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1 **TITLE: The effect of tree diversity on the resistance and recovery**
2 **of forest stands in the French Alps may depend on species**
3 **differences in hydraulic features**

4

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14

15 **Abstract**

16 As climate change should lead to an increase in the vulnerability and the sensitivity of
17 forests to extreme climatic events, quantifying and predicting their response to more severe
18 droughts remains a key task for foresters. Furthermore, recent works have suggested that tree
19 diversity may affect forest ecosystem functioning, including their response to extreme events.
20 In this study we aimed at testing whether the growth response of forest stands to stressful
21 climatic events varied between mixed and monospecific stands, under various environmental
22 conditions. We focused on beech-fir forests (*Fagus sylvatica* [L.] and *Abies alba* [L.]) and
23 beech-oak forests (*Fagus sylvatica* [L.] and *Quercus pubescent* [L.]) in the French Alps. We
24 used a dendrochronological dataset sampled in forest plots organized by triplets (one mixture
25 and two monospecific stands) distributed in six sites along a latitudinal gradient. We tested
26 (1) whether stand diversity (two-species stands vs monospecific stands) modulates the stands'
27 response to drought events in terms of productivity, (2) whether species identity may drive the
28 diversity effect on resistance and recovery, and (3) whether this can be explained by
29 interspecific interactions. We found that (1) interspecific differences in response to extreme
30 drought events (possibly due to interspecific differences in hydraulic characteristics) can
31 induce a mixture effect on stand growth, although it appeared (2) to be strongly depending on
32 species identity (positive effect only found for beech-fir mixed stands), while (3) there were
33 no significant non-additive effects of diversity on stand resistance and recovery, except for
34 some specific cases. Overall, our study shows that promoting selected mixed stands
35 management may buffer extreme drought effect on stand productivity.

36 **Key words:** Diversity, ecosystem functioning, stand growth, resistance, recovery, climate
37 change, forests, Alps

38

39 1 INTRODUCTION

40 In the upcoming decades, extreme climatic events are predicted to become more
41 frequent (Dale et al., 2001; Pachauri et al., 2015), especially water and/or heat stresses. Such
42 events affect ecosystems functioning and related services (Kellomaki et al., 2008; Malhi et al.,
43 2008; Olesen et al., 2007) directly by altering organisms' physiology, but also indirectly by
44 affecting community composition (Bertrand et al., 2011; Lenoir et al., 2008) that in turn
45 impacts ecosystem functioning (Loreau, 2001). In particular, increased extreme drought
46 frequency and intensity could be very damaging for European forest ecosystems (Babst et al.,
47 2019; Maracchi et al., 2005). However, quantifying and predicting climate change impacts on
48 ecosystem functioning remains a difficult but important task (Morin et al., 2018).

49 The functioning of forest ecosystems could be deteriorated by climate change impacts
50 (like extreme drought events), which can in turn strongly impact the services they provide. In
51 this context, it becomes crucial to better understand how forests react after a such a stressful
52 climatic event, notably their resistance and/or recovery (McCann, 2000; Van Ruijven and
53 Berendse, 2010; Vogel et al., 2012). There are various definitions of resistance or recovery
54 (Newton and Cantarello, 2015). In the present study, resistance is defined as the inverse of
55 growth reduction experienced during a stressful event, i.e. ratio between the productivity
56 during stressful year and before the stressful year (Lloret et al., 2011). Thus, the larger this
57 ratio, the stronger the resistance. Recovery is defined as the capacity of the ecosystem to
58 recover after a stressful event in terms of growth (Lloret et al., 2011), i.e. ratio between the
59 productivity after the stressful year and the productivity during the stressful year.

60 Meanwhile, numerous theoretical, empirical and experimental studies have shown that
61 species richness can strongly modify ecosystem functioning, especially productivity
62 (Cardinale et al., 2012; Hooper et al., 2005). In fact, species-rich communities may, on

63 average, show an increase in productivity in comparison to species-poor communities - and
64 especially to monocultures, a pattern called “overyielding effect”. Such a result has been
65 mainly shown in herbaceous communities, but a few experimental (Jones et al., 2005;
66 Pretzsch, 2005), observation-based (Toïgo et al., 2015) and modelling studies (Morin et al.,
67 2018, 2011) have also shown that overyielding effects may be found in tree communities.

68 Furthermore, it has also been suggested that diversity can stabilize the productivity of
69 ecosystems over time (Ives and Carpenter, 2007). This relationship was also studied in in
70 grasslands (Cardinale et al., 2007) but also in forest ecosystems (DeClerck et al., 2006;
71 Thompson et al., 2014). The stability of an ecosystem process may be quantified by several
72 metrics (Donohue et al., 2016). Most studies have focused on temporal stability describing the
73 temporal variation of an ecosystem process on the mid- or long-term (usually quantified by
74 the inverse of the coefficient of variation of the process over time (Tilman, 1999)). Many
75 studies have showed a positive relationship at the community scale (Isbell et al., 2015; Jucker
76 et al., 2014). The effects of diversity on resistance and recovery of ecosystems have been
77 much less studied than for temporal stability (Donohue et al. 2016). Yet, theoretical works
78 have suggested that diversity, especially species richness, may have a negative effect on
79 recovery (Loreau and Behera, 1999). However, only few empirical studies (usually on
80 grassland ecosystems) have been conducted on this question (Pfisterer and Schmid, 2002;
81 Tilman and Downing, 1994), and no consensus emerged from grassland studies on the effect
82 of diversity on resistance or recovery after a stressful event. Regarding forest ecosystems, the
83 very few examples available showed that community composition may have a contrasted
84 influence on resistance and recovery depending on species - i.e. positive or negative effect for
85 Arthur and Dech (2016) or Pretzsch et al. (2013); not significant for DeClerck et al (2006).
86 These results are often explained by physiological complementarity between species or by

87 environmental differences on the specific context of the studies (Grossiord et al., 2014;
88 Merlin et al., 2015).

89 Regarding the role of physiological complementarity, it is generally assumed that
90 physiological differences (e.g. specific hydraulic character) are greater at the interspecific
91 than at the intraspecific level (Cruiziat et al., 2002). This may induce contrasted responses to
92 climatic constraints between species (Desplanque et al., 1998; Lebourgeois et al., 2014, 2010;
93 Cailleret and Davi, 2010). Forest stands response to drought events should thus be different
94 between mixed and monospecific stands. Delzon (2015) and Klein et al. (2014) recently
95 summarized the main hydraulic strategies of trees to respond to extreme droughts. A first
96 strategy is the avoidance of physiological stress that refers to the mechanisms allowing a tree
97 to avoid drought effects, by relying on water storage (Meinzer et al., 2009) and stomatal
98 regulation (Collatz et al., 1991) or to a deep rooting system (Bréda et al., 2006). Second, the
99 tolerance strategy to physiological stress consists of coping with drought stress, which is
100 possible by investing in xylem resistance to cavitation or in mechanisms allowing to lower the
101 wilting point (Urli et al., 2013). Using their hydraulic characters, it is possible to rank species
102 along an “isohydric-anisohydric” gradient (Martínez-Vilalta and Garcia-Forner, 2017; Tardieu
103 and Simonneau, 1998) that relies on temporal dynamics of gas exchange and drought
104 responses, and thus on differences in stomatal sensitivity (Martínez-Vilalta and Garcia-Forner
105 2017).

106 Two others mechanisms focusing on species interactions may also be involved:
107 competition reduction and facilitation. According to several studies (Brooker et al., 2007;
108 Canham et al., 2006; Forrester and Bauhus, 2016), intra-specific competition may be, on
109 average, stronger than interspecific competition. Thus, we can expect a relaxed inter-
110 individual competition for water or light resources in mixed forests, which may directly
111 increase ecosystem resistance and recovery. Facilitation occurs when a species could

112 facilitate, without negative consequences, the establishment or maintenance of another species
113 (Callaway et al., 2002; Choler et al., 2001). Some studies have shown that interspecific
114 competition may decrease with increasing stress, consistently with the stress gradient
115 hypothesis (*SGH*, Bertness and Callaway, 1994). This hypothesis initially assumes that
116 competitive interactions should shift to facilitative ones when environmental conditions
117 become very stressful. The positive effect of mixing is therefore stronger under stressful
118 conditions. However, this pattern is challenged by more recent studies showing that in very
119 stressful conditions facilitation between species does not hold and gives way to a strong
120 competition (Holmgren and Scheffer, 2010; Maestre et al., 2009). According to these studies,
121 the species composition of the mixed stands, especially their physiological characteristics,
122 may lead to contrasting response patterns to drought. For example, a mixed stand composed
123 of species with diverging response patterns to drought could be more resistant in terms of
124 growth during a drought event than a stand composed of species with similar response
125 patterns to drought. It can be modulated by environmental conditions, such as drought
126 intensity and duration.

127 It is thus crucial to study forest response to drought events and effects on forest
128 ecosystems functioning, especially to develop relevant silvicultural management scenarios
129 buffering the sensitivity of forest stands to drought by mitigating its negative impacts on
130 growth and generally promoting forest adaptation to new climatic conditions. Some studies in
131 France show that mixed stands management could improve stand resistance to extreme
132 stressful events compare monospecific stands management (Millar et al., 2007; Seynave et al.,
133 2018). Increasing the diversity in tree community thus seems to be an efficient solution to
134 sustain forest functioning and to better preserve most of the related services that are especially
135 important in mountain forests (e.g. soil erosion control and protection against avalanches).
136 Moreover, these forests have been identified as especially vulnerable regarding climate

137 change (Courbaud et al., 2011; UNEP, 2010), especially in Alps (on which our work focuses).
138 Studying how species composition and interspecific interactions drive stand response to
139 drought is crucial, and knowing these effects could lead to relevant recommendations for
140 forest management and to maintain forest ecosystems' services.

141 In this paper, we thus addressed the three following questions:

142 (1) Is the productivity of forest stand more resistant and/or does it recover
143 faster to extreme drought events in mixed stands than in monospecific
144 ones?

145 (2) How does species identity affect the diversity effect on resistance and
146 recovery?

147 (3) Can this effect be explained by interaction between species (i.e. net
148 diversity effect)?

149 To answer these questions, we used a triplet design (Pretzsch et al., 2013b), distributed
150 along a latitudinal gradient may considering the effect of environmental conditions. Using
151 such space-for-time substitution appeared as a relevant way to assess the impact of future
152 climate change (Blois et al., 2013; Lester et al., 2014). We focused on two mixed forest types,
153 i.e. common beech (*Fagus sylvatica*) - pubescent oak (*Quercus pubescens*) and beech-silver
154 fir (*Abies alba*) forests. These mixed forests are widespread in the region, distributed along
155 strong climatic gradients, and have a critical economical importance in France. More
156 specifically, beech-fir stands are common communities in northern external Alps while beech-
157 oak stands are common in southern external Alps (Seynave et al., 2008; Tinner et al., 2013).
158 Comparing these three species is also interesting because of their physiological differences
159 (see Material and Methods section), which are likely to show various response to climatic
160 stress and especially to extreme drought events. We hypothesized that stand resistance and

161 recovery patterns depended on species richness depending mostly of composition. We expect
162 different pattern between beech-oak and beech-fir stand. We also hypothesized that mixed
163 effect is mostly explaining by additive effect.

164

165 **2 MATERIAL AND METHODS**

166 **2.1 Field sites**

167 The field design was constituted of forest plots dominated by one (monospecific
168 stands) or two tree species (mixed stands). These plots were located in six forested areas in
169 the French Alps, distributed along a latitudinal gradient with contrasted climatic conditions.
170 These sites were from North to South: Bauges, Vercors, Mont Ventoux, Luberon-Lagarde,
171 Grand Luberon and Sainte-Baume (Fig. 1 and Appendix Table A). All sites are characterized
172 by limestone bedrock, with a North to West aspect for all plots, as sites have been selected to
173 minimize variability in all environmental conditions but climate, as much as possible. This
174 gradient has been divided into two parts according to species composition of the sampled
175 stands: the northern sites (Bauges, Vercors, Mont Ventoux) with beech-fir forests, and the
176 southern sites (Luberon Lagarde, Grand Luberon, Sainte-Baume) with beech-oak forests.
177 Monospecific beech stands have been sampled in the all (six) sites. The stand structure was
178 high forest, except in Grand Luberon where stands were coppice forests.

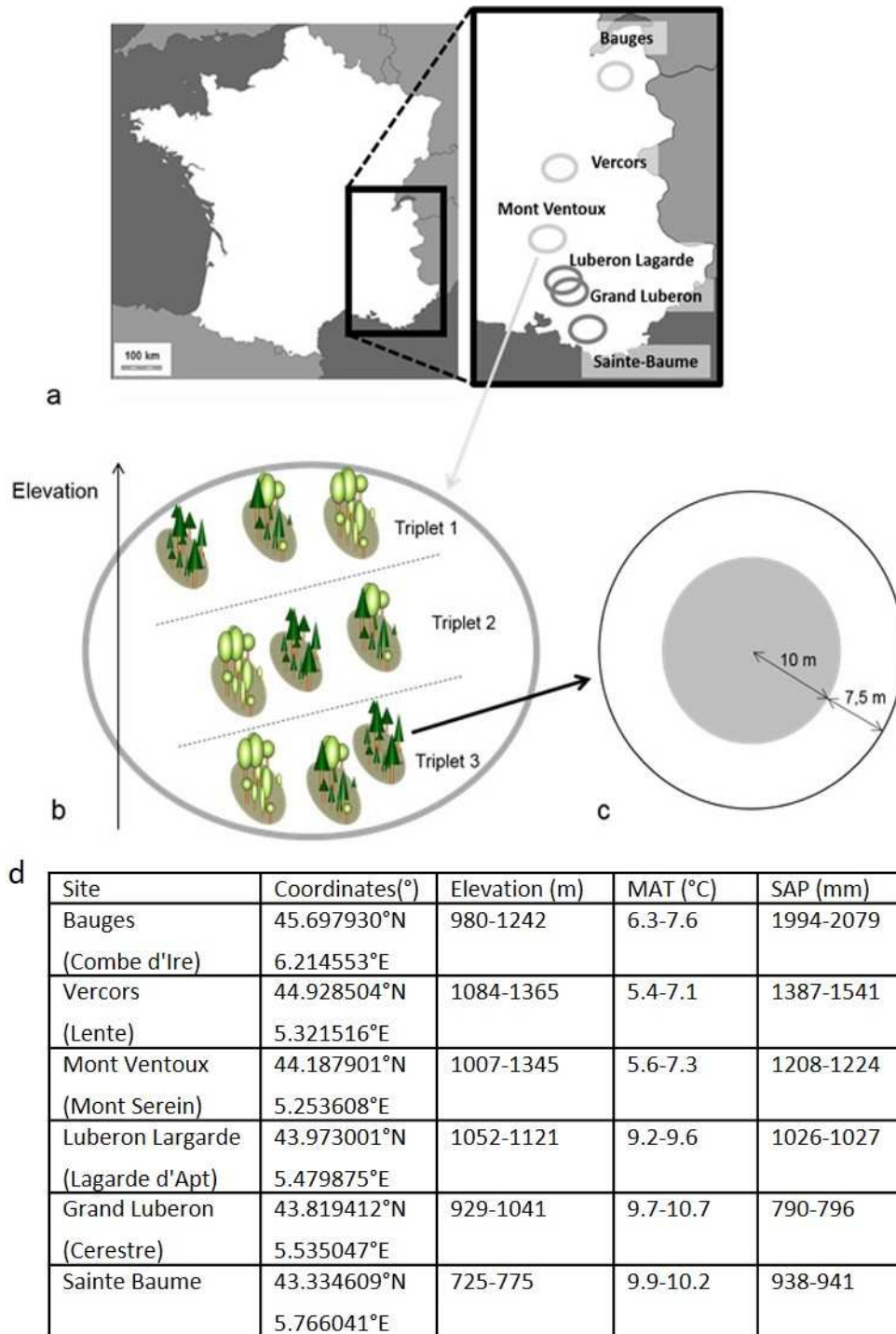
179 **2.2 Species**

180 In this study, we focused on two kinds of mixed stands: a coniferous-hardwood mixed
181 stand, with fir mixed with beech (with two late-successional species), and a hardwood-
182 hardwood mixed stand with beech and oak (late successional and mid-successional species).
183 Common beech is sensitive to dry conditions but recovers easily after extreme stressful event
184 (Lebourgeois et al., 2005). Silver fir is less sensitive to dry conditions, but grows better in

185 humid conditions (Lebourgeois et al., 2010; Mauri et al., 2016). Moreover its growing season
186 starts earlier than beech (as a coniferous species), which could affect positively its recovery
187 after a drought year (except in case of early spring drought). Pubescent oak is a mid-
188 successional species that is more light-demanding than the two other species and that better
189 tolerates shallow soils and drier atmospheric conditions than the two other species (Pasta et
190 al., 2016). We study mixed stands of two species with very different hydraulic strategies (fir -
191 coniferous and isohydric - and beech - hardwood and anisohydric), and mixed stands of two
192 species with similar hydraulic strategies (oak and beech, hardwood and anisohydric). Other
193 species were sampled in some plots when present - maple (*Acer campestre*), spruce (*Picea*
194 *abies*), and Scots pine (*Pinus sylvestris*) - but they represented less than 10% of total
195 composition for each plot in terms of basal area. As they were equally present in
196 monospecific or mixed stands, we did not consider them in this study.

197 **2.3 Plot sites**

198 The plots have been grouped in triplets at each site, i.e. the combination of a beech
199 pure stand, a fir or oak monospecific stands (i.e. target species representing at least 90% of
200 the total basal area), and a fir-beech or oak-beech mixed stands (i.e. between 40 and 60% of
201 each species, with an average of 45%). Focusing on forest mixed stands with two species
202 allowed testing complementary effects in a more precise way (Aussenac et al., 2017; Forrester
203 and Bauhus, 2016) and better identifying explanatory mechanisms at a local scale (del Rio et
204 al. 2017). All plots used in analyze (60 plots) were sampled between 2013 and 2015,
205 organized in 20 triplets (Appendix Table A).



206

207 *Figure 1: Description of the field design. (a) The study area and sites where the plots have*
 208 *been sampled. North sites (light grey circles) are Mont Ventoux, Vercors and Bauges, with*
 209 *plots sampled in beech-fir forests. South sites (dark grey circles) are in Luberon Lagarde,*
 210 *Grand Luberon and Sainte-Baume, with plots sampled in beech-oak forests. (b) Schematic*
 211 *representation of a site with three triplets of stands (one monospecific stand of species A*

212 (*beech*), one monospecific stand of species *B* (*fir* or *oak*), and one mixed stand with species *A*
213 and *B*) distributed along an elevational gradient. (c) Schematic representation of a plot, with
214 an inner circle (grey area) in which all trees with a *DBH* > 7.5 cm were sampled, and an
215 external 7.5 m wide buffer zone in which only the trees with a larger *DBH* than the median
216 *DBH* of trees in the inner circle have been sampled (dominant trees). (d) Description of the
217 sites. Coordinates: latitudinal and longitude; Elevation; *MAT*: mean annual temperature;
218 *SAP*: sum of annual precipitation.

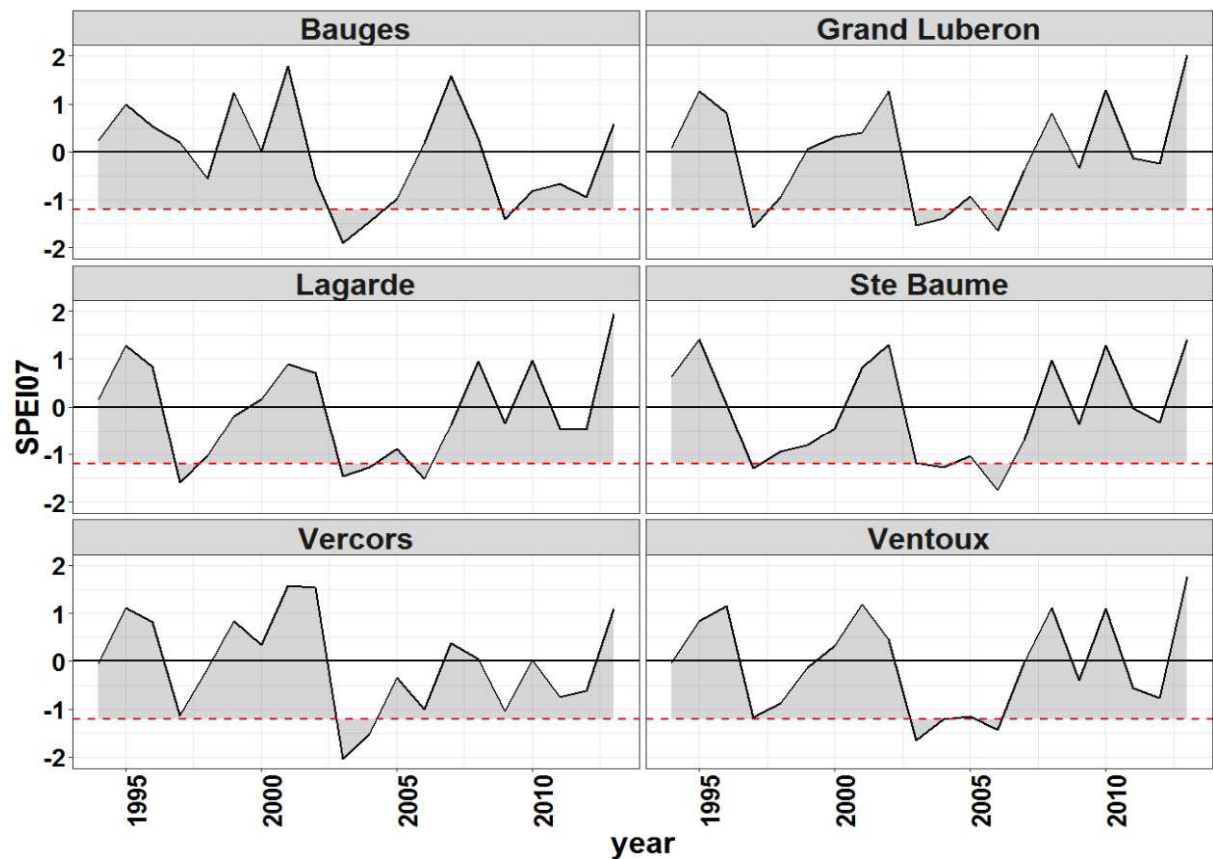
219 A plot was constituted of a 17.5 m-radius circle, including a central zone of a 10 m-
220 radius circle (Fig. 1). For each plot, slope, elevation and aspect were measured. In the central
221 zone, tree characteristics were measured (species identity, location, height, crown depth,
222 diameter at breast height [*DBH*]) and trees with a *DBH* larger than 7.5 cm were cored at
223 breast height using a Pressler borer. In coppice stands, only the largest stem of each coppice
224 (individual tree) was cored. We thus considered all the trees in a plot, regardless their status
225 (dominant or understory).

226 **2.4 Climatic data**

227 We used the Standardized Precipitation Evapotranspiration Index (*SPEI*, Vicente-
228 Serrano et al., 2013, 2010) to determine the onset, duration and magnitude of drought
229 conditions with respect to normal conditions, derived from the *SPI* (Standardized
230 Precipitation Index, Guttman, 1999), and represents a climatic water balance (Thornthwaite,
231 1948) calculated at different time scales, using the monthly (or weekly) difference between
232 precipitation and *PET* (Vicente-Serrano et al., 2013, 2010). These indexes have been already
233 used in several ecological studies analyzing radial growth data (Merlin et al., 2015; Potop et
234 al., 2014; Pretzsch et al., 2016).

235 Monthly values of precipitation and *PET* were extracted from 1km-resolution GIS
236 layers covering all France for each year from 1995 to 2013. These maps were created using
237 data from 119 and 214 non-interrupted weather stations from the Météo France network, for
238 precipitation and temperature respectively. A monthly model was created for each variable
239 using Geographically Weighted Regression (GWR, Fotheringham et al., 2002) with spatially
240 distributed variables describing topography, solar radiation, land use and distances to the seas
241 (Piedallu et al., 2016). Cross-validation was used to validate these maps, with a mean r^2
242 ranging between 0.80 for precipitation to 0.94 for mean temperature across all pixels in
243 France.

244 We calculated annual *SPEI* (Fig. 2) using *R* package *SPEI* (Vicente-Serrano et al.,
245 2010), between February and July, hereafter identified as *SPEI*₀₇, i.e. the growth period
246 (Vanoni et al., 2016). It also allowed determining the years with driest growth season of a
247 dataset. The threshold corresponding to a drought event (at the year level) affecting tree
248 growth was likely to vary between species and sites, but for the sake of simplicity we used a
249 unique threshold in our analyses. A sensitivity analysis on threshold level based on AIC
250 comparison (data not shown) showed that the best threshold was -1.17 (exploring value
251 between -0.5 and -1.5 with 0.02 step) for our dataset. This agreed with a recent experimental
252 study in grasslands that used a threshold of -1.28 (Isbell et al., 2015) and a global study based
253 on remote sensing data that used a threshold of -1 (Schwalm et al., 2017).



254

255 *Figure 2: SPEI07 (calculated between February and July) at the six studied sites (black*
 256 *lines). The horizontal red line represents the threshold defining an extreme dry event (i.e. the*
 257 *driest year's decile), with values below the threshold.*

258 2.5 Data analyses

259 Dendrochronological analyses

260 We studied growth dynamics using tree rings for the last 18 years before sampling, i.e.
 261 from 1995 to 2013. Each core has been

262 cut longitudinally. We put some chalk to improve contrast between rings. Then cores
 263 were photographed with a large-resolution camera coupled with binocular lens. Then the
 264 width of each ring was assessed with ImageJ software (<https://imagej.nih.gov/ij/index.html>),
 265 with an accuracy of 0.01 mm. All cores, i.e. 2159 trees, were cross-dated for each species
 266 using specific species pointer years, as described in Lebourgeois and Merian (2012), but

267 without series standardization. This analysis allowed ensuring that chronologies were
268 synchronized, without correcting for interannual variations amplitude. Here, productivity was
269 represented by basal area increment *BAI* instead of diameter increment in Lloret et al. (2011).
270 Diameter increments were transformed into *BAI* using measured DBH (Biondi and Qeadan,
271 2008). Some cores were too difficult to read accurately (blurred distinction between rings)
272 and were thus not reliable and have been removed for the analyses. Therefore, we finally used
273 growth time-series for 1235 trees (i.e. 924 cores removed), with 596 beeches (mean age:
274 106 ± 45 years old), 387 firs (mean age: 75 ± 38 years old) and 240 oaks (mean age: 87 ± 40
275 years old).

276 This study aimed at assessing forest productivity by sampling all trees in a plot instead
277 of sampling only some a few trees like classically done (e.g. NFI-based studies). Considering
278 all trees should allow better quantifying the competitive environment between all trees within
279 each plot. However, we did not obtain growth data for all trees due to the difficulty of reading
280 some cores, especially in the southern sites. As these unreadable cores were not equally
281 distributed across the network of plots but also inside each triplet, it was not possible to focus
282 on only the subsample of available trees (i.e. trees with a readable core) to calculate resistance
283 (R_t) and recovery (R_c) for the whole plot. To assess the productivity of the whole plot, we
284 thus had to reconstruct the temporal series of *BAI* of the missing individuals, i.e. 924 trees –
285 thus *ca.* 40% of total dataset (meaning that the number of sampled trees remains much larger
286 than what is usually done when focusing on only a few dominant trees in a plot). To do so, we
287 consider separately each species in each stand type (mixed or monospecific stand) in each
288 site. A linear model was fitted in each case to predict individual *BAI* with tree basal area,
289 using all observed rings between 1995 and 2013. With this approach, we have been able to
290 predict *BAI* time-series for each missing tree (models' estimates shown in Appendix Table B),
291 to finally obtain *BAI* time-series for each plot.

292 To assess resistance and recovery in each plot, we used annual *BAI* at the stand level,
293 for the last 18 years (1995-2013). The annual productivity at year y (BAI_y) was calculated by
294 summing the *BAI* of all trees for each plot:

$$295 \quad BAI_y = \sum_i^n BAI_{iy} \quad (1)$$

296 with n being the number of trees in the plot and BAI_{iy} being the basal area increment of tree i
297 at year y .

298 Lagged effects of drought years on resistance and recovery in terms of *BAI*

299 Contrary to a lot of studies in forest ecosystems (Lloret et al., 2011; Pretzsch et al.,
300 2013; Trouvé et al., 2017; Zang et al., 2014) that used a comparison between tree growth
301 before and after a stressful event, we used a distributed lag effect model of *SPEI*07 using the
302 *DLNM* R package (Gasparri, 2011). We included these linear lag effects of *SPEI* in a linear
303 model of stand tree growth that controls for additional covariates. More precisely, we
304 modelled stand annual basal area increment (*BAI*) as function of competitive environment
305 (*BA*), and distributed lag effect of *SPEI*. Using climate lag effect to understand trees
306 interaction allowed us to capture the past climatic context and understand the lagged climatic
307 effect, which will be important to predict the effect of climatic changes on forest ecosystems
308 (Ogle et al., 2015).

309 We modelled the drought lag effect from the current year (lag0) up to four previous
310 year (*i.e.* lag1, lag2, lag3 and lag4) with distributed lag effects based on (i) a threshold
311 function below $SPEI = -1.17$ and (ii) a linear function to represent the temporal lag effect of
312 drought on tree growth. The threshold function (i) corresponds to a transformation of *SPEI*
313 into a new variable $SPEI_t$ such as $SPEI_t = 0$ if $SPEI \geq -1.17$ and $SPEI_t = -1.17 - SPEI$, if $SPEI$
314 < -1.17 . $SPEI_t$ is a positive and increasing function drought stress intensity (whereas drought
315 stress corresponds to negative values of *SPEI*). The temporal distributed lag effect (ii) was

316 modelled using a linear model with an intercept (see Gasparrini, 2011 for model details on
 317 distributed lag effect models). This linear trend was supported by a preliminary analysis
 318 assuming the unconstrained lag effect. A distributed lag effect allows representing delayed
 319 effect of a variable (in our case $SPEI_t$) as the sum of the effect until a given number of lag
 320 years is reached (four in our case). The equation 2 shows the lag effect for a given year y :

$$321 \quad \sum_{l=0}^4 \beta_l SPEI_{t_{y-l}} \quad (2)$$

322 where the linear lag effect model is fitted by constraining the β coefficients as $\beta_l = a + b * l$,
 323 where l is the lag year (l in 0 to 4). Our distributed lag effect model is closely similar to
 324 classical representation of resilience in term of resistance and recovery (see Appendix Fig. C
 325 and Lloret et al. 2011) with the intercept at lag0 (parameter a) representing the immediate
 326 growth reduction due to drought (i.e. resistance) and the linear recovery over time (function of
 327 the parameter b) determining the recovery after stress. The parameters a and b can be
 328 estimated by recasting the equation (2) as:

$$329 \quad \sum_{l=0}^4 \beta_l SPEI_{t_{y-l}} = a * \sum_{l=0}^4 SPEI_{t_{y-l}} + b * \sum_{l=0}^4 l * SPEI_{t_{y-l}}$$

$$330 \quad = a * lag_{intercept}(SPEI_y) + b * lag_{slope}(SPEI_y), \quad (3)$$

331 with $lag_{intercept}(SPEI_y) = \sum_{l=0}^4 SPEI_{t_{y-l}}$ and $lag_{slope}(SPEI_y) = \sum_{l=0}^4 l * SPEI_{t_{y-l}}$.

332 The fully fitted model is given by the following equation:

$$333 \quad BAI_{s,t,p,y} = c_{0,s} + c_1 * BA_p + a * lag_{intercept}(SPEI_y) + b * lag_{slope}(SPEI_y) + d_t + d_{p,t} + e_{s,t,p,y} \quad (4)$$

334 where s , t , p , and y are respectively the site, triplet, the plot and the year. $c_{0,s}$ is site dependent
 335 intercept. BA_p is the total basal area and c_1 is its fitted coefficients. d_t and $d_{p,t}$ are respectively
 336 the triplet random effects and plot nested in triplet random effects and $e_{s,t,p,y}$ is the residual
 337 normal error. a and b represent respectively the immediate growth reduction due to drought
 338 (i.e. resistance, higher a means stronger resistance) and the linear recovery over time

339 (recovery, stronger b means faster/higher recovery). This model was fitted separately per
340 stand type – i.e. monospecific beech, fir and oak stand, and beech-fir and beech-oak mixed –
341 and region – North (for Bauges, Vercors, Ventoux) and South (for Luberon Lagarde, Grand
342 Luberon and Sainte-Baume) - with *lme* and DLNM with R software (R version 3.3.0).

343 Then we analyzed mixed stand response to drought events by considering the relative
344 abundance (i.e. relative basal area) of beech as an explanatory variable (model details are in
345 Appendix D). We further expected that the effect diversity on resistance may vary with
346 species proportion in mixed stands.

347 Assessing non-additive effects of mixed stands in response to an extreme drought event

348 We tested whether climatic stress may impact forest stands in the short term, i.e. at the
349 year during which the drought stress occurred (hereafter named “current year”) and the 3
350 years just after. Lloret et al. (2011) presented a framework to compute the effects of extreme
351 one-time stress on stand (or tree) productivity during and after. Here, we used resistance (R_t)
352 and recovery (R_c), defined below in (5) and (6). This metrics were calculated with BAI_y series
353 (Eq. 1), namely BAI_y during climatic stress (Dr), BAI_y in the respective pre-stress period
354 ($PreDr$), used as reference period, and BAI_y in the respective post-stress period ($PostDr$)
355 (Zang et al 2014, Lloret et al., 2011) as:

$$356 \quad R_t = Dr/PreDr \quad (5)$$

$$357 \quad R_c = PostDr/Dr \quad (6)$$

358 $PreDr$ and $PostDr$ were calculated from an average over three years (Pretzsch et al.,
359 2013). Figure C illustrates graphically the computing method. We focused on years with
360 extreme drought, meaning with $SPEI_{07} < -1.17$ (see above), meaning selected years are not the
361 them between sites.

362 To better explore the effect of diversity on forest resistance and recovery, we
 363 computed indices inspired by the Net Biodiversity Effect (*NBE*, Loreau, 1998). The *NBE*
 364 quantifies non-additive effect of species mixing, i.e. effect of interspecific interaction, on a
 365 given ecosystem process (e.g. mean productivity). We compared the productivity of a two-
 366 species stand and the predicted productivity based on the productivity of monospecific stands
 367 and the relative abundance of species in the mixed stand - under the null hypothesis that there
 368 was no effect of species interactions on ecosystem functioning. We have thus transposed this
 369 approach to define two indices for productivity resistance $R_{t_{div.eff}}$ and productivity recovery
 370 $R_{c_{div.eff}}$. In other words, this method allowed calculating non-additive effect of increasing
 371 diversity on R_t (5) or R_c (6).

372 To compute these new indices, a predicted response of mixed plots is calculated from
 373 monospecific stand plots ($R_{t_{pred}}$ or $R_{c_{pred}}$), using a predicted productivity $BAI_{pred,y}$ for each
 374 mixed plot and each year y . $BAI_{pred,y}$ was calculated using observed *BAI* of each species in
 375 monospecific stands of the corresponding triplet. Expected resistance ($R_{t_{pred}}$) and recovery
 376 ($R_{c_{pred}}$) were then assessed from $BAI_{pred,y}$ time-series. The productivity of each mixed stand
 377 could be partitioned in two parts: productivity of beech trees, productivity of accompanying
 378 species (fir or oak). The relative abundance of each species in the mixed stands (p_{Fagus} , $p_{Quercus}$
 379 or $Abies$) was calculated using the summed initial basal area of each species (i.e. basal area in
 380 1995). Thus, predicted annual productivity $BAI_{pred,y}$ of each mixed stand at year y was
 381 calculated as follows:

$$382 \quad BAI_{pred,y} = BAI_{Fagus,y} * p_{Fagus} + BAI_{Quercus\ or\ Abies,y} * p_{Quercus\ or\ Abies} \quad (6)$$

383 where $BAI_{Fagus\ or\ Quercus\ or\ Abies,y}$ were respectively beech/oak/fir monospecific stand basal area
 384 increment at year y .

385 Finally, Rt_{pred} or Rc_{pred} were compared with the observed values (Rt_{obs} or Rc_{obs}). It was
386 noteworthy that these calculations were possible because the plots within a triplet had a
387 similar structure (i.e similar basal area). In this analysis, we thus obtained $Rt_{div.eff}$ and $Rc_{div.eff}$
388 values for each triplet t :

$$389 \quad Rt_{div.eff_t} = Rt_{obs_t} - Rt_{pred_t} \quad (7)$$

$$390 \quad Rc_{div.eff_t} = Rc_{obs_t} - Rc_{pred_t} \quad (8)$$

391 $Rt_{div.eff}$ and $Rc_{div.eff}$ were analyzed separately for each site. To test whether $Rt_{div.eff}$ and
392 $Rc_{div.eff}$ values were significantly different from 0, we used on a Wilcoxon-test. Significant
393 positive or negative values means that diversity had, on average, a positive or negative non-
394 additive effect on resistance and recovery, respectively. If $Rt_{div.eff}$ and $Rc_{div.eff}$ are equal to 0, it
395 means that diversity had no non-additive effect on resistance and recovery.

396 Then, we tested how environmental conditions (here stress gradient) may affect the
397 mixed stand effect along the latitudinal gradient (Fig. 4). We computed stress gradient level
398 for each triplet (considering environmental conditions are similar within triplet) with
399 maximum beech height in beech monospecific stand plot.

400 All analyses were carried-out with R software (R version 3.3.0). The full methodology
401 is summarized in Appendix Fig. C.

402

403 **3 RESULTS**

404 **3.1 Diversity and climate effects on resistance and recovery**

405 In fir and beech stands (i.e. in the northern part of the gradient), the response of both
406 metrics to drought events are significant for the three stands. Moreover, resistance and
407 recovery varied between stands (Table 1). Mixed stands appeared to have a lower resistance

408 than monospecific stand and similar resistance than monospecific fir stands: as the estimate
 409 for monospecific beech (-0.003±0.001) was higher than estimates for monospecific fir (-
 410 0.009±0.001) and mixed stands (0.007±0.001).

<i>Dataset</i>		<i>Beech stands</i>	<i>Other pure stands (Fir or Oak)</i>	<i>Mixed stands</i>
	<i>parameters</i>	<i>Estimate (±SE)</i>	<i>Estimate (±SE)</i>	<i>Estimate (±SE)</i>
<i>Beech-Fir</i>	<i>BA</i>	0.003 (±0.002)	0.003 (±0.006)	0.006 (±0.005)
	<i>Resistance (a)</i>	-0.003 (±0.0008)	-0.009 (±0.001)	-0.007 (±0.001)
	<i>Recovery (b)</i>	0.001 (±0.0003)	0.003 (±0.0006)	0.002 (±0.0004)
<i>Beech-Oak</i>	<i>BA</i>	-0.004 (±0.002)	0.002 (±0.002)	0.0002 (±0.004)
	<i>Resistance (a)</i>	-0.001 (±0.001)	-0.0004 (±0.0008)	-0.0003 (±0.001)
	<i>Recovery (b)</i>	0.0003 (±0.0006)	0.0004 (±0.0003)	-0.0001 (±0.0005)

411 *Table 1: Models' parameters estimates tested to explain BAI for every stands, with the*
 412 *northern (with beech-fir stand, including Bauges, Vercors and Mont Ventoux, quoting here in*
 413 *decreasing latitude order) and southern (with beech-oak stand including Luberon Lagarde,*
 414 *Grand Luberon and Sainte-Baume, quoting here in decreasing latitude order) parts of the*
 415 *gradient taken separately. BA is the stand basal area, and resistance and recovery represent*
 416 *stand responses to extreme drought. Significant p-value with t-test at the 0.1 level are*
 417 *represented in bold.*

418 The recovery of all stands (represented by $lag_{slope}(SPEI)_y$, see Table 1) was
 419 significantly positive. Mixed stands recovery (estimate: 0.002±0.0004) is higher than beech
 420 stands recovery (estimate: 0.001±0.0003) but lower than fir stands recovery (estimate:
 421 0.003±0.0006).

422 In oak and beech stands (i.e. in the southern part of the gradient) (Table 1), extreme
 423 drought events did not significant affect *BAI* at stand level. Monospecific oak and beech

424 stands showed a positive recovery, contrary to mixed stands, although these trends were not
 425 significant.

426

427

	<i>BA</i>	<i>phet</i>	<i>Resistance</i> (<i>a</i>)	<i>Recovery</i> (<i>b</i>)	<i>Resistance:phet</i> (<i>a</i> ₁)	<i>Recovery:phet</i> (<i>b</i> ₁)
beech-fir stand	0.003 (±0.005)	-0.031 (±0.024)	-0.018 (±0.005)	0.004 (±0.002)	0.024(±0.011)	-0.005(±0.004)
beech-oak stand	-0.0001 (±0.003)	0.021 (±0.008)	-0.0001 (±0.005)	-0.0001 (±0.002)	-0.0004(±0.011)	-0.0002(±0.004)

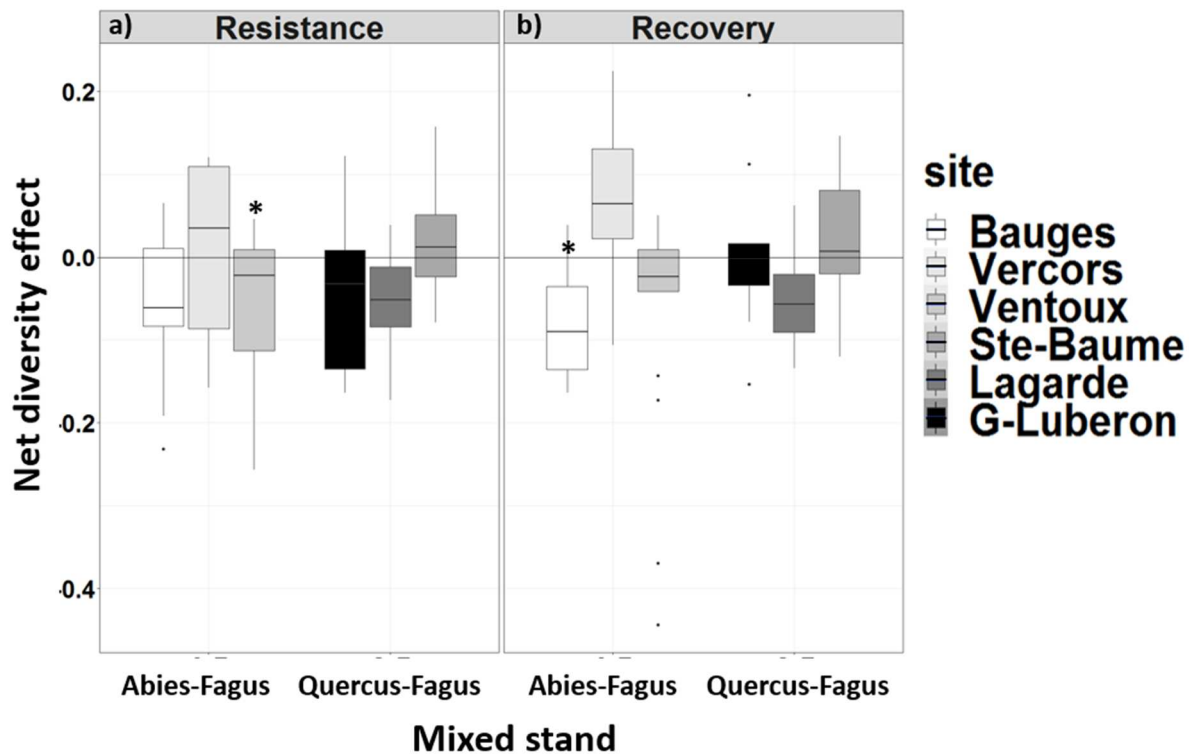
428 *Table 2: Models' parameters estimates tested to explain BAI for every stands (see Appendix*
 429 *D), with the northern (with beech-fir stands, including Bauges, Vercors and Mont Ventoux,*
 430 *quoting here in decreasing latitude order) and southern (with beech-oak stands including*
 431 *Luberon Lagarde, Grand Luberon and Sainte-Baume, quoting here in decreasing latitude*
 432 *order) parts of the gradient taken separately. BA is the stand basal area, and resistance and*
 433 *recovery represent stand responses to extreme drought. Significant p-value at the 0.05 level*
 434 *are represented in bold.*

435 For beech-fir stands, increasing beech proportion induced an increasing stand
 436 resistance (Table 2). Contrariwise, there is no significant effect of beech proportion on mixed
 437 stand recovery. For beech-oak stands, we found that beech proportion did not significantly
 438 affect stand response to drought events.

439 **3.2 Net diversity effect on resistance and recovery**

440 Using the transposition of *NBE* approach to stand resistance during a stressful event
 441 ($R_{t_{div.eff}}$) and stand recovery after a stressful event ($R_{c_{div.eff}}$), we did not find any strong effect
 442 of diversity, either for resistance and recovery (Fig. 3). However, there was a weak negative
 443 $R_{t_{div.eff}}$ for stand in Bauges and Ventoux, only significant for stands in the Ventoux site. Mixed

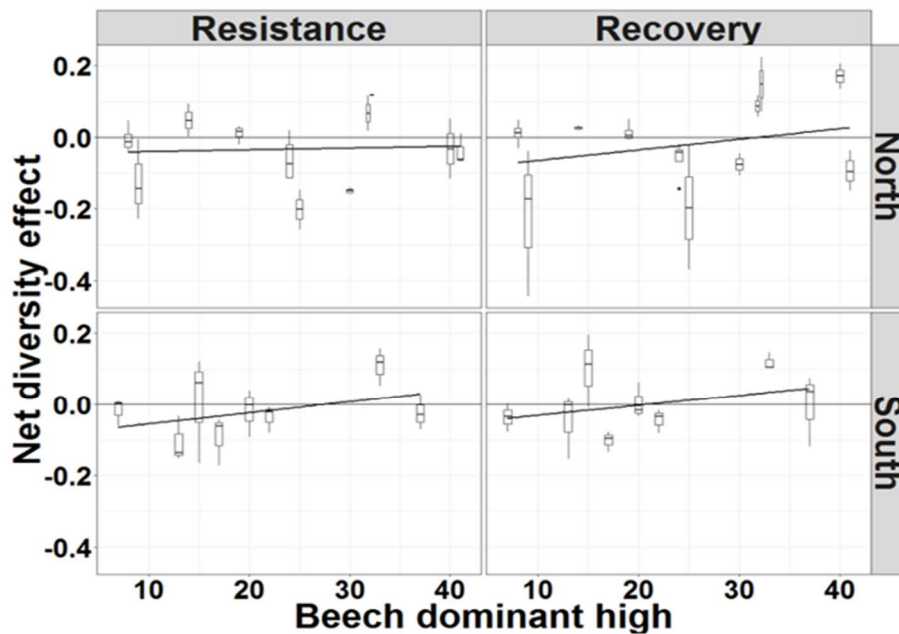
444 stands did not seem to recover faster or slower than monospecific stands, except in the Bauges
 445 site, as $R_{C_{div.eff}}$ was significantly negative. In the Vercors site, $R_{C_{div.eff}}$ seemed to be positive,
 446 but it was not significant. There was no significant $R_{t_{div.eff}}$ and recovery in mixed beech-oak
 447 stands (i.e. Southern part of the gradient).



448
 449 *Figure 3: Boxplot of $R_{t_{div.eff}}$ and $R_{C_{div.eff}}$, i.e. net diversity effect on stand resistance (a) and on*
 450 *stand recovery (b) respectively, for each site. Averages were computed with all observations*
 451 *for each site. Beech-fir stand are in Bauges, Vercors and Ventoux (quoting here in decreasing*
 452 *latitude order) and beech-oak stand are Luberon-Lagarde, Grand Luberon and Ste-Baume*
 453 *(quoting here in decreasing latitude order). For remembering only driest years were*
 454 *considered for $R_{t_{div.eff}}$ and $R_{C_{div.eff}}$ computing, i.e. 2 years by site. Significant differences with*
 455 *0 are indicated with (*).*

456 The proxy quantifying the level of environmental stress for each triplet had no
 457 significant effect on the net biodiversity effect on resistance and recovery (Fig. 4). For mixed

458 beech-oak stands, environmental stress level (assessed as the inverse of maximum beech
 459 height of the triplet) may have a marginally significant negative effect on the net biodiversity
 460 effect on stand recovery.



Model	$Rt_{div.eff} / Rc_{div.eff} \sim$	stress gradient + (maximum beech height)	Site
North	$Rt_{div.eff}$	-0.002 (± 0.002)	Bauges : 0.05 (± 0.11) Vercors: 0.08 (± 0.08) Ventoux: -0.02 (± 0.05)
	$Rc_{div.eff}$	0.002 (± 0.003)	Bauges : -0.18 (± 0.15) Vercors: 0.01 (± 0.1) Ventoux: -0.1 (± 0.06)
South	$Rt_{div.eff}$	0.003 (± 0.004)	Grand Luberon : -0.07(± 0.06) Lagarde: -0.11 (± 0.08) Ste Baume: -0.08 (± 0.13)
	$Rc_{div.eff}$	0.008 (± 0.004)	Grand Luberon : -0.08 (± 0.05) Lagarde: -0.19 (± 0.08) Ste Baume: -0.21 (± 0.12)

461

462 *Figure 4: Linear models tested to explain $Rt_{div.eff}/Rc_{div.eff}$ with a proxy of stress gradient, i.e.*
 463 *maximum beech height, for every stand with the beech-fir stand (North) and beech-oak stand*
 464 *(South) parts of the gradient taken separately. North includes plots in Bauges, Vercors and*
 465 *Mont Ventoux (quoting here in decreasing latitude order) and South includes plots in*

466 *Luberon Lagarde, Grand Luberon and Sainte-Baume (quoting here in decreasing latitude*
467 *order). Student test between mixed and monospecific stand with p-value <0.1 are in bold.*

468 **4 DISCUSSION**

469 **4.1 Resistance and recovery to extreme drought events**

470 We used two complementary approaches in the present study: the *BAI* model allowed
471 quantifying differences between the responses of monospecific and mixed stands, while the
472 $R_{t_{div.eff}}$ and $R_{C_{div.eff}}$ computing dealt with species interactions effect on stand resistance and
473 recovery. The latter approach allowed testing more precisely whether non-additive effects
474 related to species interactions might explain the diversity effect on resistance/recovery, by
475 comparing predicted and observed responses in mixed stands while removing a large part of
476 external variability - such as environmental conditions (climate, soil, topography). The
477 approach relying on the *BAI* model was more focused on the physiological differences
478 between species, by quantifying separately the effect of drought on stand *BAI* during the
479 current year and during the four years following the drought, which contrasts with other
480 studies usually only considering immediate responses (Lloret et al., 2011; Pretzsch et al.,
481 2013).

482 The analysis of stand *BAI* showed contrasted results. Regardless the metrics used, and
483 the type of mixed stands considered, mixed stands showed an intermediate response
484 compared to monospecific stands. The difference may be significant (beech-fir stands) or not
485 (beech-oak stands). We did not find any strong patterns for $R_{t_{div.eff}}$ and $R_{C_{div.eff}}$, regardless the
486 part of gradient considered, which can be explained by the strong dependencies of
487 interspecific interactions to species composition and environmental conditions.

488 Furthermore, we aimed at testing how environmental conditions may affect the mixed
489 stand effect along the latitudinal gradient (Fig. 4). However, we lacked statistical power to

490 test this effect with the modelling approach represented in equation (4), and the results were
491 not significant for $R_{t_{div.eff}}$ and $R_{C_{div.eff}}$.

492 **4.2 How mixed stands can buffer drought impact on stand growth?**

493 According to previous studies, stand resistance and recovery could vary with stand
494 composition (Arthur and Dech, 2016; Pretzsch et al., 2013, as in beech-fir stands in our
495 study), or not (DeClerck et al., 2006, as in beech-oak stands). The discrepancies among
496 studies can be explained by a species-specific effect, related to the various physiological
497 characteristics between species. As explain in introduction, it is possible to rank species along
498 an “isohydric-anisohydric” gradient (Martínez-Vilalta and Garcia-Forner, 2017; Tardieu and
499 Simonneau, 1998). For a same stress intensity, species with more anisohydric hydraulic
500 characters (e.g. oak and beech) should better resist to drought (i.e. stomata remain open longer
501 during drought stress) than species with more isohydric hydraulic characters (e.g. fir) that
502 avoid damage by quickly closing their stomata. Extreme drought events may cause damage on
503 some important organs of trees (roots, leaves or branches) because of cavitation (Delzon and
504 Cochard, 2014; Maherali et al., 2006) for anisohydric species. Previous work focusing on
505 beech, spruce and oak stand resistance (Pretzsch et al., 2013) highlighted the importance of
506 the plurality in hydraulic characters to understand differences in buffering composition effect
507 between mixed stands. Moreover, Cailleret et al. (2017) showed a general difference in
508 drought vulnerability between hardwood and coniferous species (though without considering
509 an “isohydric-anisohydric” gradient).

510 Our results confirmed that mixed stands composed of two species with similar
511 hydraulic features should show more similar responses to an extreme drought event than the
512 monospecific stands of each species, ie. beech-oak mixed stands. Since we aimed at
513 explaining variation in stand resistance through differences in hydraulic characters between

514 species, we further expected that the effect diversity on resistance may vary with species
515 proportion in mixed stands. We found that beech proportion did not significantly affect stand
516 response to drought events in oak-beech stands. This result even suggests that mixing species
517 with similar responses to drought may actually not affect effect of drought on stand growth.

518 Contrariwise, mixed stands composed by two species with contrasted hydraulic
519 features are expected to respond differently, as it was the case for fir-beech mixed stands. In
520 this case, one may expect a strong buffering effect on stand growth. First, we found that
521 monospecific beech stands were more resistant than monospecific fir stands, consistently with
522 literature (Anderegg et al., 2015; Niinemets and Valladares, 2006) and with the differences
523 between the hydraulic characters of these two species. Second, mixed beech-fir stands showed
524 an intermediate value between both monospecific stands, but not significantly different from
525 monospecific fir stands. In fact, fir contributed much more than beech to mixed stands *BAI*
526 (73 ± 0.33 % of *BAI* for fir), which may explain why the buffering effect of the mixture seemed
527 limited in comparison with monospecific fir stands in our results. Moreover, we found that
528 increasing beech proportion induced an increasing stand resistance. In other words, stand
529 resistance decreased with an increasing proportion of fir. Thus, fir appeared to drive the
530 response of mixed stands in this part of the gradient. Regarding recovery, monospecific fir
531 stands recovered faster than monospecific beech stands probably because damage after
532 extreme drought is weaker for isohydric species like fir, for instance if trees develop reverse
533 embolism strategies (Cochard, 2006; Cochard and Delzon, 2013; Taneda and Sperry, 2008),
534 as it can happen in isohydric species. Mixed stands recovery was also intermediate between
535 monospecific beech and fir stands, but the differences were not significant. To sum up, mixed
536 stands appeared to show intermediate responses in terms of resistance and recovery when
537 compared to monospecific stands. The explanations presented above remained, however, to

538 be further confirmed with more ecophysiological-based approaches on our field gradient
539 (Hochberg et al., 2018).

540 **4.3 Possible consequences for forest management in the Alps**

541 Forests currently provides a multitude of ecosystem services - like wood production,
542 protection in mountain areas or biodiversity conservation - all strongly dependent on species
543 composition. Limiting the impacts of extreme events is thus crucial in forest ecosystems to
544 promote adaptation. In mountain forests, the conservation of stand structure (basal area,
545 density, tree dominant height), without discontinuity, seems more important than species
546 composition (Lebourgeois et al., 2014; Trouvé et al., 2017) to limit soil erosion or block fall.
547 However, it is noticeable that the economical value is not equivalent between species, which
548 may temper the advantage of mixing species for some forest managers. Our study showed that
549 mixed beech-fir stands may buffer the effect of extreme drought on stand *BAI*, i.e. showed a
550 stronger resistance, than monospecific fir stands, while recovery was similar between
551 monospecific fir stands and mixed beech-fir stands. Contrariwise, there was no significant
552 buffering effect of mixture on beech-oak stands. Our results yet suggest that mixed stands
553 could be a solution to buffer extreme drought effect in some cases. Therefore, these findings,
554 together with other positive effects of diversity on ecosystem services (Gamfeldt et al., 2013;
555 van der Plas et al., 2018), may argue for the benefits of mixed forest management, instead of
556 monospecific stands. Thus, is especially true for beech-fir stands that can be more resistant to
557 future severe drought events, in comparison with monospecific fir stands, although beech is
558 currently less interesting than fir from an economic point of view. The question is less
559 problematic for the oak-beech mixture, as we found no buffering effect in mixed stands and as
560 these two species share relatively weak economic interest in this region (Southern Alps).

561 Climate change is likely to induce an economic loss for European forests (including
562 mountain forests) (Hanewinkel et al., 2013). To quantify this loss, it may be important to
563 compare the economic gain or loss of species productivity between mixed and monospecific
564 stands on longer time scale and according to various management scenarios. To do so, we
565 think that forest models considering diversity, climate and management may be key tools,
566 such as gap models (Cordonnier et al., 2018). For instance, this would allow testing whether
567 the increase in fir productivity in mixed stands relatively to monospecific ones across the next
568 decades, due to higher resistance, may counterbalance the mean loss in fir productivity due to
569 decreasing fir proportion. Our results suggest that there may be trade-off in the possible
570 management of these mixed stands: increasing beech proportion may lead to a higher stand
571 resistance but also to a loss in fir productivity, while decreasing beech proportion should
572 induce a lower resistance - possibly leading to higher mortality rate at the stand level - but
573 also the maintenance of fir productivity (Appendix Table E). In addition, the other key
574 ecosystem services (protection against erosion or avalanches for example) must also be
575 considered to draw a complete scheme about the interest of mixing for forest management.

576

577 **5 CONCLUSION**

578 According to our results, managing forest mixed stands may increase the resistance
579 and recovery of forests in future climatic conditions although this may be strongly dependent
580 on species characteristics. More works on other types of mixed stands and their response to
581 drought are required to draw a more comprehensive picture and to better assess when mixture
582 management allows to buffer climate change impacts. Meanwhile, testing silvicultural
583 scenarios under climate change with forest gap-models seems to be an interesting and

584 complementary alternative to improve our knowledge and help our decision-making to
585 maintain key ecosystem services provided by forests (Cordonnier et al., 2018).

586

587 **AUTHORS' CONTRIBUTIONS**

588 XM conceived the original question and field setup of this study; MJ and XM
589 designed the research, developed the methodology and collected the data; MJ processed and
590 analyzed the data; MJ, FL and XM led the writing of the manuscript. All authors contributed
591 critically to the draft and gave final approval for publication.

592

593 **DATA ACCESSIBILITY**

594 Data will be deposited in the Dryad Digital Repository

595

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607

608 **REFERENCES**

609 Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw,
610 J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought
611 legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349,
612 528. <https://doi.org/10.1126/science.aab1833>

613 Arthur, C.M., Dech, J.P., 2016. Species composition determines resistance to drought in dry forests of
614 the Great Lakes – St. Lawrence forest region of central Ontario. *J. Veg. Sci.* 27, 914–925.
615 <https://doi.org/10.1111/jvs.12416>

616 Aussenac, R., Bergeron, Y., Ghotsa Mekontchou, C., Gravel, D., Pilch, K., Drobyshev, I., 2017.
617 Intraspecific variability in growth response to environmental fluctuations modulates the
618 stabilizing effect of species diversity on forest growth. *J. Ecol.* 105, 1010–1020.
619 <https://doi.org/10.1111/1365-2745.12728>

620 Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century
621 redistribution in climatic drivers of global tree growth. *Sci. Adv.* 5, eaat4313.
622 <https://doi.org/10.1126/sciadv.aat4313>

623 Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–
624 193.

625 Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C.,
626 Gégout, J.-C., 2011. Changes in plant community composition lag behind climate warming in
627 lowland forests. *Nature* 479, 517–520. <https://doi.org/10.1038/nature10548>

628 Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization: Defining the
629 Biological Trend from Expected Basal Area Increment. *Tree-Ring Res.* 64, 81–96.
630 <https://doi.org/10.3959/2008-6.1>

631 Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for
632 time in predicting climate-change effects on biodiversity. *Proc. Natl. Acad. Sci.* 110, 9374–
633 9379.

634 Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe
635 drought: a review of ecophysiological responses, adaptation processes and long-term
636 consequences. *Ann. For. Sci.* 63, 625–644. <https://doi.org/10.1051/forest:2006042>

637 Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt,
638 P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S.,
639 Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K.,
640 Seifan, M., Touzard, B., Michalet, R., 2007. Facilitation in plant communities: the past, the
641 present, and the future. *J. Ecol.* 0, 070908024102002–??? [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2745.2007.01295.x)
642 [2745.2007.01295.x](https://doi.org/10.1111/j.1365-2745.2007.01295.x)

643 Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler,
644 C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H.,
645 Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G.,
646 Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.-M., Hultine, K.R., Janda, P., Kane, J.M.,
647 Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon,
648 J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S.,
649 Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi,
650 M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B.,
651 Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M.,
652 Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-
653 Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. *Glob. Change*
654 *Biol.* 23, 1675–1690. <https://doi.org/10.1111/gcb.13535>

655 Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L.,
656 Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002.
657 Positive interactions among alpine plants increase with stress. *Nature* 417, 844.

658 Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006.
659 Neighborhood analyses of canopy tree competition along environmental gradients in New
660 England forests. *Ecol. Appl.* 16, 540–554.

661 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace,
662 G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B.,
663 Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on
664 humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11148>

665 Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M.,
666 Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time
667 because of species complementarity. *Proc. Natl. Acad. Sci.* 104, 18123–18128.

668 Choat, B., Brodersen, C.R., McElrone, A.J., 2015. Synchrotron X-ray microtomography of xylem
669 embolism in *Sequoia sempervirens* saplings during cycles of drought and recovery. *New*
670 *Phytol.* 205, 1095–1105. <https://doi.org/10.1111/nph.13110>

671 Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S.,
672 Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J.,
673 Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S.,
674 Westoby, M., Wright, I.J., Zanne, A.E., 2012a. Global convergence in the vulnerability of
675 forests to drought. *Nature* 491, 752–755. <https://doi.org/10.1038/nature11688>

676 Choler, P., Michalet, R., Callaway, R.M., 2001. Facilitation and competition on gradients in alpine
677 plant communities. *Ecology* 82, 3295–3308.

678 Cochard, H., 2006. Cavitation in trees. *Comptes Rendus Phys.* 7, 1018–1026.
679 <https://doi.org/10.1016/j.crhy.2006.10.012>

680 Cochard, H., Delzon, S., 2013. Hydraulic failure and repair are not routine in trees. *Ann. For. Sci.* 70,
681 659–661. <https://doi.org/10.1007/s13595-013-0317-5>

682 Collatz, G.J., Ball, J.T., Grivet, C., Berry, J.A., 1991. Physiological and environmental regulation of
683 stomatal conductance, photosynthesis and transpiration: a model that includes a laminar
684 boundary layer. *Agric. For. Meteorol.* 54, 107–136.

685 Cordonnier, T., Kunstler, G., Courbaud, B., Morin, X., 2018. Managing tree species diversity and
686 ecosystem functions through coexistence mechanisms. *Ann. For. Sci.* 75.
687 <https://doi.org/10.1007/s13595-018-0750-6>

688 Courbaud, B., Kunstler, G., Morin, X., Cordonnier, T., 2011. What is the future of the ecosystem
689 services of the Alpine forest against a backdrop of climate change? *Rev. Géographie Alp.*
690 <https://doi.org/10.4000/rga.1317>

691 Cruiziat, P., Cochard, H., Améglio, T., 2002. Hydraulic architecture of trees: main concepts and
692 results. *Ann. For. Sci.* 59, 723–752.

693 Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J.,
694 Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Michael
695 Wotton, B., 2001. Climate Change and Forest Disturbances. *BioScience* 51, 723.
696 [https://doi.org/10.1641/0006-3568\(2001\)051\[0723:CCAFD\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2)

697 DeClerck, F.A., Barbour, M.G., Sawyer, J.O., 2006. Species richness and stand stability in conifer
698 forests of the Sierra Nevada. *Ecology* 87, 2787–2799.

699 del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K.,
700 Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D. I., Heym, M., Hurt, V.,
701 Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matovic, B., Mohren, F., Motta, R.,
702 den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Skrzyszewski, J., Sramek, V., Sterba, H.,
703 Stojanovic, D., Svoboda, M., Zlatanov, T. M. and Bravo-Oviedo A., 2017. Species
704 interactions increase the temporal stability of community productivity in *Pinus sylvestris*-
705 *Fagus sylvatica* mixtures across Europe. *J Ecol* 105:1032–1043. doi: 10.1111/1365-
706 2745.12727

707 Delzon, S., 2015. New insight into leaf drought tolerance. *Funct. Ecol.* 29, 1247–1249.
708 <https://doi.org/10.1111/1365-2435.12500>

709 Delzon, S., Cochard, H., 2014. Recent advances in tree hydraulics highlight the ecological significance
710 of the hydraulic safety margin. *New Phytol.* 203, 355–358.

711 Desplanque, C., Rolland, C., Michalet, R., 1998. Dendroécologie comparée du sapin blanc (*Abies*
712 *alba*) et de l'épicéa commun (*Picea abies*) dans une vallée alpine de France. *Can. J. For. Res.*
713 28, 737–748.

714 Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K.,
715 Jackson, A.L., Lurgi, M., McClean, D., O'Connor, N.E., O'Gorman, E.J., Yang, Q., 2016.
716 Navigating the complexity of ecological stability. *Ecol. Lett.* 19, 1172–1185.
717 <https://doi.org/10.1111/ele.12648>

718 Dunne, J.A., Saleska, S.R., Fischer, M.L., Harte, J., 2004. Integrating experimental and gradient
719 methods in ecological climate change research. *Ecology* 85, 904–916.

720 Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity
721 Relationships in Forests. *Curr. For. Rep.* 2, 45–61. <https://doi.org/10.1007/s40725-016-0031-2>

722 Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C.,
723 Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B.,
724 Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem
725 services are found in forests with more tree species. *Nat. Commun.* 4, 1340.
726 <https://doi.org/10.1038/ncomms2328>

727 Gasparrini, A., 2011. Distributed lag linear and non-linear models in R: the package *dlm*. *J. Stat.*
728 *Softw.* 43, 1.

729 Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruehlheide, H., Checko, E., Forrester, D.I.,
730 Dawud, S.M., Finer, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D.,
731 Gessler, A., 2014. Tree diversity does not always improve resistance of forest ecosystems to
732 drought. *Proc. Natl. Acad. Sci.* 111, 14812–14815. <https://doi.org/10.1073/pnas.1411970111>

733 Guttman, N.B., 1999. Accepting the standardized precipitation index: A calculation algorithm1.
734 *JAWRA J. Am. Water Resour. Assoc.* 35, 311–322.

735 Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., Zimmermann, N.E., 2013.
736 Climate change may cause severe loss in the economic value of European forest land. *Nat.*
737 *Clim. Change* 3, 203–207. <https://doi.org/10.1038/nclimate1687>

738 Hochberg, U., Rockwell, F.E., Holbrook, N.M., Cochard, H., 2018. Iso/Anisohydry: A Plant–
739 Environment Interaction Rather Than a Simple Hydraulic Trait. *Trends Plant Sci.* 23, 112–
740 120. <https://doi.org/10.1016/j.tplants.2017.11.002>

741 Holmgren, M., Scheffer, M., 2010. Strong facilitation in mild environments: the stress gradient
742 hypothesis revisited. *J. Ecol.* 98, 1269–1275. [https://doi.org/10.1111/j.1365-
743 2745.2010.01709.x](https://doi.org/10.1111/j.1365-2745.2010.01709.x)

744 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge,
745 D.M., Loreau, M., Naeem, S., others, 2005. Effects of biodiversity on ecosystem functioning:
746 a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.

747 Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., Bonin,
748 C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A.,
749 Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus,
750 P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P.,
751 Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W.,
752 Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem
753 productivity to climate extremes. *Nature* 526, 574–577. <https://doi.org/10.1038/nature15374>

754 Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. *science* 317, 58–62.

755 Jones, H.E., McNamara, N., Mason, W.L., 2005. Functioning of mixed-species stands: evidence from
756 a long-term forest experiment. *For. Divers. Funct.* 111–130.

757 Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on
758 aboveground wood production in forest ecosystems: linking patterns and processes. *Ecol. Lett.*
759 17, 1560–1569. <https://doi.org/10.1111/ele.12382>

760 Kellomaki, S., Peltola, H., Nuutinen, T., Korhonen, K.T., Strandman, H., 2008. Sensitivity of managed
761 boreal forests in Finland to climate change, with implications for adaptive management.
762 *Philos. Trans. R. Soc. B Biol. Sci.* 363, 2339–2349. <https://doi.org/10.1098/rstb.2007.2204>

763 Kirkman, L.K., Mitchell, R.J., Helton, R.C., Drew, M.B., 2001. Productivity and species richness
764 across an environmental gradient in a fire-dependent ecosystem. *Am. J. Bot.* 88, 2119–2128.

765 Klein, T., Yakir, D., Buchmann, N., Grünzweig, J.M., 2014. Towards an advanced assessment of the
766 hydrological vulnerability of forests to climate change-induced drought. *New Phytol.* 201,
767 712–716.

768 Lebourgeois, F., Bréda, N., Ulrich, E., Granier, A., 2005. Climate-tree-growth relationships of
769 European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR).
770 *Trees* 19, 385–401. <https://doi.org/10.1007/s00468-004-0397-9>

771 Lebourgeois, F., Eberlé, P., Mérian, P., Seynave, I., 2014. Social status-mediated tree-ring responses
772 to climate of *Abies alba* and *Fagus sylvatica* shift in importance with increasing stand basal
773 area. *For. Ecol. Manag.* 328, 209–218. <https://doi.org/10.1016/j.foreco.2014.05.038>

774 Lebourgeois, F., Merian, P., 2012. Principes et méthodes de la dendrochronologie. LERFOB
775 AgroPariTech Cent. Nancy 85p.

776 Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate coniferous
777 forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus*
778 *sylvestris*). *J. Veg. Sci.* 21, 364–376. <https://doi.org/10.1111/j.1654-1103.2009.01148.x>

779 Lenoir, J., Gégout, J. c., Marquet, P.A., de Ruffray, P., Brisse, E.L., 2008. A Significant Upward Shift
780 in Plant Species Optimum Elevation During the 20th Century. *Science* 320, 1763–1768.
781 <https://doi.org/10.1126/science.1157704>

782 Lester, R.E., Close, P.G., Barton, J.L., Pope, A.J., Brown, S.C., 2014. Predicting the likely response of
783 data-poor ecosystems to climate change using space-for-time substitution across domains.
784 *Glob. Change Biol.* 20, 3471–3481. <https://doi.org/10.1111/gcb.12634>

785 Lin, Y.-S., Medlyn, B.E., Duursma, R.A., Prentice, I.C., Wang, H., Baig, S., Eamus, D., de Dios, V.R.,
786 Mitchell, P., Ellsworth, D.S., de Beeck, M.O., Wallin, G., Uddling, J., Tarvainen, L.,
787 Linderson, M.-L., Cernusak, L.A., Nippert, J.B., Ocheltree, T.W., Tissue, D.T., Martin-StPaul,
788 N.K., Rogers, A., Warren, J.M., De Angelis, P., Hikosaka, K., Han, Q., Onoda, Y., Gimeno,
789 T.E., Barton, C.V.M., Bennie, J., Bonal, D., Bosc, A., Löw, M., Macinins-Ng, C., Rey, A.,
790 Rowland, L., Setterfield, S.A., Tausz-Posch, S., Zaragoza-Castells, J., Broadmeadow, M.S.J.,
791 Drake, J.E., Freeman, M., Ghannoum, O., Hutley, L.B., Kelly, J.W., Kikuzawa, K., Kolari, P.,
792 Koyama, K., Limousin, J.-M., Meir, P., Lola da Costa, A.C., Mikkelsen, T.N., Salinas, N.,

793 Sun, W., Wingate, L., 2015. Optimal stomatal behaviour around the world. *Nat. Clim. Change*
794 5, 459.

795 Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-
796 growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920.
797 <https://doi.org/10.1111/j.1600-0706.2011.19372.x>

798 Loreau, M., 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future
799 Challenges. *Science* 294, 804–808. <https://doi.org/10.1126/science.1064088>

800 Loreau, M., 1998. Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl. Acad.*
801 *Sci.* 95, 5632–5636.

802 Loreau, M., Behera, N., 1999. Phenotypic diversity and stability of ecosystem processes. *Theor.*
803 *Popul. Biol.* 56, 29–47.

804 Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient
805 hypothesis for competition and facilitation in plant communities. *J. Ecol.* 97, 199–205.
806 <https://doi.org/10.1111/j.1365-2745.2008.01476.x>

807 Maherali, H., Moura, C.F., Caldeira, M.C., Willson, C.J., Jackson, R.B., 2006. Functional coordination
808 between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees.
809 *Plant Cell Environ.* 29, 571–583. <https://doi.org/10.1111/j.1365-3040.2005.01433.x>

810 Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., Nobre, C.A., 2008. Climate Change,
811 Deforestation, and the Fate of the Amazon. *Science* 319, 169–172.
812 <https://doi.org/10.1126/science.1146961>

813 Maracchi, G., Sirotenko, O., Bindi, M., 2005. Impacts of present and future climate variability on
814 agriculture and forestry in the temperate regions: Europe. *Clim. Change* 70, 117–135.

815 Martínez-Vilalta, J., Garcia-Forner, N., 2017. Water potential regulation, stomatal behaviour and
816 hydraulic transport under drought: deconstructing the iso/anisohydric concept. *Plant Cell*
817 *Environ.* 40, 962–976. <https://doi.org/10.1111/pce.12846>

818 Mauri, A., De Rigo, D., Caudullo, G., 2016. *Abies alba* in Europe: distribution, habitat, usage and
819 threats. *Eur. Atlas For. Tree Species Publ EU Luxemb.* Pp E01493b <https://doi.org/10.1111/pce.12846>

820 <https://doi.org/10.1111/pce.12846> Cited Pages 7 9.

821 Maxime, C., Hendrik, D., 2010. Effects of climate on diameter growth of co-occurring *Fagus sylvatica*
822 and *Abies alba* along an altitudinal gradient. *Trees* 25, 265–276.
823 <https://doi.org/10.1007/s00468-010-0503-0>

824 Mayr, S., Schmid, P., Laur, J., Rosner, S., Charra-Vaskou, K., Dämon, B., Hacke, U.G., 2014. Uptake
825 of Water via Branches Helps Timberline Conifers Refill Embolized Xylem in Late Winter.
826 *Plant Physiol.* 164, 1731–1740. <https://doi.org/10.1104/pp.114.236646>

827 McCann, K.S., 2000. The diversity–stability debate. *Nature* 405, 228.

828 Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009. Xylem
829 hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension
830 with hydraulic capacitance. *Funct. Ecol.* 23, 922–930. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2435.2009.01577.x)
831 [2435.2009.01577.x](https://doi.org/10.1111/j.1365-2435.2009.01577.x)

832 Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and
833 tree size on resistance and resilience to drought in sessile oak and Scots pine. *For. Ecol.*
834 *Manag.* 339, 22–33. <https://doi.org/10.1016/j.foreco.2014.11.032>

835 Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future:
836 managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.

837 Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., Bugmann, H., 2018. Long-
838 term response of forest productivity to climate change is mostly driven by change in tree
839 species composition. *Sci. Rep.* 8. <https://doi.org/10.1038/s41598-018-23763-y>

840 Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes
841 productivity in temperate forests through strong complementarity between species: Species
842 richness promotes forest productivity. *Ecol. Lett.* 14, 1211–1219.
843 <https://doi.org/10.1111/j.1461-0248.2011.01691.x>

844 Morris, H., Plavcová, L., Cvecko, P., Fichtler, E., Gillingham, M.A.F., Martínez-Cabrera, H.I.,
845 McGlenn, D.J., Wheeler, E., Zheng, J., Ziemińska, K., Jansen, S., 2016. A global analysis of
846 parenchyma tissue fractions in secondary xylem of seed plants. *New Phytol.* 209, 1553–1565.
847 <https://doi.org/10.1111/nph.13737>

848 Newton, A.C., Cantarello, E., 2015. Restoration of forest resilience: An achievable goal? *New For.* 46,
849 645–668. <https://doi.org/10.1007/s11056-015-9489-1>

850 Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate
851 Northern Hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.

852 Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., ... Tissue,
853 D. T. (2015). Quantifying ecological memory in plant and ecosystem processes. *Ecology*
854 *Letters*, 18(3), 221–235. doi: 10.1111/ele.12399

855 Olesen, J.E., Carter, T.R., Díaz-Ambrona, C.H., Fronzek, S., Heidmann, T., Hickler, T., Holt, T.,
856 Mínguez, M.I., Morales, P., Palutikof, J.P., Quemada, M., Ruiz-Ramos, M., Rubæk, G.H.,
857 Sau, F., Smith, B., Sykes, M.T., 2007. Uncertainties in projected impacts of climate change on
858 European agriculture and terrestrial ecosystems based on scenarios from regional climate
859 models. *Clim. Change* 81, 123–143. <https://doi.org/10.1007/s10584-006-9216-1>

860 Pachauri, R.K., Mayer, L., Intergovernmental Panel on Climate Change (Eds.), 2015. *Climate change*
861 *2014: synthesis report*. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

862 Pasta, S., de Rigo, D., Caudullo, G., n.d. *Quercus pubescens* in Europe: distribution, habitat, usage and
863 threats. *Eur. Atlas For. Tree Species San-Miguel-Ayaz J Rigo Caudullo G Houst. Durrant T*
864 *Mauri Eds* 156–157.

865 Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of
866 ecosystem functioning. *Nature* 416, 84.

867 Piedallu, C., Gégout, J.-C., Lebourgeois, F., Seynave, I., 2016. Soil aeration, water deficit, nitrogen
868 availability, acidity and temperature all contribute to shaping tree species distribution in
869 temperate forests. *J. Veg. Sci.* 27, 387–399. <https://doi.org/10.1111/jvs.12370>

870 Plavcová, L., Hoch, G., Morris, H., Ghiasi, S., Jansen, S., 2016. The amount of parenchyma and living
871 fibers affects storage of nonstructural carbohydrates in young stems and roots of temperate
872 trees. *Am. J. Bot.* 103, 603–612. <https://doi.org/10.3732/ajb.1500489>

873 Potop, V., Boroneanț, C., Možný, M., Štěpánek, P., Skalák, P., 2014. Observed spatiotemporal
874 characteristics of drought on various time scales over the Czech Republic. *Theor. Appl.*
875 *Climatol.* 115, 563–581. <https://doi.org/10.1007/s00704-013-0908-y>

876 Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots.
877 Ecol. Stud. 176, 41–64.

878 Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., Kohnle, U., Nagel, J.,
879 Spellmann, H., Zasada, M., Zingg, A., 2013a. Productivity of mixed versus pure stands of oak
880 (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica*
881 L.) along an ecological gradient. Eur. J. For. Res. 132, 263–280.
882 <https://doi.org/10.1007/s10342-012-0673-y>

883 Pretzsch, H., Del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I., Bielak,
884 K., Brazaitis, G., Coll, L., 2016. Mixing of Scots pine (*Pinus sylvestris* L.) and European
885 beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with
886 water availability. For. Ecol. Manag. 373, 149–166.

887 Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in
888 mixed *versus* pure forests: evidence of stress release by inter-specific facilitation: Drought
889 stress release by inter-specific facilitation. Plant Biol. 15, 483–495.
890 <https://doi.org/10.1111/j.1438-8677.2012.00670.x>

891 Pugnaire, F.I., Luque, M.T., 2001. Changes in plant interactions along a gradient of environmental
892 stress. Oikos 93, 42–49.

893 Schwalm, C.R., Anderegg, W.R.L., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G., Litvak, M.,
894 Ogle, K., Shaw, J.D., Wolf, A., Huntzinger, D.N., Schaefer, K., Cook, R., Wei, Y., Fang, Y.,
895 Hayes, D., Huang, M., Jain, A., Tian, H., 2017. Global patterns of drought recovery. Nature
896 548, 202–205. <https://doi.org/10.1038/nature23021>

897 Seynave, I., Bailly, A., Balandier, P., Bontemps, J.-D., Cailly, P., Cordonnier, T., Deleuze, C., Dhôte,
898 J.-F., Ginisty, C., Lebourgeois, F., Merzeau, D., Paillassa, E., Perret, S., Richter, C., Meredieu,
899 C., 2018. GIS Coop: networks of silvicultural trials for supporting forest management under
900 changing environment. Ann. For. Sci. 75. <https://doi.org/10.1007/s13595-018-0692-z>

901 Seynave, I., Gégout, J.-C., Hervé, J.-C., Dhôte, J.-F., 2008. Is the spatial distribution of European
902 beech (*Fagus sylvatica* L.) limited by its potential height growth? J. Biogeogr. 35, 1851–1862.
903 <https://doi.org/10.1111/j.1365-2699.2008.01930.x>

904 Taneda, H., Sperry, J.S., 2008. A case-study of water transport in co-occurring ring-versus diffuse-
905 porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling.
906 *Tree Physiol.* 28, 1641–1651.

907 Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil
908 water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp.*
909 *Bot.* 419–432.

910 Thompson, I., Mackey, B., McNulty, S., Mosseler, A., Secretariat of the convention on the biological
911 diversity, 2014. Forest resilience, biodiversity, and climate change: a synthesis of the
912 biodiversity, resilience, stability relationship in forest ecosystems.

913 Thornthwaite, C.W., 1948. An Approach toward a Rational Classification of Climate. *Geogr. Rev.* 38,
914 55. <https://doi.org/10.2307/210739>

915 Tilman, D., 1999. The Ecological Consequences of Changes in Biodiversity: A Search for General
916 Principles. *Ecology* 80, 1455–1474. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2)
917 [9658\(1999\)080\[1455:TECOCI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2)

918 Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. *Nature* 367, 363.

919 Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E.,
920 Allen, J.R., Carraro, G., Conedera, M., others, 2013. The past ecology of *Abies alba* provides
921 new perspectives on future responses of silver fir forests to global warming. *Ecol. Monogr.* 83,
922 419–439.

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

926 Trouvé, R., Bontemps, J.-D., Collet, C., Seynave, I., Lebourgeois, F., 2017. Radial growth resilience
927 of sessile oak after drought is affected by site water status, stand density, and social status.
928 *Trees* 31, 517–529. <https://doi.org/10.1007/s00468-016-1479-1>

929 UNEP (Ed.), 2010. Mainstreaming the economics of nature: a synthesis of the approach, conclusions
930 and recommendations of teeb, The economics of ecosystems & biodiversity. UNEP, Geneva.

931 Urli, M., Porte, A.J., Cochard, H., Guengant, Y., Burlett, R., Delzon, S., 2013. Xylem embolism
932 threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiol.* 33, 672–683.
933 <https://doi.org/10.1093/treephys/tpt030>

934 van der Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala,
935 M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R.,
936 Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol,
937 B., Charbonnier, Y., Cornelissen, J.H.C., Dahlgren, J., Checko, E., Coppi, A., Dawud, S.M.,
938 Deconchat, M., De Smedt, P., De Wandeler, H., Domisch, T., Finér, L., Fotelli, M., Gessler,
939 A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H.,
940 Jaroszewicz, B., Joly, F.-X., Jucker, T., Kambach, S., Kaendler, G., Kattge, J., Koricheva, J.,
941 Kunstler, G., Lehtonen, A., Liebergesell, M., Manning, P., Milligan, H., Müller, S., Muys, B.,
942 Nguyen, D., Nock, C., Ohse, B., Paquette, A., Peñuelas, J., Pollastrini, M., Radoglou, K.,
943 Raulund-Rasmussen, K., Roger, F., Seidl, R., Selvi, F., Stenlid, J., Valladares, F., van Keer, J.,
944 Vesterdal, L., Fischer, M., Gamfeldt, L., Allan, E., 2018. Continental mapping of forest
945 ecosystem functions reveals a high but unrealised potential for forest multifunctionality. *Ecol.*
946 *Lett.* 21, 31–42. <https://doi.org/10.1111/ele.12868>

947 Vanoni, M., Bugmann, H., Nötzli, M., Bigler, C., 2016. Drought and frost contribute to abrupt growth
948 decreases before tree mortality in nine temperate tree species. *For. Ecol. Manag.* 382, 51–63.
949 <https://doi.org/10.1016/j.foreco.2016.10.001>

950 Van Ruijven, J., Berendse, F., 2010. Diversity enhances community recovery, but not resistance, after
951 drought. *J. Ecol.* 98, 81–86. <https://doi.org/10.1111/j.1365-2745.2009.01603.x>

952 Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive
953 to Global Warming: The Standardized Precipitation Evapotranspiration Index. *J. Clim.* 23,
954 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>

955 Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Begueria, S., Trigo, R., Lopez-Moreno, J.I.,
956 Azorin-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Moran-Tejeda, E., Sanchez-
957 Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes.
958 *Proc. Natl. Acad. Sci.* 110, 52–57. <https://doi.org/10.1073/pnas.1207068110>

- 959 Vogel, A., Scherer-Lorenzen, M., Weigelt, A., 2012. Grassland Resistance and Resilience after
960 Drought Depends on Management Intensity and Species Richness. PLoS ONE 7, e36992.
961 <https://doi.org/10.1371/journal.pone.0036992>
- 962 Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., Menzel, A., 2014. Patterns of drought tolerance in
963 major European temperate forest trees: climatic drivers and levels of variability. Glob. Change
964 Biol. 20, 3767–3779. <https://doi.org/10.1111/gcb.12637>