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1 MIXTURE EFFECT ON RADIAL STEM AND SHOOT GROWTH 2 DIFFERS AND VARIES WITH TEMPERATURE

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8 ABSTRACT

9 The effect of species diversity on forest productivity and its temporal stability is known to be species-
10 , climate- and site- dependent and is mostly apprehended through stem diameter. Therefore, it
11 remains largely unknown whether the mixture effect on the growth of tree crowns is similar to its
12 effect on the growth of tree diameter. However, it is commonly accepted that changes in crown
13 architecture are an important component of tree response to tree species diversity. Moreover, the
14 mixture effect on species is often asymmetric, i.e. the effect of a species A on a species B is not equal
15 to the effect of species B on A. It then appears that considering the effects of both species mixture
16 and climate on shoot growth could contrast the results coming mainly from stem growth.

17 We studied the effects of tree species mixture and temperature on the annual growth of shoots and
18 basal area of stems in *Fagus sylvatica-Quercus pubescens* and *Fagus sylvatica-Abies alba* stands along
19 a Mediterranean-Alpine gradient, for four years in five sites. The sample design was organized in 10
20 triplets: four triplets of mono- and bi-specific plots of *Quercus pubescens* and *Fagus sylvatica* and six
21 triplets of mono- and bi-specific plots of *Abies alba* and *Fagus sylvatica* along an altitudinal gradient
22 ranging from 725m to 1431m.

23 We found that the mixture effect on annual shoot volume increment (SVI) and on basal area
24 increment (BAI) was asymmetrical in seven out of 10 cases and not significant in the three remaining

25 cases. Mixture effect on SVI ranked from -56% to 157% and on BAI it ranked from -40% to 252%.
26 Eventually we found that mixture effect was dependent on the type of limiting factor for growth,
27 with at the driest sites a predominance of competition effects and at the coldest site a positive
28 mixture effect on the two species studied.

29 Branch growth appears as a variable that can be at least as informative as radial growth regarding
30 the tree response to species interactions. This implies that considering only stem diameter in the
31 diversity-productivity relationship can lead to biased conclusions on the global mixture effect on tree
32 growth, which calls for a comprehensive approach of the tree response to tree species diversity. Our
33 results are discussed in the light of the species stress tolerances and strategies to cope with
34 competition.

35 KEYWORDS

36 Diversity, productivity, temperature, temperate forest, stress gradient, species interactions

37 1.INTRODUCTION

38 1.1 DIVERSITY-PRODUCTIVITY RELATIONSHIPS IN FORESTS

39 Forest productivity is a key component of ecosystem functioning. Accumulated empirical evidence
40 showed that tree species diversity may increase forest productivity, forest stability and dampen the
41 effects of climate and of insect attack (Jactel and Brockerhoff, 2007; Jucker et al., 2014b; Liang et al.,
42 2016). The positive effects of species diversity on forest productivity are explained through niche
43 partitioning effects and facilitative effects (improvement of harsh abiotic conditions, improvement of
44 resource acquisition, protection against herbivores, (Caspersen et al., 2018; Kunz and Fichtner,
45 2019)). If niche partitioning occurs, then a higher number of species in the community can improve
46 resource uptake at the ecosystem level (Jucker et al., 2015; Schnabel et al., 2019). As light is a key
47 resource in forests, niche partitioning focusing on light capture (Forrester et al., 2019; Ishii and
48 Asano, 2010; Williams et al., 2017) has mostly been explained by the 'canopy packing' process, which

49 corresponds to a morphological complementarity between interacting trees (Pretzsch, 2014). Trees
50 with complementary architectures will have a higher interception of light and a densified structure.
51 However, the mixture effect on tree productivity is generally apprehended from tree diameter
52 increment. Results of such studies have often shown an asymmetrical effect at the species level (i.e.
53 species-specific mixture effects in a given mixed stand may be of opposite signs, Forrester et al.,
54 2018; Toigo et al., 2015) and appears highly dependent on soil and climatic conditions as well as on
55 tree species identity and characteristics (Ammer, 2019; Mina et al., 2018). Exploring mixture effects
56 on other compartments of trees is rarely done, while it seems that the joint consideration of radial
57 and branch growth along environmental gradients would allow a more detailed understanding of
58 tree responses to tree species mixture, especially those more directly linked to complementary
59 processes such as canopy packing.

60 1.2 MIXTURE EFFECT ON TREE GROWTH CAN BE MODIFIED BY SPECIES, SITE CHARACTERISTICS AND 61 CLIMATIC CONDITIONS

62 It has long been recognised that the nature and intensity of species interactions depend on the
63 growing conditions of species (Bertness and Callaway, 1994). Originally, the stress gradient
64 hypothesis states that the effect of facilitation is stronger in the most stressful environments,
65 whereas competition between species is stronger in less stressful environments. The positive effect
66 of a protective nurse plant on the survival of a beneficiary plant is a typical example (Castro et al.,
67 2004). This theory has since been refined: firstly, it would apply only when the stress gradient is not a
68 resource gradient. Thus, when the gradient considered is a resource gradient, the effect of
69 facilitation would follow a bell-shape curve with competition predominating at both ends (Holmgren
70 and Scheffer, 2010; Maestre et al., 2009). Secondly, positive effects would depend on the index used
71 to quantify competition and facilitation: if the persistence of a species through facilitation is possible
72 in extreme environments, the performance of a species would be improved only under intermediate
73 conditions of stress. Thirdly, the effect of facilitation would depend on the stress tolerance of the

74 species considered. Examples of facilitation under intermediate conditions exist in forest ecosystems,
75 mostly on seedlings: positive effect of shading in seedlings in temperate forests (Devaney et al.,
76 2020; Simard et al., 2012) and nurse shrubs and tree seedlings at intermediate drought stress
77 (Callaway, 1992; Guignabert et al., 2020). More recently, a theoretical framework has been proposed
78 linking complementary resource use and stress gradient (Forrester, 2014) suggesting that the
79 positive effect of complementary use of light resources is only possible when the water or nutrient
80 resource is sufficient. This hypothesis has been verified in boreal forests (Searle and Chen, 2020), in
81 mountain (Caspersen et al., 2018; Jourdan et al., 2020a) and along a water availability gradient
82 (Steckel et al., 2019, but see Mina et al., 2018). In addition, not only the environmental stress
83 gradient but also species ecological strategies are critical in positive mixture effect: species tolerance
84 to shade, drought and cold determines whether or not species benefit from the mixture of species
85 (Jucker et al., 2014b; Searle and Chen, 2020; Toïgo et al., 2017; Zhang et al., 2012).

86 1.3 THE IMPORTANCE OF CONSIDERING MIXTURE EFFECT ON BRANCH GROWTH

87 Tree productivity is usually apprehended either through the calculation of basal area increment
88 (Toïgo et al., 2015), tree volume increment (Pretzsch et al., 2015) or total above-ground biomass
89 increment (Jucker et al., 2014a) and thus do not explicitly consider shoot growth. Classically,
90 allometric relationships are used to assess volume and total aerial biomass of a tree from dimensions
91 more easily measurable (especially tree circumference or diameter, Vallet et al., 2006), while height
92 growth is actually estimated from stand age. These allometric relations were mostly established in
93 pure stands, while species mixture can modify height growth of trees (Vallet and Perot, 2016) or the
94 allometry between diameter and height (Forrester et al., 2018; Trouvé et al., 2017). Thus, crown
95 plasticity is an aerial characteristic of trees that is important in the response of trees to species
96 mixture. Crown competition is a primordial component of tree competition for space (Hajek et al.,
97 2015; Seidel et al., 2011). Adjusting crown growth allows a reduction in inter-specific competition
98 (Longuetaud et al., 2013). For instance, crown plasticity and inherent interspecific differences

99 contributed nearly equally in explaining patterns of overyielding, in a young plantation (Williams et
100 al., 2017). In European forests, canopy packing appears to be driven more by crown plasticity than by
101 vertical stratification (Jucker et al., 2015). The much denser and more plastic canopy space filling in
102 mixed stands may increase light interception, stand density, productivity, and growth resilience to
103 disturbances (Pretzsch, 2014). It appears then that beyond the simple consideration of tree diameter,
104 tree growth strategies reflect on all of the tree aerial compartments (Fichtner et al., 2013; Van de
105 Peer et al., 2017). If mixture effect on tree productivity is conditioned by site and climatic conditions
106 and that crown plasticity is a part of the species strategy to face competition, then branch growth
107 should also be dependent both on the neighbourhood and site conditions. However, the vast
108 majority of studies on the effect of diversity on stand productivity have relied on diameter
109 measurements, and the effect of species mixture on branch growth is thus largely under-studied.
110 Therefore, focusing on different aerial compartments of the tree may possibly shed a new light on
111 the effects of species mixture to obtain a more comprehensive picture of the forest functioning.

112 The diversity- and stability- productivity relationships in forests have been studied through different
113 complementary approaches going from experimental methods to modelling methods (Kambach et
114 al., 2019; Morin et al., 2011). At one end, experimental designs manipulating directly tree diversity
115 offer the advantage of controlling the different factors that may bias the comparison between pure
116 and mixed stands, but trees are still relatively young (Tobner et al., 2016; Van de Peer et al., 2018;
117 Williams et al., 2017). At the other end, due to the long lifespan of trees, experiments investigating
118 long term behaviour of forests are scarce, and modelling approaches allow to simulate the diversity-
119 productivity relationship on the long term (Morin et al., 2018). Between these two extremes,
120 observational data coming from national inventories allow to investigate the diversity-productivity
121 relationship in mature stands and along large environmental gradients (*e.g.* Bourdier et al., 2016;
122 Caspersen et al., 2018; Ruiz-Benito et al., 2014). Besides, in recent years the approach by triplet of
123 plots has been receiving a growing attention (*e.g.* del Río et al., 2017; Heym et al., 2017; Pretzsch et
124 al., 2020; Steckel et al., 2019; Jourdan et al., 2020a). A triplet of plots consists of a plot in a two-

125 species mixed stand and two plots in pure stands of corresponding species. The plots within a triplet
126 are established under similar site conditions allowing comparison between pure and mixed stands.
127 This approach has the advantage of being implemented in a mature forest and along controlled
128 environmental gradients.

129 1.4 OBJECTIVES AND HYPOTHESIS

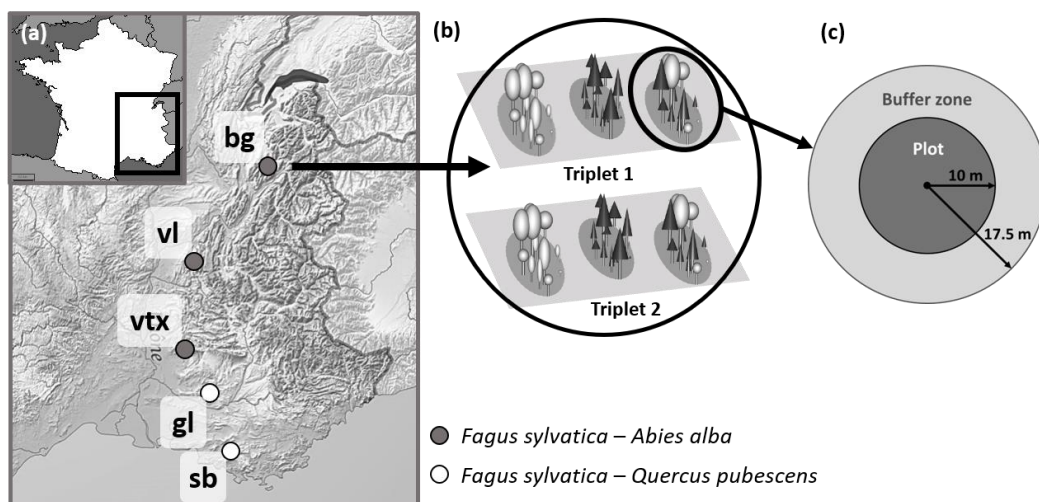
130 Through an observational design based on triplets of plots (Jourdan et al., 2020a, 2020b), this work
131 aimed at assessing and comparing the influence of tree species mixture on the growth of two aerial
132 compartments of trees: stems and branches. Two types of species mixtures (*Fagus sylvatica-Abies*
133 *alba* or *Fagus sylvatica-Quercus pubescens*) were studied at five study sites, distributed along a
134 Mediterranean-Alpine gradient of forests. These three species are major species in Europe: *Fagus*
135 *sylvatica* is found up to 2000 m of elevation in central and western Europe (Durrant et al., 2016).
136 *Quercus pubescens* has an optimum growth between 200 and 800 m of elevation but can be found
137 up to 1300 m (Pasta et al., 2016). *Abies alba*, on the other hand, is restricted to mountainous regions
138 with a distribution from 500 to 2000 m of elevation (Mauri et al., 2016). The study of beech-oak and
139 beech-fir associations along a Mediterranean-Alpine gradient is of interest on several point: (i) *Fagus*
140 *sylvatica* is a very competitive species on sites that are favourable. The environmental gradient
141 considered makes it possible to cover the limits of its growing conditions in terms of temperature
142 and precipitation with different environmental constraints (drought in the south and cold in the
143 north); (ii) In the southern sites, *Fagus sylvatica* is accompanied by *Quercus pubescens*, that is a
144 broadleaf species less tolerant to shade but more tolerant to drought (Niinemets and Valladares,
145 2006). In sites where water is a limiting factor, species growth should suffer from interspecific
146 competition, particularly in the hottest years and for the least drought-tolerant species. On the
147 other hand, in milder years, positive mixture effect should emerge from two different processes: a
148 competitive advantage for *Fagus sylvatica* and a change in resource allocation for *Quercus pubescens*
149 from stem to shoot. (iii) In the northern sites, *Fagus sylvatica* is accompanied by a coniferous species,

150 *Abies alba* that is shade- and cold-tolerant (Niinemets and Valladares 2006). We expected that
151 mixture effect would be positive on shoot and branch growth at the coldest site, particularly on
152 shade and cold tolerant species.

153 We sought to determine the effects of tree species mixture and climate on stem and branch growth
154 by (i) considering a possible interaction effect between stand composition (pure vs. mixed stand) and
155 temperature on tree growth (ii) comparing tree reaction to stand composition and temperature
156 between stem and shoot growth in pure and mixed stands.

157 2. MATERIAL AND METHODS

158 2.1 STUDY SITES AND SAMPLE DESIGN



159
160 Figure 1 Overview of the experimental design: (a) the five study sites are located in south-eastern
161 France along a latitudinal gradient going from Mediterranean area to the Alps (*sb*: Sainte-Baume; *gl*:
162 Grand-Luberon; *vtx*: Ventoux; *vl*: Vercors-Lente; *bg*: Bauges). The association of tree species in stands
163 changes according to the sites: *Fagus sylvatica* and *Quercus pubescens* in the southern sites (*sb* and
164 *gl*), *Fagus sylvatica* and *Abies alba* in the northern sites (*vtx*, *vl* and *bg*); (b) In each of the five sites,
165 the two triplets of plots are at different elevations. A triplet of plots consists in one plot in a mixed
166 stand and two plots in pure stands of the corresponding tree species; (c) Individual plots are

167 delimited as circular plots with a radius of 17.5 m made of a central area (10 m radius) where trees
168 are sampled and a buffer zone (7.5 m radius).

169

170 Study sites were located in the French Alps along a latitudinal gradient (More detailed information on
171 the experimental design is provided by Jourdan et al., 2019) and belong to the experimental network
172 GMAP (<https://oreme.org/observation/foret/gmap/>). The association of tree species in stands varied
173 across the five sites considered (Fig 1a): *Fagus sylvatica* and *Abies alba* in northern sites (Bauges,
174 Vercors-Lente, Ventoux), *Fagus sylvatica* and *Quercus pubescens* in southern sites (Grand-Luberon,
175 Sainte-Baume). Each of these sites was made of two triplets (Fig 1b) associating a plot in a two-
176 species mixed stand and the two pure plots of the corresponding species. The latitudinal gradient
177 allows testing a wide range of climatic conditions, which is necessary to study the environmental
178 determinants of the mixture effect. Each triplet of plots allowed the comparison of tree growth in
179 pure and mixed stands in homogenous environmental conditions within a site. Individual plots were
180 delimited as circular plots with a radius of 17.5 m made of a central area (10 m radius) where the
181 measurements were conducted, and a buffer zone (7.5 m radius) to ensure the plot was surrounded
182 by homogeneous conditions (Fig 1c). Forest management was restricted in the plots so that human
183 perturbation inside each stand was avoided.

184 In each triplet, air temperature was recorded every two hours with a sensor Tinytag Plus 2 - TGP-450
185 along the study period (2015-2018), and was averaged to obtain mean monthly and annual
186 temperatures at the triplet level. Monthly precipitation records were obtained from Meteo France at
187 the site level. We calculated annual soil water deficit from monthly time series of precipitation and
188 temperature and soil water holding capacity according to the Thornthwaite and Mather's methods
189 (Thornthwaite and Mather, 1957). Temperatures and annual soil water deficit in *Fagus sylvatica*-
190 *Quercus pubescens* sites were higher and precipitation lower than in *Abies alba*-*Fagus sylvatica* sites
191 (Table 1): the driest site being Grand Luberon and the wettest and coldest site being Vercors-Lente.

192 Table 1 Tree and site characteristics: stem diameter at breast height, annual stem basal area
 193 increment (BAI) and annual shoot volume increment (SVI) from 2015 to 2018 for *Fagus sylvatica*,
 194 *Quercus pubescens* and *Abies alba* in the five sites studied (*bg* Bauges; *gl* Grand Luberon; *sb* Sainte
 195 Baume; *vl* Vercors-Lente; *vtx* Ventoux), carbon to nitrogen ratio (C:N), soil water holding capacity
 196 (SWHC), precipitation (P), soil water deficit (SWD) and temperature (T). We ranked the studied sites
 197 per couple of species and from the most productive site to the least productive site (*F. sylvatica*-*Q.*
 198 *pubescens*: BAI_{sb}>BAI_{gl}; *F. sylvatica*-*A. Alba*: BAI_{bg}>BAI_{vl}>BAI_{vtx}).

199

	Variable	Species	Site				
			<i>sb</i>	<i>gl</i>	<i>bg</i>	<i>vl</i>	<i>vtx</i>
Tree characteristics (mean; q25-q75)	Stem diameter at breast height (cm)	<i>Fagus sylvatica</i>	34.1	21.7	56.8	37.7	28.6
		<i>Quercus pubescens</i>	25-39.2	19.5-24.1	46.3-59.3	25.9-48.2	23.6-34.2
	BAI (cm ²)	<i>Abies alba</i>	34.2	18.2	71.3	41.5	40.5
		<i>Fagus sylvatica</i>	27.3-41.1	15.5-23.1	52.5-82.9	35.2-51.2	30.4-46.9
		<i>Quercus pubescens</i>	6.4	3.4	20.9	10.1	5.1
		<i>Abies alba</i>	3.5-8.3	1.8-4.6	8.4-23.5	5.4-15	1.9-6.9
		<i>Quercus pubescens</i>	8.9	2.5	90.7	30.7	15.2
		<i>Abies alba</i>	6.5-9.4	1.4-3.3	55-108	17-40.1	7.7-18.4
	SVI (cm ³)	<i>Fagus sylvatica</i>	267.4	387.5	1004.3	761.6	470
		<i>Quercus pubescens</i>	67.6-315	109.9-528.8	295-1330.3	197.8-1065.8	110.3-473.1
		<i>Abies alba</i>	780.7	760.1	2443.9	3058.8	769.1
		<i>Quercus pubescens</i>	233.3-1148.4	316.2-883.7	788.4-3371.6	620.8-4106.4	230.1-980
<i>Abies alba</i>							
<i>Quercus pubescens</i>							
Site characteristics (mean; min-max)	Latitude		43.3°N-5.7°E	43.8°N-5.5°E	45.7°N-6.2°E	44.9°N-5.3°E	44.2°N-5.2°E
	Altitude (m) (triplet n°1-n°2)		736-746	872-1005	1025-1203	1137-1390	1328-1354
	C:N		18.2	14.6	14.5	14.3	19.9
	SWHC (mm)		16.5-19.9	13.7-15.8	12.9-15.7	12-16.7	18.6-21.1
	P (mm)		168	121	173	163	144
	SWD (mm)		158-174	106-130	153-180	139-177	135-149
	T (°C)		837.6	731.9	1182.4	1485.1	1159
			655-1101	500-1031	1048-1330	1377-1598	790-1471
			220	238	22	17	101
			97-346	161-338	13-35	8-32	40-177
		12.1	11.1	8.2	6.7	8.4	
		11.8-12.3	10.8-11.4	7.7- 8.6	5.7-7.7	8.0-8.9	

200 2.2 SHOOT GROWTH AND BASAL AREA INCREMENT

201 Trees were sampled during a field campaign in 2018 in 10 triplets (2 triplets at each of the five sites),
202 corresponding to 30 plots. Only dominant trees, belonging to the upper canopy layer, were selected:
203 5 co-dominant trees of the target species in pure stands, and 5 co-dominant trees of each of the two
204 species in mixed stands for a total of 20 trees per triplet or 40 trees per sites (see Table S1). Tree
205 height and diameter at breast height (1.30 m) were measured in 2018. Three to four terminal
206 branches per tree were collected in the upper part of the crown exposed to the sun. Annual shoot
207 growth in diameter and length from bud scar to bud scar for the years 2015 to 2018 were measured
208 with a calliper. Then, we combined measurements of shoot length and diameter to calculate an
209 annual shoot volume increment (SVI in cm^3). SVI was estimated as a cylinder. Finally, SVI from the
210 same year of the three to four individual branches of a tree were averaged to obtain an SVI per tree
211 for each studied year. One increment core per tree was collected from the bark to the pith at breast
212 height using a Pressler borer. The ring profiles of the selected trees were assessed by X-ray
213 microdensitometry and ring widths from 2015 to 2018 were used to calculate the annual basal area
214 increment (BAI in cm^2) of trees. BAI represents the surface of wood at breast height (1.30 m) formed
215 during the year. Tree and site characteristics are summarized in Table 1.

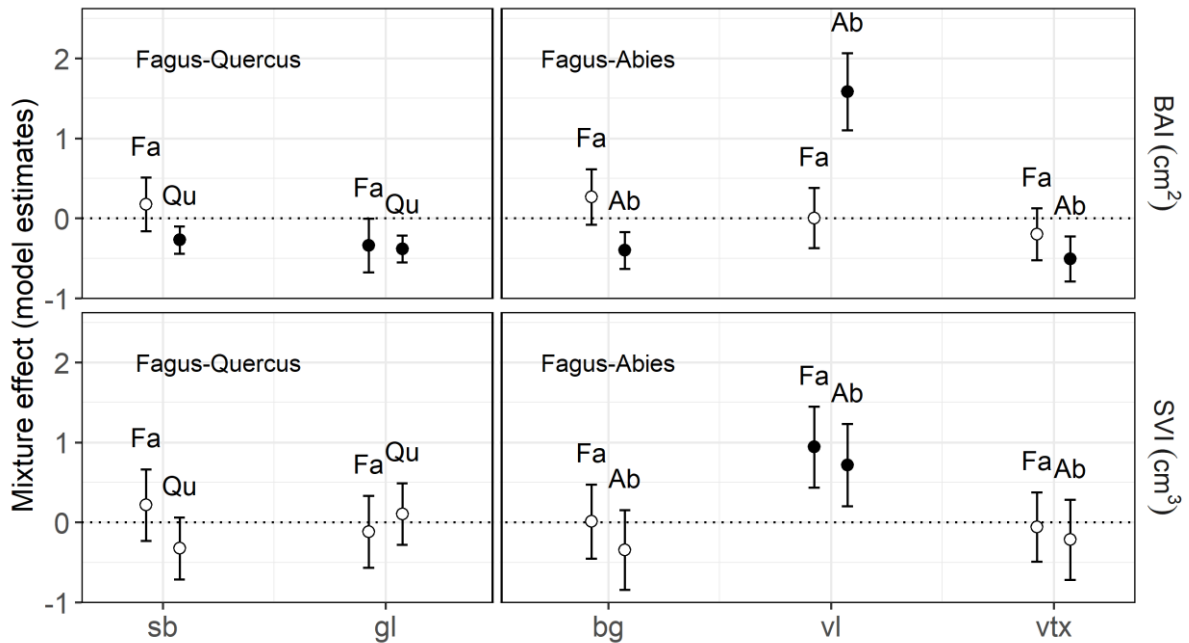
216 2.3 STATISTICAL ANALYSIS

217 To determine the effects of species mixture and climate per site and species (*Fagus sylvatica*, *Abies*
218 *alba* and *Quercus pubescens*) on SVI and BAI we used a linear mixed-effects model by species and
219 tree compartment (shoot and stem) at tree level. According to our hypotheses we integrated an
220 interaction term between site, temperature and stand composition (pure or mixed). We simplified
221 models by removing any non-significant interactions starting from the highest order level to get an
222 accurate estimate of simple effects. Moreover, we added tree diameter as covariate to account for
223 the effect of tree size on BAI and SVI. We also included a random effect at the triplet level to account
224 for the sampled design. BAI and SVI were log-transformed to ensure normality of residuals.

225 The analyses were performed with R 4.0.2 (R Core Team, 2020) and packages car, emmeans and
226 nlme for statistical analyses.

227 3. RESULTS

228 3.1 MIXTURE EFFECT ON BASAL AREA INCREMENT (BAI) AND SHOOT VOLUME INCREMENT (SVI)



229 Figure 2 Mixture effect on basal area increment (BAI) and shoot volume increment (SVI) of *Quercus*
 230 *pubescens* (Qu), *Fagus sylvatica* (Fa) and *Abies alba* (Ab) in the five studied sites (*sb*: Sainte Baume;
 231 *gl*: Grand Luberon; *bg*: Bauges; *vl*: Vercors-Lente; *vtx*: Ventoux). Dots indicate model coefficients (on
 232 the log scale). Error bars indicate confidence intervals at 95 % of model coefficients. Significant
 233 mixture effects (p-values < 0.1) are represented by black dots, non-significant effects (p-values >=
 234 0.1) are represented by white dots.
 235

236

237 *Fagus sylvatica-Quercus pubescens* stands

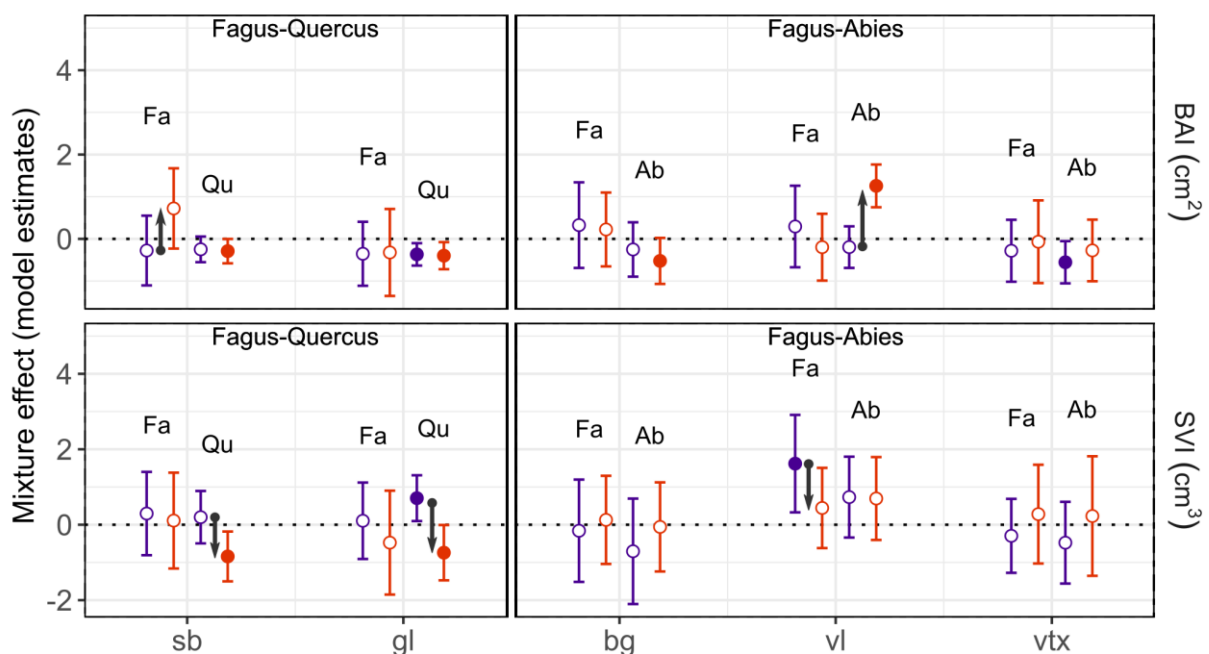
238 At the most productive site (*sb*), neither the BAI nor the SVI of *Fagus sylvatica* were significantly
 239 impacted by species mixture (Fig 2). Tree species mixture had a significant effect on BAI but not on
 240 SVI of *Quercus pubescens*: BAI of *Quercus pubescens* decreased by - 24 % when mixed with *Fagus*
 241 *sylvatica* compared to pure stands.

242 At the least productive and driest site (*gl*), BAI of *Fagus sylvatica* and *Quercus pubescens* decreased
 243 significantly by - 29 % and by - 32 %, respectively, in mixture compared to pure stand. The mixture
 244 effect on SVI was not significant neither on *Fagus sylvatica* nor on *Quercus pubescens* (Fig 2).

245 *Fagus sylvatica*-*Abies alba* stands

246 At *Fagus sylvatica*-*Abies alba* sites, BAI of *Fagus sylvatica* was never significantly impacted by the
 247 presence of *Abies alba* (Fig 2). In other cases, mixture effect depended on site condition: At the most
 248 and at the least productive site (*bg* and *vtx*, respectively), BAI of *Abies alba* decreased in mixture with
 249 *Fagus sylvatica* compared to pure stand by - 33 % and by - 0.36 %, respectively (Fig 2). Conversely SVI
 250 of *Quercus pubescens* were not significantly impacted by species mixture (Fig 2). At the coldest site
 251 (*vl*), BAI of *Abies alba* increase by + 67 % when mixed with *Fagus sylvatica* compared to pure stand.
 252 This increase was accompanied by an increased SVI in both species in mixture of + 105 % for *Abies*
 253 *alba* and of + 157 % for *Fagus sylvatica*.

254 3.2 CHANGES IN MIXTURE EFFECT ON BASAL AREA INCREMENT (BAI) AND SHOOT VOLUME
 255 INCREMENT (SVI) WITH TEMPERATURE



257 Figure 3 Model estimates of the changes in mixture effect on basal area increment (BAI) and shoot
258 volume increment (SVI) with temperature in *Quercus pubescens* (*Qu*), *Fagus sylvatica* (*Fa*) and *Abies*
259 *alba* (*Ab*) in the five studied sites (*sb* Sainte Baume; *gl* Grand Luberon; *bg* Bauges; *vl* Vercors-Lente;
260 *vtx* Ventoux). Dots indicate model coefficients (on the log scale). Error bars indicate confidence
261 interval of model coefficients. Mixture effects at a minimal and maximal temperature values are in
262 violet and in orange, respectively. Arrows represent the changes in mixture effect from a low to a
263 high value of temperature when it is significant. Significant mixture effects (p-values < 0.1) are
264 represented by violet and orange dots, not significant effect (p-values ≥ 0.1) are represented by
265 white dots.

266

267 *Quercus pubescens-Fagus sylvatica* stands

268 Mixture effect on BAI tended to be temperature-dependent only for *Fagus sylvatica* (estimates ± se:
269 1.00 ± 0.53 ; p-value = 0.06) at the most productive site (*sb*): the effect of temperature was positive
270 and significant in mixed stands (2.46 ± 0.90 ; p-value = 0.007) but not in pure stands (0.31 ± 0.81 ; p-
271 value = 0.70; Fig S1). Nevertheless, the difference in BAI in *Fagus sylvatica* between mixed stands and
272 pure stands was significant neither at low temperature nor at high temperature (Fig 3).

273 Mixture effect on SVI depended on temperature in *Quercus pubescens* in the two studied sites (*sb*: -
274 1.4 ± 0.56 ; p-value = 0.07 and *gl*: -1.44 ± 0.55 ; p-value = 0.01). At the most productive site (*sb*), the
275 effect of temperature on SVI of *Quercus pubescens* was positive and significant in pure stands
276 (2.42 ± 0.86 ; p-value = 0.006) but not significant in mixed stands (0.18 ± 0.95 ; p-value = 0.85; Fig S1);
277 the difference between SVI in mixed and pure stands going from not significant (Fig 3) at a minimal
278 annual value of temperature (11.8 °C) to a decrease in SVI of - 57 % in mixed stand compared to pure
279 stand at a maximal annual value of temperature (12.3 °C). At the least productive and driest site (*gl*),
280 the effect of temperature was not significant in pure stand (0.62 ± 0.70 ; p-value = 0.4), but was
281 negative in mixed stand (-1.46 ± 0.71 ; p-value = 0.04): the difference between SVI in mixed and pure

282 stands going from an increase of + 102 % in SVI in mixed stand compared to pure stand (Fig 3) at a
283 minimal value of temperature (10.7 °C) to a decrease of - 52 % in SVI in mixed stands compared to
284 pure stands (Fig 3) at a maximal value of temperature (12.3 °C).

285 *Abies alba-Fagus sylvatica* stands

286 At the coldest site (*vl*), mixture effect on BAI of *Abies alba* depended on temperature (1.45 ± 0.29 ; p-
287 value < 0.001). An elevation of annual temperature caused a decrease in BAI of *Abies alba* in pure
288 stands ($- 0.67 \pm 0.10$; p-value < 0.001) but not in mixed stands (0.05 ± 0.10 ; p-value = 0.6; Fig S1): the
289 difference between BAI in mixed and pure stands going from non-significant (Fig 2) at a minimal
290 value of annual temperature (5.7 °C) to an increase in BAI of 252 % in mixed stand compared to pure
291 stand at a maximal value of annual temperature (7.7 °C). In *Fagus sylvatica* the change in mixture
292 effect with BAI was not significant. Conversely mixture effect on SVI of *Fagus sylvatica* depended on
293 temperature ($- 1.18 \pm 0.65$; p-value = 0.07). The positive effect of temperature on SVI of *Fagus*
294 *sylvatica* was lower in mixed stand (1.75 ± 0.66 ; p-value = 0.009) compared to pure stand ($2.33 \pm$
295 0.63 ; p-value = 0.0003; Fig S1): the difference between SVI in mixed and pure stands going from an
296 increase of 405 % (Fig 2) at a minimal value of annual temperature (5.7 °C) to a non-significant
297 difference at a high value of temperature (7.7 °C).

298 4. DISCUSSION

299 Despite the fact that most of the studies dealing with the diversity-productivity relationship in forests
300 rely on tree diameter increment, we found that mixture effects on shoot volume increment do not
301 mirror the mixture effect on stem growth. Mixture effect was more often neutral on branch growth
302 than on stem growth along the studied stands, while positive mixture effect changed with
303 temperatures and site conditions. We also found that on the driest site (*gl*) in *Fagus sylvatica*-
304 *Quercus pubescens* stands, the negative effect of competition was predominant, as opposed to the
305 coldest site (*vl*) where the effect of mixing on branch and stem growth was positive.

306

307 4.1 ASYMMETRIC MIXTURE EFFECT BETWEEN BRANCH AND STEM GROWTH

308 Mixture effect on branch growth did not necessarily mirror mixture effect on stem growth as
309 illustrated by the case of beech in Vercors-Lente. This implies that considering only stem diameter in
310 the diversity-productivity relationship can lead to an under- or an overestimation of the mixture
311 effect. An asymmetric mixture effect may be caused by species strategies in response to competition.
312 In plastic species such as oaks, an elongation of the stem with a development of the branches to
313 access the light is typical of a competition avoidance strategy (MacFarlane and Kane, 2017; Pretzsch
314 and Rais, 2016; Van de Peer et al., 2017) especially in mixture with species with low crown
315 transparency such as *Fagus sylvatica*. *Fagus sylvatica*, on its side, tends to increase its branchiness, at
316 least in the young stages (Van de Peer et al., 2017), its branch length increment being uncorrelated
317 to light availability (Hajek et al., 2015). We did not observe any competition avoidance effects in
318 *Abies alba* mixed with *Fagus sylvatica*, which highlights the fact that strategies to face competition
319 are highly species-specific. This lack of branch response to mixture can be explained by a weak crown
320 plasticity related to competition in shade-tolerant coniferous species (Vieilledent et al., 2010).

321 4.2 POSITIVE EFFECT OF MIXTURE ON STEM AND BRANCH GROWTH DEPENDS ON SITE AND 322 TEMPERATURE

323 Radial stem of *Fagus sylvatica* was affected by intraspecific or interspecific competition at the site
324 with the lowest soil field capacity with *Quercus pubescens*, at the edge of its distribution range. In
325 young development stages, beech growing in harsh environmental conditions tend to outcompete
326 oak (Van de Peer et al., 2018) likely because interspecific interactions at such young development
327 stages rely more on species growth rates than at later development stages. Moreover, negative
328 mixture effect on both stems and branches appear when temperature increases, replacing the
329 competition avoidance strategy for *Quercus pubescens*. Such pattern has already been pointed out in
330 forests at the global scale, with an increase of the positive mixture effect on productivity with
331 increasing precipitation (Jactel et al., 2018). Complementarity between species could occur if

332 resources such as water and nutrients are not limiting for growth (Forrester, 2014) and the southern-
333 most sites that we studied are the driest of the latitudinal gradient. Yet, a transition from
334 competition to facilitation with abiotic stress exist in forests (He et al., 2013). The only positive
335 mixture effect on both branch and stem growth that we found occurred in the coldest site supporting
336 the hypothesis of a complementary use of light resource. Thus, *Abies alba* can benefit from a better
337 light absorption and a more efficient use of light in mixture, which is accompanied by a higher growth
338 in height (Forrester and Albrecht, 2014). However, our results show that mixture effect on tree
339 crown do not necessarily reflect on stem growth in diameter (see beech in *gl*). The fact that a positive
340 effect on *Fagus sylvatica* shoot was observed in only one of the study sites is most probably due to
341 the particularity of the Mediterranean-Alpine gradient. It is also known that beech is a species which
342 benefits from a competitive reduction in mixture, reflected in an enlarged crown size (Dieler and
343 Pretzsch, 2013). On one side our results confirm that shoot growth may increase in case of
344 competition reduction (Pretzsch and Rais, 2016) and prove that this effect is also varying with
345 temperature. On the other side, this result is consistent with the idea that the nature of abiotic stress
346 determines the mixture effect. Contexts where species are more limited by temperatures than by
347 drought favours positive mixture effects (Toigo et al., 2015) possibly through species
348 complementarity or facilitative effect *via* the control of microclimatic conditions by forest cover that
349 benefit to the dynamics of the associated vegetation (Zellweger et al., 2020).

350 5. CONCLUSION

351 Mixture effect on growth of stems and branches can be asymmetrical. Our results prove that tree
352 crown is a key component of the productivity-diversity relationship. The nature of mixture effect on
353 stems and branches was strongly dependent on the geographical context and on the type of abiotic
354 factor limiting growth: tree species in a Mediterranean context can be particularly subject to
355 interspecific competition, while we highlighted a positive effect of species complementarity on stem
356 and branch growth in the coldest and wettest mountainous site. It then appears that the

357 consideration of tree crown along with stem productivity in the diversity-productivity relationship in
358 forest is needed to further understand and quantify the effect of mixing on tree productivity.

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