinearity. All predictors were standardized to account for differences in measurement units.

211 The plot aspect was considered as random effect. Since the response variable (tree growth resistance)
212 did not satisfy the normal distribution criterion (Shapiro–Wilk test), the gamma family was set in the
213 GLMEs (**Fig. S1**). This analysis was carried out using the *glmer* function of the *lme4* R package
214 (Bates et al. 2007). Marginal and conditional R^2 values (R^2_m and R^2_c , respectively), accounting for
215 the variability due to fixed and fixed plus random factors, respectively, of fitted models were
216 computed using “*r2_nakagawa*” function of the “*performance*” R package (Lüdecke et al. 2021). VIF
217 was calculated using the *vif* function in the *car* R package (Fox et al. 2007).

218 **3. Results**

219 **3.1 Quantification of release events in thinned plots**

220 Sampled oak trees were relatively young, with a mean age of 43 years in thinned plots and of 51 years
221 in unthinned ones. In both cases, oaks presented both positive trends of mean BAI series up to the
222 1970s, representing the vigorous juvenile phase of growth during a wet-cool decade (**Fig. 2**). Scots
223 pines showed higher growth rates than oaks, but also more interannual variability, with an exceptional
224 BAI reduction in years 1992-1993 (**Fig. 2b**). In 1989, both species and plots featured a drop in BAI
225 due to an exceptional dry year.

226 After 1984, oaks in thinned plots showed a growth release. For the following years, up to 2004 the
227 oaks BAI values remained higher in thinned plots. The mean BAI change (BC) of oaks in 1984 for
228 thinned plots was 100%, but close to 0% for Scots pines and oaks in unthinned plots (**Fig. 3a**). The
229 differences between the first and third quartiles in BC values were much larger in the thinned plots
230 suggesting greater individual variability following the treatment. Trees featuring higher release levels
231 were the ones which, at the date of thinning, had smaller diameters (**Fig. 3b**). Trees DBH in 1984 and
232 BC were negatively related in thinned plots ($r = -0.63$, $p < 0.05$).

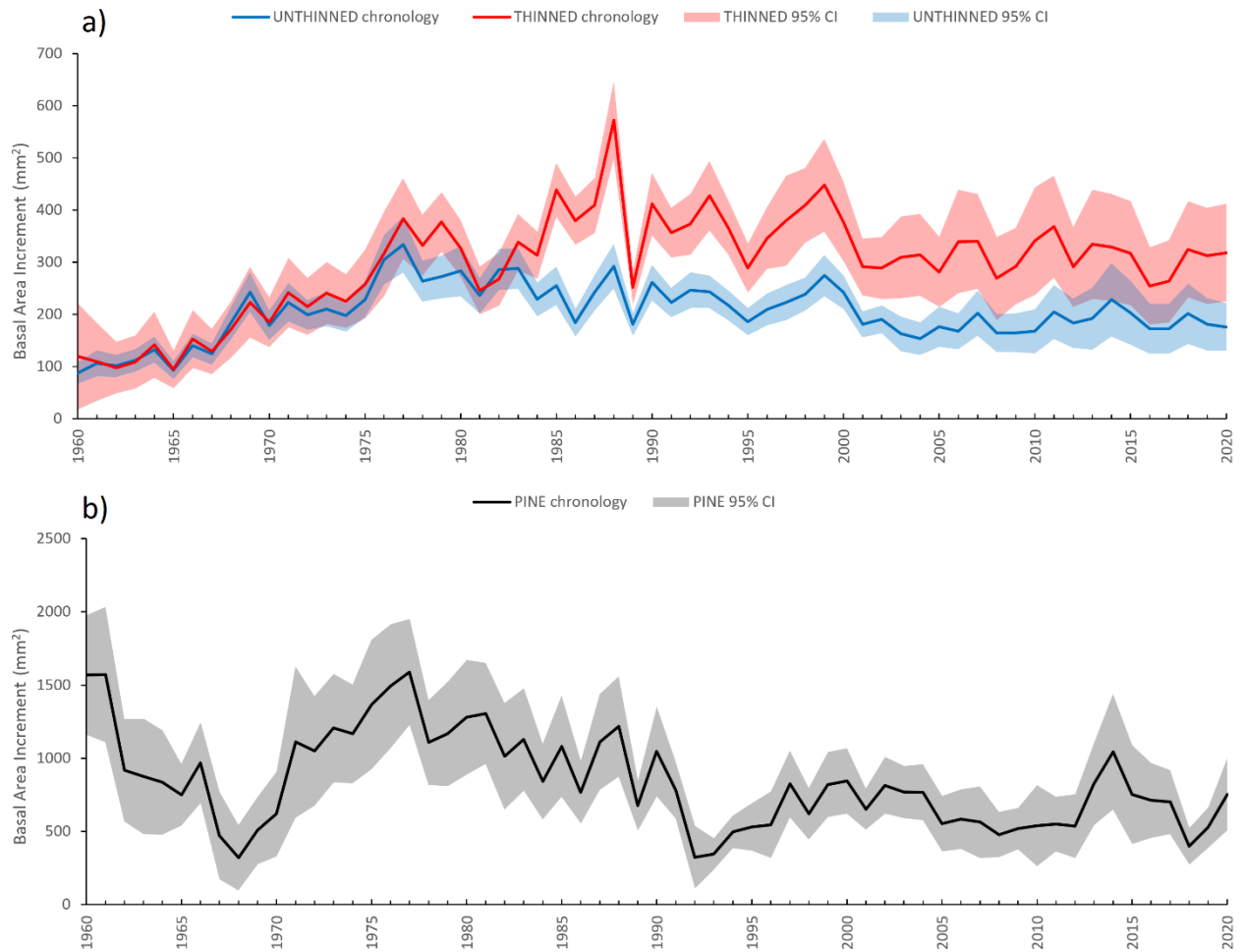


Figure 2. a) Basal area increment (BAI) chronologies of oaks in thinned (red line) and unthinned (blue line) plots and bootstrapped confidence intervals (95% CIs). b) BAI chronology of Scots pines and bootstrapped confidence intervals (95% CIs).

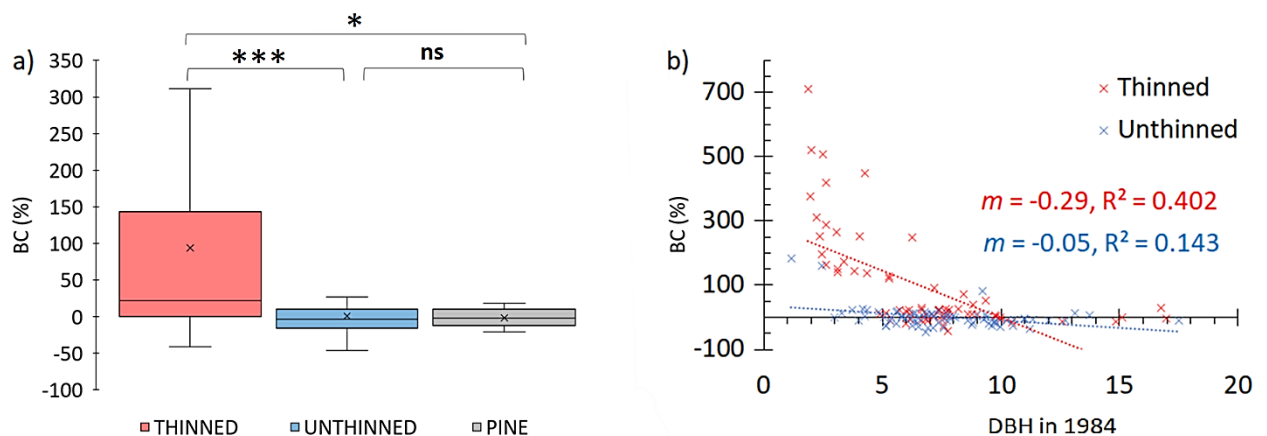


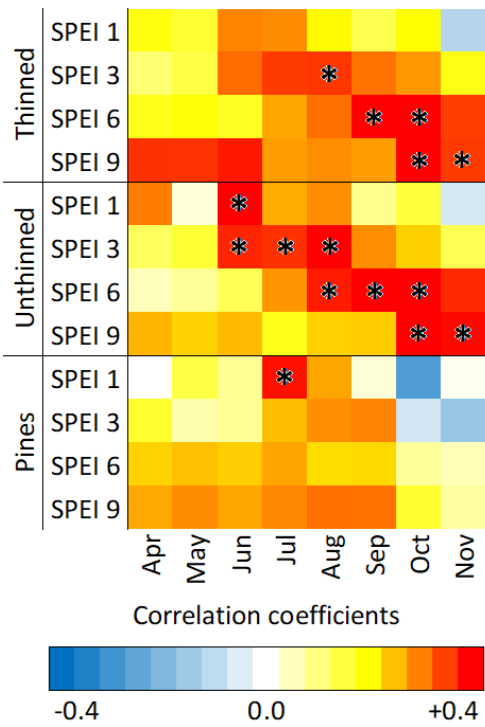
Figure 3: (a) Box plots of basal area increment (BAI) change (BC) after the thinning in 1984 in thinned and unthinned oak plots and in *P. sylvestris* (pine) series. Significant differences in BC (%) between groups were tested with paired two-sided Student's t-Test. Significance levels: ns (not significant) $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. (b) Scatter plot relating oak diameter (DBH) in 1984 with BAI change (BC) in thinned (red cross) and unthinned (blue cross) plots; the slope of the lines is denoted by the letter m .

245 **3.2 Growth response to drought events**

246 In the post thinning interval (1984–2020), we found a significant BAI response to the 1-month SPEI
 247 values for June in unthinned plots, whereas no significant correlation was found for thinned plots
 248 indicating a low responsiveness to short term changes in soil water availability (**Fig. 4**). The highest
 249 and significant correlation coefficients in *P. sylvestris* trees were found between indexed BAI and
 250 July 1-month SPEI, indicating a higher sensitivity to shorter drought events than oaks in thinned plots
 251 and a more similar response to oaks without thinning. The 3-month (June, July, and August) SPEI
 252 showed positive relationships with oak BAI for unthinned plots and only in August for thinned plots.
 253 Correlation coefficients for oaks in thinned and unthinned plots were high and significant for October
 254 6- and 9-month long SPEIs. The moving correlation analyses revealed a progressive loss of
 255 significance of the correlations with the June 1-month SPEI in thinned plots, while the values
 256 remained higher and significant in the unthinned plots. However, no difference between thinned and
 257 unthinned plots for 6- and 9-month long SPEIs was found in moving correlation analyses (**Figs. 5** and
 258 **S3**).

259 Exceptional dry growing seasons, with SPEI below the threshold of -1.28, occurred in 1967, 1986,
 260 1989, 1995 and 2012 (**Fig. S2**). In terms of resistance, the 1989 drought affected more severely
 261 studied trees, causing abrupt BAI growth reductions in both oaks (-40.5%) and pines (-40.1%). On
 262 the other hand, the 2012 drought event did not severely reduce growth of oaks and had a low effect
 263 on pines. *P. sylvestris* series showed remarkable differences with oaks in 1967 and 1995 (**Fig. 6**),
 264 when their resistance to drought was lower and higher than oaks, respectively.

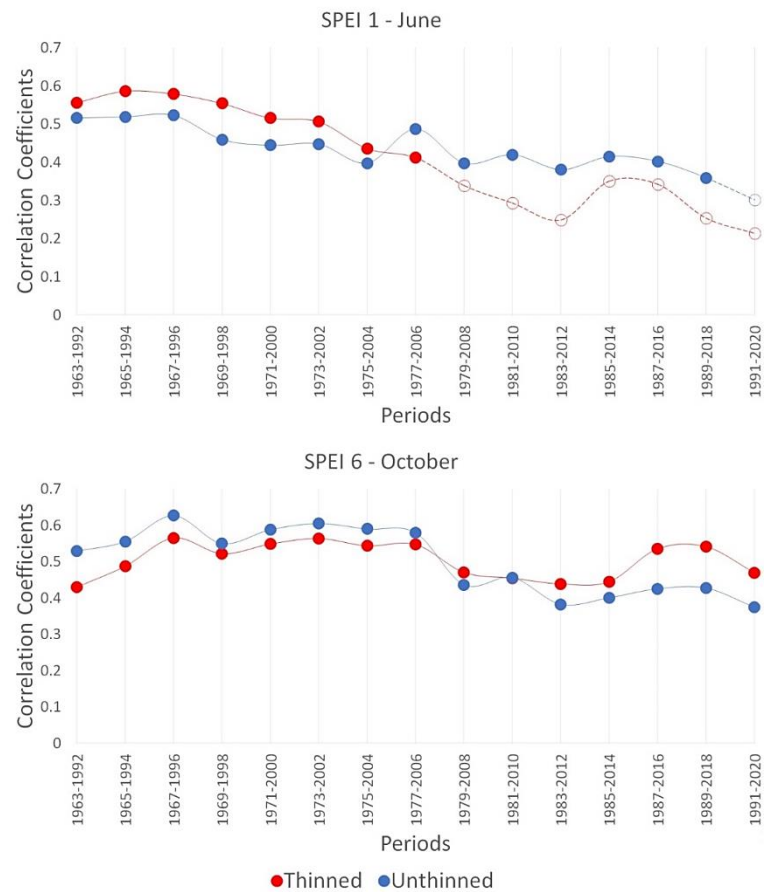
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266

267 **Figure 4.** Correlation coefficients between mean indexed BAI standard chronologies and 1-, 3-, 6- and 9-
 268 month SPEI index, for the period 1984-2020. Asterisks are overlapped when 95% bootstrap confidence interval
 269 was significant.

270 Generally, oaks and pines have high recovery rates ($R_c > 1$) after drought (**Fig. 6**). Consequently,
 271 four years after the drought events BAI values were close to pre-disturbance levels, with resilience
 272 values close to one. On average, recovery periods for both pines and oaks occurred in one or two
 273 years, with exception of the 1967 drought when pines required four years and the ones in 1989 and
 274 1995 when most oaks needed more than two years to recover. Relative resilience indices showed
 275 distributions similarly to recovery indices (**Figs. 6 and S4**), and they were inversely proportional to
 276 the resistance index.



277 **Figure 5.** Pearson's correlation coefficients calculated using 30-year moving windows between mean indexed
 278 BAI standard chronologies and June 1-month SPEI index and October 6-month SPEI. Filled dots for significant
 279 95% bootstrap confidence interval. Period of analysis is 1963-2020. All results are plotted in Figure S3.
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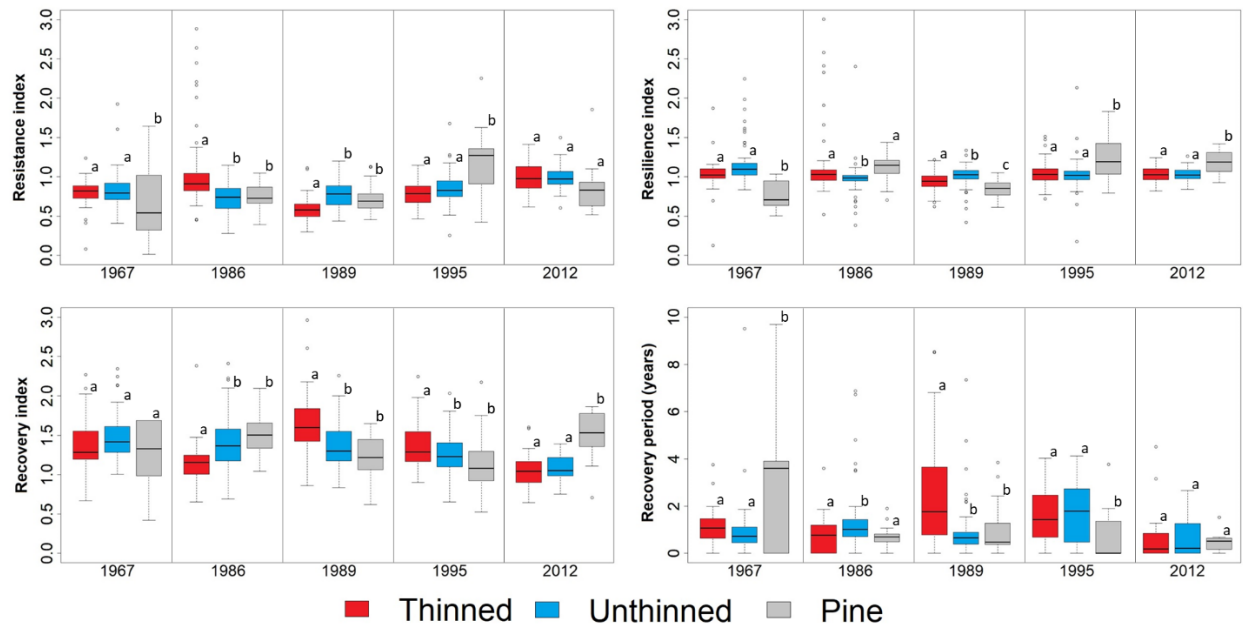


Figure 6. Boxplots showing resistance, recovery and resilience indices and recovery period (years) of *Q. subpyrenaica* trees in thinned (red) and unthinned (blue) plots and *P. sylvestris* trees (grey) for drought events of the years 1967, 1986, 1989, 1995 and 2012 (see also Fig. S2). Relative resilience indices calculated in *Q. subpyrenaica* trees in thinned and unthinned plots are plotted in Figures S4. Significant differences between groups (paired two-sided Student's t-Test with $\alpha=0.05$) were represented by overhead letters.

3.3 Variability of resilience components

The October 9-month SPEI index was selected as a main drought driver of oak growth for the computation of climate growth correlation at individual tree level in the common period 1984–2002 (CorrSPEI). Within this time interval, we analyzed three exceptional droughts (1986, 1989 and 1995; cf. **Fig. S2**) using GLMEs.

Generally, thinned plots showed higher resistance values in 1986 and lower in 1989 than unthinned plots (**Table 2**). In 1986 and 1989, RW had a significant negative effect over resistance in unthinned stands. In the second event, MS and CorrSPEI parameters presented negative influences on growth resistance, especially for thinned plots. In the 1995 drought, there was not significant difference among thinned and unthinned plots, resistance was negatively related to RW and MS. For the same event, the only parameter with significant weight was the correlation coefficient between SPEI and BAI in unthinned plots (**Table 2**).

Thinned plots showed a significantly lower resilience after the 1986 severe drought. However, larger oaks from thinned plots showed lower levels of relative resilience in the 1989 and higher in the 1995 drought. Mean sensitivity had a significant positive (1986) and negative (1989) weight on resilience, especially for thinned stands. CorrSPEI was often positively related to resilience, especially in 1989 and 1995. Finally, the relative resilience was not influenced by either tree DBH or

305 tree age, but it depended more on CorrSPEI (positive relationship) and slightly on ring width and
306 mean sensitivity (**Table 2**).

307 In all models performed, slope aspect always explained a very little portion of the variance.
308 Moreover, the values of conditional and marginal R^2 were similar indicating that most variability in
309 growth resistance to drought was accounted for by fixed factors (**Table 2**).

310 **Table 2.** Summary statistics (*t* values) of Generalized Linear Mixed-Effects models fitting tree growth resistance, recovery, resilience and relative resilience in
311 the three drought years studied (1986, 1989 and 1995). Variables are abbreviated as: dbh, diameter at breast height; RW, mean ring width; MS, mean sensitivity;
312 CorrSPEI, correlation coefficients of October 9-month SPEI index and the BAI chronology. In the case of fixed factors, NA indicates the parameter not included
313 in the model, whereas in the case of the random factor (slope aspect) NA was used when the calculation of the conditional R^2 (R^2_c) was not possible due to
314 variance equal to 0. Bold values are statistically significant. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.
315

Resistance	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	+8.73***	+11.15***	+5.59***	+15.51***	+9.29***	+11.16***	+12.10***	+11.16***	+7.89***
Age	NA	NA	+0.31	NA	NA	-1.81	NA	NA	+0.28
dbh	-1.26	-1.36	NA	-2.15*	-0.18	NA	+1.00	+2.04*	NA
RW	-0.81	-0.38	-1.99*	-0.19	-0.83	-2.30*	-2.21*	-2.92**	-0.99
MS	+0.40	+0.01	-0.44	-3.65***	-3.07**	-1.36	-4.05***	-3.81***	-0.92
CorrSPEI	-0.33	-1.12	+0.37	-2.75**	-1.69	-2.60**	-1.43	-0.39	-1.85
Thinning (dummy)	+3.31***	NA	NA	-5.47***	NA	NA	-0.72	NA	NA
Slope aspect variance	<0.01	0	<0.01	<0.01	0.01	0	<0.01	<0.01	<0.01
R ² m	0.07	0.04	0.03	0.18	0.05	0.15	0.13	0.21	0.06
R ² c	0.09	NA	0.07	0.19	0.07	NA	0.14	0.26	0.09

Recovery	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	+9.36***	+8.50***	+5.79***	+8.082***	+7.67***	+5.69***	+8.52***	+9.72***	+5.93***
Age	NA	NA	NA	NA	NA	+0.18	NA	NA	-0.73
dbh	+0.45	<i>+0.91</i>	+0.53	-0.16	-0.41	NA	-1.69	-1.13	NA
RW	-1.61	-1.67	-1.56	+1.25	+1.33	+0.57	+2.19*	+1.99*	+0.07
MS	+0.06	-0.50	+0.52	+1.13	+0.43	+0.93	+3.62***	+2.95**	+1.49
CorrSPEI	+1.28	+0.98	+1.37	+3.43***	+1.62	+2.89***	+6.06***	+2.45*	+5.62***
Thinning (dummy)	-4.41***	NA	NA	+3.31***	NA	NA	-0.18	NA	NA
Slope aspect variance	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.00	<0.01
R ² m	0.268	0.107	0.090	0.426	0.247	0.189	0.446	0.457	0.352
R ² c	0.334	0.259	0.175	0.448	0.303	0.247	0.462	NA	0.410

Resilience	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	+8.01***	+6.01***	+7.35***	+18.35***	+19.00***	+11.44***	+11.74***	+11.76***	+8.64***
Age	NA	NA	NA	NA	NA	-1.63	NA	NA	-1.07
dbh	-2.35*	-1.25	+1.29	-2.92**	-1.94	NA	-1.61	1.85	NA
RW	+1.91	+1.66	-2.26*	+0.75	+1.93	-2.10*	-0.11	-0.04	-2.34*
MS	+3.77***	+2.36*	+0.32	-2.27*	-3.28**	+0.72	-0.22	+0.04	-0.16
CorrSPEI	+0.71	-0.60	+2.12*	+2.28*	+1.99*	+1.73	+4.38***	+2.16*	+3.88***
Thinning (dummy)	+0.47	NA	NA	-2.65**	NA	NA	+0.53	NA	NA
Slope aspect variance	0.00	<0.01	<0.01	<0.01	0.00	<0.01	<0.01	<0.01	0.00
R ² m	0.293	0.319	0.106	0.176	0.188	0.147	0.147	0.129	0.243
R ² c	NA	0.336	0.140	0.185	NA	0.185	0.165	0.205	NA

Relative resilience	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	+20.00***	+15.42	+13.73***	+21.72***	+18.49***	+13.53***	+21.72***	+13.69***	+13.84***
Age	NA	NA	NA	NA	NA	-0.37	NA	NA	-0.39
dbh	+0.06	+0.28	+1.26	-1.48	-1.32	NA	-1.48	-0.85	NA
RW	-1.43	-0.76	-2.37*	+1.72	+1.76	-1.69	1.72	+2.23*	-0.87
MS	+1.29	+0.36	+1.00	+3.28**	-0.86	1.05	+3.28**	+2.18*	+1.88
CorrSPEI	+1.70	+0.84	+2.08*	+6.67***	1.65	+3.12**	+6.67***	+2.87**	+5.77***
Thinning (dummy)	-3.10**	NA	NA	0.05	NA	NA	0.05	NA	NA
Slope aspect variance	<0.00	<0.01	<0.01	<0.01	0.00	<0.01	<0.01	0.00	<0.01
R ² m	0.169	0.024	0.219	0.176	0.188	0.147	0.529	0.484	0.503
R ² c	0.231	0.152	0.226	0.185	NA	0.185	0.530	NA	0.505

317 **4. Discussion**

318 **4.1 Effects of thinning on oak radial growth**

319 Thinning enhanced radial growth in *Q. subpyrenaica* trees, an effect lasted for over 20 years and
320 slightly decreasing probably in relation to canopies closure. Other studies on other oak species
321 confirm the lasting duration of the positive effect of thinning on growth (Cutter et al. 1991; Mayor et
322 al. 1993; Cañellas et al 2004). The *Q. subpyrenaica* response after these treatments depended on stem
323 diameter, with smaller stems featuring more plastic response and showing a higher relative growth
324 improvement than larger individuals. This could be related to the suppressed position of the
325 dominated layer that promptly enhanced radial growth after the canopy opened by thinning. The
326 larger trees, which had already reached a dominant or codominant position within the stand, exhibited
327 fewer release effects. This response could be due to higher competition among stems of the same
328 individual, as reported by Corcuera et al. (2006) for multi-stemmed *Quercus pyrenaica* coppice trees.
329 Juodvalkis et al. (2005) also reported similar results demonstrating that an increase of tree volume
330 could be achieved only when thinning 10-30 years-old oak (*Quercus robur*) stands, whereas at older
331 ages the positive effect of thinning is buffered by overaging. On the other hand, the larger trees were
332 the most favoured by thinning due to their greater capacity of resource uptake (soil water and
333 nutrients) and allocation occurring after thinning in a study on *Q. pyrenaica* coppice stands in central
334 Spain (Cañellas et al 2004). However, an imbalance between stem diameter and parent root system
335 size could occur after a thinning treatment in coppice stands, resulting in smaller trees not necessarily
336 suppressed in root water uptake by bigger individuals.

337 **4.2 Effects of thinning on climate-growth relationships**

338 Since *Q. subpyrenaica* has shown a wide range of ecophysiological adjustments in response to
339 drought stress in experiments based on seedlings, even wider than their parental taxa (Himrane et al.
340 2004), it is important to assess the growth responses to water shortage of adult trees inhabiting
341 formerly coppiced forests as has been done in *Q. faginea* (Alla and Camarero 2012). In our study,
342 climate-growth analysis confirmed the key role of water availability in limiting tree stem growth, in
343 line with other studies on Mediterranean deciduous oaks (Corcuera et al. 2004, Camarero et al. 2016,
344 Martínez-Sancho et al. 2021). Growth and productivity of oaks was linked to more consistently to
345 longer (i.e 6 to 9 months) droughts. However, in unthinned plots growth was linked to early summer
346 (June) drought conditions, similarly to what Di Filippo et al. (2010) found in Turkey oak (*Quercus*
347 *cerris* L.). Moving windows analysis revealed that this effect was also significant in oaks located in
348 thinned plots, but it lost its significance following the thinning treatment. Correlations values between
349 oak growth and longer droughts (6- to 9-month SPEIs) did not show differences between thinned and
350 unthinned plots and remained stable even after treatment.

351 Scots pine growth exhibited positive correlations to 1-month July SPEI, therefore being more
352 sensitive to short-term droughts than *Q. subpyrenaica* in thinned plots. The different ecophysiological
353 strategies of coexisting pines and oaks to withstand summer drought were well described by Martín-
354 Gómez et al. (2017). They found that the anisohydric oaks presented a faster recovery of predawn
355 water potential after summer drought than the pines. This is probably associated with more accessible
356 and deeper soil water tables which could explain specific response to longer droughts. These authors
357 also reported a stronger negative effect of drought stress on long-term growth in pines, relying on
358 shallower soil water tables, compared with oaks.

359 In our study, the exceptional growth reduction featured in Scots pine in 1992-1993 period (**Fig.**
360 **2b**) was not related to severe drought conditions, suggesting an impact of other abiotic or biotic
361 disturbances such as the defoliator pine processionary moth, *Thaumetopoea pityocampa* (Camarero
362 et al. 2022). In addition, cold winter conditions (January and February were cold in 1992) could also
363 have contributed to the sharp decrease in Scots pine growth (Matisons et al. 2019).

364 **4.3 Impact of severe droughts on growth resilience**

365 The oak *Q. subpyrenaica* is a ring-porous species with anisohydric behavior, maintaining higher
366 transpiration and physiological activity under mild-to moderate drought conditions (Corcuera et al.
367 2004, Himrane et al. 2004, Tognetti et al. 2007). However, during very dry summer conditions, *Q.*
368 *subpyrenaica* reduces transpiration rates showing high recovery rates after the first seasonal
369 precipitation in early fall (Martín-Gómez et al. 2017). The exceptionally and successive droughts
370 detected in the study site from the 1980s onwards, also investigated by other authors for nearby
371 forested areas in Spain (Camarero et al. 2015, 2016, 2018; Manrique-Alba et al. 2022), could explain
372 an intensification of the coupling between oak growth and water deficit. Differently from *Q. ilex* and
373 *Q. faginea* mixed coppice forests in a drier area of eastern Spain (Camarero et al. 2016), *Q.*
374 *subpyrenaica* in our study site proved highly resistant to the 2012 drought event in both thinned and
375 unthinned plots, perhaps because it was less severe in the Spanish Pre-Pyrenees. The other selected
376 drought events affected differently studied plots: the 1967 and 1995 ones produced similar effects
377 regardless of thinnings, whereas in 1986 and 1989 the resistance values differed between thinned and
378 unthinned plots. Specifically, in 1986 the growth reduction on thinned oak plots was mitigated by the
379 release of the post-thinning phase. In 1989 drought induced a more pronounced growth reduction in
380 oaks of thinned plots. Nevertheless, also in concomitance of severe droughts events absolute BAI
381 values in thinned plots were significantly higher than those recorded in unthinned plots, in line with
382 the results obtain by Aldea et al. (2017) in thinned, mixed pine-oak stands.

383 Most trees recovered pre-disturbance growth levels within one or two years, confirming global
384 analyses of post-drought growth recovery (Anderegg et al. 2015), with wider interquartile ranges for

385 the recovery periods after the 1989 drought, when some oaks and pines took up to six years to fully
386 recover growth levels.

387 The fitted GLMEs confirmed the opposite influence of thinning on resilience components (Rs, Rc,
388 Rs and RR) in oak trees during the 1986 and 1989 droughts, while in 1995 the differences between
389 thinned and unthinned plots were not significant. Tree-level drought sensitivity assessed with
390 CorrSPEI generally had a higher weight than structural (DBH and age) and growth (RW and MS)
391 parameters on resilience components. As expected, CorrSPEI was negatively related to drought Rs
392 but positively related to Rc, Rs and RR. Oaks trees with larger DBH feature higher resilience against
393 severe droughts and shorten the time to regain pre-drought growth rates (Camarero et al., 2016;
394 Colangelo et al. 2017, González de Andrés et al. 2021). However, we are not able to claim a clear
395 role of stem diameter on resilience components, with an opposite effect during 1995 drought as
396 compared to 1986 and 1989 droughts.

397 Inter-annual growth variability estimated with mean sensitivity statistics (MS) is negatively related
398 with drought resistance only in thinned plots and for the 1989 and 1995 events. The growth release
399 following the thinning enhanced the MS in oaks trees making drought influence on growth more
400 noticeable. Instead, competition in unthinned plots explains the production of complacent growth
401 series and the lack of significance of MS in GLMs.

402 Soil and topographic features such as aspect and/or relative position of forest along the slope could
403 also influence the effect of drought on tree growth (Lloret et al 2004). In our study case, little
404 differences of slope aspects did not change oaks resilience components, with no differences detected
405 by GLMEs in sensitivity between SE- and wetter SW-oriented slopes. A larger number of plots
406 distributed at different aspects could help for better investigating this aspect.

407 Our results are supported by the outcomes of a recent meta-analysis showing a high variability of
408 stand competition influence over tree growth resilience after drought (Castagneri et al. 2022). Our
409 initial hypothesis of greater resistance and resilience of thinned plots oaks cannot be always
410 confirmed but only for the first severe drought occurred after the treatment. A possible explanation
411 is that forest management strategies such as thinning induce only short-term benefits but may not
412 result in long-term adaptation to global change, that could be achieved promoting changes in species
413 or genetic composition (Vilà-Cabrera et al. 2018).

414 **5. Conclusions**

415 *Q. subpyrenaica* stem radial growth showed a moderate post-thinning release especially in trees with
416 lower DBH. Thinning induced long-lasting growth increase, reversed only by severe droughts.
417 Following drought events reducing the amount of stored wood biomass, could lengthen the post-
418 drought recovery time (usually 1-2 years), postpone the turnover cycle and the timing of other
419 silvicultural treatments. At the same time, thinning could reduce competition between individuals for
420 soil water, causing dieback, especially in overaged coppice stands. We argue that future studies
421 should carefully plan and monitor thinning treatments in similar seasonally dry oak coppices which
422 probably respond more positively to thinning treatments carried out during wetter decades and in
423 regular intervals shorter than 20 years.

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