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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.

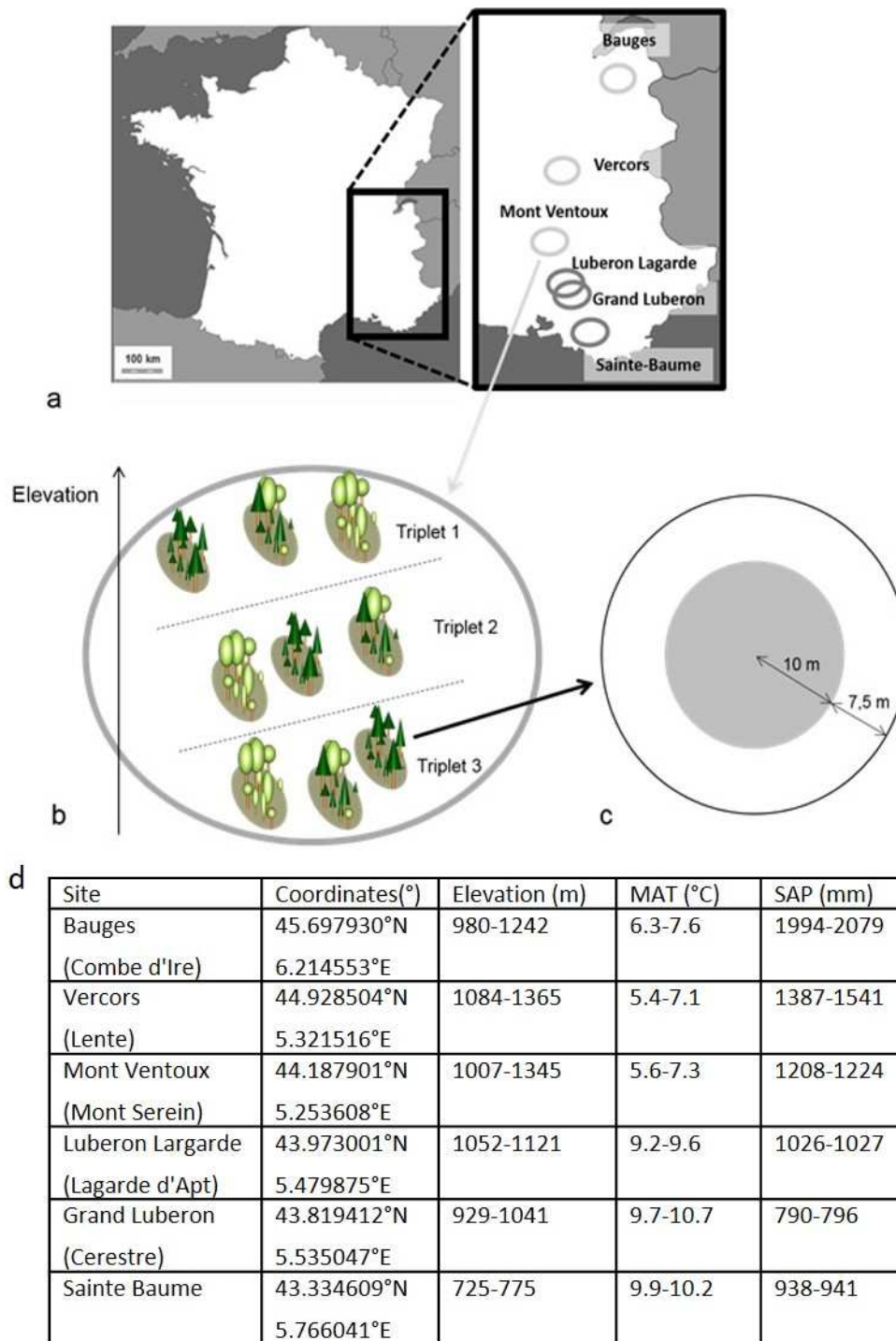
### 179 **2.2 Species**

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 Largarde,*  
 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.

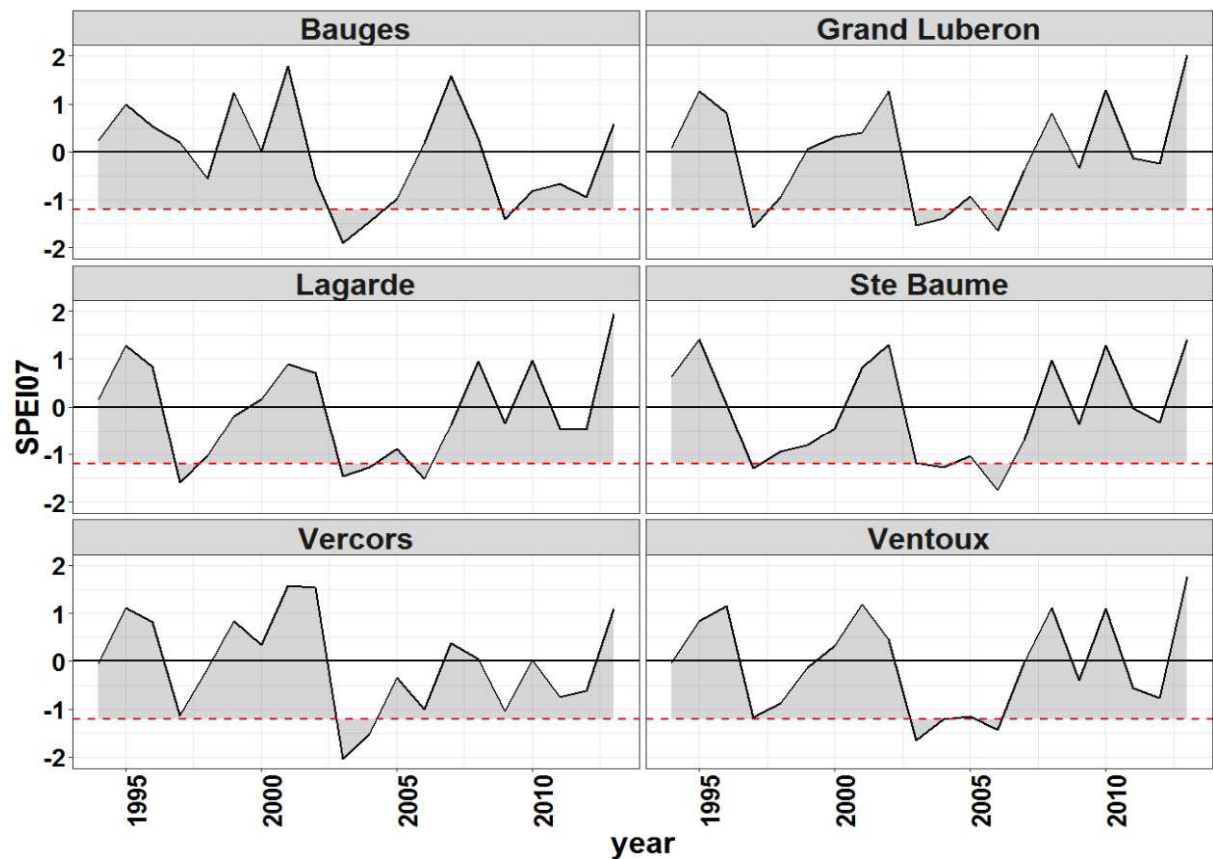
219 A plot was constituted of a 17.5 m-radius circle, including a central zone of a 10 m-  
220 radius circle (Fig. 1). For each plot, slope, elevation and aspect were measured. In the central  
221 zone, tree characteristics were measured (species identity, location, height, crown depth,  
222 diameter 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*<sub>07</sub>, 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  $106\pm 45$  years old), 387 firs (mean age:  $75\pm 38$  years old) and 240 oaks (mean age:  $87\pm 40$   
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  $\beta$  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>
<b><i>Beech-Fir</i></b>	<i>BA</i>	0.003 (±0.002)	0.003 (±0.006)	0.006 (±0.005)
	<i>Resistance (a)</i>	<b>-0.003</b> (±0.0008)	<b>-0.009</b> (±0.001)	<b>-0.007</b> (±0.001)
	<i>Recovery (b)</i>	<b>0.001</b> (±0.0003)	<b>0.003</b> (±0.0006)	<b>0.002</b> (±0.0004)
<b><i>Beech-Oak</i></b>	<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> <sub>1</sub> )	<i>Recovery:phet</i> ( <i>b</i> <sub>1</sub> )
beech-fir stand	0.003 (±0.005)	-0.031 (±0.024)	<b>-0.018</b> (±0.005)	<b>0.004</b> (±0.002)	<b>0.024(±0.011)</b>	-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)

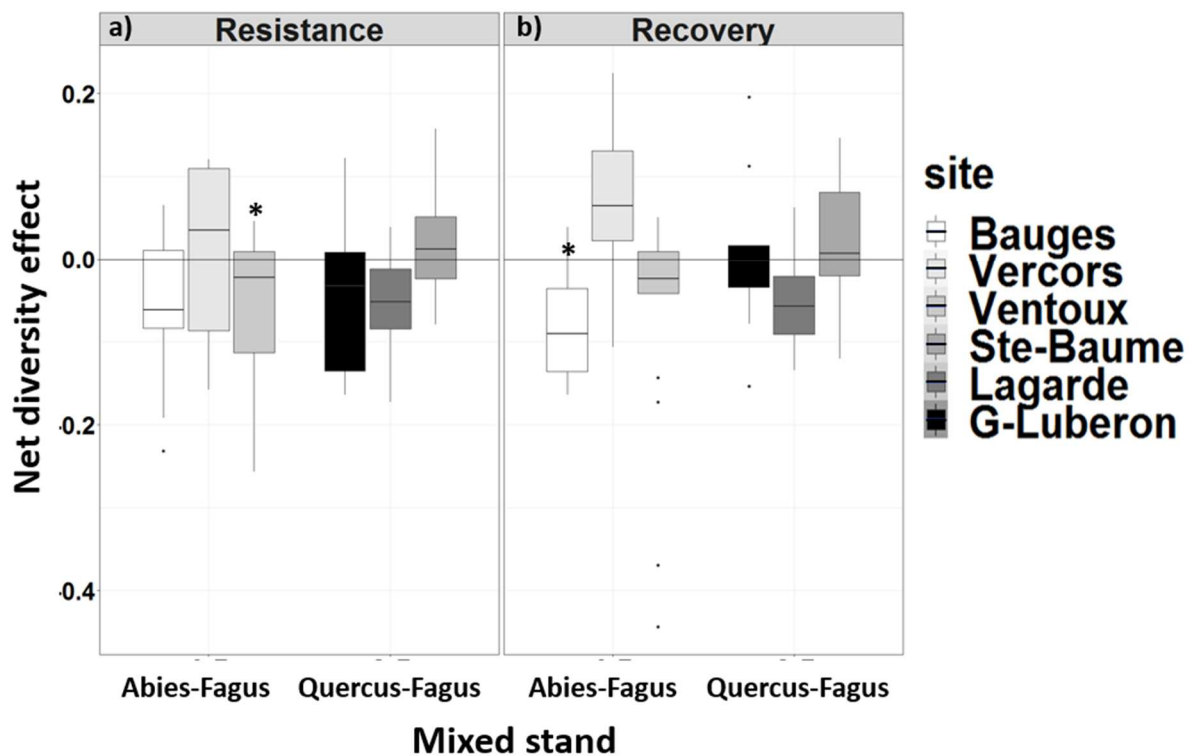
428 *Table 2: Models' parameters estimates tested to explain BAI for every stands (see Appendix*  
 429 *D), with the northern (with beech-fir stands, including Bauges, Vercors and Mont Ventoux,*  
 430 *quoting here in decreasing latitude order) and southern (with beech-oak stands including*  
 431 *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

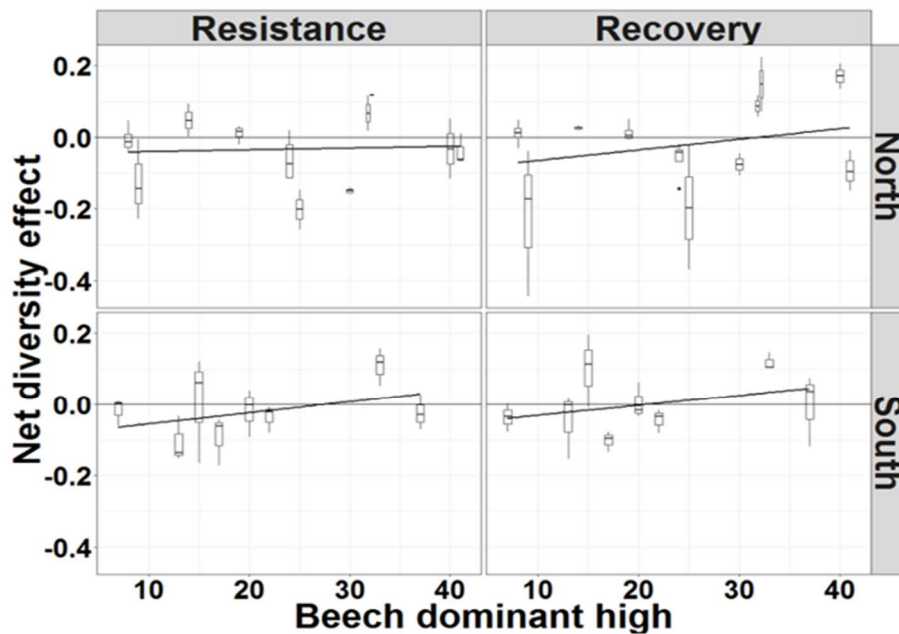
444 stands did not seem to recover faster or slower than monospecific stands, except in the Bauges  
 445 site, as  $R_{C_{div.eff}}$  was significantly negative. In the Vercors site,  $R_{C_{div.eff}}$  seemed to be positive,  
 446 but it was not significant. There was no significant  $R_{t_{div.eff}}$  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 ( $\pm 0.002$ )	Bauges : 0.05 ( $\pm 0.11$ ) Vercors: 0.08 ( $\pm 0.08$ ) Ventoux: -0.02 ( $\pm 0.05$ )
	$Rc_{div.eff}$	0.002 ( $\pm 0.003$ )	Bauges : -0.18 ( $\pm 0.15$ ) Vercors: 0.01 ( $\pm 0.1$ ) Ventoux: -0.1 ( $\pm 0.06$ )
South	$Rt_{div.eff}$	0.003 ( $\pm 0.004$ )	Grand Luberon : -0.07( $\pm 0.06$ ) Lagarde: -0.11 ( $\pm 0.08$ ) Ste Baume: -0.08 ( $\pm 0.13$ )
	$Rc_{div.eff}$	<b>0.008 (<math>\pm 0.004</math>)</b>	Grand Luberon : -0.08 ( $\pm 0.05$ ) Lagarde: <b>-0.19 (<math>\pm 0.08</math>)</b> Ste Baume: <b>-0.21 (<math>\pm 0.12</math>)</b>

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 ( $73 \pm 0.33$  % 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

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