1 **Are pine-oak mixed stands in Mediterranean mountains more resilient**

2 **to drought than their monospecific counterparts?**

3 Francisco Muñoz-Gálvez[1], Asier Herrero[2], Esther Pérez-Corona[3], Enrique Andivia[3]

4 [1] Terrestrial Ecosystem Ecology and Conservation Research Group, Department of

5 Ecology, Universidad Autónoma de Madrid, Madrid, Spain.

6 [2] Forest Ecology and Restoration Group, Department of Life Sciences, University of

7 Alcala, Alcalá de Henares, Spain.

8 [3] Department of Biodiversity, Ecology and Evolution, Universidad Complutense de

9 Madrid, Madrid, Spain.

10   **Abstract**

11   Climate change projections point to an increase in the intensity and frequency of extreme

12   drought events with important negative impacts on forest functioning. Predicting these

13   impacts constitutes a crucial challenge for forest managers and for the maintenance of

14   ecosystem services supply. Promoting mixed stands seems a promising strategy for

15   adapting forest ecosystems to ongoing climate change. However, some uncertainty exists

16   regarding whether mixed stands can improve growth resilience to extreme drought events.

17   Here, we aim to assess tree growth response to drought in mixed and monospecific stands

18   of *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. in central Spain. We built tree-ring

19   chronologies, and evaluated tree growth sensitivity to water availability and growth

20   resilience components to extreme droughts using linear mixed models. We found

21   contrasting species- and climate-specific responses to admixture. *Q. pyrenaica* growth

22   was significantly higher in mixed than in monospecific stands in years without water

23   limitations, while *P. sylvestris* showed higher growth in mixed stands under dry

24   conditions. Consequently, *P. sylvestris* and *Q. pyrenaica* showed higher resistance and

25   recovery to drought in mixed than monospecific stands, respectively. However, *Q.*

26   *pyrenaica* was more resistant in monospecific than mixed stands. Our results highlight

27   the importance of water availability and species-specific responses when evaluating

28   admixture effects on drought vulnerability. Overall, we show positive effects of

29   admixture on tree growth and resilience components for both *P. sylvestris* and *Q.*

30   *pyrenaica*, supporting admixture as a management option for adaptation of Mediterranean

31   mountain forests to climate change.

32   **Keywords:** Climate change, complementarity, forest management, growth stability,

33   *Pinus sylvestris*, *Quercus pyrenaica*, tree diversity.

34

1. Introduction

Climate change is globally altering forest composition, structure and functioning (Allen et al., 2010, 2015; Ruiz-Benito et al., 2017), which ultimately compromises the provision of key ecosystem services to human well-being (Nelson et al., 2013). Mediterranean forests can be especially vulnerable ecosystems due to its high exposition to climate change (Lindner et al., 2010). Over the last century, temperature increased in the Mediterranean basin by 1.4 ºC (Cramer et al., 2018), exacerbating drought impacts on tree growth and triggering drought-induced mortality events (Greenwood et al., 2017; Gazol et al., 2018; Madrigal-González et al., 2018). Climate change scenarios project a worrisome increase of 2-5 ºC along 21st century coupled with a decrease in precipitation of up to 30%, and a higher frequency and intensity of extreme drought events (IPCC, 2018; Spinoni et al., 2018). Thus, there is an urgent need to improve our knowledge about forest response to extreme droughts and to adequate management strategies to enhance long-term forest resilience.

Admixture, i.e. the increase in tree species diversity, may contribute to stabilize forest functioning and ecosystem services supply in response to disturbances (Gamfeldt et al., 2013). Several studies have showed a positive relationship between tree diversity and forest productivity at different spatial scales (Paquette and Messier, 2010; Ruiz-Benito et al., 2014; Pretzsch et al., 2015, 2019; Liang et al., 2016; Jactel et al., 2018). Admixture can also stabilize forest productivity and reduce growth sensitivity to climatic variability (del Río et al., 2017). All this body of evidence has led to the promotion of mixed stands in forestry practice worldwide (Bolte et al., 2010). However, some studies have reported a decrease in the magnitude of the positive effect of tree diversity on forest productivity with drought stress (Jactel et al., 2018; Toïgo et al., 2015). Furthermore, there is some uncertainty regarding admixture effects on the stability of forest

60   productivity to extreme drought events (Grossiord, 2019). In this regard, growth

61   resilience, i.e. the capacity of individuals to restore pre-disturbance growth rates after a

62   disturbance (Holling, 1996; Lloret et al., 2011), is an increasingly adopted concept to

63   evaluate forest stability to extreme droughts (Nikinmaa et al., 2020). Despite some

64   evidence of positive effects of admixture on resilience to drought (Lebourgeois et al.,

65   2013; Gazol and Camarero, 2016; Steckel et al., 2020), other studies reported species- or

66   site-specific effects (Pretzsch et al., 2013; Grossiord et al., 2014; Mölder and Leuschner,

67   2014; Merlin et al., 2015; Granda et al., 2018; Jourdan et al., 2019a, 2019b). In addition,

68   few studies have been conducted in Mediterranean areas (Granda et al., 2018), hampering

69   our ability to make a correct assessment of admixture as an appropriate management

70   option for adaptation of Mediterranean forests to climate change.

71   Admixture positive effects on forest productivity are commonly interpreted on the

72   basis of complementarity, which includes both competition reduction and facilitation

73   mechanisms (Ammer, 2019). On one hand, competition reduction usually occurs through

74   niche partitioning, due to inter-specific differences in physiology, morphology and

75   phenology, leading to disparate resource acquisition strategies (Forrester, 2014; Forrester

76   and Bauhus, 2016). On the other hand, facilitation implies that one species increases the

77   performance of coexisting species (Callaway, 1995). Active hydraulic redistribution

78   (Querejeta et al., 2003; Zapater et al., 2011) and nocturnal water release (Prieto et al.,

79   2012) are examples of facilitative mechanisms that result in increased soil moisture.

80   These complementarity effects have been also associated with the biodiversity-stability

81   relationship (Loreau and de Mazancourt, 2013), although other mechanisms such as

82   temporal shifts in species interactions (del Río et al., 2017) and asynchronic species-

83   specific responses to environmental fluctuations (Morin et al., 2014) have been also

84   proposed.

85   Most of the research on complementarity effects on forest ecosystems have been

86 conducted in forests without severe water limitations, where light-related interactions

87 drive complementarity effects (e.g. Bayer et al., 2013; Pretzsch, 2014; Forrester and

88 Bauhus, 2016). In seasonally dry areas, such as the Mediterranean basin, admixture

89 positive effects rely on reducing competition for water and/or improving water

90 availability (Jucker et al., 2014; Ruiz-Benito et al., 2014). Mediterranean tree species

91 show a wide variety of water use strategies associated with different structural and

92 physiological adaptations, such as stomatal behaviour (isohydric vs. anisohydric species)

93 and rooting strategy (taproot vs superficial) (Zavala et al., 2000; Moreno-Gutiérrez et al.,

94 2012; del Castillo et al., 2016; Martín-Gómez et al., 2017). This suggests the existence of

95 complementarity mechanisms among species that would reduce competition for water in

96 mixed forests and thus, enhance resilience to extreme droughts. However, whether

97 admixture modifies tree responses to drought compared to monospecific stands is still

98 under debate (Grossiord, 2019).

99   Mediterranean Iberian forests are excellent models for the evaluation of admixture

100 effects on drought impacts (Vilà-Cabrera et al., 2018). Many of the current coniferous

101 forests of the Iberian Peninsula (mainly *Pinus* spp.) are the result of large-scale

102 afforestation policies during the 20th century (Vadell et al., 2016). The lack of subsequent

103 forest management has resulted in structurally and functionally homogeneous even-aged

104 dense stands (Villar-Salvador, 2016), which often show low growth rates (Gómez-

105 Aparicio et al., 2009), high mortality (Sánchez-Salguero et al., 2012), lack of regeneration

106 (Ruiz-Benito et al., 2012), and high vulnerability to fires and pests (Maestre and Cortina,

107 2004). In this context, the admixture of oaks (*Quercus* spp.) in pine monospecific stands

108 can be considered as a powerful tool to manage Mediterranean forests in the face of

109   climate change (Pausas et al., 2004), by both spreading drought-impact risk among

110   multiple species and beneficial complementarity effects.

111   In this study, we compared tree growth response to drought conditions in mixed

112   and monospecific stands of Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus*

113   *pyrenaica* Willd.) in central Spain. These species are frequently mixed in extensive areas

114   of Iberian mountains at the ecotone between monospecific pine and oak stands (Sánchez

115   de Dios et al., 2019). We employed a stand-level "triplet design" coupled with tree-ring

116   data to analyze the effect of water availability on tree growth at an annual scale in both

117   monospecific and mixed stands. Following this approach, we also quantified growth

118   resilience, and associated components (resistance and recovery), to extreme drought

119   events occurred during the last decades using the indices proposed by Lloret et al. (2011).

120   Due to functional differences between target species regarding shade tolerance, leaf habit,

121   rooting depth and water use strategies (del Castillo et al., 2016; Martín-Gómez et al.,

122   2017; Moreno-Gutiérrez et al., 2012), we hypothesized lower drought-induced growth

123   reductions and higher resilience to extreme droughts in mixed than monospecific stands

124   due to complementarity effects.

125   **2. MATERIAL AND METHODS**

126   **2.1. Study area**

127   The study was conducted in the Sierra de Guadarrama National Park, in the centre

128   of the Iberian Peninsula (40º 50' 26'' N; 3º 49' 34'' W). Climate is continental

129   Mediterranean, characterized by cold winters and warm and dry summers, with

130   precipitations concentrated in autumn and spring. Mean annual temperature and total

131   precipitation is 11.4ºC and 555.7 mm, respectively (period 1961-2018; data from CRU

132   TS3.10 database, Harris et al. (2014)). *P. sylvestris* is the dominant tree species at high

133   altitude, co-occurring with *Q. pyrenaica* at intermediate altitude (1,200-1,600 m a.s.l.),

134 although the later can also be found forming extensive monospecific stands. Understory

135 species vary with altitude, being *Pteridium aquilinum* ((L.) Kuhn)*, Genista florida* (L.),

136 *Ilex aquifolium* (L.) and *Crataegus monogyna* (Jacq.) the most representative species.

137 **2.2. Sampling design**

138   We selected six independent forest sites on the southern face of the Sierra de

139 Guadarrama at an altitude that ranged from 1,286 to 1,544 m a.s.l. (Table 1). At each site

140 we selected 15 stands of 20 x 20 m (0.04 ha) following a triplet design. Thus, we sampled

141 five monospecific stands of each species (100% of the basal area) and five mixed stands

142 (basal area of the dominant tree species was lower than 70%). Field sampling was carried

143 out from November 2018 to February 2019. We selected one tree in each monospecific

144 stand and two trees (one of each species) in mixed stands (hereinafter focal trees). Focal

145 trees were selected in the centre of the stand, and they were all dominant or co-dominant

146 with no sign of vigour decline (i.e. defoliation or dry branches) or physical damages (e.g.

147 due to snow or herbivory). In mixed stands, the distance between focal trees was lower

148 than 5 m. We recorded the diameter at breast height (DBH) of each target tree and each

149 neighboring tree within a circular plot of 7 m radius measured from the focal tree. We

150 calculated the basal area of the circular plot and the Lorimer's distance-independent

151 competition index (LCI) (Lorimer, 1983) as:

152
$$LCI_i = \sum_{j=1}^{n} DBH_j / DBH_i$$

153 where DBH_i is the diameter at breast height of the target tree i, and DBH_j is the diameter

154 at breast height of the neighboring tree j.

155 **2.3. Dendroecological methods**

156   We extracted one wood core per target tree at breast height using a Pressler

157   increment borer (5 mm; Haglöf, Sweden). Wood cores were processed following standard

158   dendrochronological methods (Fritts, 1976). First, wood cores were air-dried and glued

159   on wooden supports. Then, they were sanded using sandpapers of progressively finer

160   grains to maximize the visibility of the tree rings. Tree growth series were visually cross-

161   dated using pointer years (Yamaguchi, 1991). Wood cores were scanned at 1,200 dpi

162   resolution (EPSON® Perfection v800) and tree-ring widths were measured to the nearest

163   0.01 mm using ImageJ® (Schneider et al., 2012).

164   Ring-width series were converted to basal area increment (BAI) assuming stem

165   growth is approximately concentric:

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

167   where r_t and r_{t-1} are the stem radius at the end and at the beginning of a given annual ring,

168   respectively. BAI reflects whole tree growth better than the one-dimensional growth of

169   tree ring width (Biondi and Qeadan, 2008). We also quantified annual tree size as the

170   basal area of the tree for the whole BAI series, representing the increase in size with

171   ageing. Even though the oldest tree was dated to 1905, we selected as study period 1961-

172   2018 for the robustness of statistical analysis (70% of the target trees in 1961).

173   **2.4. Identification of extreme drought events**

174   We used the CRU TS3.10 database (Harris et al., 2014) to characterized the

175   climate of the study sites for the period 1961-2018. Annual mean temperature and annual

176   precipitation from this database were highly correlated (r = 0.89 and 0.74, respectively

177   using common years) with data from the nearest meteorological station (Navacerrada, 25

178   km far from the closest site and at 1,894 m a.s.l). Water availability (P-PET) was

179   characterized as the difference between annual precipitation and potential

180   evapotranspiration (PET) following Bigler et al. (2006). PET was calculated following

181   Thornthwaite (1948). We calculated P-PET from October of the previous year to

182   September of the present year to account for the influence of previous year conditions on

183   the current growing season (Madrigal-González et al., 2017a).

184   Drought events were identified as extremely dry years with a significant reduction

185   on tree growth (Schweingruber et al., 1990). Specifically, we selected as extreme

186   droughts those years where P-PET was below the 15th percentile of the time series (i.e. P-

187   PET values under -251.4 mm) and where at least 60% of the sampled trees showed a BAI

188   reduction of at least 20% relative to the BAI average in the three preceding years. We

189   selected 1986, 1995, 2005, 2012 and 2017 as extreme drought events (Fig. S1).

190   **2.5. Resistance, resilience and recovery to drought events**

191   To evaluate growth responses to selected drought events, we calculated growth

192   resistance, resilience and recovery indices following Lloret et al. (2011):

$$Resistance = Dr/PreDr$$

$$Resilience = PostDr/PreDr$$

$$Recovery = PostDr/Dr$$

196   where Dr is the BAI the year of the drought event and PreDr and PostDr the mean BAI

197   for three years before and after the drought event, respectively. We only calculated

198   resistance index in 2017 since growth series finished in 2018. We also characterized water

199   availability differences between evaluated periods as:

$$PPET_{resistance} = PPET_{dr} - PrePPET$$

$$PPET_{resilience} = PostPPET - PrePPET$$

202
$$PPET_{recovery} = PostPPET - PPET_{dr}$$

203 where P-PET$_{dr}$ is the annual P-PET value the year of the drought event and PreP-PET and

204 PostP-PET are the mean annual P-PET for three years before and after the drought event,

205 respectively.

2.6. Data analysis

207   To analyse tree growth response to biotic and abiotic factors in mixed and

208 monospecific stands, we modelled BAI using a linear mixed model (LMM). BAI was log-

209 transformed to achieve homocedasticity. Tree identity nested within forest site was

210 included as random effect to account for lack of independence resulting from repeated

211 measurements within trees and forest sites. We also used an autoregressive correlation

212 structure (AR1) to remove first-order autocorrelation in tree growth series (Pinheiro et

213 al., 2018). We considered as fixed effects annual tree size, stand type (mixed and

214 monospecific), species (*P. sylvestris* and *Q. pyrenaica*), annual water availability (P-PET)

215 and the Lorimer's competition index (LCI). To compare species growth sensitivity to

216 drought and competition between stand types, we included in the model the interactions

217 species × stand type × P-PET and species × stand type × LCI. A polynomial function was

218 used for tree size because tree growth capacity increases until trees reach maturity and

219 stabilize or decrease afterwards (Richards, 1959). Since growth-size relationships can be

220 species-specific (Das, 2012), we also included in the model the interaction species × size.

221 Continuous predictor variables were standardized (i.e. the mean was subtracted from each

222 value and divided by the standard deviation) to allow comparisons across model-

223 estimated parameters (Zuur et al., 2009).

224   To evaluate growth stability to drought events in mixed and monospecific stands,

225 we fitted independent LMM for each growth resilience component (resilience, resistance

226 and recovery). Since different drought events were evaluated, we included tree identity

227 nested within forest site as random effect. Growth resilience components were log-

228 transformed to achieve homocedasticity. To evaluate whether resilience components are

229 modulated by stand type and drought intensity, we included as fixed effect in the model

230 the interaction species × stand type × P-PET$_{dr}$. We also included the interaction species ×

231 tree size, and LCI and the P-PET difference between the periods considered for the

232 calculation of resilience components (P-PET$_{ret}$, P-PET$_{res}$ and P-PET$_{rec}$) as covariates in

233 the models (Andivia et al., 2020; DeSoto et al., 2020).

234   For both group of models, we built all alternative models and selected the most

235 parsimonious ones based on the Akaike Information Criterion corrected for small sample

236 sizes (AICc) (Burnham and Anderson, 2002) using as threshold two units of AICc (Zuur

237 et al., 2009). All statistical analyses were performed in R (R v3.5.2; R Core Team, 2018)

238 using the packages *nlme* (Pinheiro et al., 2018) and *MuMIn* (Barton, 2016).

239 3. RESULTS

240 3.1. Stand structure and tree characteristics

241 Stand structure size and the age of target trees varied among selected forest sites (Table

242 1). In general, *Q. pyrenaica* monospecific stands were denser than mixed and *P. sylvestris*

243 monospecific stands, while LCI values showed no clear trend among stand types (Table

244 1). The age at 1.3 m and DBH of target trees ranged from 15 to 113 years and from 22 to

245 54 cm for *P. sylvestris*, while ranged from 30 to 110 years and from 15 to 55 cm for *Q.*

246 *pyrenaica*, respectively. Studied species showed similar tree age and DBH (mean ± SD)

247 in both stand types. *P. sylvestris* age was 73.1 ± 20.0 and 81.9 ± 21.5, and the DBH was

248 31.7 ± 12.8 cm and 28.7 ± 11.4 cm in mixed and monospecific stands, respectively. *Q.*

249 *pyrenaica* age was 62.7 ± 15.5 and 61.9 ± 17.6, and the DBH was 12.3 ± 7.8 cm and 12.1

250 ± 5.6 cm in mixed and monospecific stands, respectively.

251 **Table 1.** Stand structure and characteristics of target trees for the studied forest sites.

252 CAN: Canencia, MIR: Miraflores, MOR: Morcuera, NAV: Navafría, PNA: Peña Alta,

253 SMP: Santa María del Paular. Mix: mixed stands, MoP: Monospecific stands of *P.*

254 *sylvestris*, MoQ: Monospecific stands of *Q. pyrenaica*. Tree age at 1.3 m (No. years);

255 DBH: Diameter at Breast Height (cm); LCI: Lorimer's distance-independent Competition

256 Index; Density: number of trees per hectare. Showed values are mean ± SD. For each

257 forest site altitude and coordinates are showed.

| Site	Stand	Tree age	DBH	LCI	Density
CAN	Mix	77.2 ± 12.5	25.6 ± 14.0	6.0 ± 1.9	864 ± 539
1341 m	MoP	67.4 ± 31.2	25.8 ± 14.3	7.6 ± 2.2	897 ± 527
40.84, -3.77	MoQ	51.6 ± 14.2	14.6 ± 8.1	6.7 ± 3.8	1,546 ± 884
MIR	Mix	67.4 ± 7.5	23.5 ± 11.4	10.4 ± 4.3	994 ± 178
1287 m	MoP	77.0 ± 6.6	28.1 ± 7.3	12.9 ± 2.7	1196 ± 74
40.82, -3.79	MoQ	67.8 ± 6.2	11.7 ± 6.4	8.5 ± 4.9	2,274 ± 492
MOR	Mix	63.2 ± 11.9	17.7 ± 14.3	13.0 ± 10.6	1,182 ± 479
1544 m	MoP	73.2 ± 3.3	34.9 ± 9.7	6.4 ± 1.8	546 ± 187
40.84, -3.80	MoQ	64.2 ± 6.3	10.2 ± 5.1	15.8 ± 12.8	3,898 ± 876
NAV	Mix	73.7 ± 27.2	14.1 ± 10.6	19.8 ± 13.8	2,417 ± 569
1530 m	MoP	105.0 ± 2.2	32.1 ± 8.3	13.1 ± 4.5	1,052 ± 404
40.98, -3.79	MoQ	52.6 ± 1.9	11.8 ± 4.1	20.8 ± 7.2	3,482 ± 872
PNA	Mix	63.8 ± 20.7	21.5 ± 14.5	13.2 ± 9.6	1,195 ± 312
1536 m	MoP	82.0 ± 31.6	22.9 ± 10.6	13.1 ± 3.8	1,546 ± 587
40.98, -3.80	MoQ	85.0 ± 21.6	12.7 ± 4.8	16.2 ± 12.7	3,366 ± 536
SMP	Mix	62.0 ± 22.5	18.4 ± 14.9	17.0 ± 17.2	1,098 ± 647
1288 m	MoP	86.6 ± 15.4	34.6 ± 12.5	9.7 ± 3.8	923 ± 354
40.86, -3.89	MoQ	47.0 ± 17.6	14.3 ± 5.5	14.8 ± 8.6	1,507 ± 922

258

259

260

261

3.2. Abiotic and biotic drivers of tree growth

263 Target trees showed high inter-annual variability in tree growth, especially for *P.*

264 *sylvestris* (Fig. 1). *P. sylvestris* showed greater mean BAI over the study period (1961-

265 2018) than *Q. pyrenaica* (16.9 ± 0.2 cm^2 and 10.2 ± 0.2 cm^2, respectively). Stand type

266 also influence tree growth (Fig. 1), since both species showed greater BAI in mixed than

267 in monospecific stands (18.8 ± 0.3 *vs* 14.9 ± 0.2 cm^2 for *P. sylvestris* and 11.0 ± 0.3 *vs*

268 9.2 ± 0.2 cm^2 for *Q. pyrenaica*, respectively). Yet, BAI differences between forest types

269 were more evident after the 80's, especially for *P. sylvestris*.
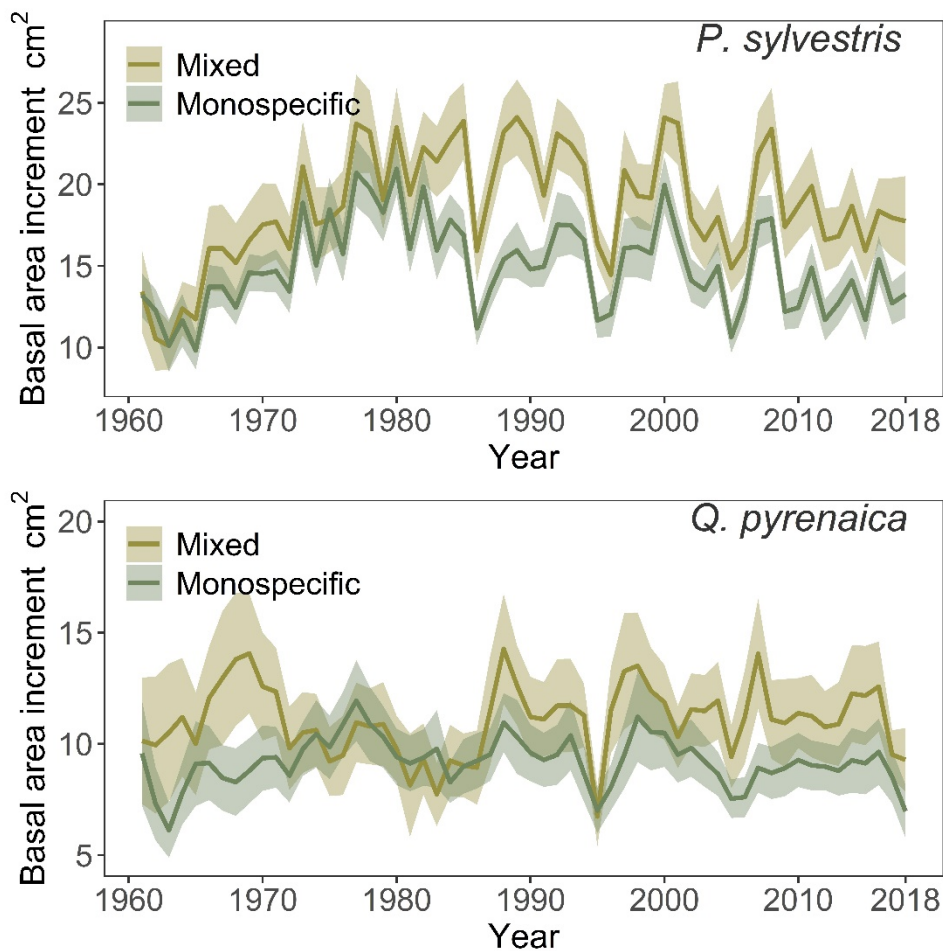
270

271 **Figure 1:** Basal area increment pattern (mean ± standard error) over the study period for

272 each study species and stand type.

273   The most parsimonious growth model included the triple interaction species ×

274   stand type × P-PET, the pairwise interaction species × tree size, and the main effect of

275   the LCI (Table S1). The model explained 47% of variance for random and fixed effects

276   (conditional R^2) and 46% of variance for fixed effects only (marginal pseudo-R^2). As

277   expected, tree size effect on BAI was species-specific and tree growth was negatively

278   related to LCI (Table S2). Although P-PET had a positive effect on tree growth, growth

279   sensitivity to P-PET was determined by the interaction between tree species and stand

280   type (Table S2). *P. sylvestris* showed a higher tree growth sensitivity to P-PET (i.e. higher

281   model slope) in monospecific than in mixed stands, resulting in greater BAI in mixed

282   stands in years with low water availability (Fig. 2). On the contrary, *Q. pyrenaica* growth

283   sensitivity to P-PET was much higher in mixed than in monospecific stands. *Q. pyrenaica*

284   showed greater BAI in mixed than monospecific stands, especially in years with high

285   water availability (Fig. 2).

286
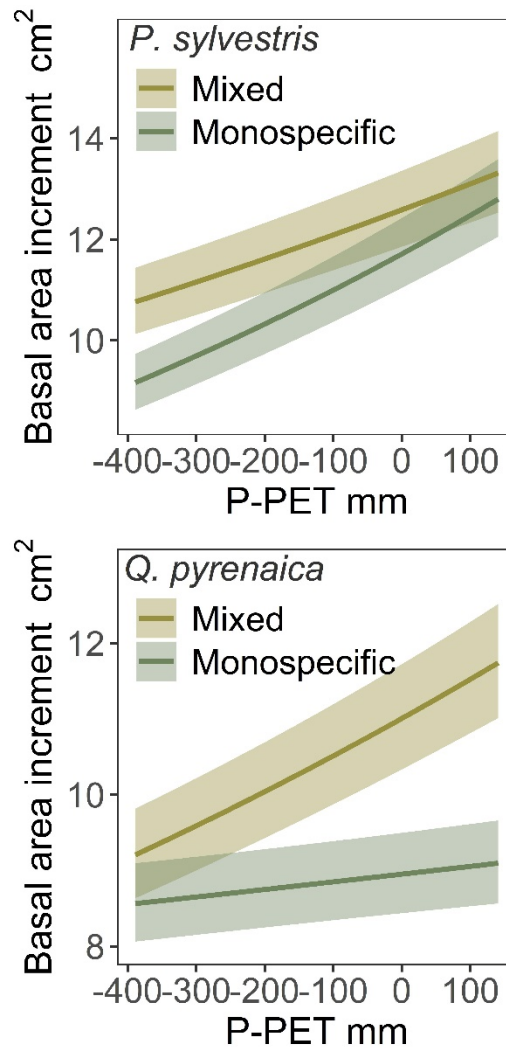
Figure 2: Predicted annual basal area increment (± 95% confidence interval) in response to annual water availability (P-PET) for each study species and stand type.

3.3. Growth resilience in response to drought events

The most parsimonious models for growth resilience components included different fixed effects. Growth resistance was affected by the interaction species × stand type (Table S3). While *P. sylvestris* was more resistant to drought events in mixed than in monospecific stands (0.87 ± 0.02 and $0.81 \pm 0.02$, respectively), *Q. pyrenaica* showed the opposite trend (0.87 ± 0.03 and 0.96 ± 0.03, respectively) (Fig. 3a, Table S4). Growth recovery was also affected by the interaction species × stand type (Table S5). *Q. pyrenaica* showed a greater recovery after drought events in mixed than in monospecific stands (1.48 ± 0.07 and 1.19

297   ± 0.04, respectively), whereas *P. sylvestris* showed similar recovery in both stand types

298   (1.28 ± 0.04 and 1.39 ± 0.04) (Fig. 3b, Table S5). In addition, growth recovery was also

299   affected by differences in water availability after drought (P-PET$_{rec}$) and by the

300   interaction species × drought intensity (P-PET$_{dr}$). Both species showed greater recovery

301   with increasing P-PET$_{rec}$ and decreasing P-PET$_{dr}$, respectively (Table S6). However, the

302   increase in recovery with decreasing drought intensity was higher in *Q. pyrenaica* than in

303   *P. sylvestris* (estimated model slopes ± SE, 0.35 ± 0.05 and 0.14 ± 0.05, respectively; Fig

304   4a, Table S6).

305   Growth resilience was also affected by water availability differences between the

306   post- and the pre-drought periods (P-PET$_{res}$) and by the interaction species × drought

307   intensity (P-PET$_{dr}$) (Table S7). However, we did not find any effect of stand type on

308   growth resilience (Fig. 3c). Growth resilience was negatively related to P-PET$_{res}$

309   (estimated model slope ± SE, -0.20 ± 0.06). Analogously to growth recovery, resilience

310   increased with decreasing drought intensity, especially in *Q. pyrenaica* (estimated model

311   slopes ± SE, 0.46 ± 0.06 and 0.002 ± 0.06, respectively) (Fig 4b). Growth resilience was

312   also affected by the interaction species × tree size. Growth resilience decreased with tree

313   size in *P. sylvestris*, but no effect was found in *Q. pyrenaica* (estimated model slopes ±

314   SE, 0.07 ± 0.02 and 0.02 ± 0.02, respectively; Table S8).

315
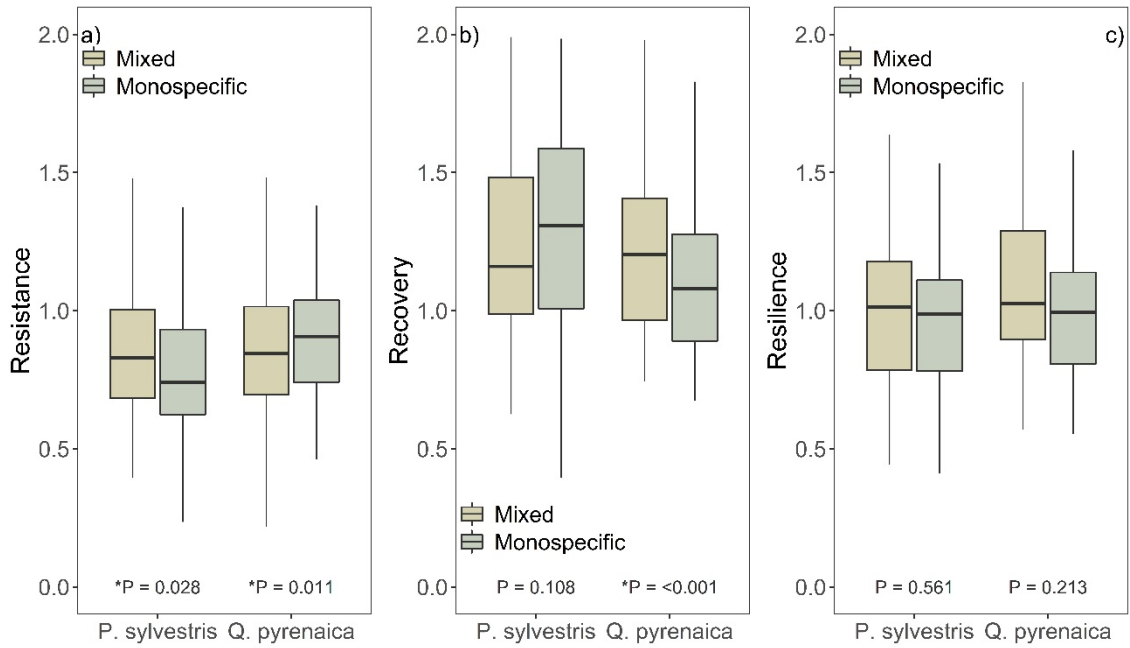
Figure 3: Boxplots of growth resistance (a), recovery (b) and resilience (c) for study species and stand type. For each boxplot, the P-value of the comparison between stand types is showed. Asterisks show significant interactions (P < 0.05). Boxes are 95% and 5% percentile values, whiskers depict maximum and minimum values and the solid lines indicate the median.

321
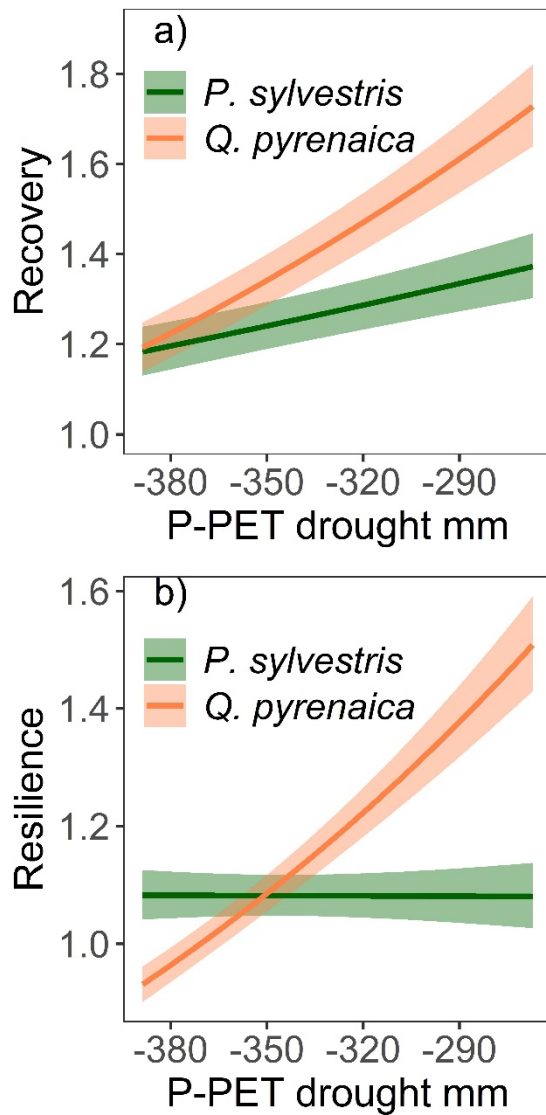
Figure 4: Model prediction (± 95% confidence interval) for growth recovery (a) and resilience (b) for each study species in response to drought intensity (P-PET$_{dr}$).

4. DISCUSSION

4.1. Admixture effects on tree growth and resilience components

Our results show beneficial effects of admixture on tree growth for the widely distributed sub-Mediterranean *Q. pyrenaica* and boreal *P. sylvestris* in drought-limited

331   Mediterranean mountains. Admixture positive effects on tree growth response to water

332   availability were species-specific, which resulted in contrasting effects on the different

333   components of growth resilience to extreme drought events. *P. sylvestris* showed higher

334   growth in mixed than in monospecific stands in years with low water availability, which

335   also resulted in a higher growth resistance to extreme droughts in mixed stands. On the

336   contrary, growth differences between mixed and monospecific stands increased with

337   increasing water availability for *Q. pyrenaica*, showing higher recovery after extreme

338   drought events in mixed stands. On the one hand, these results can help to clarify the

339   ongoing debate on the relationship between tree diversity and resilience to drought in

340   forest ecosystems, pointing to the importance of species- and climate-specific effects. On

341   the other hand, our results have key implications for forest management, suggesting

342   *P.sylvestris*-*Q. pyrenaica* mixed stands as an adaptation solution for mid-elevation forests

343   in the Iberian Peninsula under increased aridity.

344   The positive effect of admixture on tree growth can be explained by

345   complementarity due to both mechanisms, facilitation and competition reduction (Loreau

346   and Hector., 2001; Callaway, 2007; Brooker et al., 2008). According to the stress gradient

347   hypothesis (Bertness and Callaway, 1994), positive interactions among species are more

348   common in areas with high environmental stress, which is the case of drought-limited

349   forests in Mediterranean mountains (e.g. Gómez-Aparicio et al., 2004). On the one hand,

350   competition reduction relies on inter-specific differences in resource acquisition

351   strategies. Study species show remarkable differences in shade tolerance, leaf phenology,

352   water-use strategy, and root structure (Niinemets and Valladares, 2006; Poyatos et al.,

353   2008; Río and Sterba, 2009). Among them, vertical rooting stratification is a key

354   complementarity mechanism in drought-limited forest ecosystems (Grossiord, 2019). In

355   this regard, some studies in mixed stands showed that conifers have access to shallower

356 water resources while oak species can access deeper ones due to a more extensive and

357 deep root system (Poyatos et al., 2008; del Castillo et al., 2016; Martín-Gómez et al.,

358 2017). On the other hand, facilitation could occur through hydraulic lift by oak species

359 under moderate and severe drought conditions, which increases water availability in the

360 upper soil horizons for the admixed species (Querejeta et al., 2003; Zapater et al., 2011).

361   The higher growth during dry years and resistance to extreme droughts for *P.*

362 *sylvestris* in mixed than monospecific stands might be driven mainly by water-related

363 facilitation mechanisms. Hydraulic lift can increase not only water availability for *P.*

364 *sylvestris*, but also root growth and functioning as well as nutrient availability due to

365 positive effects of increasing humidity on organic matter decomposition and

366 mineralization (Rothe and Binkley, 2001; Richards et al., 2010; Prieto et al., 2012, del

367 Castillo et al., 2016). Competition reduction in response to low water availability seems

368 not to play a prevailing role in our study since admixture showed neutral effects on *Q.*

369 *pyrenaica* growth in dry years. In fact, *Q. pyrenaica* showed higher resistance to extreme

370 droughts in monospecific than in mixed stands. Accordingly, Steckel et al., (2020)

371 showed a reduction of admixture positive effects on *Q. robur* and *Q. petraea* response to

372 drought in driest sites when co-occuring with *P. sylvestris*.

373   Interestingly, admixture positive effects on *Q. pyrenaica* growth emerged with

374 increasing water availability. Reduced inter-specific competition coupled to higher

375 above- and below-ground competitive capacity could allow *Q. pyrenaica* to maximize

376 light and nutrient capture in mixed stands under non-limited water conditions

377 (Longuetaud et al., 2013; Madrigal-González et al., 2016), which might also explain the

378 higher recovery of *Q. pyrenaica* after extreme droughts in mixed than in monospecific

379 stands. In addition, functional differences in leaf traits between study species can also

380 improve mineralization and decomposition processes, ultimately increasing nutrient

381   availability in mixed stands (Rothe and Binkley, 2001; Andivia et al., 2016; Santonja et

382   al., 2017). Despite *P. sylvestris* is also likely to benefit from increased nutrient

383   availability, competition for light could offset positive admixture effects under moderate

384   to high water availiability conditions due to larger leaf areas. In this context, *Q. pyrenaica*

385   could be favoured over *P. sylvestris* due to its broad-leaved habit and higher tolerance to

386   shade (Zavala et al., 2000; Niinemets and Valladares, 2006).

387   **4.2. Growth resilience components**

388   To analyze growth resilience components, we simultaneously considered all extreme

389   drought events occurred during recent decades (1986-2018), which represents a more

390   realistic approach to assess overall growth response to drought than analyzing each event

391   separately. In fact, under ongoing climate change, trees are exposed to recurrent extreme

392   drought events (Spinoni et al., 2018), which has been proved to reduce the resilience

393   capacity of forest tree species (Andivia et al., 2020; Serra-Maluquer et al., 2018).

394   However, by doing so, we did not account for specific details about drought onset and

395   duration of each event, which could influence species drought sensitivity (Hoffmann et

396   al., 2018). To partly avoid this, we followed recent recommendations to quantify growth

397   resilience (DeSoto et al., 2020; Schwarz et al., 2020). Specifically, we evaluated growth

398   resilience components after controlling for among-events differences in drought intensity

399   ($PPET_{dr}$) and water availability differences between growth periods ($PPET_{re}$, $PPET_{res,}$

400    $PPET_{rec}$).

401   Decreasing drought intensity and differences in water availability between post-

402   and drought periods had a positive effect on growth recovery of both species. This agrees

403   with other studies pointing to the importance of site climatic conditions on growth

404   recovery capacity (Gazol et al., 2017; Steckel et al., 2020). Decreasing drought intensity

405   also increased resilience for *Q. pyrenaica*, but not for *P. sylvestris*. This, and the higher

406   effect of decreasing drought intensity on *Q. pyrenaica* recovery, might be partly explained

407   by the anisohydric behavior of oaks, i.e. the preservation of transpiration rates at low

408   water potential (Fernández-De-Uña et al. 2017, Martín-Gómez et al. 2017). Thus, *Q.*

409   *pyrenaica* might take advantage of increased water availability, and faster refilling of soil

410   water reserves with decreasing drought intensity, to maximize post-drought tree growth,

411   and thus recovery and resilience. In fact, oak species at dry sites show positive drought

412   legacies (Anderegg et al., 2015). On the contrary, the isohydric behavior of *P. sylvestris*

413   (i.e. tight stomatal control under drought conditions; Irvine et al., 1998), seems to respond

414   to specific drought threshold through prolonged stomata closure, reducing photosynthesis

415   and depleting carbohydrate reserves, which might ultimately impair post-drought growth.

416   Finally, the negative effect of differences in water availability between post- and pre-

417   drought periods on resilience may reflect a negative legacy of moderate dry conditions

418   during pre-disturbance period on post-drought growth. We also considered tree size when

419   evaluating growth resilience components, since size strongly influences tree growth

420   dynamics and thus resilience capacity (Andivia et al., 2020). Tree size was negatively

421   related to growth resilience for *P. sylvestris*, which contrasts to previous studies with this

422   species using different size categories (Merlin et al., 2015). Larger trees can be more

423   exposed to drought due to their greater foliar biomass and the dominant position in the

424   stand (Martín-Benito et al., 2008), which might increase water demand and respiration

425   costs affecting post-drought recovery.

426   Contrary to our hypothesis, we did not find differences in species resilience

427   capacity mediated by stand type. These results can be related to reported trade-offs

428   between growth resistance and recovery (Hodgson et al., 2015; Hoffmann et al., 2018).

429   This trade-off might explain the observed higher recovery in mixed stands and higher

430   resistance in monospecific ones for *Q. pyrenaica*. The lack of this trade-off for *P.*

431 *sylvestris*, which showed higher resistance in mixed than monospecific stands but similar

432 recovery, could be due to the above-mentioned strong negative drought legacy effects

433 reported for conifer species (Anderegg et al., 2015), which could impair post-drought

434 recovery in both type of stands.

435 **4.3. Implications for forest management**

436 Our results showed positive effects of admixture on tree growth and resilience

437 components for both *P. sylvestris* and *Q. pyrenaica*. The positive effect of admixture on

438 *P. sylvestris* growth response during dry years and resistance to extreme droughts can be

439 critical at the southern distribution limit of the species under increased aridity conditions.

440 In addition, enhancement of *Q. pyrenaica* tree growth in years without water limitations,

441 suggests that increasing tree diversity can also contribute to increase the productivity of

442 Mediterranean mountain forests (Río and Sterba, 2009). On the other hand, we found a

443 negative effect of competition on tree growth irrespectively of species identity and the

444 type of stand analysed, which suggests that thinning is a key tool to improve forest

445 resilience and response to drought, in agreement with previous studies (Kohler et al.,

446 2010; Sohn et al. 2016). This is especially relevant for monospecific conifer stands in the

447 Iberian peninsula, since lack of forest management during the last decades have led to

448 dense stands with a high vulnerability to drought, fires and pests (Maestre and Cortina,

449 2004; Gómez-Aparicio et al., 2011; Sánchez-Salguero et al., 2012). However, drought

450 impacts on forest dynamics rely not only on tree growth responses but also on recruitment

451 and mortality (Allen et al., 2010; Madrigal-González et al., 2017b). Thus, further studies

452 should also evaluate admixture effects on other demographic rates to provide a

453 comprehensive view of the response of mixed stand to drought events (Andivia et al.,

454 2020; Madrigal-González et al., 2017b). This is of pivotal importance to properly evaluate

455 tree diversity effects on forest resilience, but also to design forest management strategies

456 oriented to guarantee the long-term persistence of mixed stands.

457

458 **5. CONCLUSIONS**

459 Our results suggest that mixed stands of *P. sylvestris* and *Q. pyrenaica* are less vulnerable

460 to drought than their monospecific counterparts, corroborating positive complementarity

461 effects between contrasting functional species. Thus, this study contributes to the growing

462 body of evidences supporting admixture as a management option for adaptation of forests

463 to climate change. Promoting mixed stands of pine and oak species may contribute to

464 increase forest productivity while reducing vulnerability to climatic disturbances.

465 However, positive effects on tree growth and resilience were species-specific and

466 contingent upon water availability, which suggests that further studies should include

467 more species combination and the whole environmental gradient over the natural area

468 where species co-occur.

469

478

Declaration of interests: None

480

REFERENCES

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, 1–55. https://doi.org/10.1890/ES15-00203.1

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Ammer, C., 2019. Diversity and forest productivity in a changing climate. New Phytol. 221, 50–66. https://doi.org/10.1111/nph.15263

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and ther implications for carbon cycle models. Science (80-.). 349, 528–531. https://doi.org/10.1017/CBO9781107415324.004

Andivia, E., Rolo, V., Jonard, M., Formánek, P., Ponette, Q., 2016. Tree species identity mediates mechanisms of top soil carbon sequestration in a Norway spruce and European beech mixed forest. Ann. For. Sci. 73, 437–447.

501   https://doi.org/10.1007/s13595-015-0536-z

502 Andivia, E., Ruiz-Benito, P., Diaz-Martínez, P., Carro-Martínez, N., Zavala, M.,

503   Madrigal-González, J., 2020. Inter-specific tolerance to recurrent droughts of pine

504   species revealed in saplings rather than adult trees. For. Ecol. Manage. 459.

505 Barton, K., 2016. MuMIn: multi model inference: model selection and model averaging

506   based on information criteria.

507 Bayer, D., Seifert, S., Pretzsch, H., 2013. Structural crown properties of Norway spruce

508   (Picea abies [L.] Karst.) and European beech (Fagus sylvatica [L.]) in mixed versus

509   pure stands revealed by terrestrial laser scanning. Trees - Struct. Funct. 27, 1035–

510   1047. https://doi.org/10.1007/s00468-013-0854-4

511 Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol.

512   Evol. https://doi.org/10.1016/0169-5347(94)90088-4

513 Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an

514   inciting mortality factor in scots pine stands of the Valais, Switzerland. Ecosystems

515   9, 330–343. https://doi.org/10.1007/s10021-005-0126-2

516 Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization:

517   Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Res.

518   64, 81–96. https://doi.org/10.3959/2008-6.1

519 Bolte, A., Ammer, C., Löf, M., Nabuurs, G.-J., Schall, P., Spathelf, P., 2010. Adaptative

520   forest management: a prerequisite for sustainable forestry in the face of climate

521   change., in: Sustainable Forest Management in Changing World: An European

522   Perspective. Springer, Dordrecht, pp. 115–139. https://doi.org/10.1007/978-90-481-

523   3301-7

524 Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G.,

525   Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L.,

526   Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz,

527   C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008.

528   Facilitation in plant communities: The past, the present, and the future. J. Ecol. 96,

529   18–34. https://doi.org/10.1111/j.1365-2745.2007.01295.x

530 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a

531   practical information-theorethical approach. Springer, New York, NY, US.

532 Callaway, R.M., 2007. Positive interactions and interdependence in plant communities.

533   Springer, Missoula, U.S.A. https://doi.org/10.1007/978-1-4020-6224-7

534 Callaway, R.M., 1995. Possitive interactions among plants. Bot. Rev. 61, 306–349.

535 Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.P., Iglesias, A., Lange, M.A.,

536   Lionello, P., Llasat, M.C., Paz, S., Peñuelas, J., Snoussi, M., Toreti, A., Tsimplis,

537   M.N., Xoplaki, E., 2018. Climate change and interconnected risks to sustainable

538   development in the Mediterranean. Nat. Clim. Chang. 8, 972–980.

539   https://doi.org/10.1038/s41558-018-0299-2

540 Das, A., 2012. The effect of size and competition on tree growth rate in old-growth

541   coniferous forests. Can. J. For. Res. 42, 1983–1995. https://doi.org/10.1139/x2012-

542   142

543 de Dios, R.S., Velázquez, J.C., Ollero, H.S., 2019. Classification and mapping of Spanish

544   mediterranean mixed forests. IForest 12, 480–487. https://doi.org/10.3832/ifor2817-

545   012

546 del Castillo, J., Comas, C., Voltas, J., Ferrio, J.P., 2016. Dynamics of competition over

547   water in a mixed oak-pine Mediterranean forest: Spatio-temporal and physiological

548   components. For. Ecol. Manage. 382, 214–224.

549   https://doi.org/10.1016/j.foreco.2016.10.025

550 del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I.,

551   Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Heym,

552   M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Makrickiene, E., Matović, B.,

553   Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G.,

554   Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Zlatanov,

555   T.M., Bravo-Oviedo, A., 2017. Species interactions increase the temporal stability

556   of community productivity in Pinus sylvestris–Fagus sylvatica mixtures across

557   Europe. J. Ecol. 105, 1032–1043. https://doi.org/10.1111/1365-2745.12727

558 DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T.,

559   Amoroso, M.M., Bigler, C., Camarero, J.J., Čufar, K., Gea-Izquierdo, G., Gillner,

560   S., Haavik, L.J., Hereş, A.M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T.,

561   Levanič, T., Linares, J.C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner,

562   B., Sangüesa-Barreda, G., Stojanovic, D.B., Suárez, M.L., Villalba, R., Martínez-

563   Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk

564   in trees. Nat. Commun. 11, 1–9. https://doi.org/10.1038/s41467-020-14300-5

565 Fernández-de-Uña, L., Rossi, S., Aranda, I., Fonti, P., González-González, B.D.,

566   Cañellas, I., Gea-Izquierdo, G., 2017. Xylem and Leaf Functional Adjustments to

567   Drought in Pinus sylvestris and Quercus pyrenaica at Their Elevational Boundary.

568   Front. Plant Sci. 8, 1200. https://doi.org/10.3389/fpls.2017.01200

569 Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-

570   species forests: From pattern to process. For. Ecol. Manage. 312, 282–292.

571 https://doi.org/10.1016/j.foreco.2013.10.003

572 Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity

573 Relationships in Forests. Curr. For. Reports 2, 45–61.

574 https://doi.org/10.1007/s40725-016-0031-2

575 Fritts, H.C., 1976. Tree rings and climate. Academic Press.

576 Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-

577 Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson,

578 E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher

579 levels of multiple ecosystem services are found in forests with more tree species.

580 Nat. Commun. 4. https://doi.org/10.1038/ncomms2328

581 Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience

582 to an extreme drought. J. Ecol. 104, 1063–1075. https://doi.org/10.1111/1365-

583 2745.12575

584 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., de

585 Luis, M., Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C.,

586 Martín-Hernández, N., Martínez del Castillo, E., Ribas, M., García-González, I.,

587 Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares, L.A., Hevia, A., Tomás-

588 Burguera, M., Galván, J.D., 2018. Forest resilience to drought varies across biomes.

589 Glob. Chang. Biol. 24, 2143–2158. https://doi.org/10.1111/gcb.14082

590 Gazol, A., Ribas, M., Gutiérrez, E., Camarero, J.J., 2017. Aleppo pine forests from across

591 Spain show drought-induced growth decline and partial recovery. Agric. For.

592 Meteorol. 232, 186–194. https://doi.org/10.1016/j.agrformet.2016.08.014

593 Gómez-Aparicio, L., García-Valdés, R., Ruiz-Benito, P., Zavala, M.A., 2011.

594   Disentangling the relative importance of climate, size and competition on tree

595   growth in iberian forests: implications for forest management under globar change.

596   Glob. Chang. Biol. 17, 2400–2414.

597 Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004.

598   Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs

599   as nurse plants. Ecol. Appl. 14, 1128–1138. https://doi.org/10.1890/03-5084

600 Gòmez-Aparicio, L., Zavala, M.., Bonet, F.J., Zamora, R., 2009. Are pine plantations

601   valid tools for restoring Mediterranean forests? An assessment along gradients of

602   climatic conditions, stand density and distance to seed sources. Ecol. Appl. 19,

603   2124–2141.

604 Granda, E., Gazol, A., Camarero, J.J., 2018. Functional diversity differently shapes

605   growth resilience to drought for co-existing pine species. J. Veg. Sci. 29, 265–275.

606   https://doi.org/10.1111/jvs.12617

607 Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen,

608   C.D., Fensham, R., Laughlin, D.C., Kattge, J., Bönisch, G., Kraft, N.J.B., Jump,

609   A.S., 2017. Tree mortality across biomes is promoted by drought intensity, lower

610   wood density and higher specific leaf area. Ecol. Lett. 20, 539–553.

611   https://doi.org/10.1111/ele.12748

612 Grossiord, C., 2019. Having the right neighbors: how tree species diversity modulates

613   drought impacts on forests. New Phytol. https://doi.org/10.1111/nph.15667

614 Grossiord, C., Granier, A., Gessler, A., Jucker, T., Bonal, D., 2014. Does Drought

615   Influence the Relationship Between Biodiversity and Ecosystem Functioning in

616   Boreal Forests? Ecosystems 17, 394–404. https://doi.org/10.1007/s10021-013-

617   9729-1

618   Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of

619   monthly climatic observations - the CRU TS3.10 Dataset. Int. J. Climatol. 34, 623–

620   642. https://doi.org/10.1002/joc.3711

621   Hodgson, D., McDonald, J.L., Hosken, D.J., 2015. What do you mean, "resilient"?

622   Trends Ecol. Evol. 30, 503–506. https://doi.org/10.1016/j.tree.2015.06.010

623   Hoffmann, N., Schall, P., Ammer, C., Leder, B., Vor, T., 2018. Drought sensitivity and

624   stem growth variation of nine alien and native tree species on a productive forest site

625   in Germany. Agric. For. Meteorol. 256–257, 431–444.

626   https://doi.org/10.1016/j.agrformet.2018.03.008

627   Holling, C.S., 1996. Engineering resilience versus ecological resilience., in: Schulze, P.

628   (Ed.), Engineering within Ecological Constraints. Washington: National Academy,

629   pp. 31–41.

630   IPCC, 2018. Summary for Policymakers, in: Global Warming of 1.5°C. An IPCC Special

631   Report on the Impacts of Global Warming of 1.5°C above Pre-Industrial Levels and

632   Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening

633   the Global Response to the Threat of Climate Change,. Génova, Suiza, p. 32.

634   https://doi.org/10.1017/CBO9781107415324

635   Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of Pinus sylvestris to

636   drought: stomatal control of transpiration and hydraulic conductance. Tree Physiol.

637   18, 393–402. https://doi.org/10.1093/TREEPHYS/18.6.393

638   Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X., Pretzsch, H.,

639   Castagneyrol, B., 2018. Positive biodiversity–productivity relationships in forests:

640   Climate matters. Biol. Lett. 14, 12–15. https://doi.org/10.1098/rsbl.2017.0747

641   Jourdan, Marion, Kunstler, G., Morin, X., 2019. How neighbourhood interactions control

642   the temporal stability and resilience to drought of trees in mountain forests. J. Ecol.

643   1–12. https://doi.org/10.1111/1365-2745.13294

644   Jourdan, M., Lebourgeois, F., Morin, X., 2019. The effect of tree diversity on the

645   resistance and recovery of forest stands in the French Alps may depend on species

646   differences   in   hydraulic   features.   For.   Ecol.   Manage.   450,   1–41.

647   https://doi.org/10.1016/j.foreco.2019.117486

648   Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., Coomes,

649   D.A., 2014. Competition for light and water play contrasting roles in driving

650   diversity-productivity relationships in Iberian forests. J. Ecol. 102, 1202–1213.

651   https://doi.org/10.1111/1365-2745.12276

652   Kohler, M., Sohn, J., Nägele, G., Bauhus, J., 2010. Can drought tolerance of Norway

653   spruce (Picea abies (L.) Karst.) be increased through thinning? Eur. J. For. Res. 129,

654   1109–1118. https://doi.org/10.1007/s10342-010-0397-9

655   Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce Abies alba

656   tree-ring sensitivity to summer drought in the Vosges mountains, western Europe.

657   For. Ecol. Manage. 303, 61–71. https://doi.org/10.1016/j.foreco.2013.04.003

658   Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D.,

659   McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B.,

660   Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J.,

661   Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D.,

662   Tchebakova, N., Fischer, M., Watson, J. V., Chen, H.Y.H., Lei, X., Schelhaas, M.J.,

663   Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S.,

664   Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-

665   Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F.,

666   Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R.,

667   Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L.,

668   Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje,

669   C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R.,

670   Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel,

671   V., Engone-Obiang, N.L., Ferreira, L. V., Odeke, D.E., Vasquez, R.M., Lewis, S.L.,

672   Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in

673   global forests. Science (80-.). 354. https://doi.org/10.1126/science.aaf8957

674 Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J.,

675   Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010.

676   Climate change impacts, adaptive capacity, and vulnerability of European forest

677   ecosystems. For. Ecol. Manage. 259, 698–709.

678   https://doi.org/10.1016/j.foreco.2009.09.023

679 Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of

680   successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–

681   1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x

682 Longuetaud, F., Piboule, A., Wernsdörfer, H., Collet, C., 2013. Crown plasticity reduces

683   inter-tree competition in a mixed broadleaved forest. Eur. J. For. Res. 132, 621–634.

684   https://doi.org/10.1007/s10342-013-0699-9

685 Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: A synthesis

686   of underlying mechanisms. Ecol. Lett. 16, 106–115.

687   https://doi.org/10.1111/ele.12073

688 Loreau M., Hector. A., 2001. Partitioning selection and complementarity in biodiversity

689   experiments. Nature 412, 72–76.

690 Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in

691   natural hardwood stands. For. Ecol. Manage. 6, 343–360.

692 Madrigal-González, J., Andivia, E., Zavala, M.A., Stoffel, M., Calatayud, J., Sánchez-

693   Salguero, R., Ballesteros-Cánovas, J., 2018. Disentangling the relative role of

694   climate change on tree growth in an extreme Mediterranean environment. Sci. Total

695   Environ. 642, 619–628. https://doi.org/10.1016/j.scitotenv.2018.06.064

696 Madrigal-González, J., Ballesteros-Cánovas, J.A., Herrero, A., Ruiz-Benito, P., Stoffel,

697   M., Lucas-Borja, M.E., Andivia, E., Sancho-García, C., Zavala, M.A., 2017a. Forest

698   productivity in southwestern Europe is controlled by coupled North Atlantic and

699   Atlantic Multidecadal Oscillations. Nat. Commun. 8, 1–8.

700   https://doi.org/10.1038/s41467-017-02319-0

701 Madrigal-González, J., Herrero, A., Ruiz-Benito, P., Zavala, M.A., 2017b. Resilience to

702   drought in a dry forest: Insights from demographic rates. For. Ecol. Manage. 389,

703   167–175. https://doi.org/10.1016/j.foreco.2016.12.012

704 Madrigal-González, J., Ruiz-benito, P., Ratcliffe, S., Calatayud, J., 2016.

705   Complementarity effects on tree growth are contingent on tree size and climatic

706   conditions across Europe. Sci. Rep. 6, 11. https://doi.org/10.1038/srep32233

707 Maestre, F.T., Cortina, J., 2004. Are Pinus halepensis plantations useful as a restoration

708   tool in semiarid Mediterranean areas? For. Ecol. Manage. 198, 303–317.

709   https://doi.org/10.1016/j.foreco.2004.05.040

710 Martín-Benito, D., Cherubini, P., Del Río, M., Cañellas, I., 2008. Growth response to

711   climate and drought in Pinus nigra Arn. trees of different crown classes. Trees -

712   Struct. Funct. 22, 363–373. https://doi.org/10.1007/s00468-007-0191-6

713   Martín-Gómez, P., Aguilera, M., Pemán, J., Gil-Pelegrín, E., Ferrio, J.P., 2017.
714   Contrasting ecophysiological strategies related to drought: the case of a mixed stand
715   of Scots pine (Pinus sylvestris) and a submediterranean oak (Quercus subpyrenaica).
716   Tree Physiol. 37, 1478–1492. https://doi.org/10.1093/treephys/tpx101

717   McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut,
718   J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant
719   survival and mortality during drought: Why do some plants survive while others
720   succumb   to   drought?   New   Phytol.   https://doi.org/10.1111/j.1469-
721   8137.2008.02436.x

722   Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand
723   composition and tree size on resistance and resilience to drought in sessile oak and
724   Scots   pine.   For.   Ecol.   Manage.   339,   22–33.
725   https://doi.org/10.1016/j.foreco.2014.11.032

726   Mölder, I., Leuschner, C., 2014. European beech grows better and is less drought sensitive
727   in mixed than in pure stands: Tree neighbourhood effects on radial increment. Trees
728   - Struct. Funct. 28, 777–792. https://doi.org/10.1007/s00468-014-0991-4

729   Moreno-Gutiérrez, C., Dawson, T.E., Nicolás, E., Querejeta, J.I., 2012. Isotopes reveal
730   contrasting water use strategies among coexisting plant species in a mediterranean
731   ecosystem.   New   Phytol.   196,   489–496.   https://doi.org/10.1111/j.1469-
732   8137.2012.04276.x

733   Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M., Bugmann, H., 2014.
734   Temporal stability in forest productivity increases with tree diversity due to
735   asynchrony   in   species   dynamics.   Ecol.   Lett.   17,   1526–1535.

736   https://doi.org/10.1111/ele.12357

737   Nelson, E.J., Kareiva, P., Ruckelshaus, M., Arkema, K., Geller, G., Girvetz, E., Goodrich,

738   D., Matzek, V., Pinsky, M., Reid, W., Saunders, M., Semmens, D., Tallis, H., 2013.

739   Climate change's impact on key ecosystem services and the human well-being they

740   support   in   the   US.   Front.   Ecol.   Environ.   11,   483–493.

741   https://doi.org/10.1890/120312

742   Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of

743   temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547.

744   https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

745   Nikinmaa, L., Lindner, M., Cantarello, E., Jump, A.S., Siedl, R., Winkel, G., Muys, B.,

746   2020. Review the use of resilience concepts in forest sciences. Curr. For. Reports.

747   Paquette, A., Messier, C., 2010. The effect of biodiversity on tree productivity: from

748   temperate   to   boreal   forests.   Glob.   Ecol.   Biogeogr.   20,   170–180.

749   https://doi.org/10.1111/j.1466-8238.2010.00592.x

750   Pausas, J.G., Blade, C., Valdecantos, A., Seva, J.P., Fuentes, D., Alloza, J.A., Vilagrosa,

751   A., Bautista, S., Cortina, J., Vallejo, R., 2004. Pines and oaks in the restoration of

752   Mediterranean landscapes of Spain: New perspectives for an old practice - a review.

753   Plant Ecol. 171, 209–220.

754   Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R., 2018. Linear and Nonlinear Mixed

755   Effects Models.

756   Poyatos, R., Llorens, P., Piñol, J., Rubio, C., 2008. Response of Scots pine (Pinus

757   sylvestris L.) and pubescent oak (Quercus pubescens Willd.) to soil and atmospheric

758   water deficits under Mediterranean mountain climate. Ann. For. Sci. 65.

759   https://doi.org/10.1051/forest:2008003

760   Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species

761   stands compared with monocultures. For. Ecol. Manage. 327, 251–264.

762   https://doi.org/10.1016/j.foreco.2014.04.027

763   Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G.,

764   Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K.,

765   Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F.,

766   Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J.,

767   Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M.,

768   Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A.,

769   2015. Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris

770   L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient

771   through Europe. Eur. J. For. Res. 134, 927–947. https://doi.org/10.1007/s10342-

772   015-0900-4

773   Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought

774   stress in mixed versus pure forests: Evidence of stress release by inter-specific

775   facilitation. Plant Biol. 15, 483–495. https://doi.org/10.1111/j.1438-

776   8677.2012.00670.x

777   Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K.,

778   Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvod, K.,

779   Jansons, A., de-Dios-García, J., Löf, M., Aldea, J., Korboulewsky, N., Reventlow,

780   D.O.J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette,

781   Q., Sitko, R., Fabrika, M., Svoboda, M., Černý, J., Wolff, B., Ruíz-Peinado, R., del

782   Río, M., 2019. Stand growth and structure of mixed-species and monospecific stands

783   of Scots pine (Pinus sylvestris L.) and oak (Q. robur L., Quercus petraea (Matt.)

784   Liebl.) analysed along a productivity gradient through Europe. Eur. J. For. Res.

785   https://doi.org/10.1007/s10342-019-01233-y

786 Prieto, I., Armas, C., Pugnaire, F.I., 2012. Water release through plant roots: New insights

787   into its consequences at the plant and ecosystem level. New Phytol. 193, 830–841.

788   https://doi.org/10.1111/j.1469-8137.2011.04039.x

789 Querejeta, J.I., Egerton-Warburton, L.M., Allen, M.F., 2003. Direct nocturnal water

790   transfer from oaks to their mycorrhizal symbionts during severe soil drying.

791   Oecologia 134, 55–64. https://doi.org/10.1007/s00442-002-1078-2

792 Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of

793   mixed tree plantations on the nutrition of individual species: A review. Tree Physiol.

794   30, 1192–1208. https://doi.org/10.1093/treephys/tpq035

795 Richards, F.J., 1959. A flexible growth function for empirical use. J. Exp. Bot. 10, 290–

796   301. https://doi.org/10.1093/jxb/10.2.290

797 Río, M. Del, Sterba, H., 2009. Comparing volume growth in pure and mixed stands of

798   Pinus sylvestris and Quercus pyrenaica. Ann. For. Sci. 66.

799   https://doi.org/10.1051/forest/2009035

800 Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: A

801   synthesis. Can. J. For. Res. 31, 1855–1870. https://doi.org/10.1139/x01-120

802 Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., Zavala, M.A.,

803   2014. Diversity increases carbon storage and tree productivity in Spanish forests.

804   Glob. Ecol. Biogeogr. 23, 311–322. https://doi.org/10.1111/geb.12126

805 Ruiz-Benito, P., Gómez-Aparicio, L., Zavala, M.A., 2012. Large-scale assessment of

806   regeneration and diversity in Mediterranean planted pine forests along ecological

807   gradients. Divers. Distrib. 18, 1092–1106. https://doi.org/10.1111/j.1472-

808   4642.2012.00901.x

809   Ruiz-Benito, P., Ratcliffe, S., Zavala, M.A., Martínez-Vilalta, J., Vilà-Cabrera, A., Lloret,

810   F., Madrigal-González, J., Wirth, C., Greenwood, S., Kändler, G., Lehtonen, A.,

811   Kattge, J., Dahlgren, J., Jump, A.S., 2017. Climate- and successional-related

812   changes in functional composition of European forests are strongly driven by tree

813   mortality. Glob. Chang. Biol. 23, 4162–4176. https://doi.org/10.1111/gcb.13728

814   Sánchez-Salguero, R., Navarro-Cerrillo, R.M., Swetnam, T.W., Zavala, M.A., 2012. Is

815   drought the main decline factor at the rear edge of Europe? The case of southern

816   Iberian pine plantations. For. Ecol. Manage. 271, 158–169.

817   https://doi.org/10.1016/j.foreco.2012.01.040

818   Santonja, M., Fernandez, C., Proffit, M., Gers, C., Reiter, I.M., Cramer, W., Baldy, V.,

819   2017. Plant litter mixture partly mitigates the negative effects of extended drought

820   on soil biota and litter decomposition in a Mediterranean oak forest.

821   Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of

822   image analysis. Nat. Methods. https://doi.org/10.1038/nmeth.2089

823   Schwarz, J.A., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J.,

824   2020. Quantifying growth responses of trees to drought - a critique of the Lloret-

825   indicators and recommendations for future studies. Curr. For. Reports.

826   https://doi.org/https://doi.org/10.32942/osf.io/5ke4f

827   Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., Bräker, O.U., 1990. Identification,

828   presentation and interpretation of event years and pointer years in

829   dendrochronology. Dendrochronologia 8, 9–38.

830   Serra-Maluquer, X., Mencuccini, M., Martínez-Vilalta, J., 2018. Changes in tree
831   resistance, recovery and resilience across three successive extreme droughts in the
832   northeast   Iberian   Peninsula.   Oecologia   187,   343–354.
833   https://doi.org/10.1007/s00442-018-4118-2

834   Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016. Heavy and frequent thinning
835   promotes drought adaptation in Pinus sylvestris forests. Ecol. Appl. 26, 2190–2205.
836   https://doi.org/10.1002/eap.1373

837   Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., Dosio, A., 2018. Will drought events
838   become more frequent and severe in Europe? Int. J. Climatol. 38, 1718–1736.
839   https://doi.org/10.1002/joc.5291

840   Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll,
841   L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M.,
842   Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B.,
843   Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine
844   (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) –
845   Site water supply and fertility modify the mixing effect. For. Ecol. Manage. 461,
846   117908. https://doi.org/10.1016/j.foreco.2020.117908

847   Team, R.C., 2018. R: A language and environment for statistical computing.

848   Thornthwaite, C.W., 1948. An Approach toward a Rational Classification of Climate.
849   Geogr. Rev. 38, 55–94.

850   Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., 2015.
851   Overyielding in mixed forests decreases with site productivity. J. Ecol. 103, 502–
852   512. https://doi.org/10.1111/1365-2745.12353

853   Vadell, E., de-Miguel, S., Pemán, J., 2016. Large-scale reforestation and afforestation

854   policy in Spain: A historical review of its underlying ecological, socioeconomic and

855   political dynamics. Land use policy 55, 37–48.

856   https://doi.org/10.1016/j.landusepol.2016.03.017

857   Vilà-Cabrera, A., Coll, L., Martínez-Vilalta, J., Retana, J., 2018. Forest management for

858   adaptation to climate change in the Mediterranean basin: A synthesis of evidence.

859   For. Ecol. Manage. 407, 16–22. https://doi.org/10.1016/j.foreco.2017.10.021

860   Villar-Salvador, P., 2016. Restoration of Spanish pine plantations: A main challenge for

861   the 21st century. Reforesta 53–66. https://doi.org/10.21750/refor.1.04.4

862   Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living

863   trees. Can. J. For. Res. 21, 414–416.

864   Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., Granier, A., 2011. Evidence

865   of hydraulic lift in a young beech and oak mixed forest using 18O soil water

866   labelling. Trees - Struct. Funct. 25, 885–894. https://doi.org/10.1007/s00468-011-

867   0563-9

868   Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and trade-offs in Mediterranean

869   plant communities: the case of mixed holm oak (Quercus ilex L)-Aleppo pine (Pinus

870   halepensis Mill.) forests. Bot. Rev. 66, 119–149.

871   Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects

872   models and extensions in ecology with R. Springer.

873