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2

3 **Title: Mixing beech with fir or pubescent oak does not help mitigate drought exposure at**
4 **the limit of its climatic range**

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22 **Keywords**

23 mixed forests; species interactions; drought; carbon isotope composition; hydrogen isotope
24 composition; *Fagus sylvatica*; *Abies alba*; *Quercus pubescens*; southeastern France

25

26 **Abstract:**

27 In the context of climate change, it remains unclear whether mixed-species forests will help
28 mitigate the impacts of future droughts and, if so, through which processes. As European beech
29 (*Fagus sylvatica*) is one of the major European species, it is crucial to evaluate its response to
30 drought when mixed with species with contrasted functional traits and in contrasted climatic
31 conditions, particularly at the limit of its climatic range. This study aimed to (i) characterize the
32 effects of tree species interactions on the drought exposure of beech in south-eastern France,
33 and (ii) determine whether belowground water uptake complementarity underlies these effects.
34 We focused on beech-silver fir (*Abies alba*) and beech-pubescent oak (*Quercus pubescens*)
35 forests across six sites in the French pre-Alps, a region at the limit of the climatic range for
36 beech. We used a triplet approach to compare the tree-ring carbon isotope composition ($\delta^{13}\text{C}$)
37 of these species in pure and two-species mixed stands during a period of very dry years, and
38 used water hydrogen isotope composition ($\delta^2\text{H}$) in the xylem to identify water uptake sources.
39 Overall, we found no clear mixture effect pattern on beech physiological functioning among
40 sites and triplets. In beech-fir sites, mixing beech with fir had no effect on beech $\delta^{13}\text{C}$ values
41 during dry years. In beech-oak sites, mixture effects on beech were mostly neutral, although
42 sometimes beech suffered from a stronger exposure to drought in mixed stands. Our study
43 emphasizes the impact of the tree sampling design on the outcome of studies on forest
44 biodiversity-ecosystem functioning relationships. Limiting tree sampling to dominant trees
45 when analyzing stand-level relationships may bias these outcomes. We evidenced differences

46 in water uptake sources between beech and fir, but not between beech and oak during a dry
47 summer. However, these patterns did not help explain the lack of species mixture effects, or
48 existence thereof, at the triplet scale. Our study demonstrates that managing beech in mixed
49 stands with silver fir or pubescent oak at the limit of beech climatic range does not buffer
50 drought impacts on beech during dry years. In the long term, with more frequent extreme
51 droughts, promoting beech-fir mixtures will not be detrimental to beech drought response, while
52 beech may suffer in mixtures with pubescent oak.

53 **1. Introduction**

54 European forest ecosystems are expected to be highly impacted by ongoing climate change
55 (Hanewinkel et al., 2013) through an increase in temperatures and more frequent and intense
56 droughts (IPCC, 2014; Lehner et al., 2017). Drought-induced stress can lead to a loss of vitality
57 and to mortality for trees, caused by hydraulic failure and carbon starvation (McDowell et al.,
58 2008; Hartmann et al., 2018). This will be especially true in southern parts of the European
59 temperate and Mediterranean regions (Lindner et al., 2010). There is therefore a strong need for
60 new management strategies to help forest owners mitigate current and future drought impacts
61 (Bolte et al., 2009).

62 European beech (*Fagus sylvatica* L.) is an essential species in European forests: its natural
63 distribution covers most of continental Europe and it is the most abundant broad-leaved forest
64 tree in Central Europe (Dittmar et al., 2003). Beech is a drought-sensitive species and is
65 especially vulnerable when the soil water deficit is severe and prolonged (Gessler et al., 2007).
66 Model-based projections predict that climate change will likely induce a reduction in beech-
67 dominated forests in southern Europe (Cheaib et al., 2012; Hanewinkel et al., 2013). Growth
68 declines for beech have already been reported in recent decades (Charru et al., 2017), especially
69 at its southern range limits (Jump et al., 2006).

70 Managing temperate forests with higher tree species diversity has been identified as one
71 management strategy that can improve forest productivity (e.g. Toïgo et al., 2015; Liang et al.,
72 2016; Ammer, 2019) and other ecosystem functions (Brockerhoff et al., 2017), such as
73 resistance to disturbances (Jactel et al., 2017). In particular, it has been shown that beech
74 productivity improves in mixed forests compared to pure ones, particularly when beech is
75 admixed with silver fir (*Abies alba* Mill.) or other coniferous species (e.g. Toïgo et al., 2015;
76 Pretzsch and Forrester, 2017). However, it is still not clear whether mixed-species forests also

77 contribute to mitigating drought impacts (Grossiord, 2019), which in turn would have an effect
78 on forest vitality and productivity. In the case of beech, contrasted effects of species interactions
79 have been found under drought conditions. Some studies demonstrate lower drought exposure
80 of beech in mixed stands (e.g. Pretzsch et al., 2013; Metz et al., 2016), but others conclude that
81 the mixture effect is neutral (e.g. Schwarz and Bauhus, 2019). Furthermore, contrasted results
82 were found when comparing the effects of the same species mixture, including beech, among
83 different sites (Schäfer et al., 2017; González de Andrés et al., 2018; Jourdan et al., 2019b).

84 Two factors have been identified as major drivers for the variability in the outcome of mixture
85 effects on the mitigation of drought impacts: the importance of functional variability among
86 species and the effect of site climatic conditions (Forrester, 2014; Forrester and Bauhus, 2016).
87 First, the outcomes are species-dependent: species with more contrasted functional traits in
88 terms of physiology, phenology or morphology (e.g. root depth, stomatal control, physical traits
89 involved in xylem resistance to embolism), are more likely to show complementarity effects,
90 especially for drought responses (Grossiord, 2019). Secondly, even if the given species mixture
91 potentially mitigates drought impacts, the degree of the effect may vary with site-level
92 environmental conditions (Forrester and Bauhus, 2016). Forrester and Bauhus (2016) suggested
93 a theoretical framework, as a generalization of the stress gradient hypothesis (Bertness and
94 Callaway, 1994), in which positive mixture effects are expected to be stronger when resources
95 are scarce, for example along a declining precipitation gradient or during severe drought events.
96 In accordance with this framework, Grossiord et al. (2014c, 2014b) found negative or neutral
97 effects in more humid sites and positive effects in drier ones (Grossiord et al., 2014b, 2014c).
98 However, the relationship between mixture effects and a resource gradient may not be linear
99 but may rather emerge from threshold points of resource availability (de Streel et al., 2020).

100 Such patterns could be explained by the fact that positive mixture effects may not be strong
101 enough to compensate for the increasing environmental constraints in extremely dry sites and

102 that positive mixture effects on drought response could disappear with strong water stress (e.g.
103 de Streel et al., 2020).

104 The outcome of studies on the effects of species mixing may also depend on how the trees were
105 sampled. To date the typical approach has been to limit the sampling design to dominant trees
106 when examining mixture effects on the response of trees to drought, particularly as measured
107 by carbon isotope composition ($\delta^{13}\text{C}$) (Grossiord et al., 2014c; Metz et al., 2016; Schwarz and
108 Bauhus, 2019). However, not including light-suppressed trees in these analyses could bias the
109 overall patterns of mixture effects, as the drought sensitivity of suppressed and dominant trees
110 may differ (Mérian and Lebourgeois, 2011). Including all trees for a more complete
111 representation of the forest stand could help in understanding the variability of mixture effects
112 on drought responses.

113 The processes behind mixture effects on drought exposure are linked to spatial or temporal
114 resource partitioning among species due to competition, facilitation, or niche differentiation for
115 resource acquisition and use (Ammer, 2019; Grossiord, 2019). At aboveground level, this may
116 result in, for example, differences in canopy packing and shading effects (Ishii and Asano,
117 2010; Jucker et al., 2015; Grossiord 2019). At belowground level, complementarity for water
118 uptake and niche differentiation among species could result in a lesser exposure to decreased
119 soil water content during extreme drought events (Forrester, 2014), but these processes have
120 rarely been experimentally tested in the field (Grossiord et al., 2014a; Goisser et al., 2016).

121 Further studies for species diversity effects on beech drought exposure are therefore necessary
122 to identify whether or not tree-species mixing might mitigate drought impacts and maintain
123 beech productivity, particularly along the southern margins of beech distribution in Europe
124 where climate change is occurring the fastest. To address these questions, we studied the effect
125 of species mixture on beech drought exposure during a period with severe summer droughts, in

126 forest plots of different species compositions distributed across six sites in south-eastern France
127 with contrasting climate conditions. We studied two widespread species mixtures with beech
128 in mountainous areas of south-eastern France: beech associated with silver fir (*Abies alba* Mill.)
129 in the northern part of the region, and beech associated with pubescent oak (*Quercus pubescens*
130 Willd.) in the southern part. These two accompanying species are likely to show
131 complementarity effects with beech as they have contrasted physiological functioning, i.e.
132 contrasted water transport systems and phenology between beech (deciduous species) and fir
133 (evergreen conifer), and contrasted drought and shade tolerance between beech and pubescent
134 oak (Niinemets and Valladares, 2006). We sampled all trees in the stands, including both
135 dominant and light suppressed trees. We used stable carbon isotope composition ($\delta^{13}\text{C}$) in tree
136 rings from dry years to examine the effect of species composition on tree exposition to drought
137 (Grossiord et al., 2014c; Metz et al., 2016). Tree ring analysis provided us with an integrative
138 measurement of past drought effects on tree functioning (McCarroll and Loader, 2004). Tree-
139 ring $\delta^{13}\text{C}$ is expressed as a negative value that increases (less negative values) when a tree is
140 exposed to increased water stress (Saurer et al., 1995). It indirectly reflects the compromise
141 between carbon and water acquisition and use at leaf and plant level (Farquhar et al., 1982).
142 Finally, to assess potential water-use complementarity mechanisms, we looked at differences
143 in water uptake sources between species. To do so, we measured the stable hydrogen isotope
144 composition ($\delta^2\text{H}$) in branch xylem water (Dawson, 1993; West et al., 2006).

145 We specifically addressed the following questions:

- 146 1. Is beech physiological functioning ($\delta^{13}\text{C}$) during dry years influenced by site-specific
147 environmental conditions?
- 148 2. Is beech $\delta^{13}\text{C}$ during dry years different between pure and mixed stands?
- 149 3. Can potential mixture effects be explained by complementarity in species water uptake
150 sources?

151 2. Material and Methods

152 2.1. Field design

153 We selected six sites in the French pre-Alps on limestone bedrock (Fig. 1a, see also Jourdan et
154 al., 2019b) spanning a wide range of climatic conditions (Fig. 2). At each site, we used a triplet
155 approach, i.e. an ensemble of three plots: one plot in pure stands of each studied species and
156 one plot in a mixed stand of the same two species (Fig. 1b). All the triplets were located on
157 north-facing slopes. The three plots within each triplet were as close to each other as possible
158 and with a similar slope (Table A1). The soil textures and gravel contents were similar within
159 a triplet. At each site, two sets of such triplets were selected in order to cover local variability
160 in environmental conditions and stand structure, resulting in six plots per site (Fig. 1b). Plot
161 elevations ranged from 700 m to 1400 m (Table A1).

162 Figure 1 HERE; size: 2 columns; B&W

163 European beech (*Fagus sylvatica* L.) was present at all six sites and was mixed with either silver
164 fir (*Abies alba* Mill.) in the three northern sites (S1 to S3) or with pubescent oak (*Quercus*
165 *pubescens* Willd.) in the three southern ones (S4 to S6) (Fig. 1a). In pure plots, the focal species
166 accounted for at least 80% of the total basal area and in the mixed plots each focal species
167 accounted for at least 40% of the total basal area (Table A2). Other tree species present in the
168 plots represented less than 20% of the total basal area and were mostly in the understory of the
169 canopy (Table 1, Table A2). The trees from both focal species in the mixed stands were mixed
170 on a stemwise intermingling pattern (del Río et al., 2018). Sites S1 to S4 were located in forests
171 with continuous-cover management whereas sites S5 and S6 had limited management. To limit
172 direct management effects, we only worked in stands where no thinning operations had been
173 conducted for at least the last two decades. All the stands were located in mature forests with
174 an uneven-aged high forest structure, except for S5, which was in a coppice forest. Individual

175 plots were circular with a radius of 17.5 m (area = 962 m²) and consisted of a central area (10
176 m radius, area = 314 m²) where the measurements were conducted, plus a buffer zone (7.5 m
177 radius) to ensure the plot was surrounded by homogeneous conditions (Fig. 1c).

178 Table 1 HERE; size: 1.5 columns

179 2.2. *Climate data*

180 Climatic variables were extracted from the mesoscale SAFRAN reanalysis of the Météo France
181 national observation network data (Quintana-Seguí et al., 2008). As SAFRAN was initially
182 designed for mountainous areas, it was the best-estimated source of daily climatic data for our
183 study region. The precision of the climate data was relevant at the site scale, but not at the triplet
184 scale, as the SAFRAN analysis covers France with an 8 km × 8 km grid and is calculated for
185 the average elevation of the corresponding grid. We used the SAFRAN long-term climate data
186 to estimate the average cumulative annual precipitation and the mean annual temperature per
187 site over a 20-year period (1994-2013) (Fig. 2; Table A3).

188 Figure 2 HERE; size: 1 column; B&W

189 2.3. *Choice and characterization of dry years*

190 Jourdan et al. (2019b) calculated the standardized precipitation evapotranspiration index (SPEI,
191 Vicente-Serrano et al., 2010) for each of the six sites for the months of February to July, i.e. the
192 growth period, of each year from 1994 to 2013 (see Fig. 2 in Jourdan et al., 2019b). SPEI is a
193 standardized index that makes it possible to identify dry years for a given site, but not to
194 compare drought intensity among sites. This enabled us to choose the period of dry years
195 relative to each site within the 1994-2013 period for tree-ring carbon isotope composition ($\delta^{13}\text{C}$)
196 analyses. We targeted the 2003-2007 period because it was representative of a series of severe
197 dry years for all sites. Indeed, this period was on average much drier in terms of precipitation

198 across sites than the 20-year average for 1994-2013 (Fig. 2), but was also hotter during the
199 summer months (Table A3).

200 To characterize the water stress during these dry years, we used the daily forest water balance
201 model BILJOU© (Granier et al., 1999). We estimated the daily relative extractable water
202 (REW, unitless) for each site based on daily climate data over the 1994-2013 period. REW is
203 the ratio between available soil water and the maximum extractable water (water holding
204 capacity) and varies from field capacity (REW=1) to permanent wilting point (REW=0). Water
205 stress is assumed to occur when REW drops below a threshold of 0.4 under which stomatal
206 conductance, and therefore leaf gas exchange, is gradually reduced (Granier et al., 1999). The
207 BILJOU© model has a daily time step and requires daily climatic input variables (mean air
208 temperature, precipitation, wind speed, global radiation, and humidity) as well as soil water
209 holding capacity and leaf area index (LAI). We used SAFRAN daily climatic variables at the
210 site scale. We fixed soil water holding capacity at 100 mm since we were not able to
211 characterize the plot soil profiles precisely. Nevertheless, we tested the BILJOU© model with
212 different soil water holding capacity values but this did not change the ranking of the sites in
213 terms of water stress (data not shown). Similarly, we used a single LAI value (i.e. $7.0 \text{ m}^2 \text{ m}^{-2}$)
214 for all the sites as a standard value for mature forests. Adapting this value to the different sites
215 did not change the ranking of the sites. For each year at each site, an annual number of days
216 when REW is below 0.4 was calculated, which allowed to quantify water stress levels (Table
217 A3).

218 *2.4. Tree measurements*

219 *2.4.1. Dendrometry*

220 In 2014, in the central area of each of the 36 plots, Jourdan et al. (2019b) surveyed all of the
221 trees with a diameter at breast height (DBH, cm) greater than 7.5 cm and recorded their DBH

222 and total height. They also cored the trunk of all trees with a DBH greater than 7.5 cm in the
223 plots at a height of 1.3 m with a Pressler increment borer (Haglöf, Sweden) in 2014-2015. In
224 coppice stands, they only cored the largest stem of each clump of coppice shoots (individual
225 tree). Some cores were too difficult to date accurately and were discarded from further analyses,
226 leaving a total of 792 trees sampled (368 beech, 222 fir and 202 pubescent oak trees),
227 representing all the diameter classes and different strata in the canopy. On these cores, Jourdan
228 et al. (2019b) measured tree-ring width for the 1994-2013 period and performed cross-dating
229 for each species according to specific pointer years.

230 2.4.2. Carbon isotope composition ($\delta^{13}\text{C}$)

231 We used these tree cores to analyse the stable carbon isotope composition ($\delta^{13}\text{C}$) of each tree
232 in the tree-rings of the selected period (2003-2007). Using a scalpel under a stereomicroscope,
233 we extracted the tree-rings (including earlywood and latewood) that corresponded to the target
234 period (2003-2007) as one pooled block for all five years. We used whole wood tissue for our
235 analyses as it shows the same trends as cellulose-only isotopic measurements and allowed us to
236 analyze a larger number of trees (McCarroll and Loader, 2004). For each tree, the tree-rings of
237 the 2003-2007 period were kept as one sample. We ground them into a fine powder, then
238 weighed around 1 mg of powder for each sample in tin capsules for the isotopic analysis. We
239 used a different technique when the dry mass of the 2003-2007 tree-ring sample was less than
240 6 mg (15 samples out of 792) to avoid any loss of matter in the grinding process. These 15
241 samples were cut into four quarters perpendicularly to the tree-ring axis with a scalpel instead
242 of being ground. For each of these samples, we then analyzed separately three out of four
243 subsamples for isotopic composition and used the average of these three $\delta^{13}\text{C}$ values. The fourth
244 subsample was kept as a spare in case further analyses should be needed on these samples.

245 The $^{13}\text{C}/^{12}\text{C}$ ratios of each wood sample were analyzed with an isotope-ratio mass spectrometer
246 (IRMS, Isoprime 100, Isoprime Ltd., Cheadle Hulme, UK) coupled with an elemental analyzer
247 (EA, Elementar vario, ISOTOPE cube, Elementar Analysen Systeme GmbH, Hanau, Germany)
248 at the SILVATECH platform (Silvatech, INRAE, 2018. Structural and functional analysis of
249 tree and wood Facility, Nancy, France). The results were expressed as carbon isotope
250 composition $\delta^{13}\text{C}$ (‰) relative to the international standard Vienna Pee Dee Bee Belemnite (V-
251 PDB) (IAEA, 1995) following Eq. 1:

$$252 \quad \delta^{13}\text{C} (\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \quad (1)$$

253 where R_{sample} and R_{standard} represent the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and the V-PDB standard,
254 respectively (Farquhar et al., 1982). The mass spectrometer had a precision of ± 0.2 ‰ for $\delta^{13}\text{C}$
255 values.

256 In this study, we used two sets of $\delta^{13}\text{C}$ data for our statistical analyses. First, we used all the
257 $\delta^{13}\text{C}$ values to characterize the response of all the trees, individually or at the stand level,
258 hereafter called “all trees”. Second, we used a subsample of pre-selected dominant trees in each
259 plot, hereafter called “dominant-tree subsample”, to analyze the effect of mixture on the $\delta^{13}\text{C}$
260 of the trees without any confounding factor related to light availability in the canopy (McCarroll
261 and Loader, 2004). These dominant trees were selected according to the following criteria: (i)
262 they were in the biggest diameter class in each plot, (ii) they had a crown illumination index
263 (Dawkins index) of 4 or 5, meaning that they received direct vertical light (Clark and Clark,
264 1992), (iii) they were well mixed with the other species on a stem-to-stem basis in the mixed
265 stands, and (iv) they were suitable for branch sampling by climbers (see $\delta^2\text{H}$ section). We then
266 randomly chose between four and seven of these dominant trees per species in each plot, leading
267 to a total of 240 dominant trees (beech = 121, fir = 57, pubescent oak = 62) out of a total of 792
268 trees measured for $\delta^{13}\text{C}$.

269 One caveat should be noted concerning our $\delta^{13}\text{C}$ measurements: we were able to compare $\delta^{13}\text{C}$
270 functioning during dry years between pure and mixed plots, but we were not able to use the
271 difference in $\delta^{13}\text{C}$ between a reference wet year and a dry year to estimate tree drought
272 resistance, as some studies have done to detect mixture effects (e.g., Grossiord et al., 2014c;
273 Schwarz and Bauhus, 2019). Indeed, during the period from 1994 to 2013, we were not able to
274 find any years that were wet enough to serve as a reference across all sites. Moreover, as growth
275 is very slow at some of the sites with a Mediterranean influence, we would not have been able
276 to cut out single yearly tree-rings precisely enough. Other studies have also used absolute values
277 of $\delta^{13}\text{C}$, as we did, albeit usually over a longer-term chronology (González de Andrés et al.,
278 2018; de Streel et al., 2020). Moreover, in a study looking at tree diversity effects on drought
279 responses using $\delta^{13}\text{C}$, the same trends were found with differences in $\delta^{13}\text{C}$ between a wet and a
280 dry year (Grossiord et al., 2014c) than with absolute $\delta^{13}\text{C}$ values for the dry years only
281 (Grossiord, 2014, p.48). We therefore focused our analyses on mixture effects on tree
282 functioning during dry years by comparing values between pure and mixed stands, expecting
283 more negative $\delta^{13}\text{C}$ values for beech in mixed stands as compared to pure ones if the presence
284 of oak or fir in the mixture induced less competition for water resources.

285 *2.4.3. Xylem water $\delta^2\text{H}$*

286 To estimate among-tree differences in water uptake sources, we used a method that relies on
287 the natural abundance of stable hydrogen isotopes in the xylem water from branches (Dawson,
288 1993). During dry spells, an isotopic gradient for hydrogen is established in the top layers of
289 the soil (Clark and Fritz, 1997). The hydrogen isotope composition ($\delta^2\text{H}$, ‰) of water flowing
290 in the xylem, which is the raw sap coming up from the roots, represents the mean signature of
291 all the water sources for the tree's rooting system. Due to very rocky shallow soils, we were not
292 able to obtain a full soil profile at all of our sites. To address niche partitioning in water uptake

293 sources, we therefore analyzed differences in $\delta^2\text{H}$ values within triplets, but we were not able
294 to quantitatively estimate a depth of water uptake by trees.

295 We sampled the same trees selected for the dominant-tree subsample of $\delta^{13}\text{C}$ analyses. To
296 determine the $\delta^2\text{H}$ of the xylem water, we sampled a 30 to 40-cm-long branch from each
297 dominant tree in the summer of 2018 during a dry spell at five sites, for a total of 200 samples.
298 We could not visit S4 that year for technical reasons, and therefore we do not have $\delta^2\text{H}$ values
299 for that site. Professional climbers cut the branches out of the upper third of the tree crown. We
300 removed bark tissue immediately with a knife to prevent phloem sap from mixing with xylem
301 water. Five-centimeter-long samples were then cut from the branches and placed into closed
302 airtight glass vials and stored in cool conditions.

303 Once in the lab, we stored the branch samples in cool chambers at 4°C to reduce the risk of
304 evaporation. We then extracted water from the branch samples through cold trapping with a
305 custom-made static vacuum cryogenic distillation system (West et al., 2006). The water from
306 the branch samples was evaporated by heating the sampling tube in a water bath (65°C), then
307 condensed with liquid nitrogen for 90 minutes in a collection tube. The extracted water was
308 analyzed for $^2\text{H}/^1\text{H}$ ratios with an elemental analyzer (EA, EuroPyrOH; EuroVector, Milano,
309 Italy) coupled to an isotope ratio mass spectrometer (Isoprime IRMS; Elementar, Manchester,
310 UK) at the SILVATECH platform (Silvatech, INRAE, 2018. Structural and functional analysis
311 of tree and wood Facility, Nancy, France). The $^2\text{H}/^1\text{H}$ ratio of each water sample was
312 determined from six subsamples of $0.2\ \mu\text{L}$ of extracted water and only the last three
313 measurements were kept, then averaged for each sample. The first three measurements were
314 discarded to avoid any bias related to a potential “memory effect”, meaning a contamination
315 from the previous sample analyzed. The results were expressed as $\delta^2\text{H}$ relatively to the
316 international Vienna-standard mean ocean water standard (V-SMOW) following Eq. 2:

317
$$\delta^2\text{H} (\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \quad (2)$$

318 where R_{sample} and R_{standard} represent the $^2\text{H}/^1\text{H}$ ratios of the sample and of the V-SMOW standard
 319 (IAEA, 1995). The mass spectrometer used in this study had a precision of $\pm 2.0 \text{ ‰}$ for $\delta^2\text{H}$
 320 values.

321 We weighed the branch samples after cryo-distillation and placed them in a drying oven for 48
 322 h at 65°C to check if all the water had been extracted. If part of the water had not been
 323 completely extracted, we applied a correction to the $\delta^2\text{H}$ values since the extracted water had
 324 less of the heavier isotope (^2H) than the water remaining in the branch. We calculated the
 325 theoretical fractionation of the hydrogen isotopes with Eq. 3 to obtain a corrected $\delta^2\text{H}$ value
 326 (Araguás-Araguás et al., 1995):

327
$$\delta^2H_{\text{corr}} = \delta^2H_{\text{measured}} - \left(\frac{F^{(1/\alpha)} - F}{F - 1} * 1000 \right) \quad (3)$$

328 where $\delta^2\text{H}_{\text{measured}}$ is the known measured value, $\delta^2\text{H}_{\text{corr}}$ the expected real value if there had been
 329 no fractionation during extraction, F the fraction of water remaining in the branch, and α a fixed
 330 factor specific to the isotope measured (^2H) and to the extraction temperature (65°C). Factor α
 331 is calculated from Eq. 4 (Majoube, 1971):

332
$$10^3 * \ln(\alpha) = a * \left(\frac{10^6}{T_K^2} \right) + b * \left(\frac{10^3}{T_K} \right) + c \quad (4)$$

333 where T_K is the extraction temperature in degrees Kelvin, and a , b , and c are fixed factors for
 334 ^2H defined in Majoube (1971) with $a = 24.844$, $b = -76.248$, and $c = 52.612$ (Clark and Fritz,
 335 1997). We applied this correction to all the samples with a water-extraction percentage less than
 336 100%.

337 *2.5. Data analysis*

338 All data analyses were conducted including either all trees or those in the dominant-tree
339 subsample.

340 2.5.1. Variability of $\delta^{13}\text{C}$ values in pure stands

341 To assess the variability of $\delta^{13}\text{C}$ values among sites and species, we compared $\delta^{13}\text{C}$ values in
342 the pure stands only. First, for site effects, we studied the differences in $\delta^{13}\text{C}$ values among the
343 six pure beech stands, and among the three stands of pure fir and pure pubescent oak, following
344 the model:

$$345 \quad \delta^{13}\text{C} \sim \text{Site} + \text{Triplet} + \text{Site:Triplet} \quad (5)$$

346 We used a linear model for each species with *Site* (S1 to S6) and *Triplet* (1 or 2) as factor
347 variables. We further tested the interaction between *Site* and *Triplet* to reveal the differences
348 between the two triplets at each site.

349 Second, we tested for differences in $\delta^{13}\text{C}$ values between the two species (beech and fir, or
350 beech and oak) in pure stands, following the model:

$$351 \quad \delta^{13}\text{C} \sim \log(\text{DBH}) + \text{Species} + \log(\text{DBH}) : \text{Species} + 1|\text{Triplet ID} \quad (6)$$

352 We used a linear mixed model with *Species* as a two-level factor (beech vs. fir, or beech vs.
353 oak) and $\log(\text{DBH})$ of the individual tree as a continuous variable. The interaction between
354 $\log(\text{DBH})$ and *Species* was also included in the model. *Triplet ID* was used as a random factor
355 (*Triplet ID* is a six-level factor for each type of mixture, identified by site and triplet number,
356 e.g. S1:2 for site 1, triplet 2). The introduction of individual tree DBH as a covariate was used
357 as a proxy for light availability, as the biggest trees within triplets are the ones with the most
358 access to light while smaller trees represent the understory trees. This approach allowed us to
359 take into account the confounding factor related to light availability in the canopy and its effect

360 on $\delta^{13}\text{C}$ (McCarroll and Loader, 2004). We used the log transformation of DBH to obtain a
361 linear relationship between $\log(\text{DBH})$ and $\delta^{13}\text{C}$ values .

362 2.5.2. Mixture effects on $\delta^{13}\text{C}$

363 We analyzed the effect of species mixture on $\delta^{13}\text{C}$ values separately by type of mixture (beech-
364 fir or beech-oak) with three different types of analyses that made it possible to test for a mixture
365 effect at different levels. First, we tested the mixture effect on individual $\delta^{13}\text{C}$ values by species
366 separately for the beech-fir and beech-oak sites with all six triplets together following the linear
367 mixed-effect model:

$$368 \quad \delta^{13}\text{C} \sim \log(\text{DBH}) + \text{Mixture} + \log(\text{DBH}) : \text{Mixture} + 1|\text{Triplet ID} \quad (7)$$

369 with *Mixture* (pure vs. mixed stands) as a fixed two-level factor, $\log(\text{DBH})$ of each tree as a
370 continuous variable, and *Triplet ID* as a random factor (*Triplet ID* is a six-level factor for each
371 type of mixture, identified by site and triplet number, e.g. S1:2 for site 1, triplet 2). The
372 interaction between $\log(\text{DBH})$ and *Mixture* was also included in the model.

373 Second, we tested the same effect separately for each triplet with the following linear model for
374 each species and triplet:

$$375 \quad \delta^{13}\text{C} \sim \log(\text{DBH}) + \text{Mixture} + \log(\text{DBH}) : \text{Mixture} \quad (8)$$

376 with *Mixture* as a two-level factor (pure vs. mixed stands), $\log(\text{DBH})$ as a covariate. The
377 interaction between $\log(\text{DBH})$ and *Mixture* was also included in the model.

378 Finally, to evaluate any effect of mixture on stand-level functioning, we used a metric called
379 “Net Biodiversity Effect” (NBE, %), adapted for complex traits such as $\delta^{13}\text{C}$ by Grossiord et
380 al. (2013) from Loreau and Hector (2001). We calculated NBE for the dominant-tree subsample
381 only (NBE_{dom}) because with all trees we would not have been able to separate the effects of
382 light availability vs. water availability.

383 NBE_{dom} on the average $\delta^{13}\text{C}$ of a given mixture of species is the difference between the observed
 384 averaged $\delta^{13}\text{C}$ in the mixture ($\delta^{13}\text{C}_O$, ‰) and the expected averaged $\delta^{13}\text{C}$ in the mixture ($\delta^{13}\text{C}_E$,
 385 ‰) calculated with species values in pure stands:

$$386 \quad NBE_{dom} = \delta^{13}\text{C}_O - \delta^{13}\text{C}_E = \sum_{i=1}^2 (\delta^{13}\text{C}_{O_i} * P_{O_i}) + \sum_{i=1}^2 (\delta^{13}\text{C}_{E_i} * P_{O_i}) \quad (9)$$

387 where $\delta^{13}\text{C}_{O_i}$ is the observed average $\delta^{13}\text{C}$ value for dominant trees of species *i* in mixed stands,
 388 $\delta^{13}\text{C}_{E_i}$ is the average $\delta^{13}\text{C}$ value for dominant trees of species *i* in its respective pure stand and
 389 P_{O_i} is the proportion of species *i* in the mixed plot in terms of basal area.

390 We calculated NBE_{dom} values for each triplet. Based on the precision of the mass spectrometer
 391 used for the isotopic measurements in this study (± 0.2 ‰), NBE_{dom} values were considered
 392 different from 0.0 ‰ when the difference between observed and expected mixed stand values
 393 was greater than ± 0.4 ‰. A positive difference means that the observed mixed stand had a
 394 higher $\delta^{13}\text{C}$ value than expected based on values from the corresponding pure stands. A negative
 395 difference means that the observed mixed stand had a lower $\delta^{13}\text{C}$ value than expected from
 396 pure-stand values. Since there was only one value per triplet, no statistical analyses were
 397 possible for this variable, though we were able to compare results across triplets.

398 2.5.3. $\delta^2\text{H}$ analysis

399 To test for differences in water uptake sources between species and between pure and mixed
 400 stands, we analyzed $\delta^2\text{H}$ data separately by type of mixture (beech-fir or beech-oak). We used
 401 a linear mixed model including *Triplet ID* as a random factor to test for differences between
 402 species and pure or mixed stands. We used the following model:

$$403 \quad \delta^2\text{H} \sim \text{Species} + \text{Mixture} + \text{Species:Mixture} + 1|\text{Triplet ID} \quad (10)$$

404 with *Species* a two-level factor (beech and fir, or beech and oak), *Mixture* a two-level factor
405 (pure or mixed), and *Triplet ID* a random factor (*Triplet ID* is a six-level factor for each type of
406 mixture, identified by site and triplet number, e.g. S1:2 for site 1, triplet 2).

407 2.5.4. *Statistical analyses*

408 All analyses were performed with R software version 3.6.2 (R Core Team, 2019). Linear mixed
409 effect models were conducted with the `lme` function of the NLME package (Pinheiro et al.,
410 2019). Analyses of variance following linear models or linear mixed models were conducted
411 with the `Anova` function (Type II SS) from the CAR package (Fox and Weisberg, 2019) and
412 post-hoc multiple comparisons were made with the `glht` function (Tukey contrasts) in the
413 MULTCOMP package (Hothorn et al., 2008). We graphically assessed normality and
414 homoscedasticity of all model residuals. For mixed effect models, we used a pseudo R-squared
415 in the R package MUMIN (Barton, 2019) to determine the variance explained by both the fixed
416 terms only (marginal coefficient of determination, R^2_m) and the entire model including the
417 random terms (conditional coefficient of determination, R^2_c).

418

419 3. Results

420 3.1. Site and species patterns of $\delta^{13}\text{C}$ in pure stands

421 3.1.1. Site and triplet effects on $\delta^{13}\text{C}$ within species

422 In pure beech stands, mean $\delta^{13}\text{C}$ values for the selected dry years for all sampled trees ranged
423 from $-27.9 \pm 0.8 \text{ ‰}$ at S1:1 to $-25.7 \pm 0.5 \text{ ‰}$ at S2:2 (Fig. 3a). There was a significant site effect
424 on $\delta^{13}\text{C}$ values (Eq. 5, $P < 0.001$): the trees at S1 had significantly lower $\delta^{13}\text{C}$ values than at the
425 other five sites (Fig. 3a). Mean $\delta^{13}\text{C}$ values differed significantly between the two triplets of a
426 site at S6 only (Fig. 3a). The range for the dominant-tree subsample was similar to the range for
427 all trees, but the $\delta^{13}\text{C}$ values were higher, with beech mean $\delta^{13}\text{C}$ values ranging from $-27.6 \pm$
428 0.4 ‰ at S1:2 to $-25.4 \pm 0.4 \text{ ‰}$ at S4:2 (Fig. 4a). As for all trees, there was a significant site
429 effect on $\delta^{13}\text{C}$ values (Eq. 5, $P < 0.001$): the trees at S1 had significantly lower $\delta^{13}\text{C}$ values than
430 the trees at the other five sites (Fig. 4a).

431 In pure fir stands, mean $\delta^{13}\text{C}$ values for all sampled trees ranged from $-28.0 \pm 0.6 \text{ ‰}$ at S1:2 to
432 $-25.2 \pm 0.3 \text{ ‰}$ at S3:1 (Fig. 3b). There was a significant site effect on $\delta^{13}\text{C}$ values (Eq. 5, $P <$
433 0.001): the trees at S1 had significantly lower $\delta^{13}\text{C}$ values than the trees at S2 and S3 (Fig. 3b).
434 Mean $\delta^{13}\text{C}$ values differed significantly between the two triplets of a site at S3 only (Fig. 3b).
435 For the dominant-tree subsample, the range was narrower and the $\delta^{13}\text{C}$ values were higher, with
436 fir mean $\delta^{13}\text{C}$ values ranging from $-26.9 \pm 0.7 \text{ ‰}$ at S1:2 to $-24.8 \pm 0.3 \text{ ‰}$ at S3:2 (Fig. 4b). As
437 for all trees, there was a significant site effect on $\delta^{13}\text{C}$ values (Eq. 5, $P < 0.001$): the trees at S1
438 had significantly lower $\delta^{13}\text{C}$ values than the trees at the other five sites (Fig. 4b).

439 In pure pubescent oak stands, mean $\delta^{13}\text{C}$ values for all sampled trees ranged from -26.1 ± 0.3
440 ‰ at S6:1 to $-24.8 \pm 0.4 \text{ ‰}$ at S4:2 (Fig. 3c). There was a significant site effect on $\delta^{13}\text{C}$ values
441 (Eq. 6, $P < 0.001$): all three sites had significantly different $\delta^{13}\text{C}$ values (Fig. 3c). For the
442 dominant-tree subsample, the range was narrower, but the mean $\delta^{13}\text{C}$ values were similar to all

443 trees: oak mean $\delta^{13}\text{C}$ values ranged from -25.9 ± 0.7 ‰ at S6:1 to -24.5 ± 0.4 ‰ at S4:2 (Fig.
444 4c). We observed no significant differences among the three sites or between triplets within
445 sites (Fig. 4c).

446 Figure 3 HERE; size: 2 columns; Colour online, B&W in print

447 Figure 4 HERE; size: 2 columns; Colour online, B&W in print

448 3.1.2. Species differences in $\delta^{13}\text{C}$

449 For pure stands including data for all the trees, species effect was not significant between beech
450 and fir in the more northern sites ($P = 0.38$), but was significant between beech and oak in the
451 more southern sites ($P < 0.001$). When including $\log(\text{DBH})$ as a covariate in the model (Eq. 6),
452 $\log(\text{DBH})$ was always significant. Beech had significantly lower $\delta^{13}\text{C}$ values than fir in the
453 northern sites or than oak in the southern sites (Table B1). The interaction between $\log(\text{DBH})$
454 and $\delta^{13}\text{C}$ was significant with all trees (Table B1), meaning that the slope of the relationship
455 between $\log(\text{DBH})$ and $\delta^{13}\text{C}$ values differed between species, although it was always positive.
456 In the northern sites, fir had a stronger positive slope ($b=1.76$) than beech ($b=0.85$). In the
457 southern sites, beech had a stronger positive slope ($b=2.23$) than oak ($b=0.85$).

458 For pure stands with only the dominant-tree subsample, species effect was significant for beech-
459 fir sites ($P < 0.001$) and for beech-oak sites ($P < 0.01$) with or without $\log(\text{DBH})$ in the model.
460 When including $\log(\text{DBH})$ in the models (Eq. 6), $\log(\text{DBH})$ was not significant, nor was the
461 interaction between *Species* and $\log(\text{DBH})$ (Table B1). Beech had significantly lower $\delta^{13}\text{C}$
462 values than fir in the northern sites or than oak in the southern sites (Table B1). Mean species
463 $\delta^{13}\text{C}$ values of the dominant-tree subsample was -26.5 ± 0.4 ‰ for beech and -25.8 ± 0.3 ‰ for
464 fir at the northern sites, whereas it was -25.8 ± 0.2 ‰ for beech and -25.3 ± 0.3 ‰ for oak at
465 the southern sites.

466 3.2. Mixture effects on $\delta^{13}\text{C}$

467 3.2.1. Effect of *dbh*

468 Before analyzing the mixture effects on $\delta^{13}\text{C}$ values, we assessed the effect of $\log(\text{DBH})$ in both
469 the global (Eq. 7) and triplet-level (Eq. 8) models for each species. The effect of $\log(\text{DBH})$ was
470 significant for all four global models when all the sampled trees were included (Table 2). At
471 the triplet-level, $\log(\text{DBH})$ was significant for beech, except at S1:2 and S2:2. It was significant
472 for all fir triplets and for half of the oak triplets (Table 3). The positive relationships between
473 $\delta^{13}\text{C}$ values and $\log(\text{DBH})$ are consistent with expectations from the literature and with the
474 impact of canopy light gradients on leaf or needle $\delta^{13}\text{C}$ (McCarroll and Loader, 2004). When
475 only the dominant-tree subsample was used in the models, the effect of $\log(\text{DBH})$ on $\delta^{13}\text{C}$ was
476 not significant in the global models nor in most triplets, except at S4:2 for beech and S2:2 for
477 fir (Table 2, Table 3). The absence of significant effects for the dominant-tree subsample was
478 probably the consequence of our sampling design: this subsample only included trees that
479 received direct vertical light and for which the possible impact of canopy light gradients on
480 $\delta^{13}\text{C}$ (McCarroll and Loader, 2004) was not expected.

481 Table 2 HERE; size: 2 columns

482 Table 3 HERE; size: 2 columns

483 3.2.2. Beech-fir sites

484 At the tree level for the global model, there were no significant mixture effects on $\delta^{13}\text{C}$ values
485 during the selected dry years, either for all trees or the dominant-tree subsample (Table 2). This
486 result indicates that beech and fir trees in the mixed stands had statistically similar $\delta^{13}\text{C}$ values
487 to their values in pure stands for a given DBH (Table 2). The interaction between $\log(\text{DBH})$
488 and *Mixture* was significant for fir with all trees: both pure and mixed stands had a positive
489 relationship between $\log(\text{DBH})$ and $\delta^{13}\text{C}$ values, but pure stands had a stronger slope ($b=1.69$)

490 than mixed stands ($b=1.35$). Despite this difference in the slopes of the relationship, it did not
491 result in a statistical difference between pure and mixed stands. We also included the interaction
492 term for the dominant-tree subsample alone, although we did not expect any interaction between
493 $\log(DBH)$ and *Mixture* as (i) trees of this subsample should receive the same levels of light and
494 (ii) because none of the triplets, except one for fir, had a significant $\log(DBH)$ effect. There was
495 a small interaction effect for fir in the global model with dominant trees (Table 2).

496 At the triplet level (Table 3, Fig. 5a, 6a), there were no significant mixture effects for beech in
497 any of the triplets, either for all trees or the dominant-tree subsample. For fir, at the triplet level
498 for all trees, a significant mixture effect was found for triplets S1:1 and S2:1 only. In both these
499 triplets, the models predicted higher $\delta^{13}C$ values in mixed stands than in pure stands (Table 3).
500 For fir, only triplet S3:2 had a significant interaction between $\log(DBH)$ and *Mixture*: the pure
501 stand had a steeper slope ($b=2.22$) than the mixed stand ($b=1.33$). There were no significant
502 interactions between $\log(DBH)$ and *Mixture* for beech. There was no mixture effect for fir with
503 the dominant-tree subsample except for triplet S2:2 (Table 3). Triplet S1:1 for fir had a
504 significant interaction effect when including all trees (Table 3), but this was probably driven by
505 the differences in DBH of the dominant trees between stands (Table 1).

506 Three triplets had NBE_{dom} values close to 0.0 ‰ and the three other triplets had values below -
507 0.4 ‰ (Fig. 7).

508 3.2.3. Beech-oak sites

509 When including all trees in the global model, we found a significant mixture effect on beech
510 $\delta^{13}C$, with higher $\delta^{13}C$ values in mixed stands compared to pure ones (Fig. 5b, Table 2). There
511 was no significant effect for oak (Fig. 5b, Table 2). We no longer observed the significant effect
512 for beech when we restricted the analysis to the dominant-tree subsample (Fig. 6b, Table 2).
513 The interaction between $\log(DBH)$ and *Mixture* was not significant for either species (Table 2).

514 At the triplet level, we observed significant mixture effects for both beech and oak (Table 3).
515 For beech, when including all the trees, $\delta^{13}\text{C}$ values were higher in mixed stands than in pure
516 stands in triplets S4:2 and S5:2 (Table 3). This result held true for the beech dominant-tree
517 subsample at S4:2, but not at S5:2 (Table 3). S4:2 was the only triplet with a significant
518 interaction effects between $\log(\text{DBH})$ and *Mixture* for beech (Table 3), with a steeper slope for
519 mixed stands ($b= 3.78$) than pure stands ($b=1.69$). However, this did not change the mixture
520 effect for this triplet. For oak, when all the trees were included, $\delta^{13}\text{C}$ values were significantly
521 lower in mixed stands at S4:2 and significantly higher at S5:1 (Table 3). We did not observe
522 these effects for oak when testing the dominant-tree subsample only (Table 3). There were no
523 interaction effects between $\log(\text{DBH})$ and *Mixture* for oak (Table 3).

524 In this region, there was a trend toward the lack of a net biodiversity effect: most NBE_{dom} values
525 were close to 0.0 ‰ (Fig.7), except in triplet S6:1 where it was below -0.4 ‰.

526 Figure 5 HERE; size: 1 column; Colour online, B&W in print

527 Figure 6 HERE; size: 1 column; Colour online, B&W in print

528 Figure 7 HERE; size: 1.5 column; Colour online, B&W in print

529 3.3. Xylem-water $\delta^2\text{H}$

530 At the beech-fir sites, we observed a significant interaction effect between *Species* and *Mixture*
531 ($P=0.002$) (Table B2). There was a significant mixture effect on the $\delta^2\text{H}$ values for beech, but
532 not for fir. More specifically, beech $\delta^2\text{H}$ values were lower in mixed stands than in pure stands,
533 except for triplet S3:2 (Fig. 8). There was also a significant difference between species for $\delta^2\text{H}$
534 values in both pure and mixed stands ($P<0.001$) (Table B2): beech $\delta^2\text{H}$ values were lower than
535 those of fir, except in triplet S1:1 (Fig. 8). The difference between beech and fir was larger in
536 mixed stands (estimate: 15.3 ± 1.4 ‰) than in pure stands (estimate: 9.1 ± 1.3 ‰).

537 In beech-oak sites, we observed no mixture effect on $\delta^2\text{H}$ values for either beech or oak ($P=0.33$)
538 (Fig. 8), no differences between species ($P=0.71$), and no interaction effect ($P=0.16$) (Table
539 B2).

540 Figure 8 HERE; size: 2 columns; Colour online, B&W in print

541 **4. Discussion**

542 *4.1. Variability of $\delta^{13}\text{C}$ values in pure stands*

543 *4.1.1. Site effect for beech*

544 Our range of mean $\delta^{13}\text{C}$ values in beech tree-rings for pure stands was close to those reported
545 in the literature (Fig. 3a, 4a). For instance, in Germany, at the heart of beech's distribution
546 range, mean beech $\delta^{13}\text{C}$ value was -26.7‰ during the very dry year of 2003 (Schwarz and
547 Bauhus, 2019). In northern Spain, the southern-most area of beech distribution, mean $\delta^{13}\text{C}$ value
548 was -26.5‰ at a drier lower-elevation site and -27.5‰ at a wetter higher-elevation site for the
549 period 2000 to 2003 (Peñuelas et al., 2008). We therefore recorded one of the least negative
550 mean $\delta^{13}\text{C}$ values for beech published to date, i.e. $-25.4 \pm 0.4\text{‰}$ at S4:2 for the dominant-tree
551 subsample (Fig.4a). The origin of the high $\delta^{13}\text{C}$ values observed in our study can be explained
552 (i) by our choice to select, by design, a range of years characterized by severe summer droughts
553 (2003-2007), which undoubtedly triggered high tree water use efficiency (Saurer et al., 1995),
554 and (ii) by the fact that some of our sites were at the range limit of precipitation and temperature
555 conditions for beech in Europe (Fig. 2).

556 We found that the mean $\delta^{13}\text{C}$ values for beech in pure stands did not differ among sites except
557 at S1, either for all trees or for the dominant-tree subsample (Fig. 3a, 4a), though we had
558 expected stronger differences due to the wide range of climatic conditions across our sites (Fig.
559 2). Plant tissue $\delta^{13}\text{C}$ is a functional trait that is highly sensitive to differences in environmental
560 conditions (Farquhar et al., 1989). However, different environmental conditions can have
561 opposite effects on $\delta^{13}\text{C}$ values, and the lack of difference in $\delta^{13}\text{C}$ among the five sites (S2 to
562 S6) could be explained by a combination of conditions acting in opposite directions. We explain
563 the significantly lower mean $\delta^{13}\text{C}$ values for beech at S1 (Fig. 3a, 4b) by the fact that S1 has
564 the wettest and coolest climate among the six sites (Fig.2). Site S1 also had relatively low water

565 stress and was the least affected by water deficit during the period 2003-2007 covered by our
566 study (Table A3).

567 4.1.2. *Species differences*

568 The pure beech stands had significantly lower $\delta^{13}\text{C}$ values than did fir or oak in the respective
569 sites (Table B1). This indicated lower mean water use efficiency for beech, even though the
570 magnitude of the differences between species remained low. For beech and fir, lower $\delta^{13}\text{C}$
571 values for beech are consistent with the study by Schwarz and Bauhus (2019) during the 2003
572 drought in Germany and Croatia. For beech and pubescent oak, to our knowledge, no studies
573 have compared $\delta^{13}\text{C}$ values of mature pubescent oak with other species. Differences in $\delta^{13}\text{C}$
574 values among species can be explained by physiological and morphological characteristics
575 (McCarroll and Loader, 2004) or by differences in canopy structure in pure stands. Yet, we
576 included a dendrometric variable ($\log(\text{DBH})$) in the statistical tests to take these characteristics
577 into account when testing for species differences. Species effects remained significant in the
578 models with the dominant-tree subsample while the effect of $\log(\text{DBH})$ did not (Table B1). We
579 can therefore conclude that species differences in $\delta^{13}\text{C}$ were mainly related to intrinsic
580 differences among species in water use efficiency, and not just to canopy structure factors.

581 As expected, a large part of the variability in $\delta^{13}\text{C}$ values was explained by the $\log(\text{DBH})$
582 variable when we included all trees (Table B1). The relationship between $\delta^{13}\text{C}$ values and
583 $\log(\text{DBH})$ was always positive. This is consistent with the fact that gradients in light availability
584 in the canopy strongly influence $\delta^{13}\text{C}$ values (McCarroll and Loader, 2004). The slopes of this
585 relationship differed between species: fir always had a stronger slope than beech in northern
586 sites, indicating that small fir trees were more suppressed for light than small beech trees in
587 their respective pure stands. As both species have high shade tolerance (Niinemets and
588 Valladares, 2006), this could simply be due to the canopy structure of fir trees leading to lower

589 light availability for dominated fir trees. Beech had a stronger slope than oak in the southern
590 sites, indicating that small beech trees were more suppressed for light than small oak trees in
591 pure stands. As beech is more shade tolerant than oak (Niinemets and Valladares, 2006), this
592 could be explained by the fact that small beech trees are growing in light-suppressed
593 environments whereas oak trees, even when small, seem to only grow in environments with a
594 higher light availability leading to less variability in $\delta^{13}\text{C}$ values. These results show that in
595 addition to intrinsic species differences in water use efficiency, canopy structure and light
596 interception also influenced water and carbon functioning in pure stands .

597 *4.2. Mixture effects on $\delta^{13}\text{C}$*

598 *4.2.1. Beech-fir sites*

599 For beech, there was no mixture effect on $\delta^{13}\text{C}$ values during dry years when mixed with fir
600 (Table 2 & 3, Fig. 5a & 6a), despite strong differences in functional traits between these two
601 species. The lack of mixture effect is consistent with several studies on beech-fir mixtures. For
602 instance, at the same sites, Jourdan et al. (2019a) reported no effect of the proportion of fir on
603 the drought resistance of beech, estimated with growth data at the neighborhood tree-to-tree
604 level. In another study in Romania, no mixture effect was observed for beech on $\delta^{13}\text{C}$
605 differences between a wet and a dry year, either at the species level (Forrester et al., 2016) or
606 at the stand level (Grossiord et al., 2014c). Recently, Schwarz & Bauhus (2019) looked at the
607 resistance to a drought event for four sites with beech-fir mixtures in Germany and Croatia and
608 found no mixture effect on $\delta^{13}\text{C}$, even though they observed long-term positive effects of
609 mixture on radial growth.

610 For fir, the influence of mixture on $\delta^{13}\text{C}$ values during dry years was more variable (Table 2 &
611 3, Fig. 5a & 6a). We observed that mixture effects for fir differed among sites, between triplets
612 within a given site, or according to the type of dataset we used. This suggests that local

613 environmental conditions and stand structure strongly influenced the outcome of the tests for
614 fir and that mixture effects may play a minor role in explaining observed differences.
615 Consequently, we cannot conclude that including fir in mixtures with beech will mitigate fir
616 exposure to drought. The existing literature has highlighted contrasted patterns for fir in
617 mixtures with beech. Some studies observed that the sensitivity of fir to drought was reduced
618 when mixed with beech in drier sites (Lebourgeois et al., 2013; Gazol and Camarero, 2016),
619 while other studies found no effect (Forrester et al., 2016; Schwarz and Bauhus, 2019), or even
620 a negative effect (Jourdan et al., 2019a). Differences in site conditions could explain
621 discrepancies in the observed patterns between our results and previous studies, as mixture
622 effects may change along resource gradients (Forrester and Bauhus, 2016). The interaction
623 effects detected for fir, with all trees, between $\log(DBH)$ and stand composition suggest that
624 there was less variability in $\delta^{13}C$ values due to light availability in mixed stands. In pure stands,
625 small fir trees had lower light availability (more negative $\delta^{13}C$ values) than in mixed ones. This
626 could be explained by the fact that fir trees in mixed stands received more light than in pure
627 stands due to canopy opening with the presence of beech and to phenological differences
628 between fir and beech. However, these interactions did not impact the detected mixture effects.

629 At the stand level with both species, there was no single mixture effect pattern among sites and
630 triplets for beech-fir sites (Fig. 7). NBE_{dom} was either neutral or negative, meaning that mixtures
631 had more negative $\delta^{13}C$ values, and potentially lower water stress, than expected from pure
632 stands. Within each site, triplet NBE_{dom} values were often neutral for one triplet and negative
633 for the other one. As a reminder, these triplets were not selected as replicates, but were designed
634 to cover local variations in environmental conditions and stand structure; within-site variability
635 was therefore not surprising. The neutral or negative NBE_{dom} values could be explained by
636 differences in above-ground features, such as stand structure, proportion of shaded subcanopy
637 or canopy packing levels, or in below-ground processes, such as complementarity or facilitation

638 for water acquisition (Grossiord, 2019). The species-interaction effects between beech and fir
639 for some triplets may be attenuated or even masked by local differences in environmental
640 conditions, which could not be controlled for in these stands (Metz et al., 2016). Furthermore,
641 opposite processes that may strongly influence photosynthesis (e.g. light gradients) or water
642 use (e.g. depth of water uptake) in mixed forests may actually cancel each other out and result
643 in the absence of overall mixture effects (Forrester and Bauhus, 2016). However, the overall
644 result of NBE_{dom} for mixed beech-fir stands is that $\delta^{13}C$ values were never less negative than
645 expected, suggesting a potentially lower water stress in mixtures. These results differ from the
646 mixture effects tested for each species separately. Differences between species-level and stand-
647 level results have been observed before (Forrester et al., 2016) and can result from opposite
648 trends of mixture effects between the species (Toigo et al., 2015). For the overall stand $\delta^{13}C$
649 values, beech-fir mixtures were not detrimental in terms of functioning during dry years. We
650 will discuss potential differences in water sources among species and stand composition below;
651 however, we were not able to characterize above-ground influences in the current study.

652 4.2.2. Beech-oak sites

653 The presence of pubescent oak did not decrease beech exposure to drought. In fact, with all
654 trees in the global model (Table 2) and for two individual triplets (Table 3), the interaction with
655 pubescent oak even led to higher beech $\delta^{13}C$ values, indicating a higher drought exposure of
656 beech in mixed stands compared to pure ones. In the global model (Table 2) and in one of these
657 two triplets (S5:2, Table 3), the absence of any mixture effect for the dominant-tree subsample
658 suggested that these effects might be related to the social status of the trees, even though we
659 were not able to demonstrate this. The interaction effect between $\log(DBH)$ and $\delta^{13}C$ values in
660 S4:2 for beech was opposite to what was observed for fir: there was less variability in $\delta^{13}C$
661 values due to light availability in the pure stand than in the mixed one. However, this effect was
662 mostly driven by a few bigger trees in the pure stand (Table 1) and did not affect the observed

663 mixture effect. Comparing these results with previous work on beech-pubescent oak mixtures
664 is impossible as this is the first study to look at beech $\delta^{13}\text{C}$ response in interaction with
665 pubescent oak. Beech $\delta^{13}\text{C}$ responses when mixed with another oak species (sessile oak,
666 *Quercus petraea*) in German forests indicated that it was less exposed to drought than in pure
667 stands (Forrester et al., 2016). Compared to sessile oak, pubescent oak is more drought tolerant
668 (Niinemets and Valladares, 2006) and could be more competitive than sessile oak when mixed
669 with beech. Furthermore, when looking at growth response patterns to drought in mixture with
670 different oak species, beech showed very inconsistent results so far, with positive (Pretzsch et
671 al., 2013; *Quercus petraea*), negative (Vanhellemont et al., 2019; *Quercus robur*) or neutral
672 (Jourdan et al., 2019a; *Quercus pubescens*) patterns. Our results underline the current
673 uncertainty on the choice of silvicultural practices that forest managers must make today to
674 mitigate drought impact on beech productivity along its southern margins under future climate
675 conditions.

676 The presence of beech did not influence the physiological functioning of pubescent oak during
677 dry summers in this region (Fig. 5b, 6b, Table 2, 3). As with beech, we were not able to reveal
678 any general trend for beech-oak interactions under severe drought conditions. Our study
679 suggests that, at least in this region, managing pubescent oak with beech does not lead to clear
680 mitigation of climate change impacts on oak response to drought.

681 4.2.3. *Impact of sampling design and use of absolute $\delta^{13}\text{C}$ values*

682 Our results emphasize how the sampling design (all trees or dominant ones only) and level of
683 analysis (tree or stand) of diversity-ecosystem functioning studies may influence the outcome
684 of mixture effect tests. Limiting the sampling design to dominant trees when looking at mixture
685 effects on the $\delta^{13}\text{C}$ response of trees to drought has been the typical approach to date (Grossiord
686 et al., 2014c; Metz et al., 2016; Schwarz and Bauhus, 2019). However, we show that this choice

687 may bias the outcome of these mixture effect tests. Selecting dominant trees only is, indeed,
688 pertinent with regards to $\delta^{13}\text{C}$, as dominant trees are those with the greatest sunlit leaf areas and
689 therefore potential carbon (photosynthesis) and water (transpiration) exchange with the
690 atmosphere. However, not including suppressed trees in these analyses may bias the stand-level
691 patterns of mixture effects, as the sensitivity to drought of suppressed and dominant trees in
692 mixed stands may differ (Mérian and Lebourgeois, 2011). This highlights the need for a
693 standardization of protocols in mixed-species forest studies in accordance with the goal of the
694 study (e.g. ecophysiological or forest management questions).

695 A limitation of this study, as mentioned in the methods, was the use of absolute $\delta^{13}\text{C}$ values for
696 dry years instead of the difference in $\delta^{13}\text{C}$ between wet and dry years. Calculating a difference
697 between the $\delta^{13}\text{C}$ of a wet and a dry year would allow analyzing a direct response of trees to
698 drought and compare this response in pure and mixed stands independently of the micro-
699 environmental variability among stands within a given triplet. However, in a study looking at
700 diversity effects on drought responses of $\delta^{13}\text{C}$, the same trends were found with $\delta^{13}\text{C}$ differences
701 between wet and dry years (Grossiord et al., 2014c) than with absolute $\delta^{13}\text{C}$ values for the dry
702 years only (Grossiord, 2014, p.48). Then, this methodological caveat should not prevent us from
703 interpreting mixture effects, especially since we took precautions to avoid over-interpreting
704 these effects at the triplet scale.

705 *4.3. Complementarity in water uptake sources*

706 *4.3.1. Beech-fir sites*

707 At the more northern beech-fir sites, during the 2018 summer drought, we observed a plasticity
708 in the depth of water uptake for beech at these sites between pure and mixed stands (Fig. 8),
709 which is consistent with the known plasticity of the species in terms of rooting traits and depth
710 of water uptake (Brinkmann et al., 2018). When competing with fir, beech seemed to have a

711 deeper mean depth of water uptake than when competing with beech only. These results are in
712 accordance with previous studies which show a shift of beech fine roots down to deeper soil
713 horizons when competing with coniferous tree species (Bolte and Villanueva, 2006; Grossiord
714 et al., 2014a). Plasticity in functional traits can be the result of abiotic or biotic interactions
715 (Valladares et al., 2007). Therefore, the shift in beech water uptake depth could be explained
716 either by a response to the competition with fir roots in the same soil horizons, or by a response
717 to a depletion in soil water availability in the topsoil (Brinkmann et al., 2018).

718 In the mixed stands, xylem $\delta^2\text{H}$ values showed that beech tended to uptake water from deeper
719 soil layers than fir did (Table B2, Fig 8), suggesting niche complementarity for water uptake
720 between the two species. This kind of complementarity between species in water use is assumed
721 to partly explain positive biodiversity-ecosystem functioning relationships (Grossiord, 2019).
722 However, it has rarely been linked to mixture effects on plant growth (Mueller et al., 2013;
723 Bachmann et al., 2015) or functional traits under drought (Verheyen et al., 2008; Goisser et al.,
724 2016). In our study, the absence of a clear mixture effect on $\delta^{13}\text{C}$ for both beech and fir, despite
725 a complementarity in water uptake, may be explained by several factors. First, our results did
726 not allow us to quantify the real gain in soil water availability during these dry periods for
727 beech. Indeed, the shift in $\delta^2\text{H}$ between pure and mixed stands was slight (10 ‰ on average)
728 and may indicate only a small difference in water uptake depth and soil water content. Second,
729 below-ground processes may not be the main drivers of the mixture effects for these species in
730 the study region. Above-ground processes could well be the major drivers, but they were not
731 tested in this study. Third, as discussed by Goisser et al. (2016), the impact of species mixture
732 on soil water availability may vary across seasons. The time scale of the processes associated
733 with our $\delta^2\text{H}$ or $\delta^{13}\text{C}$ approaches were different: $\delta^2\text{H}$ gave a one-shot image of the mean
734 signature of soil water extracted during the summer, whereas the $\delta^{13}\text{C}$ values gave an integrated
735 measurement of carbon and water acquisition and use over five years with dry summers.

736

4.3.2. Beech-oak sites

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For the more southern beech-oak sites, there were no signs of complementarity or niche

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differentiation in water acquisition for either species (Table B2, Fig. 8). This result is consistent

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with the absence of mixture effects on $\delta^{13}\text{C}$ for beech and pubescent oak in most triplets. The

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absence of plasticity in water uptake for beech when mixed with pubescent oak is interesting to

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note in comparison to the beech-fir sites. It suggests that the presence of pubescent oak did not

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induce any changes in beech water uptake compared to pure beech stands. The shallow soils in

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our sites (especially S5) might be one reason for the absence of differences in rooting depth

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between the species. We did not find data in the literature on rooting depth of pubescent oak.

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However, Lebourgeois and Jabiol (2002) have shown that beech rooting depth, compared to

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two other oak species (*Quercus petraea* and *Quercus robur*), is more sensitive to constraints

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but also that in the absence of strong constraints, beech and oak species rooting profiles are

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similar. In this part of the beech distribution area, during extreme dry summers, beech and

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pubescent oak displayed a functional redundancy in their below-ground water uptake. Mixing

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these two species to improve beech access to soil water in southern France may not be an

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appropriate forest management strategy.

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753 **5. Conclusion**

754 Our study was designed to help decision-making for beech forest management strategies
755 adapted to more frequent and extreme droughts in the future, particularly at the limits of the
756 distribution area of beech. Overall, we found no major mixture effect on drought exposure for
757 beech, although there was a high variability in the outcome of mixture effects at the triplet scale.
758 In the northern part of our study, mixing beech with fir had no effect on beech $\delta^{13}\text{C}$ values
759 during dry years. This result is in accordance with a growing body of literature showing the
760 lack of a species-interaction effect on beech drought resistance. Managing mixed stands of
761 beech and fir does not seem to help mitigate drought impacts for either of the two species,
762 despite an observed complementarity in water uptake. In the southern part of our study, mixture
763 effects on beech were mostly neutral, although beech seemed to be more exposed to drought in
764 mixed stands with pubescent oak at some sites. In a region at the limits of the distribution area
765 of beech, this study allowed us to conclude that managing beech in mixed stands with silver fir
766 or pubescent oak does not buffer drought impacts during dry years. Yet, in the long term, as
767 extreme droughts will become more frequent, beech-fir mixtures should not be detrimental to
768 beech response to drought, while it might be in mixtures with pubescent oak. In the
769 southernmost distribution regions of beech, an overall assessment of multi-criteria potential
770 benefits for each type of mixture should then be conducted in order to take management
771 decisions.

772

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778

779 **CRedit authorship contribution statement**

780 **Soline Martin-Blangy**: Conceptualization, Methodology, Investigation, Formal analysis,
781 Visualization, Writing - original draft. **Marie Charru**: Conceptualization, Methodology,
782 Investigation, Writing - original draft, Supervision. **Sylvain Gérard**: Investigation, Writing -
783 review & editing. **Hervé Jactel**: Conceptualization, Resources, Project administration, Funding
784 acquisition, Writing - review & editing. **Marion Jourdan**: Resources, Investigation, Writing -
785 review & editing. **Xavier Morin**: Conceptualization, Investigation, Resources, Writing -
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804

805 **References**

- 806 Ammer, C., 2019. Diversity and forest productivity in a changing climate. *New Phytol.* 221,
807 50–66. <https://doi.org/10.1111/nph.15263>
- 808 Araguás-Araguás, L., Rozanski, K., Gonfiantini, R., Louvat, D., 1995. Isotope effects
809 accompanying vacuum extraction of soil water for stable isotope analyses. *J. Hydrol.* 168,
810 159–171. [https://doi.org/10.1016/0022-1694\(94\)02636-P](https://doi.org/10.1016/0022-1694(94)02636-P)
- 811 Bachmann, D., Gockele, A., Ravenek, J.M., Roscher, C., Strecker, T., Weigelt, A., Buchmann,
812 N., 2015. No Evidence of Complementary Water Use along a Plant Species Richness
813 Gradient in Temperate Experimental Grasslands. *PLoS One* 10, e0116367.
814 <https://doi.org/10.1371/journal.pone.0116367>
- 815 Barton, K., 2019. MuMIn: Multi-Model Inference. R package version 1.43.15.
- 816 Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.*
817 9, 187–191. [https://doi.org/10.1016/0169-5347\(94\)90087-6](https://doi.org/10.1016/0169-5347(94)90087-6)
- 818 Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.-J., Schall, P., Spathelf, P., Rock, J.,
819 2009. Adaptive forest management in central Europe: Climate change impacts, strategies
820 and integrative concept. *Scand. J. For. Res.* 24, 473–482.
821 <https://doi.org/10.1080/02827580903418224>
- 822 Bolte, A., Villanueva, I., 2006. Interspecific competition impacts on the morphology and
823 distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea*
824 *abies* (L.) Karst.). *Eur. J. For. Res.* 125, 15–26. [https://doi.org/10.1007/s10342-005-0075-](https://doi.org/10.1007/s10342-005-0075-5)
825 5
- 826 Brinkmann, N., Eugster, W., Buchmann, N., Kahmen, A., 2018. Species-specific differences in
827 water uptake depth of mature temperate trees vary with water availability in the soil. *Plant*
828 *Biol.* 21, 71–81. <https://doi.org/10.1111/plb.12907>
- 829 Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-
830 Olabarria, J.R., Lyver, P.O.B., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I.D., van
831 der Plas, F., Jactel, H., 2017. Forest biodiversity, ecosystem functioning and the provision
832 of ecosystem services. *Biodivers. Conserv.* 26, 3005–3035.
833 <https://doi.org/10.1007/s10531-017-1453-2>
- 834 Charru, M., Seynave, I., Hervé, J.-C., Bertrand, R., Bontemps, J.-D., 2017. Recent growth
835 changes in Western European forests are driven by climate warming and structured across
836 tree species climatic habitats. *Ann. For. Sci.* 74, 33. [https://doi.org/10.1007/s13595-017-](https://doi.org/10.1007/s13595-017-0626-1)
837 0626-1
- 838 Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrière, E., François, C., Gritti, E.S.,
839 Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P., 2012. Climate change impacts
840 on tree ranges: model intercomparison facilitates understanding and quantification of
841 uncertainty. *Ecol. Lett.* 15, 533–544. <https://doi.org/10.1111/j.1461-0248.2012.01764.x>
- 842 Clark, D.A., Clark, D.B., 1992. Life History Diversity of Canopy and Emergent Trees in a
843 Neotropical Rain Forest. *Ecol. Monogr.* 62, 315–344. <https://doi.org/10.2307/2937114>
- 844 Clark, I.D., Fritz, P., 1997. Chapter 4: Groundwater, in: *Environmental Isotopes in*
845 *Hydrogeology.* CRC Press, Boca Raton, pp. 79–108.
846 <https://doi.org/10.1201/9781482242911>

- 847 Dawson, T.E., 1993. Water Sources of Plants as Determined from Xylem-Water Isotopic
848 Composition: Perspectives on Plant Competition, Distribution, and Water Relations, in:
849 Ehleringer, J.R., Hall, A.E., Farquhar, G.D. (Eds.), *Stable Isotopes and Plant Carbon-*
850 *Water Relations*. Academic Press, San Diego, pp. 465–496.
851 <https://doi.org/https://doi.org/10.1016/B978-0-08-091801-3.50040-4>
- 852 de Streel, G., Collet, C., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Brazaitis, G., Coll, L.,
853 Drössler, L., Forrester, D., Heym, M., Löf, M., Pach, M., Pretzsch, H., Ruiz-Peinado, R.,
854 Skrzyszewski, J., Stankevičiūtė, J., Svoboda, M., Verheyen, K., Zlatanov, T., Bonal, D.,
855 Ponette, Q., 2020. Contrasting patterns of tree species mixture effects on wood $\delta^{13}\text{C}$ along
856 an environmental gradient. *Eur. J. For. Res.* 139, 229–245.
857 <https://doi.org/10.1007/s10342-019-01224-z>
- 858 del Río, M., Pretzsch, H., Alberdi, I., Bielak, K., Bravo, F., Brunner, A., Condés, S., Ducey,
859 M.J., Fonseca, T., von Lüpke, N., Pach, M., Peric, S., Perot, T., Souidi, Z., Spathelf, P.,
860 Sterba, H., Tijardovic, M., Tomé, M., Vallet, P., Bravo-Oviedo, A., 2018. Characterization
861 of Mixed Forests, in: Bravo-Oviedo, A., Pretzsch, H., del Río, M. (Eds.), *Dynamics,*
862 *Silviculture and Management of Mixed Forests. Managing Forest Ecosystems, Vol 31.*
863 Springer International Publishing, Cham, pp. 27–71. [https://doi.org/10.1007/978-3-319-](https://doi.org/10.1007/978-3-319-91953-9_2)
864 [91953-9_2](https://doi.org/10.1007/978-3-319-91953-9_2)
- 865 Dittmar, C., Zech, W., Elling, W., 2003. Growth variations of Common beech (*Fagus sylvatica*
866 L.) under different climatic and environmental conditions in Europe—a dendroecological
867 study. *For. Ecol. Manage.* 173, 63–78. [https://doi.org/10.1016/S0378-1127\(01\)00816-7](https://doi.org/10.1016/S0378-1127(01)00816-7)
- 868 Farquhar, G., O’Leary, M., Berry, J., 1982. On the Relationship Between Carbon Isotope
869 Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. *Aust. J.*
870 *Plant Physiol.* 9, 121. <https://doi.org/10.1071/PP9820121>
- 871 Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon Isotope Discrimination and
872 Photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40, 503–537.
873 <https://doi.org/10.1146/annurev.pp.40.060189.002443>
- 874 Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-
875 species forests: From pattern to process. *For. Ecol. Manage.* 312, 282–292.
876 <https://doi.org/10.1016/j.foreco.2013.10.003>
- 877 Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity
878 Relationships in Forests. *Curr. For. Reports* 2, 45–61. [https://doi.org/10.1007/s40725-016-](https://doi.org/10.1007/s40725-016-0031-2)
879 [0031-2](https://doi.org/10.1007/s40725-016-0031-2)
- 880 Forrester, D.I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., Grossiord, C.,
881 2016. Drought responses by individual tree species are not often correlated with tree
882 species diversity in European forests. *J. Appl. Ecol.* 53, 1725–1734.
883 <https://doi.org/10.1111/1365-2664.12745>
- 884 Fox, J., Weisberg, S., 2019. *An {R} Companion to Applied Regression*, Third. ed. Sage,
885 Thousand Oaks, CA.
- 886 Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience to an
887 extreme drought. *J. Ecol.* 104, 1063–1075. <https://doi.org/10.1111/1365-2745.12575>
- 888 Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007.
889 Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* 21,
890 1–11. <https://doi.org/10.1007/s00468-006-0107-x>

- 891 Goisser, M., Geppert, U., Rötzer, T., Paya, A., Huber, A., Kerner, R., Bauerle, T., Pretzsch, H.,
892 Pritsch, K., Häberle, K.H., Matyssek, R., Grams, T.E.E., 2016. Does belowground
893 interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem
894 growth in *Picea abies*? *For. Ecol. Manage.* 375, 268–278.
895 <https://doi.org/10.1016/j.foreco.2016.05.032>
- 896 González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.-H., Sangüesa-
897 Barreda, G., Castillo, F.J., 2018. Tree-to-tree competition in mixed European beech-Scots
898 pine forests has different impacts on growth and water-use efficiency depending on site
899 conditions. *J. Ecol.* 106, 59–75. <https://doi.org/10.1111/1365-2745.12813>
- 900 Granier, A., Bréda, N., Biron, P., Villette, S., 1999. A lumped water balance model to evaluate
901 duration and intensity of drought constraints in forest stands. *Ecol. Modell.* 116, 269–283.
902 [https://doi.org/10.1016/S0304-3800\(98\)00205-1](https://doi.org/10.1016/S0304-3800(98)00205-1)
- 903 Grossiord, C., 2019. Having the right neighbors: how tree species diversity modulates drought
904 impacts on forests. *New Phytol.* <https://doi.org/10.1111/nph.15667>
- 905 Grossiord, C., 2014. “Impact of tree species diversity on water and carbon relations in European
906 forests.” PhD Thesis, Université de Lorraine, Nancy. 156 p.
907 <https://doi.org/https://www.theses.fr/2014LORR0155>
- 908 Grossiord, C., Gessler, A., Granier, A., Berger, S., Bréchet, C., Hentschel, R., Hommel, R.,
909 Scherer-Lorenzen, M., Bonal, D., 2014a. Impact of interspecific interactions on the soil
910 water uptake depth in a young temperate mixed species plantation. *J. Hydrol.* 519, 3511–
911 3519. <https://doi.org/10.1016/j.jhydrol.2014.11.011>
- 912 Grossiord, C., Granier, A., Gessler, A., Jucker, T., Bonal, D., 2014b. Does Drought Influence
913 the Relationship Between Biodiversity and Ecosystem Functioning in Boreal Forests?
914 *Ecosystems* 17, 394–404. <https://doi.org/10.1007/s10021-013-9729-1>
- 915 Grossiord, C., Granier, A., Gessler, A., Scherer-Lorenzen, M., Pollastrini, M., Bonal, D., 2013.
916 Application of Loreau & Hector’s (2001) partitioning method to complex functional
917 traits. *Methods Ecol. Evol.* 4, 954–960. <https://doi.org/10.1111/2041-210X.12090>
- 918 Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Checko, E., Forrester,
919 D.I., Dawud, S.M., Finer, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal,
920 D., Gessler, A., 2014c. Tree diversity does not always improve resistance of forest
921 ecosystems to drought. *Proc. Natl. Acad. Sci.* 111, 14812–14815.
922 <https://doi.org/10.1073/pnas.1411970111>
- 923 Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., Zimmermann, N.E., 2013.
924 Climate change may cause severe loss in the economic value of European forest land. *Nat.*
925 *Clim. Chang.* 3, 203–207. <https://doi.org/10.1038/nclimate1687>
- 926 Hartmann, H., Moura, C.F., Anderegg, W.R.L., Ruehr, N.K., Salmon, Y., Allen, C.D., Arndt,
927 S.K., Breshears, D.D., Davi, H., Galbraith, D., Ruthrof, K.X., Wunder, J., Adams, H.D.,
928 Bloemen, J., Cailleret, M., Cobb, R., Gessler, A., Grams, T.E.E., Jansen, S., Kautz, M.,
929 Lloret, F., O’Brien, M., 2018. Research frontiers for improving our understanding of
930 drought-induced tree and forest mortality. *New Phytol.* 218, 15–28.
931 <https://doi.org/10.1111/nph.15048>
- 932 Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric
933 Models. *Biometrical J.* 50, 346–363.

- 934 Houston Durrant, T., de Rigo, D., Caudullo, G., 2016. *Fagus sylvatica* and other beeches in
935 Europe: distribution, habitat, usage and threats, in: Miguel-Ayanz, J., de Rigo, D.,
936 Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree
937 Species. Publ. Off. EU, Luxembourg, p. e012b90+.
- 938 IAEA, 1995. Reference and Intercomparison Materials for Stable Isotopes of Light Elements,
939 IAEA-TECDOC-825. Vienna.
- 940 IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II
941 and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change
942 [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)].
- 943 Ishii, H., Asano, S., 2010. The role of crown architecture, leaf phenology and photosynthetic
944 activity in promoting complementary use of light among coexisting species in temperate
945 forests. *Ecol. Res.* 25, 715–722. <https://doi.org/10.1007/s11284-009-0668-4>
- 946 Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-
947 Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree Diversity
948 Drives Forest Stand Resistance to Natural Disturbances. *Curr. For. Reports* 3, 223–243.
949 <https://doi.org/10.1007/s40725-017-0064-1>
- 950 Jourdan, M., Kunstler, G., Morin, X., 2019a. How neighbourhood interactions control the
951 temporal stability and resilience to drought of trees in mountain forests. *J. Ecol.* 1365-
952 2745.13294. <https://doi.org/10.1111/1365-2745.13294>
- 953 Jourdan, M., Lebourgeois, F., Morin, X., 2019b. The effect of tree diversity on the resistance
954 and recovery of forest stands in the French Alps may depend on species differences in
955 hydraulic features. *For. Ecol. Manage.* 450, 117486.
956 <https://doi.org/10.1016/j.foreco.2019.117486>
- 957 Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize
958 canopy packing in mixed-species forests. *Funct. Ecol.* 29, 1078–1086.
959 <https://doi.org/10.1111/1365-2435.12428>
- 960 Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the
961 southern range edge of *Fagus sylvatica*. *Glob. Chang. Biol.* 12, 2163–2174.
962 <https://doi.org/10.1111/j.1365-2486.2006.01250.x>
- 963 Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-
964 ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol.*
965 *Manage.* 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>
- 966 Lebourgeois, F., Jabiol, B., 2002. Enracinements comparés du Chêne sessile, du Chêne
967 pédonculé et du Hêtre. Réflexions sur l'autécologie des essences. *Rev. For. Française* 17.
968 <https://doi.org/10.4267/2042/4898>
- 969 Lehner, F., Coats, S., Stocker, T.F., Pendergrass, A.G., Sanderson, B.M., Raible, C.C.,
970 Smerdon, J.E., 2017. Projected drought risk in 1.5°C and 2°C warmer climates. *Geophys.*
971 *Res. Lett.* 44, 7419–7428. <https://doi.org/10.1002/2017GL074117>
- 972 Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D.,
973 McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Herault, B.,
974 Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J.,
975 Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova,
976 N., Fischer, M., Watson, J. V., Chen, H.Y.H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle,

- 977 D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A.,
978 Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonke, B., Tavani, R., Zhu, J.,
979 Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto,
980 C., Frizzera, L., Ba azy, R., Oleksyn, J., Zawi a-Nied wiecki, T., Bouriaud, O., Bussotti,
981 F., Finer, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L.,
982 Gonmadje, C., Marthy, W., OBrien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho,
983 R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V.,
984 Engone-Obiang, N.L., Ferreira, L. V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich,
985 P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests.
986 *Science* (80-). 354, aaf8957–aaf8957. <https://doi.org/10.1126/science.aaf8957>
- 987 Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl,
988 R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate
989 change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For.*
990 *Ecol. Manage.* 259, 698–709. <https://doi.org/10.1016/j.foreco.2009.09.023>
- 991 Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity
992 experiments. *Nature* 412, 72–76. <https://doi.org/10.1038/35083573>
- 993 Majoube, M., 1971. Fractionnement en oxygène 18 et en deutérium entre l’eau et sa vapeur. *J.*
994 *Chim. Phys.* 68, 1423–1436. <https://doi.org/10.1051/jcp/1971681423>
- 995 McCarroll, D., Loader, N.J., 2004. Stable isotopes in tree rings. *Quat. Sci. Rev.* 23, 771–801.
996 <https://doi.org/10.1016/j.quascirev.2003.06.017>
- 997 McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J.,
998 Sperry, J., West, A., Williams, D.G., Yezpe, E.A., 2008. Mechanisms of plant survival and
999 mortality during drought: why do some plants survive while others succumb to drought?
1000 *New Phytol.* 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- 1001 Mérian, P., Lebourgeois, F., 2011. Size-mediated climate–growth relationships in temperate
1002 forests: A multi-species analysis. *For. Ecol. Manage.* 261, 1382–1391.
1003 <https://doi.org/10.1016/j.foreco.2011.01.019>
- 1004 Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D., Ammer, C.,
1005 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European
1006 beech. *Glob. Chang. Biol.* 22, 903–920. <https://doi.org/10.1111/gcb.13113>
- 1007 Mueller, K.E., Tilman, D., Fornara, D. a., Hobbie, S.E., 2013. Root depth distribution and the
1008 diversity–productivity relationship in a long-term grassland experiment. *Ecology* 94, 787–
1009 793. <https://doi.org/10.1890/12-1399.1>
- 1010 Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of
1011 temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
1012 [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2)
- 1013 Peñuelas, J., Hunt, J.M., Ogaya, R., Jump, A.S., 2008. Twentieth century changes of tree-ring
1014 $\delta^{13}\text{C}$ at the southern range-edge of *Fagus sylvatica*: Increasing water-use efficiency does
1015 not avoid the growth decline induced by warming at low altitudes. *Glob. Chang. Biol.* 14,
1016 1076–1088. <https://doi.org/10.1111/j.1365-2486.2008.01563.x>
- 1017 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2019. nlme: Linear and Nonlinear
1018 Mixed Effects Models. R package version 3.1-143.
- 1019 Pretzsch, H., Forrester, D.I., 2017. Stand Dynamics of Mixed-Species Stands Compared with

- 1020 Monocultures, in: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), *Mixed-Species Forests*.
1021 Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 117–209. [https://doi.org/10.1007/978-](https://doi.org/10.1007/978-3-662-54553-9_4)
1022 [3-662-54553-9_4](https://doi.org/10.1007/978-3-662-54553-9_4)
- 1023 Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress
1024 in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant*
1025 *Biol.* 15, 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- 1026 Quintana-Seguí, P., Le Moigne, P., Durand, Y., Martin, E., Habets, F., Baillon, M., Canellas,
1027 C., Franchisteguy, L., Morel, S., 2008. Analysis of Near-Surface Atmospheric Variables:
1028 Validation of the SAFRAN Analysis over France. *J. Appl. Meteorol. Climatol.* 47, 92–
1029 107. <https://doi.org/10.1175/2007JAMC1636.1>
- 1030 R Core Team, 2019. *R: A Language and Environment for Statistical Computing*, R Foundation
1031 for Statistical Computing. Vienna, Austria.
- 1032 Saurer, M., Siegenthaler, U., Schweingruber, F., 1995. The climate-carbon isotope relationship
1033 in tree rings and the significance of site conditions. *Tellus B* 47, 320–330.
1034 <https://doi.org/10.1034/j.1600-0889.47.issue3.4.x>
- 1035 Schäfer, C., Grams, T.E.E., Rötzer, T., Feldermann, A., Pretzsch, H., 2017. Drought stress
1036 reaction of growth and $\delta^{13}\text{C}$ in tree rings of European beech and Norway spruce in
1037 monospecific versus mixed stands along a precipitation gradient. *Forests* 8.
1038 <https://doi.org/10.3390/f8060177>
- 1039 Schwarz, J.A., Bauhus, J., 2019. Benefits of Mixtures on Growth Performance of Silver Fir
1040 (*Abies alba*) and European Beech (*Fagus sylvatica*) Increase With Tree Size Without
1041 Reducing Drought Tolerance. *Front. For. Glob. Chang.* 2, 1–18.
1042 <https://doi.org/10.3389/ffgc.2019.00079>
- 1043 Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., 2015. Overyielding
1044 in mixed forests decreases with site productivity. *J. Ecol.* 103, 502–512.
1045 <https://doi.org/10.1111/1365-2745.12353>
- 1046 Valladares, F., Gialoni, E., Gómez, J.M., 2007. Ecological limits to phenotypic plasticity. *New*
1047 *Phytol.* 176, 749–763. <https://doi.org/10.1111/j.1469-8137.2007.02275.x>
- 1048 Vanhellefont, M., Sousa-Silva, R., Maes, S.L., Van den Bulcke, J., Hertzog, L., De Groote,
1049 S.R.E., Van Acker, J., Bonte, D., Martel, A., Lens, L., Verheyen, K., 2019. Distinct growth
1050 responses to drought for oak and beech in temperate mixed forests. *Sci. Total Environ.*
1051 650, 3017–3026. <https://doi.org/10.1016/j.scitotenv.2018.10.054>
- 1052 Verheyen, K., Bulteel, H., Palmborg, C., Olivié, B., Nijs, I., Raes, D., Muys, B., 2008. Can
1053 complementarity in water use help to explain diversity-productivity relationships in
1054 experimental grassland plots? *Oecologia* 156, 351–361. [https://doi.org/10.1007/s00442-](https://doi.org/10.1007/s00442-008-0998-x)
1055 [008-0998-x](https://doi.org/10.1007/s00442-008-0998-x)
- 1056 Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index
1057 Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index.
1058 *J. Clim.* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- 1059 West, A.G., Patrickson, S.J., Ehleringer, J.R., 2006. Water extraction times for plant and soil
1060 materials used in stable isotope analysis. *Rapid Commun. Mass Spectrom.* 20, 1317–1321.
1061 <https://doi.org/10.1002/rcm.2456>

1062 **Tables**

1063 **Table 1** Plot characteristics: mean DBH (cm) and range by species for all trees in each site,
 1064 triplet, and plot.

Site	Triplet	Plot	DBH (cm)			
			Beech	Fir	Oak	Other sp.
S1	1	Pure beech	41.9 (8-105)	–	–	19.1 (13.4-24.2)
S1	1	Pure fir	8.3 (8.3-8.3)	37 (8.6-92.9)	–	21.5 (10.5-49.3)
S1	1	Mixed	39 (28.3-49.7)	22.9 (7.6-38.2)	–	18.5 (9.2-34.4)
S1	2	Pure beech	47 (28.3-59.8)	14.1 (5.7-28.6)	–	–
S1	2	Pure fir	–	32.6 (8-79.9)	–	26.7 (13.1-50)
S1	2	Mixed	42.4 (9.5-76.4)	28.3 (7.3-91.7)	–	45.2 (45.2-45.2)
S2	1	Pure beech	16.5 (8.3-46.8)	–	–	19.4 (14.3-26.7)
S2	1	Pure fir	–	24.2 (8-42)	–	23.6 (23.6-23.6)
S2	1	Mixed	14.2 (7.3-40.1)	19.6 (7.6-57.3)	–	10.2 (8.6-14.3)
S2	2	Pure beech	47.4 (35.3-58.3)	17.3 (12.7-23.9)	–	–
S2	2	Pure fir	15.3 (15.3-15.3)	42.4 (15.6-57.3)	–	–
S2	2	Mixed	36.8 (30.2-44.2)	27.7 (12.7-57.6)	–	–
S3	1	Pure beech	25.3 (9.2-38.8)	–	–	–
S3	1	Pure fir	18.8 (18.1-19.4)	35.9 (15-47.7)	–	–
S3	1	Mixed	14.9 (7.6-23.9)	44.8 (9.5-59.8)	–	–
S3	2	Pure beech	29.9 (16.6-53.5)	20.4 (20.4-20.4)	–	–
S3	2	Pure fir	19.2 (8-30.2)	17.1 (7.3-41.7)	–	15 (10.8-19.1)
S3	2	Mixed	24 (16.2-32.1)	15.2 (7.3-60.5)	–	30.6 (28.6-32.5)
S4	1	Pure beech	24.9 (7.6-68.1)	–	–	13.3 (11.8-14.3)
S4	1	Pure oak	11.4 (7.6-15.3)	–	18.3 (7.6-42.7)	10.7 (7.6-15.9)
S4	1	Mixed	16.1 (8.6-24.5)	–	20.7 (11.1-27.4)	18.9 (8.3-39.8)
S4	2	Pure beech	22.6 (8.6-64.3)	–	11.1 (11.1-11.1)	–
S4	2	Pure oak	13.4 (13.4-13.4)	–	15.2 (8.9-24.8)	9.7 (9.2-10.2)
S4	2	Mixed	14.4 (7-27.7)	–	17.1 (12.1-22.9)	13.8 (12.4-15.3)
S5	1	Pure beech	17.1 (7.3-28.6)	–	12.9 (8.9-16.9)	13.7 (8-19.4)
S5	1	Pure oak	–	–	18.7 (10.5-32.5)	18.6 (9.2-29)
S5	1	Mixed	14.5 (8-22)	–	14.7 (7.6-21)	10.4 (7.3-16.2)
S5	2	Pure beech	16.6 (7-27.1)	–	–	13.8 (8.3-23.6)
S5	2	Pure oak	–	–	15.6 (10.8-22.9)	10.1 (7-13.4)
S5	2	Mixed	13.7 (7.3-23.6)	–	15.9 (7.6-20.7)	9.2 (7-15.3)
S6	1	Pure beech	40.4 (29.6-53.2)	–	–	16 (9.9-29)
S6	1	Pure oak	–	–	36.1 (28-45.5)	12.8 (7-22.3)
S6	1	Mixed	30.6 (9.5-45.2)	–	34.6 (20.4-42.3)	15.5 (7.3-34.4)
S6	2	Pure beech	19.6 (7.6-35.7)	–	17.2 (14-19.4)	13.3 (7.6-25.5)
S6	2	Pure oak	–	–	19 (9.9-38.2)	8.2 (7-9.9)
S6	2	Mixed	21.3 (8.6-31.8)	–	18 (8.3-26.7)	11.3 (7.6-15.9)

1065

1066 *Note:* Other tree species represent less than 20% of the total basal area of the plots (12% on average). Most
1067 common species are *Acer pseudoplatanus*, *Acer campestre*, *Ilex aquifolium*, *Sorbus torminalis* and *Taxus*
1068 *baccata*.

1069

1070

1071 **Table 2** Linear mixed model output for *Mixture* effects and $\log(\text{DBH})$ on $\delta^{13}\text{C}$ by type of
 1072 mixture and species (Eq. 7).

	Beech-fir sites						Beech-oak sites					
	Beech			Fir			Beech			Oak		
	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>
All trees	154			213			191			189		
$\log(\text{DBH})$	27	1	<.001***	268	1	<.001***	185	1	<.001***	21	1	<.001***
<i>Mixture</i>	0	1	0.77	2	1	0.13	26	1	<.001*** $\delta^{13}\text{C}_m > \delta^{13}\text{C}_p$	1	1	0.35
$\log(\text{DBH})$: <i>Mixture</i>	0	1	0.52	4	1	0.04*	1	1	0.24	1	1	0.30
$R^2_m (R^2_c)$	0.16 (0.65)			0.40 (0.76)			0.41 (0.68)			0.10 (0.46)		
Dominant-tree subsample	52			48			50			58		
$\log(\text{DBH})$	0	1	0.58	3	1	0.07	0	1	0.90	1	1	0.27
<i>Mixture</i>	2	1	0.21	1	1	0.25	0	1	0.49	2	1	0.15
$\log(\text{DBH})$: <i>Mixture</i>	2	1	0.14	5	1	0.02*	4	1	0.05	1	1	0.35
$R^2_m (R^2_c)$	0.03 (0.52)			0.10 (0.62)			0.06 (0.26)			0.05 (0.32)		

1073

1074 *Note:* Stars indicate significant $\log(\text{DBH})$, *Mixture* and interaction effects. *Mixture* is a two-level factor (pure vs.
 1075 mixed). For significant *Mixture* effects, the direction of the estimate is indicated by $\delta^{13}\text{C}_p > \delta^{13}\text{C}_m$ if pure stands
 1076 have a higher $\delta^{13}\text{C}$ estimate than mixed stands (i.e. mixture improves response to water stress compared to pure
 1077 stands), and $\delta^{13}\text{C}_m > \delta^{13}\text{C}_p$ if mixed stands have a higher $\delta^{13}\text{C}$ estimate than pure stands. χ^2 : chi square test results
 1078 for type “II” ANOVA. *df*: degrees of freedom. *P*: p-value for fixed terms. *Triplet ID* is used as a random factor in
 1079 all eight models. A pseudo R-squared for mixed effect models was used to determine the variance explained by
 1080 the two fixed terms only (marginal coefficient of determination, R^2_m) and the entire model including the random
 1081 terms (conditional coefficient of determination, R^2_c).

1082

1083 **Table 3** Model p-values for *Mixture* effects, $\log(DBH)$ on $\delta^{13}C$ by triplet and species (Eq. 8).

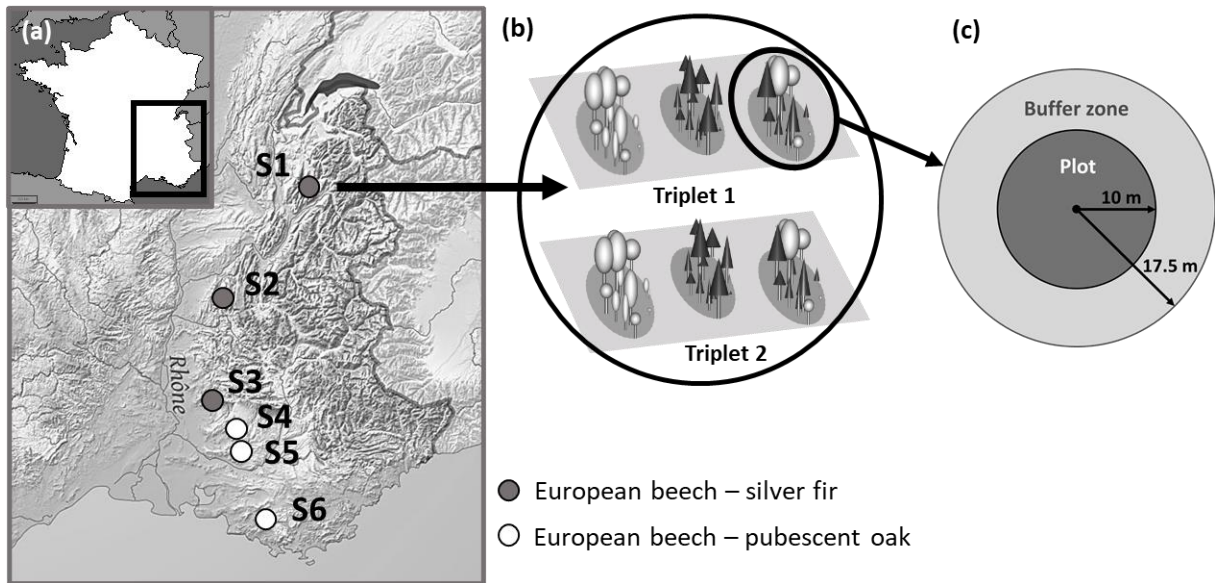
Site+Triplet	Beech			Fir			Oak		
	P - $\log(DBH)$	P - <i>Mixture</i>	P - $\log(DBH)$: <i>Mixture</i>	P - $\log(DBH)$	P - <i>Mixture</i>	P - $\log(DBH)$: <i>Mixture</i>	P - $\log(DBH)$	P - <i>Mixture</i>	P - $\log(DBH)$: <i>Mixture</i>
All trees									
S1:1	0.03*	0.13	0.67	<0.001***	<0.01** $\delta^{13}C_m > \delta^{13}C_p$	0.7	-	-	-
S1:2	0.18	0.24	0.31	<0.001***	0.94	0.15	-	-	-
S2:1	<0.001***	0.62	0.45	<0.001***	<0.01** $\delta^{13}C_m > \delta^{13}C_p$	0.35	-	-	-
S2:2	0.42	0.85	0.61	<0.001***	0.66	0.09	-	-	-
S3:1	0.03*	0.44	0.62	<0.01**	0.09	0.77	-	-	-
S3:2	<0.01**	0.54	0.82	<0.001***	0.87	0.04*	-	-	-
S4:1	<0.001***	0.06	0.6	-	-	-	0.04*	0.47	0.49
S4:2	<0.001***	<0.001*** $\delta^{13}C_m > \delta^{13}C_p$	<0.01**	-	-	-	0.02*	0.02* $\delta^{13}C_p > \delta^{13}C_m$	0.75
S5:1	<0.001***	0.32	0.39	-	-	-	0.06	<0.01** $\delta^{13}C_m > \delta^{13}C_p$	0.83
S5:2	<0.001***	<0.001*** $\delta^{13}C_m > \delta^{13}C_p$	0.15	-	-	-	0.81	0.09	0.67
S6:1	<0.01**	0.12	0.19	-	-	-	0.21	0.53	0.56
S6:2	<0.001***	0.22	0.95	-	-	-	<0.01**	0.55	0.88
Dominant-tree subsample									
S1:1	0.88	0.97	0.53	0.48	0.93	0.02*	-	-	-
S1:2	0.17	0.09	0.17	0.09	0.68	0.46	-	-	-
S2:1	0.95	0.54	0.59	0.10	0.57	0.61	-	-	-
S2:2	0.51	0.52	0.51	<0.01**	0.04* $\delta^{13}C_p > \delta^{13}C_m$	0.05	-	-	-
S3:1	0.45	0.48	0.86	0.40	0.34	0.28	-	-	-
S3:2	0.30	0.98	0.07	0.87	0.06	0.24	-	-	-
S4:1	0.76	0.47	0.55	-	-	-	0.22	0.37	0.65
S4:2	<0.001***	<0.001*** $\delta^{13}C_m > \delta^{13}C_p$	<0.001***	-	-	-	0.63	0.18	0.47
S5:1	0.62	0.53	0.78	-	-	-	0.48	0.62	0.43
S5:2	0.51	0.06	0.7	-	-	-	0.36	0.21	0.43
S6:1	0.19	0.19	0.93	-	-	-	0.31	0.96	0.09
S6:2	0.98	0.18	0.42	-	-	-	0.81	0.44	0.44

1084 *Note:* Stars indicate significant $\log(DBH)$, *Mixture* or interaction effects. *Mixture* is a two-level factor (pure vs.
1085 mixed). For significant *Mixture* effects, the direction of the estimate is indicated by $\delta^{13}C_p > \delta^{13}C_m$ if pure stands
1086 have a higher $\delta^{13}C$ estimate than mixed stands (i.e. mixture improves response to water stress compared to pure
1087 stands), and $\delta^{13}C_m > \delta^{13}C_p$ if mixed stands have a higher $\delta^{13}C$ estimate than pure stands.

1088

1089 **Figures**

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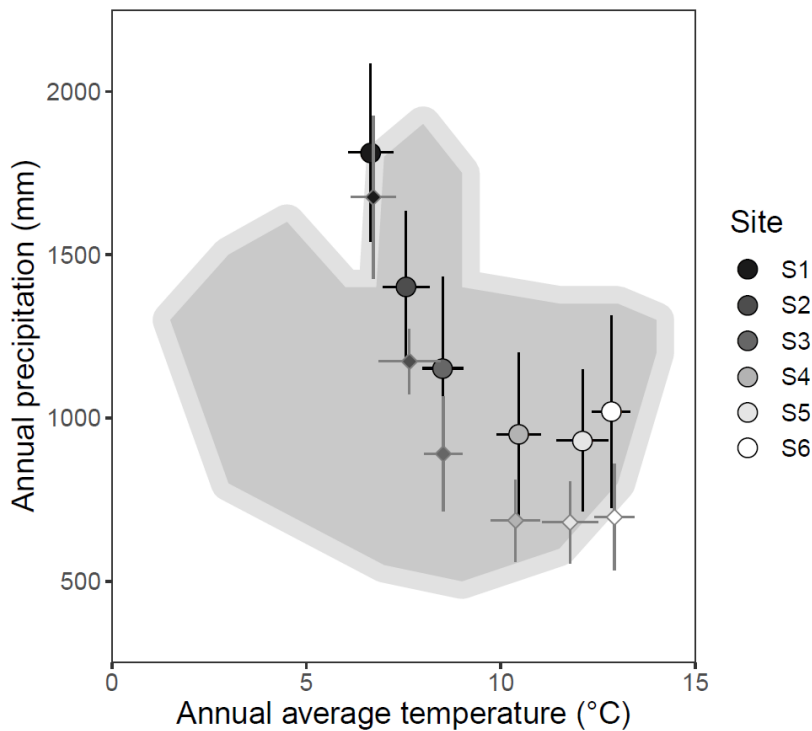
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1093 **Fig. 1.** Field design of the GMAP network (Mediterranean and Alpine Plot Gradient, set up by
1094 X. Morin in 2013). **(a)** Study area and location of the six sites in south-eastern France. Dark
1095 points (sites S1 to S3) represent northern sites with European beech (*Fagus sylvatica*) and silver
1096 fir (*Abies alba*) forests. White points (sites S4 to S6) represent southern sites with European
1097 beech and pubescent oak (*Quercus pubescens*) forests. The sites are located in the following
1098 mountain ranges of the French pre-Alps: Bauges (S1), Vercors (S2), Ventoux (S3), Lubéron
1099 Lagarde (S4), Grand Lubéron (S5), Sainte-Baume (S6). **(b)** Schematic representation of a site,
1100 with the two triplets per site. Each triplet is made up of two pure plots in monospecific stands
1101 and one mixed plot in a mixed-species stand. **(c)** Representation of an individual plot. Plots are
1102 circular with a central plot area (10 m radius) and a buffer zone (7.5 m radius). All the trees in
1103 the central plot with a DBH > 7.5 cm were sampled.

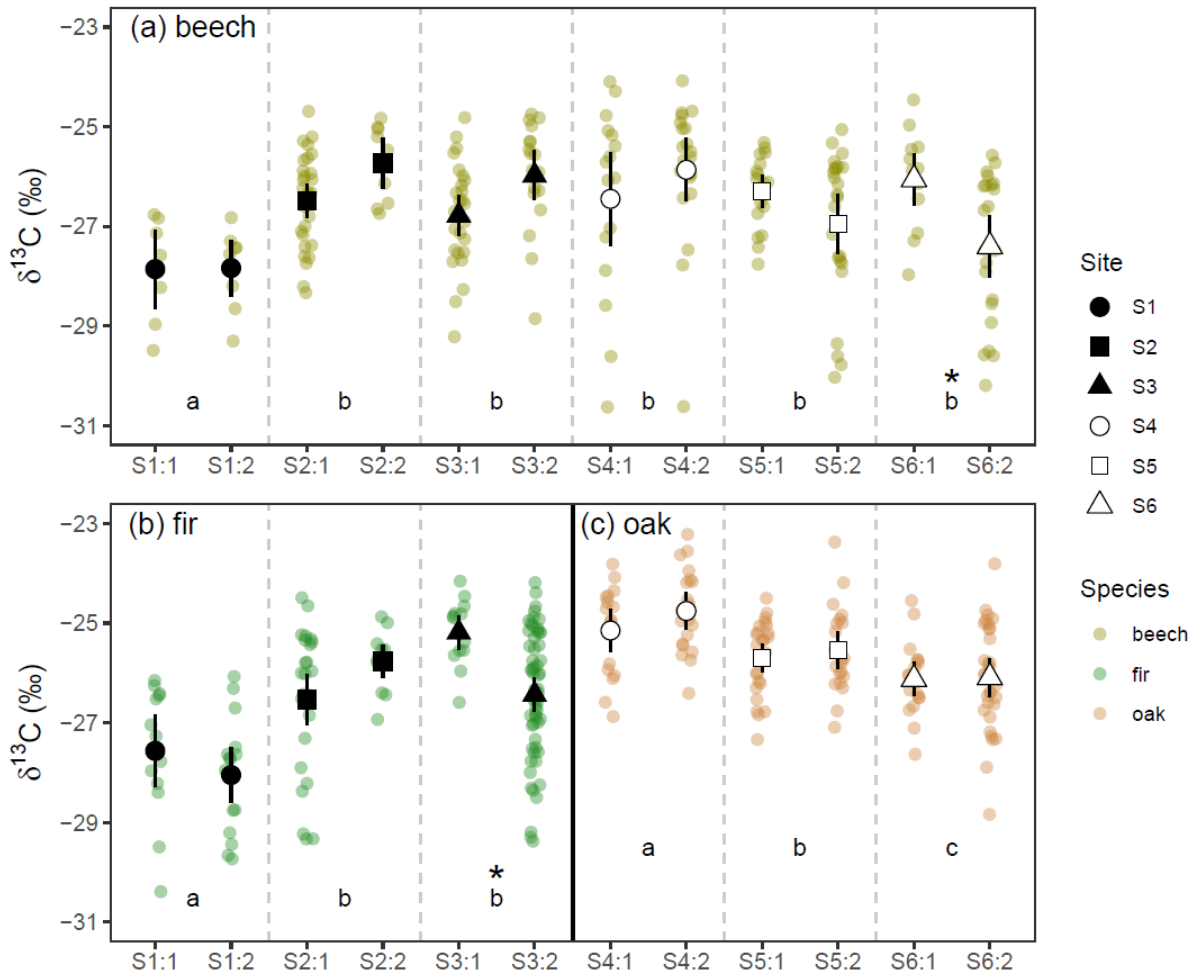
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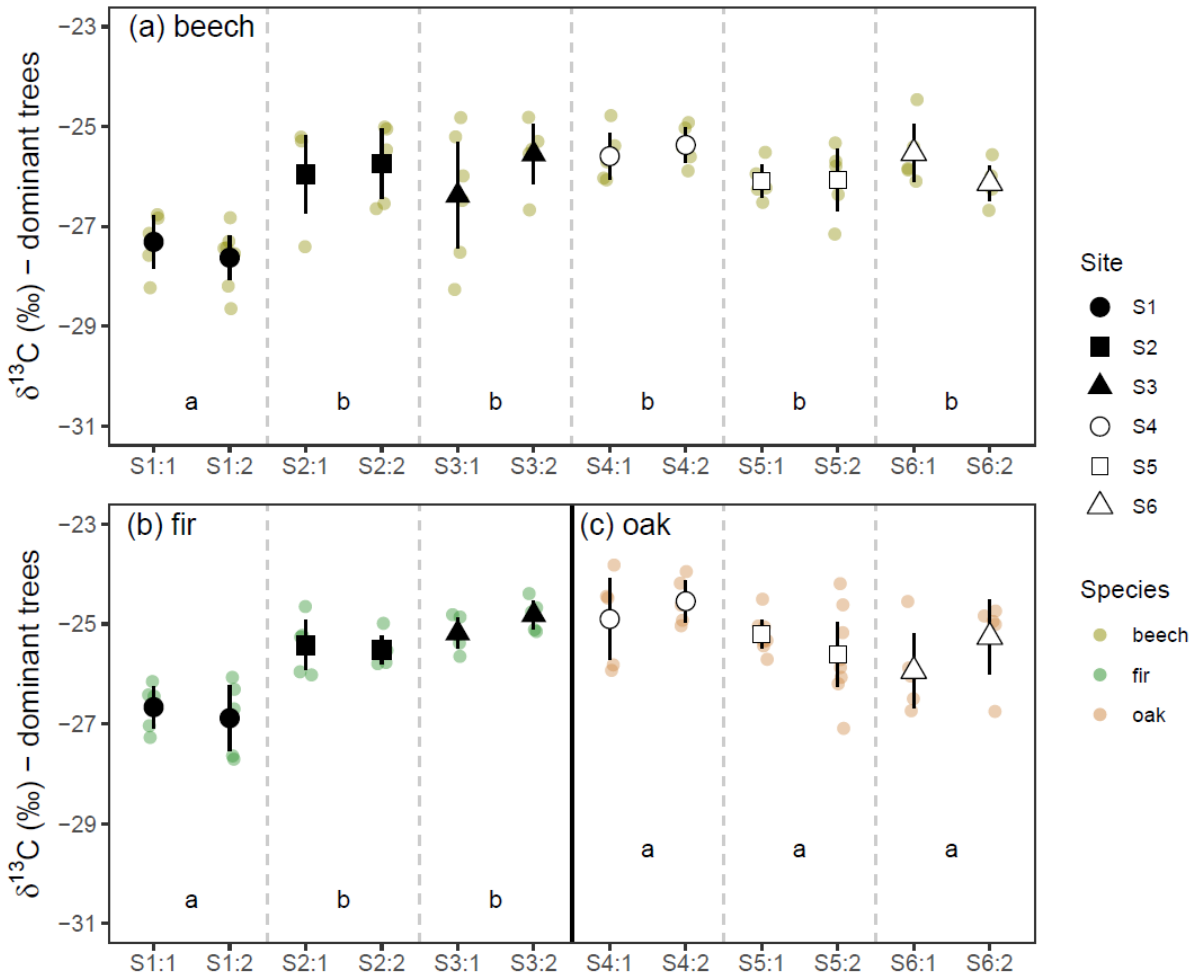
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1107 **Fig. 2.** Climate-space diagram of presence for beech in Europe, study site annual average
1108 temperature and annual sum of precipitation 20-year averages. The shaded area represents
1109 observed beech presence in Europe in all national forest inventories in terms of annual climatic
1110 conditions for temperature and precipitation (adapted from the European Atlas of Forest Tree
1111 Species, Houston Durrant et al., 2016). Large circular points represent the 20-year averages
1112 (1994-2013) from the SAFRAN weather data for each of our study sites. Small diamond points
1113 represent the 5-year averages of the selected dry years (2003-2007) for each site. The x-axis is
1114 the annual average of daily average temperatures. The y-axis is the annual sum of daily
1115 precipitation. Error bars represent \pm one standard deviation around the mean.



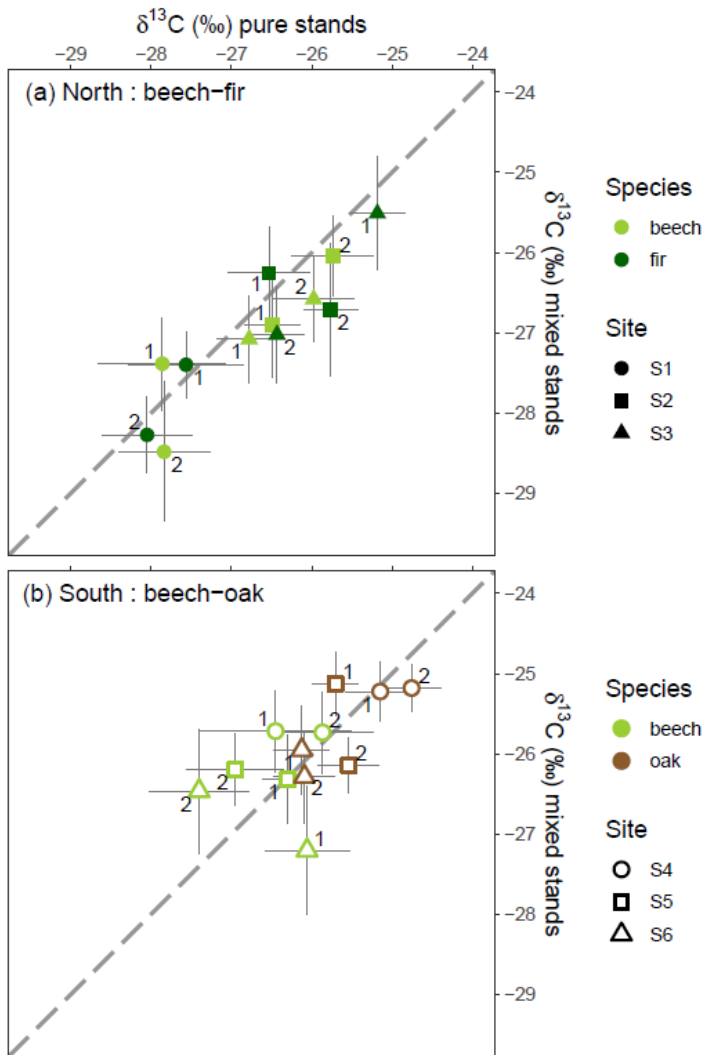
1117

1118 **Fig. 3.** Tree-ring $\delta^{13}\text{C}$ values for all the trees sampled in pure stands, by site and triplet, for (a)
 1119 beech, (b) fir, and (c) oak. Closed and open symbols with error bars (95% confidence intervals)
 1120 show mean plot values. Letters at the bottom of each graph indicate results for differences
 1121 among sites by species (Eq. 5). The pure plots of the two triplets within each site are shown
 1122 separately (i.e. S1:1 is triplet 1 in site S1). Stars indicate significant differences between the
 1123 triplets of a site in pure stands of the same species (Eq. 5). Dots in the background represent
 1124 individual tree data. For individual points, a jitter function is used to add a small amount of
 1125 random noise on the x-axis to show overlapping points.



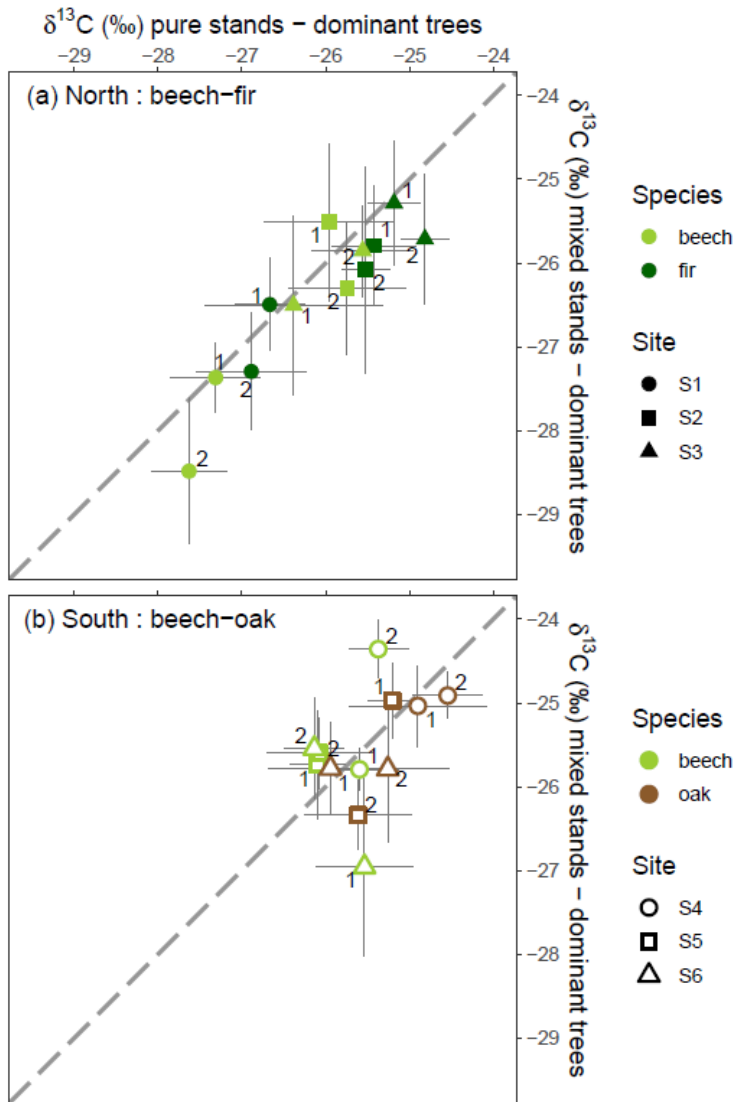
1127

1128 **Fig. 4.** Tree-ring $\delta^{13}\text{C}$ values for all the trees in the dominant-tree subsample for pure stands,
 1129 by site and triplet for (a) beech, (b) fir, and (c) oak. Closed and open symbols with error bars
 1130 (95% confidence intervals) show mean plot values. Letters at the bottom of each graph indicate
 1131 results for differences among sites by species (Eq. 5). The pure plots of the two triplets within
 1132 each site are shown separately (i.e. S1:1 is triplet 1 in site S1). Stars indicate significant
 1133 differences between the two triplets of a site in pure stands of the same species (none here) (Eq.
 1134 5). Dots in the background represent individual tree data. For individual points, a jitter function
 1135 is used to add a small amount of random noise on the x-axis to show overlapping points.



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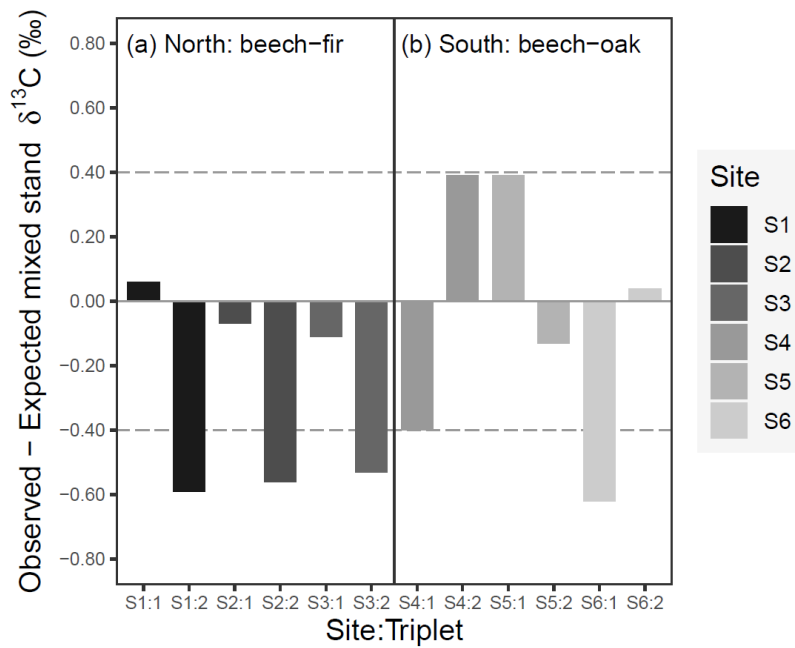
1138 **Fig. 5.** Mean tree-ring $\delta^{13}\text{C}$ values of all the sampled trees in pure versus mixed stands by
 1139 species, site and triplet for (a) beech-fir sites (S1 to S3, closed symbols) and (b) beech-oak sites
 1140 (S4 to S6, open symbols). Symbols with error bars (95% confidence intervals) show mean plot
 1141 values for pure (x-axis) vs. mixed (y-axis) stands. Numbers 1 and 2 represent the triplet number
 1142 within the site. The dashed lines are the identity lines of slope 1 and intercept 0.



1144

1145 **Fig. 6.** Mean tree-ring $\delta^{13}\text{C}$ values of the dominant-tree subsample for pure versus mixed stands
 1146 by species, site and triplet for (a) beech-fir sites (S1 to S3, closed symbols) and (b) beech-oak
 1147 sites (S4 to S6, open symbols). Symbols with error bars (95% confidence intervals) show mean
 1148 plot values for pure (x-axis) vs. mixed (y-axis) stands. Numbers 1 and 2 represent the triplet
 1149 number within the site. The dashed lines are the identity lines of slope 1 and intercept 0.

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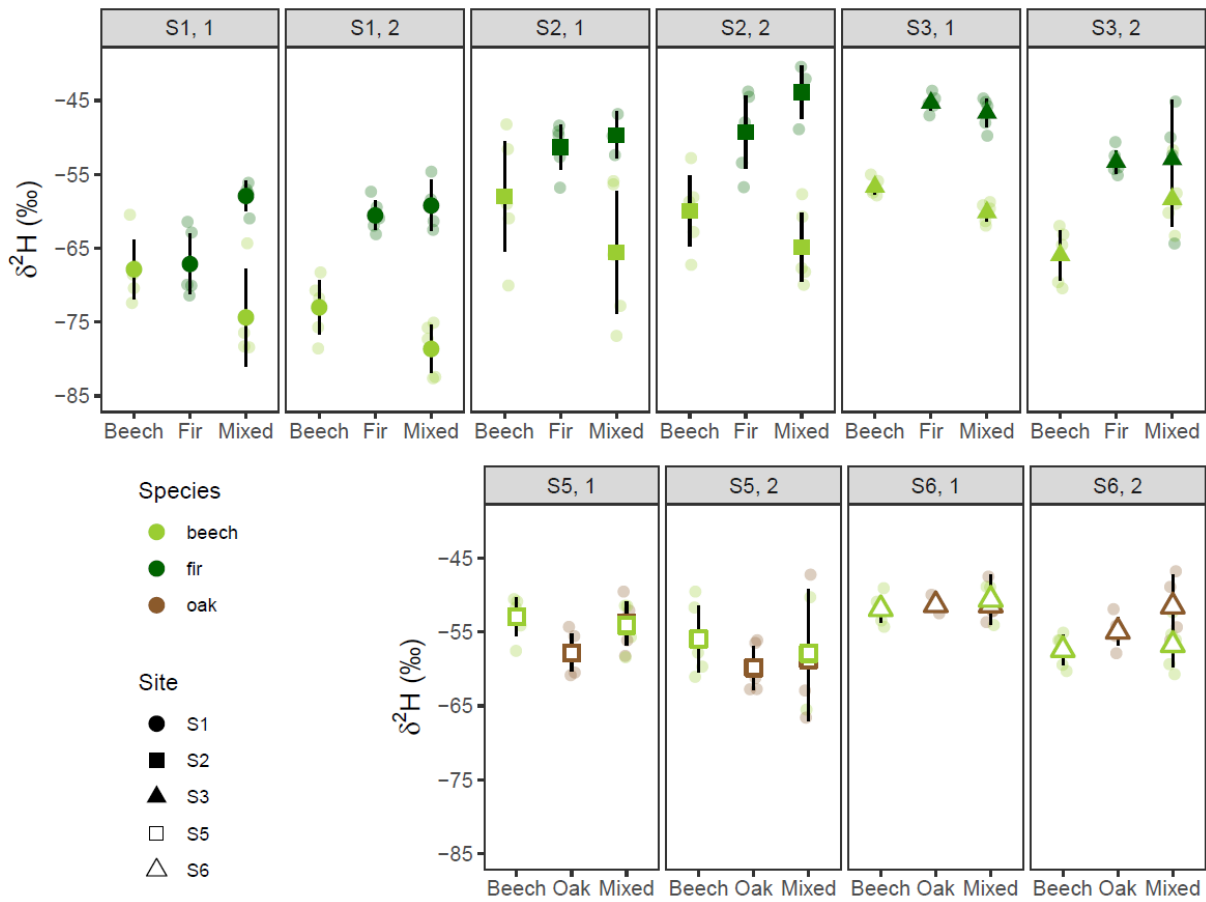


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1152 **Fig. 7.** Net Biodiversity Effect (NBE) for $\delta^{13}\text{C}$ values at the stand level (see Eq. 9) for the
1153 dominant-trees subsample. Differences under 0.4 ‰ are considered as not different from 0.0
1154 ‰. A positive NBE means that the observed mixed stand had a higher (less negative) $\delta^{13}\text{C}$ value
1155 than expected based on data from pure stands. A negative NBE means that the observed mixed
1156 stand had a lower (more negative) $\delta^{13}\text{C}$ value than expected based on data from pure stands.

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1161 **Fig. 8.** Xylem-water $\delta^2\text{H}$ values of the dominant-tree subsample by triplet and species. Each
 1162 box represents a triplet with values for both species (beech-fir in the top line and beech-oak in
 1163 the bottom line). The x-axis represents the different plots within a triplet (two pure plots and
 1164 one mixed plot). Closed and open symbols with error bars (95% confidence intervals) show
 1165 mean plot values. Dots in the background represent individual tree data. For site S5:1 in the
 1166 mixed plot, the average for beech and oak overlap. No data could be recorded at site S4.

Appendices

Appendix A : Additional plot characteristics

See Tables A1-A3

Table A1 Environmental characteristics of the triplets.

Site	Triplet	Triplet ID	Lat. (°N)	Lon. (°E)	Mean Elevation (m)	Mean Slope (°)
S1	1	S1:1	45.70548	6.2192	1198	21
S1	2	S1:2	45.71188	6.21625	1025	18
S2	1	S2:1	44.90231	5.3513	1390	20
S2	2	S2:2	44.9411	5.32774	1137	11
S3	1	S3:1	44.17788	5.24168	1354	27
S3	2	S3:2	44.18707	5.25234	1328	27
S4	1	S4:1	43.97376	5.48	1094	13
S4	2	S4:2	43.97661	5.47961	1082	12
S5	1	S5:1	43.8203	5.53343	1005	26
S5	2	S5:2	43.82269	5.53423	889	34
S6	1	S6:1	43.33197	5.77038	736	8
S6	2	S6:2	43.33281	5.77328	746	12

Table A2 Stand structure for each plot, triplet and site. Plot dendrometric variables include: the dominant height of the plot (H_{dom} , in m) and the basal area of all stems by plot and species (in $\text{m}^2 \text{ha}^{-1}$).

Site	Triplet	Plot	H_{dom} (m)	Basal area ($\text{m}^2 \text{ha}^{-1}$)				Total
				Beech	Fir	Oak	Other sp.	
S1	1	Pure beech	37	80.3	–	–	4.5	84.8
S1	1	Pure fir	30	0.2	81.0	–	8.5	89.7
S1	1	Mixed	28	27.4	29.6	–	4.3	61.4
S1	2	Pure beech	34	46.0	5.5	–	–	51.5
S1	2	Pure fir	34	–	62.5	–	7.4	69.9
S1	2	Mixed	33	32.7	45.5	–	5.1	83.3
S2	1	Pure beech	16	24.9	–	–	3.0	27.9
S2	1	Pure fir	22	–	50.5	–	1.4	51.9
S2	1	Mixed	18	16.0	18.9	–	1.4	36.2
S2	2	Pure beech	33	63.0	2.4	–	–	65.5
S2	2	Pure fir	30	0.6	64.4	–	–	65.0
S2	2	Mixed	26	27.5	19.2	–	–	46.7
S3	1	Pure beech	22	62.0	0.2	–	–	62.2
S3	1	Pure fir	16	0.9	47.5	–	0.8	49.3
S3	1	Mixed	18	17.6	39.4	–	–	57.0
S3	2	Pure beech	20	58.5	1.0	–	–	59.6
S3	2	Pure fir	17	14.1	52.1	–	1.2	67.5
S3	2	Mixed	20	32.0	20.5	–	4.7	57.3
S4	1	Pure beech	20	42.5	–	–	1.3	43.8
S4	1	Pure oak	12	1.3	–	25.3	2.0	28.6
S4	1	Mixed	16	12.5	–	24.2	9.8	46.5
S4	2	Pure beech	19	41.9	–	0.3	–	42.2
S4	2	Pure oak	13	1.0	–	19.0	0.7	20.6
S4	2	Mixed	15	35.5	–	11.9	1.7	49.1
S5	1	Pure beech	13	24.7	–	0.9	11.9	37.5
S5	1	Pure oak	11	–	–	34.4	9.7	44.1
S5	1	Mixed	11	15.2	–	13.0	8.0	36.2
S5	2	Pure beech	16	30.5	–	–	8.0	38.5
S5	2	Pure oak	10	–	–	24.3	4.2	28.5
S5	2	Mixed	12	11.9	–	12.0	5.4	29.3
S6	1	Pure beech	30	54.8	–	–	13.3	68.1
S6	1	Pure oak	19	–	–	61.6	18.2	79.8
S6	1	Mixed	21	23.3	–	24.2	22.5	70.0
S6	2	Pure beech	20	32.5	–	3.0	7.7	43.2
S6	2	Pure oak	16	–	–	33.4	0.5	33.9
S6	2	Mixed	19	22.3	–	21.2	8.1	51.7

Table A3 Average summer rainfall and summer temperature for 4-month summer periods (June to September) at each site calculated over two time periods and mean number of days with water stress (REW < 0.4) over 2003-2007 from BILJOU© model.

Site	Name of region	Summer Rain (mm)	Summer Rain (mm)	Mean summer temp. (°C)	Mean summer temp. (°C)	Mean number of days with water stress
		1994-2013	2003-2007	1994-2013	2003-2007	2003-2007
S1	Bauges	619 (±50)	581 (±158)	13.7 (±0.41)	14.3 (±1.34)	1
S2	Vercors	429 (±48)	332 (±46)	14.5 (±0.41)	15.1 (±0.93)	52
S3	Ventoux	293 (±39)	221 (±35)	15.6 (±0.37)	16.2 (±1.01)	94
S4	Lubéron Lagarde	246 (±38)	172 (±36)	17.8 (±0.37)	18.2 (±1.08)	105
S5	Grand Lubéron	227 (±30)	169 (±40)	19.8 (±0.35)	20.2 (±1.16)	107
S6	Sainte-Baume	212 (±39)	158 (±56)	20.1 (±0.37)	20.7 (±0.93)	108

Appendix B : Additional model results

See Tables B1-B2

Table B1 Linear mixed model output for *Species* effect, $\log(DBH)$ and their interaction on $\delta^{13}C$ values in pure stands by type of mixture (Eq. 6).

	Beech-fir sites				Beech-oak sites			
	χ^2	<i>df</i>	<i>P</i>	post-hoc	χ^2	<i>df</i>	<i>P</i>	post-hoc
All trees		228				238		
log(DBH)	183	1	<.001***		113	1	<.001***	
Species	7	1	<.01**	beech<fir	92	1	<.001***	beech<oak
log(DBH):Species	17	1	<.001***		24	1	<.001***	
<i>R2m (R2c)</i>	<i>0.30 (0.72)</i>				<i>0.40 (0.61)</i>			
Dominant-tree subsample		54				56		
log(DBH)	0	1	0.61		0	1	0.48	
Species	11	1	<.001***	beech<fir	7	1	<.01**	beech<oak
log(DBH):Species	0	1	0.72		4	1	0.06	
<i>R2m (R2c)</i>	<i>0.09 (0.63)</i>				<i>0.18 (0.28)</i>			

Note: Stars indicate significant $\log(DBH)$, *Species* and interaction effects. *Species* is a two-level factor (beech-fir or beech-oak). For significant *Species* effects, the direction of the estimate is indicated by beech<fir (beech<oak) because fir (oak) trees have a higher $\delta^{13}C$ estimate than beech stands. χ^2 : chi square test results for type “II” ANOVA. *df*: degrees of freedom. *P*: p-value for fixed terms. *Triplet ID* is used as a random factor in all four models. A pseudo R-squared for mixed effect models was used to determine the variance explained by the two fixed terms only (marginal coefficient of determination, R^2_m) and the entire model including the random terms (conditional coefficient of determination, R^2_c).

Table B2 Linear mixed model output for *Species* effect, *Mixture* and their interaction on $\delta^2\text{H}$ of the dominant-tree subsample by type of mixture (Eq. 10).

	Beech-fir sites				Beech-oak sites		
	χ^2	<i>df</i>	<i>P</i>	post-hoc	χ^2	<i>df</i>	<i>P</i>
Dominant-tree subsample		104				65	
Species	149	1	<0.001***	beech<fir	0	1	0.71
Mixture	0	1	0.61		1	1	0.33
Species:Mixture	10	1	0.002**	beech: m<p fir: m=p pure: beech<fir mixed: beech<fir	2	1	0.16
<i>R</i> ² _m (<i>R</i> ² _c)	0.36 (0.75)				0.03 (0.32)		

Note: Stars indicate significant *Species*, *Mixture* and interaction effects. *Species* is a two-level factor (beech-fir or beech-oak); *Mixture* is also a two-level factor (pure vs. mixed). For significant *Species* effects, the direction of the estimate is indicated by beech<fir because fir trees have a higher $\delta^2\text{H}$ estimate than beech. Post-hoc results for the *Species:Mixture* interaction are similarly indicated. χ^2 : chi square test results for type “II” ANOVA. *df*: degrees of freedom. *P*: p-value for fixed terms. *Triplet ID* is used as a random factor in both models. A pseudo R-squared for mixed effect models was used to determine the variance explained by the two fixed terms only (marginal coefficient of determination, R^2_m) and the entire model including the random terms (conditional coefficient of determination, R^2_c).