

**Tree diversity effects on forest productivity:
disentangling the effects of tree species addition vs.
substitution**

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1 TREE DIVERSITY EFFECTS ON FOREST PRODUCTIVITY: 2 DISENTANGLING THE EFFECTS OF TREE SPECIES ADDITION VS. 3 SUBSTITUTION

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15 ABSTRACT

16 1. Mixture effect on stand productivity is usually apprehended through a substitutive approach,
17 whereby productivity in mixed stands is compared to productivity in monocultures, at equivalent stand
18 density. This approach has proved that in many cases mixed stands perform better than monospecific
19 forests, however, we do not yet have a solid theory about species behaviour in the mixture or even
20 guidelines for combining species. The addition of a second tree species to an existing mono-specific
21 stand has received much less consideration. Yet, this approach has the potential to separate the
22 facilitation effect from the complementarity effect.

23 2. We compared the effect of tree species substitution vs. addition on the productivity of maritime
24 pine and silver birch in a young tree diversity experiment implemented in 2008 in SW France.

25 3. Substituting pines with birches to create two-species mixtures resulted in an increase of tree
26 productivity at stand level beyond what was expected from monocultures (i.e.,overyielding). In
27 contrast, creating mixture through the addition of birches to pine stands had no effect on the maritime
28 pine stand productivity (transgressive mixture effect not significant). This absence of effect is produced
29 by two distinct density-dependence responses at an individual level.

30 4. Our results allow clarifying the cases in which a mixed stand can be considered as an alternative to
31 a monoculture of a productive species. In particular, the addition of a pioneer and soil low-demanding
32 species during young developmental stages is a possibility to diversify the stand and potentially to
33 increase ecosystem services without altering the productivity of the target species.

34 KEYWORDS

35 *Betula pendula*; *Pinus pinaster*; *biodiversity*; *ecosystem functioning*; *overyielding*; *transgressive*
36 *overyielding*; *forest*

37 INTRODUCTION

38 1§ CHALLENGES AND DETERMINANTS OF MIXED PLANTATIONS.

39 Despite ample evidence that mixed stands provide more ecosystem services than monospecific forests
40 under various ecological conditions (Baeten et al., 2019), most planted forests are still managed as
41 monocultures. Moving towards ecologically intensive and sustainable forest management requires a
42 sound understanding of the drivers that could improve or hamper the benefits of mixed forests (Felton
43 et al., 2010). Tree species diversity has well documented positive effects on tree productivity (Gamfeldt
44 et al., 2013). Such positive effects are driven by both complementarity and selection effects (Loreau &
45 Hector, 2001). Complementarity mostly refers to niche partitioning processes whereby mixed stands
46 are better able to capture resources than monospecific stands (Jucker et al., 2015), and to facilitation,
47 where one species in the mixture benefit to the others, e.g. via improved resource quality (N-fixing
48 species) acquisition (water uplifting), or protection against herbivores (Caspersen et al., 2018; Kunz et
49 al., 2019). Selection effect refers to situations where a highly productive species recruited in the mixed
50 stand drives positive mixture effect (Fox, 2005; Loreau & Hector, 2001). However, recent studies have
51 highlighted that positive diversity-productivity relationship is strongly context-dependent. For
52 instance, species functional characteristics or stand structure can modify the shape and strength of the
53 diversity-productivity relationship (Forrester, 2014; Grossman et al., 2017). Disentangling drivers of
54 the mixture effect require innovative conceptual framework supported by novel experimental
55 approaches based on stand density, a major component of stand structure that can be controlled by
56 thinning operations.

57 2§ STAND DENSITY A KEY DETERMINANT OF MIXTURE EFFECT ON STAND PRODUCTIVITY

58 Stand density influences the degree of canopy closure, which in turn participate in the regulation of
59 light transmittance, the interception of water precipitations, belowground competition for water and

60 can modify understory microclimate, understory vegetation, and soil biodiversity (Baeten et al., 2019;
61 Gaudio et al., 2011; Henneron et al., 2017; Ligot et al., 2014; Perot et al., 2017). Stand density is also a
62 major driver of tree-tree competition, being used to calculate several competition indices in forest
63 (Biging & Dobbertin, 1992). Due to the considerable effects of tree density on canopy packing and
64 abiotic factors in forest stands, it is surprising that only a few studies addressing the effect of tree
65 diversity on productivity in temperate forest explicitly questioned the importance of stand density
66 (Forrester, 2014; Jucker et al., 2016). Yet, complementarity among species and intra-specific
67 competition both intensify with stand density. This was documented in mixed stands of late-
68 successional species (Amoroso & Turnblom, 2006; Forrester et al., 2013) of slow- with fast-growing
69 tree species (Condés et al., 2013) and of species with contrasted shade tolerance (del Rio & Sterba,
70 2009). However, it remains unclear how the mixture effect can possibly be modified by stand density,
71 especially in young plantations of fast-growing tree species.

72 3§ CONTROLLING STAND DENSITY TO COMPARE MONOCULTURES TO MIXED STANDS: OVERYIELDING, 73 THE CLASSICAL INDEX BASED ON SPECIES SUBSTITUTION

74 Our understanding of the diversity-productivity relationship in mixed forests is further hampered by
75 unresolved methodological issues. The net biodiversity effect generally simply compares the observed
76 productivity of a mixture to a theoretical mixture assembled with the same proportion of trees drawn
77 from the component monocultures (Loreau, 1998; Loreau & Hector, 2001). As such, overyielding can
78 be seen as a measure of changes in stand productivity due to the substitution of a species by others.
79 Estimating the effect of species mixture on productivity through overyielding has several advantages.
80 First, it provides a quantitative estimate of the net biodiversity effect on stand productivity (Tobner et
81 al., 2016). Second, because it compares the productivity of the mixture to the weighted productivity
82 of the component monocultures, it allows addressing whether the mixture performs better than the
83 average of monocultures (*overyielding*) or the most productive monoculture (*transgressive*
84 *overyielding*).

85 4§ LIMITATIONS LINKED TO SPECIES SUBSTITUTION AND ITS RELATED OVERYIELDING

86 The use of overyielding estimate has also several shortcomings. First, because it is inherently defined
87 at the stand level, overyielding does not account for species-specific responses to tree diversity and
88 knowing which species benefits or not from the mixture is of primary importance, particularly when it
89 comes to harvest species at different times because of differences in growth patterns. Still the effects
90 of tree diversity may not be symmetrical (del Rio & Sterba, 2009), which is a major concern to
91 understand the functioning of mixed species forests. As a consequence, considering the mixture effect
92 on species productivity and on individual tree productivity is a first step to disentangle the mechanisms

93 underlying the diversity-productivity relationship (Nadrowski et al., 2010). Moreover, from a practical
94 point of view, the conversion of monocultures to mixed stands through species substitution is not
95 without management problems. On the one hand, the silviculture of mixed stands, particularly in cases
96 of intimate mixing, is complicated by the difference in growth rates of the different species and the
97 lack of knowledge about the optimum growing space for trees of each species. On the other hand,
98 wood product processing chains are often specialized in a limited number of species and may not be
99 able to offer a market for substitute species.

100 5§ SPECIES ADDITION AS AN ALTERNATIVE TO SPECIES SUBSTITUTION

101 An alternative to species substitution is the addition of a new species within an existing stand. A species
102 addition could be less constraining than species substitution by making it possible to keep the same
103 harvesting rate for the target tree species, for example in the case of alternate-row mixing. Second if
104 resource complementarity cannot be distinguished from facilitation through species substitution, any
105 gain of productivity observed through species addition should be the signature of facilitative processes
106 (i.e. comparison of one tree species productivity with vs. without any heterospecific neighbours). So,
107 either species addition or substitution should be considered to design and manage mixed-species
108 forests and dedicated experiments are needed to disentangle their specific effects on productivity.

109 5§ OBJECTIVES AND TESTED HYPOTHESES

110 Using a long-term tree diversity experiment, we experimentally uncoupled the effect of species
111 addition vs. substitution on forest stand productivity while controlling for stand and species-specific
112 density to gain further insight into the mechanisms underlying the effect of species addition and
113 substitution. We focused on two-species mixtures of maritime pine (*Pinus pinaster Ait.*) and silver birch
114 (*Betula pendula Roth*) at two stand densities. Although the two species studied are fast-growing
115 species, they are nevertheless distinct in terms of growth dynamics and tree sizes. In the case of species
116 substitution, we expected a positive global mixture effect (ME) with a positive specific effect for both
117 pine and birch. By contrast we anticipated a negative transgressive effect (TME) as birch is notably less
118 productive than maritime pine in the local conditions of the experiment. In the case of species addition,
119 we hypothesized opposite patterns of response: a negative ME due to increased competition between
120 trees (due to higher tree density) but a positive TME due to a tree packing effect and a weak
121 competition from silver birch in pine stands. Lastly, we expected that all mixture effects would intensify
122 with stand density.

123 METHODS

124 Both maritime pine and silver birch are light demanding, fast-growing tree species and native to the
125 site. The area of distribution of maritime pine is mainly restricted to Spain, the south-west of France
126 and the north-west of Italy. Maritime pine is a highly drought tolerant species and a major species of
127 production in France yielded exclusively in monoculture. Conversely silver birch is widely distributed
128 across Europe from the Atlantic to eastern Siberia. Silver birch is yielded in the Northern and Eastern
129 Europe and despite the interest shown by these countries, in the Atlantic this tree species is
130 depreciated (Hynynen et al., 2010).

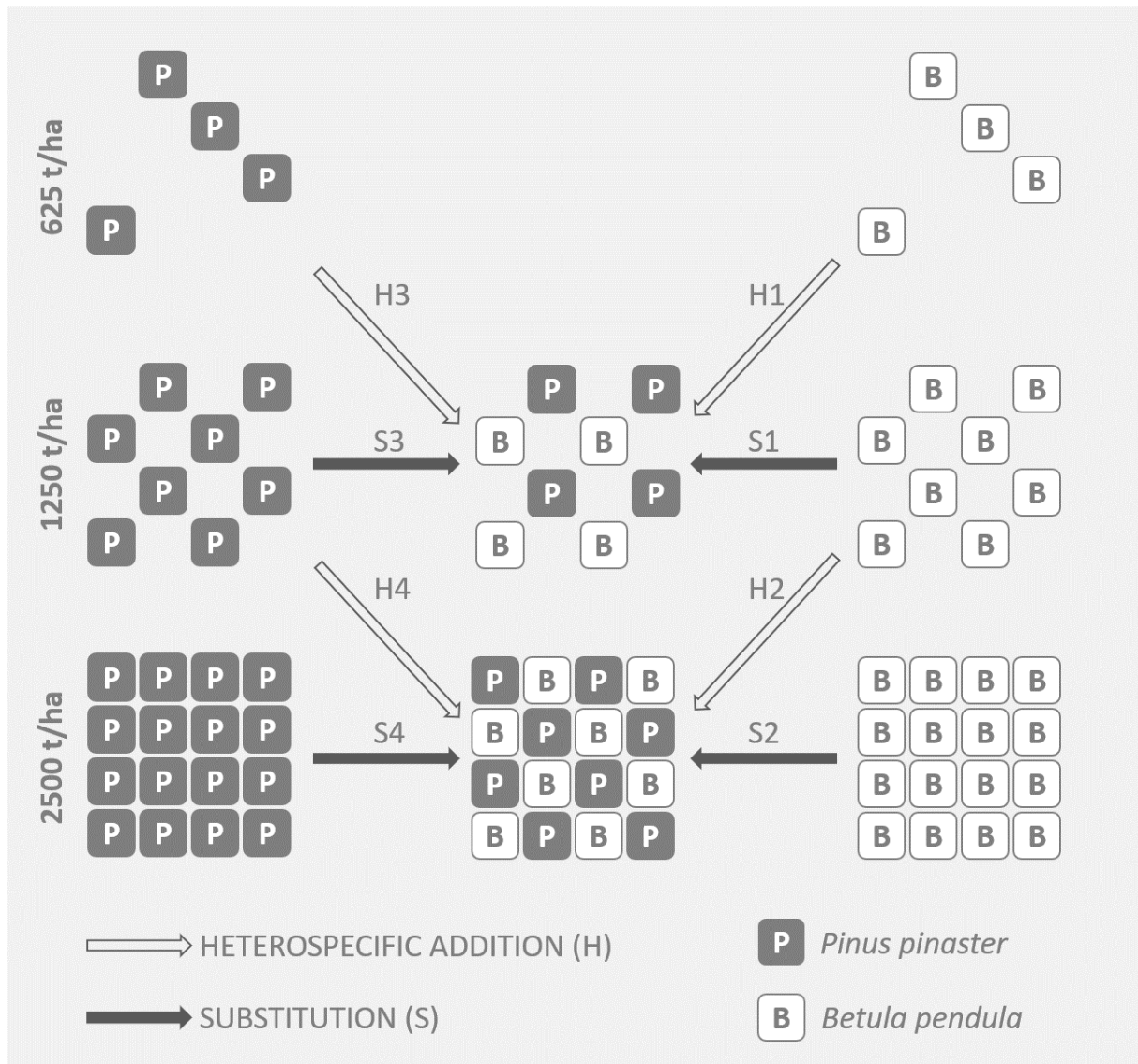
131 EXPERIMENTAL DESIGN

132 The ORPHEE experiment is located 40km south of Bordeaux (44°44'00" N, 00° 46'00" W) and belongs to the
133 worldwide Tree Diversity Network (TreeDivNet). The experimental plantation was established in 2008
134 on a clear cut of former maritime pine stands on a sandy podzol. Stumps were removed and the site
135 was ploughed and fertilized with phosphorus and potassium before planting. In total, 25 600 trees of
136 five native species (Silver birch, *Betula pendula*; pedunculate oak, *Quercus robur*; Pyrenean oak,
137 *Quercus pyrenaica*; holm Oak, *Quercus ilex* and maritime pine, *Pinus pinaster*) were planted within a
138 12ha area. Eight blocks were established, with 32 plots in every block, corresponding to the 31 possible
139 combinations of one to five species, with an additional replicate of the combination of five species.
140 Each plot contained 10 rows of 10 trees planted 2 m apart, resulting in 100 trees per plot, with a plot
141 area of 400 m². The total initial stand density was therefore 2500 tree per hectare in each plot. Tree
142 species mixtures were established according to a substitutive design, keeping the total tree number
143 (n=100) equal in all plots. Within plots, individual trees from different species were planted in a regular
144 alternate pattern, such that a tree from a given species had at least one neighbour from each of the
145 other species within a 2 m radius. Plots were three meters apart and were randomly distributed within
146 blocks. The entire experimental site was fenced to prevent grazing by mammalian herbivores.

147 PLOT SELECTION

148 The present study analyses growth data collected in 2014 (7 years-old) on the target trees at the center
149 of the plots in order to avoid edge effects (measured planting locations = 36). Importantly, at this time
150 of plot development, oak trees were on average 112 cm high and have a negligible growth in diameter,
151 whereas pines and birches were on average five times taller than oaks (563 and 510 cm high,
152 respectively). As a consequence, oak trees were confounded with the understorey vegetation. By
153 considering oak seedlings as part of the understorey vegetation we therefore focused solely on birch
154 and pine growth. However we do not deny the existence of belowground interactions as the
155 understorey can represent a large part of the fine root biomass in maritime pine stands (Bakker et al.,

156 2006). But the three oak species represent only a few individuals among the 25 species found in the
157 understorey (i.e. the most common are *Molinia caerulea*, *Ulex minor* and *Pteridium aquilinum* Corcket
158 et al., 2020), which allows us to reasonably assume that the impact of these relatively few oak
159 individuals on the productivity of pine and birch at these developmental stages is negligible. We tested
160 the effect of species addition and substitution on tree and stand volume by selecting monocultures
161 and mixed stands of birch and pine at equal stand density: the “high-density plots” (2500 t/ha) had
162 100 pines or 100 birches for monoculture plots or a mixture of 50 pines and 50 birches. The “medium-
163 density plots” (1250t/ha) had 50 pines or 50 birches for monoculture plots, or a mixture of 25 pines
164 and 25 birches. We completed the sampling by selecting “low-density plots” as monocultures (625
165 t/ha) with 25 pines or 25 birches (figure 1). To avoid bias when comparing volume of mixed stands and
166 monocultures we eventually selected plots with less than 15% of dead trees as an optimal balance
167 between the number of plots per treatments and the number of trees per plot (Supporting Information
168 Table S1).



169

170

171 Figure 1 Schematic representation of the experimental treatments consisting in three levels of stand
 172 density (low: 625t/ha, medium: 1250t/ha and high: 2500t/ha) and stand compositions, from left to
 173 right: *Pinus pinaster* in monocultures, mixed *Betula pendula* - *P. pinaster* stands (proportion of 50% of
 174 each species) and monoculture stands of *B. pendula*. Arrows indicate the between-treatment
 175 comparisons disentangling heterospecific addition (solid arrows) and species substitution (black
 176 arrows). Arrows are numbered according to the different experimental treatments compared in the
 177 result section.

178 DENDROMETRIC DATA

179 We measured the height of every 36 innermost planted trees at the center of every plot using a
 180 graduate pole, each year from 2008 to 2014. We therefore measured 36, 18 or 9 pines or birches in
 181 the high, medium and low-density plots, respectively. We also measured circumferences at 1.30m
 182 from 2012 to 2014 on 7 randomly chosen pines and 7 randomly chosen birches per plot, irrespective
 183 of plot composition. We used height-circumference relationships to estimate the circumferences of
 184 trees that have not been measured in 2014 (Supporting Information Figure S1), then we estimated
 185 tree volume following the generic model developed by (Deleuze et al., 2014). We assigned a minimum
 186 volume of 0.01m³/ha to the few trees below 1.30m in height (corresponding to the minimum volume
 187 found in the data set). Eventually we estimated dimensions of missing trees by averaging diameter,
 188 height and volume of trees in the plot. Given the negligible tree dimensions at the time of plantation
 189 (2008) volumes of trees in 2014 were used as a measure of tree productivity (i.e. volume increment:
 190 VI). Stand dendrometric characteristics are summarized in table 1.

191

192 Table 1 Mean (minimal-maximal) values of tree height, tree circumference and plot basal area of
 193 maritime pine (*Ppin*) and silver birch (*Bpen*) in monocultures (*mo*) and mixed stands (*mx*) at the three
 194 stand densities studied: low (625 t/ha), medium (1250 t/ha) and high (2500 t/ha).

		Stand density				
		Low Mo	Medium Mo	Mx	High Mo	Mx
Plot basal area (m ² /ha)	<i>Bpen</i>	1.41 0.84-2.25	2.39 0.80-4.62		3.55 1.71-5.10	
	<i>Ppin</i>	7.22 6.17-8.30	11.4 4.69-14.7		17.2 11.3-21.3	
	<i>Bpen + Ppin</i>			7.42 4.54-9.10		11.2 8.24-14.7
Tree height (cm)	<i>Bpen</i>	526 85-764	537 120-900	513 106-795	517 95-791	508 148-729
	<i>Ppin</i>	570 232-706	575 133-801	581 250-780	571 200-810	567 161-795
Tree circumference at breast height (cm)	<i>Bpen</i>	16.6 2.4-26.7	14.9 1.52-28.2	13.3 1.5-28.5	13.0 2.3-24.2	12.0 1.1-22.5
	<i>Ppin</i>	37.6 9.5-51	33.4 0.7-50.2	36.1 10.1-49.9	29.1 5.3-45.2	30.6 2.6-47

195

196 TRANSGRESSIVE MIXTURE EFFECT AND MIXTURE EFFECTS FOR SPECIES SUBSTITUTION AND ADDITION
197 We calculated two integrated indices of mixture effect for heterospecific addition and species
198 substitution: mixture effect (ME) and transgressive mixture effect (TME). These indices were adapted
199 from the classic calculation of transgressive overyielding and overyielding. Transgressive overyielding
200 and overyielding are two standardized indices of mixture effect on stand productivity calculated by
201 comparing monocultures to mixed stands at a same stand density (i.e. in case of species substitution).
202 Yet, the major difference between species substitution and species addition is that total stand density
203 increases from monoculture to mixed stands in an additive design, while it is kept constant in a
204 substitutive design. It follows that the reference monoculture used to calculate ME and TME differed
205 between additive and substitutive designs. We calculated TME the same way for species substitution
206 and species addition at medium and high stand density ($n = 2500$ t/ha and $n = 1250$ t/ha) by comparing
207 the mean total stand volume increment (SVI) of stands between mixed stands (mx) and monoculture
208 stands (mo) of the most productive species, i.e. maritime pine (Fig. 2):

$$209 \quad TME = (SVI_{mx} - SVI_{mo.pine}) / SVI_{mo.pine} \quad \text{Eq. 1}$$

210 Where SVI_{mx} was the stand volume increment since plantation of mixed stands averaged per block;
211 SVI_{mo} the stand volume increment in monoculture of birch or pine averaged per block.

212 The mixture effect (ME) was calculated for each block separately at medium and high levels of stand
213 density ($n = 2500$ t/ha and $n = 1250$ t/ha) as:

$$214 \quad ME = (SVI_{mx} - SVI_{exp}) / SVI_{exp} \quad \text{Eq. 2}$$

215 where SVI_{mx} was the observed volume increment of mixed pine-birch stands and SVI_{exp} was the
216 expected volume increment of mixed stands. While SVI_{mx} was the same for both species substitution
217 and species addition, SVI_{exp} differed between the additive and substitutive scenarios.

218 For species substitution, the calculation of $SVI_{exp.sub}$ was:

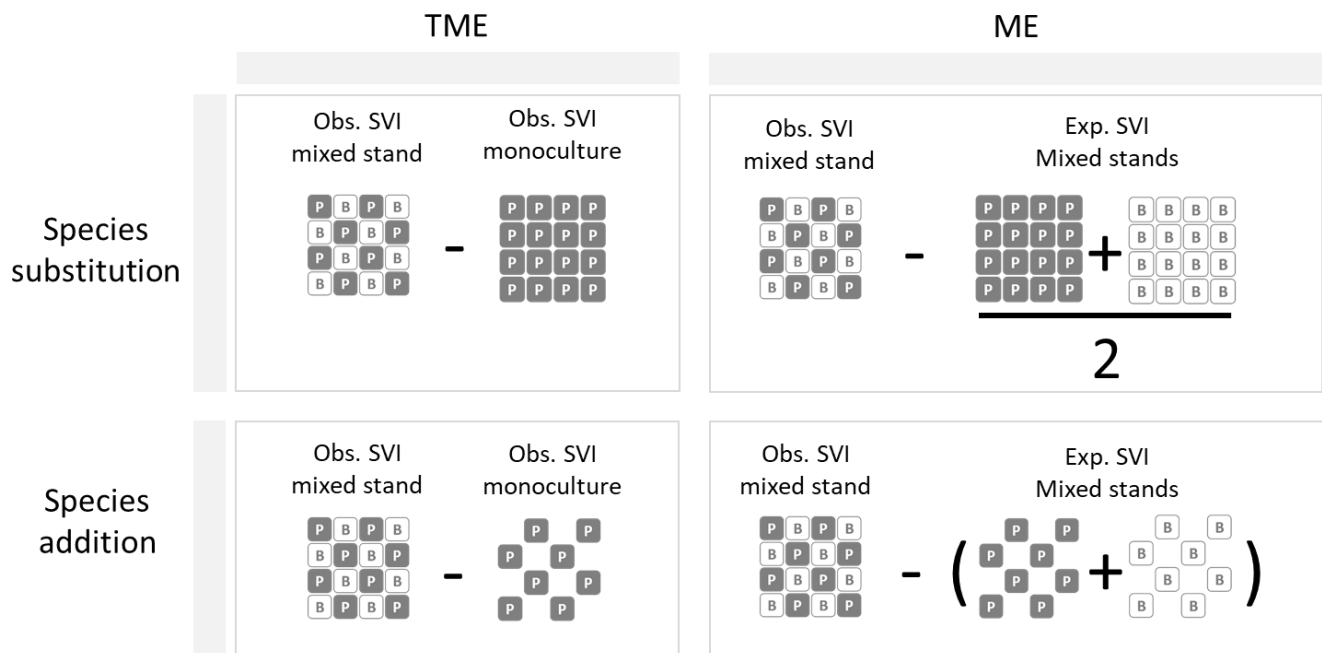
$$219 \quad SVI_{exp.sub} = 0.5 \times SVI_{mo.pine} + 0.5 \times SVI_{mo.birch} \quad \text{Eq. 3}$$

220 where $SVI_{mo.pine}$ and $SVI_{mo.birch}$ were the stand volume increment of pine and birch monocultures
221 averaged per block and 0.5 corresponds to the species proportion.

222 For species addition, we compared SVI_{mx} to $SVI_{exp.add}$ at an equal number of trees per species. Thus, for
223 a SVI_{mx} at a density of n trees, we derived $SVI_{exp.add}$ by summing volume increments in monocultures of
224 $n/2$ trees (see Figure 2):

$$225 \quad SVI_{exp.add.n} = SVI_{mo.pine} \cdot n/2 + SVI_{mo.birch} \cdot n/2 \quad \text{Eq. 4}$$

226 Figure 2 Schematic representation of the calculations of transgressive mixture effect (TME) and
 227 mixture effect (ME) of stand volume increment (SVI) for species substitution and species addition
 228 based on observed (obs.) values and expected (exp.) values.



229

230 STATISTICAL ANALYSES

231 All the analyses were performed with R 3.2.5 and functions gam, lme and glht in packages mgcv, nlme
 232 and multcomp.

233 We conducted separate analyses at the stand and tree levels by fitting a set of linear mixed effect
 234 models. At the plot level, we analysed four response variables: (i) total stand volume increment (SVI)
 235 estimated by summing tree volumes at plot level, (ii) mixture effect (ME) resulting from a species
 236 substitution (ME_{sub}) and from a species addition (ME_{add}) and (iv) transgressive mixture effect (TME)
 237 resulting from a species substitution (TME_{sub}) and from a species addition (TME_{add}). We completed the
 238 analyses at the plot level by considering also tree volume increment (TVI) of maritime pine and silver
 239 birch individual trees in monocultures and mixed plots.

240 Models of SVI and TVI included the effects of stand density (low, medium and high) and tree diversity
 241 (monoculture vs. two-species mixture) as fixed effect factors. Models of ME and TME included the
 242 effects of stand density (high and medium) and mixture scenario (substitution vs. addition) as fixed
 243 effect factors. We added Block as a random effect estimating between-block variability, except for
 244 analyses conducted at the level of individual tree where we nested plot within block to account for the
 245 non-independence of multiple trees sampled within the same plots and blocks.

246 To consider the residual heteroscedasticity, analyses of SVI and TVI were carried out by introducing a
247 variance model into the linear mixed models allowing unequal variance among experimental
248 treatments (Pinheiro & Bates, 2006).

249 RESULTS

250 TREE SPECIES SUBSTITUTION

251 The substitution of silver birch by maritime pine multiplied significantly SVI by 3.6 at medium stand
252 density (Figure 3, $38.8 \pm 5.67 \text{ m}^3/\text{ha}$, $n=18$; S1 in Figure 1) as well as at high stand density (Figure 3,
253 $56.6 \pm 10.6 \text{ m}^3/\text{ha}$, $n=8$; S2 in Figure 1). Conversely, species substitution of maritime pine by silver birch
254 decreased significantly SVI by 35% (Figure 3, S3 in Figure 1) and 36% (Figure 3, S4 in Figure 1) at medium
255 and high stand density.

256 Birch-pine mixtures obtained through the substitution scenario were significantly less productive than
257 the most productive (pine) monoculture ($\text{TME}_{\text{sub}} < 0$, Figure 4) at both medium (-0.35 ± 0.08 , $n=8$) and
258 high (-0.35 ± 1.45 , $n=8$) species density. Mixture effect (ME_{sub} , figure 4) indicated that pine-birch
259 mixtures was marginally significantly more productive (overyielding) than their component
260 monocultures at medium (0.10 ± 0.14 , $n=8$) and at high stand density (0.10 ± 0.20 , $n=8$, Figure 4).

261 Species substitution had opposite effects on TVI (tree volume increment) of the two studied species at
262 medium stand density: a substitution of maritime pine by silver birch caused a significant increase of
263 15% in pine TVI (Figure 5), but a significant reduction of 23% in birch TVI (Figure 5). At high stand
264 density, species substitution did not have any significant effect on TVI of silver birch or maritime pine
265 (Figure 5).

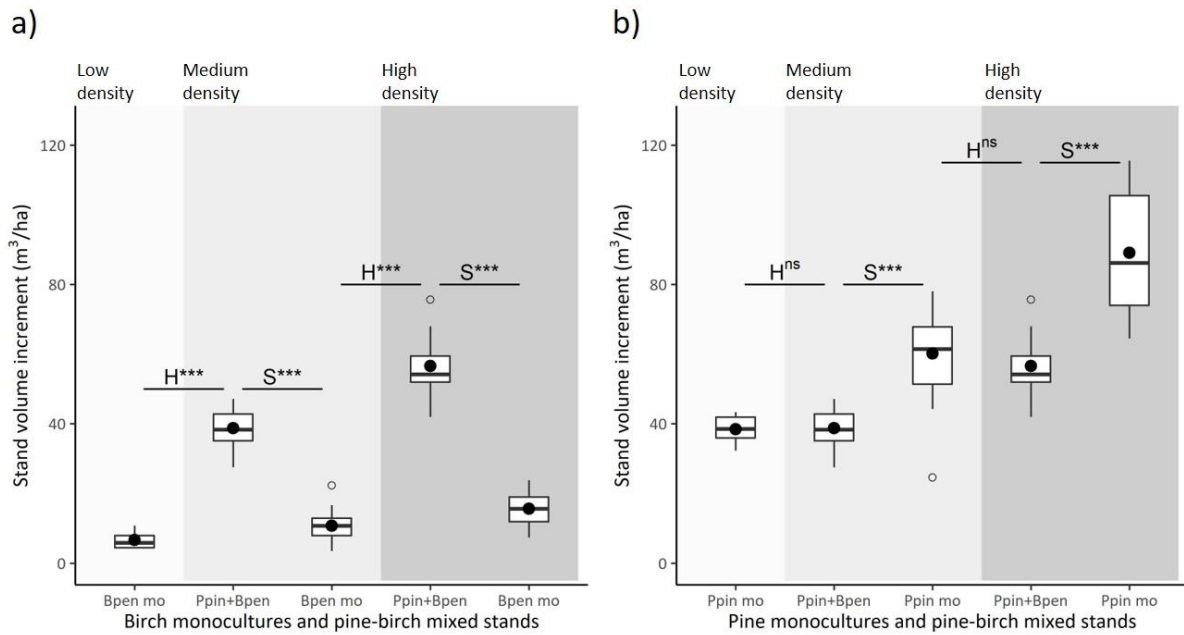
266 HETEROSPECIFIC TREE ADDITION

267 Heterospecific species addition of maritime pine in silver birch stands multiplied significantly SVI by 5.8
268 at medium stand density (Figure 3, H1 in Figure 1) and by 5.2 at high stand density (H3 in Figure 1).
269 Heterospecific species addition of silver birch in maritime pine stands did not have any significant
270 effect on SVI neither at medium stand density (Figure 3, H3 in Figure 1) nor at high stand density (H4
271 in Figure 1).

272 ME_{add} indicated that pine-birch mixtures were significantly less productive (underyielding) than their
273 component monocultures at intermediate (-0.14 ± 0.07 , $n=8$) and at high stand density (-0.19 ± 0.16 , $n=8$,
274 Figure 4). TME_{add} at medium (0.01 ± 0.10 , $n=6$) and high (-0.05 ± 0.20 , $n=8$) stand density were not

275 significantly different from zero indicating that SVI of mixed stands did not differ from SVI of pine in
276 monoculture, i.e. no transgressive overyielding (Figure 4).

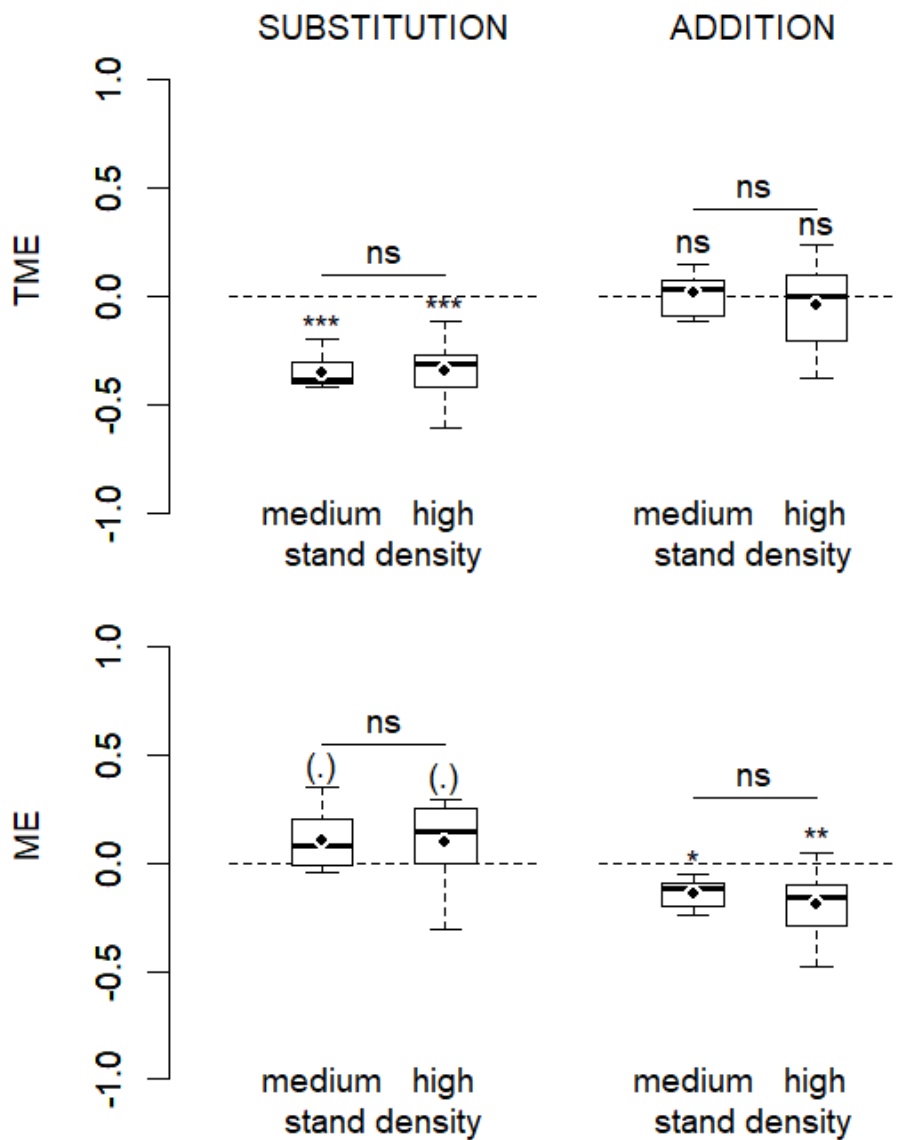
277 Heterospecific addition of silver birch in monoculture of maritime pine did not cause any significant
278 change in TVI of maritime pine at medium stand density (Figure 5) but a significant reduction of 17%
279 (Figure 5) at high stand density. Heterospecific addition of maritime pine in in monoculture of silver
280 birch caused a significant reduction in TVI of silver birch of 42% (Figure 5) and 36% (Figure 5) at medium
281 and high stand density, respectively.



282

283 Figure 3 Stand volume increment (SVI) for different plot composition: in monoculture (mo) the SVI is
 284 the sum of tree volume increment of the target species; in mixed plots (Ppin + Bpen) the SVI cumulates
 285 the tree volume increment of silver birch (Bpen) and maritime pine (Ppin). Effect of heterospecific
 286 addition (H, see solid arrows in Figure 1) and species substitution (S, see black arrows in Figure 1) on
 287 stand volume increment (SVI) of silver birch (a) and maritime pine (b) at low, medium and high stand
 288 density. Black dots indicate mean values. Significance at a level of 5% were indicated by stars (.) 0.1 >
 289 p-values > 0.05; * 0.05 > p-values > 0.01; ** 0.01 > p-values > 0.001; *** p-values > 0.001; ns no
 290 significant effect). Note that SVI_{Ppin + Bpen} of the medium and high density mixed stands are the same in
 291 a) and b).

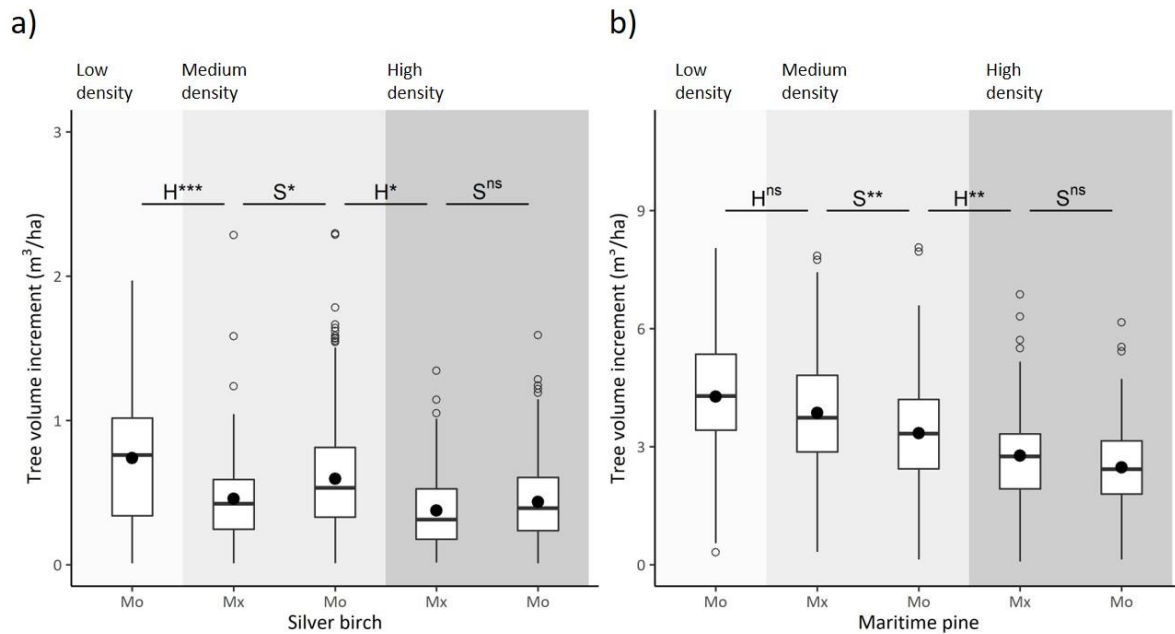
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293

294 Figure 4 Transgressive mixture effect (TME) and mixture effect (ME) at the stand level for species
295 substitution and species addition at medium and high stand density. Black dot indicates the mean
296 effects. Significance at a level of 5% were indicated by stars ((.) 0.1 > p-values > 0.05; * 0.05 > p-values
297 > 0.01; ** 0.01 > p-values > 0.001; *** p-values > 0.001; ns no significant effect)

298



299

300 Figure 5 Effect of heterospecific species addition (H) and species substitution (S) on tree volume
301 increment (TVI) of silver birch (*Betula pendula*) (a) and maritime pine (*Pinus pinaster*) (b) at low,
302 medium and high stand density and in monoculture (Mo) or mixed (Mx) plots. Black dots indicate mean
303 values. Significance at a level of 5% were indicated by stars ((.) 0.1 > p-values > 0.05; * 0.05 > p-values
304 > 0.01; ** 0.01 > p-values > 0.001; *** p-values > 0.001; ns no significant effect). Note that the scales
305 of the two figures (m³/ha) are different.

306 DISCUSSION

307 Our study assessed the role of tree species addition and species substitution in mixture effect in stands
308 at an early age. We highlighted that when controlling for stand density, overyielding in young silver
309 birch – maritime pine stands was due to a relaxation of intra-individual competition for pine.
310 Conversely addition of silver birch (the least productive species) in a maritime pine stand (the most
311 productive species) did not have a negative impact on stand productivity, which implies a non-
312 significant transgressive mixture effect. Eventually stand density had little impact on the mixture
313 effects tested and rather contribute to the species responses at an individual scale.

314 1§ SPECIES SUBSTITUTION TRIGGERED OVERYIELDING IN MIXTURE OF TWO PIONEER SPECIES

315 Respective growth rates of tree species are crucial for interactions between species in the early stages
316 of development of mixed forests and our results confirm that positive effects of biodiversity on
317 productivity are mainly due to selection effect (Tobner et al., 2016) i.e. a fast-growth and productive
318 species driving ecosystem functioning. Competitive advantage is common in young forests and positive
319 diversity-productivity relationship at this stage are often attributed in a lesser extent to
320 complementarity, particularly in harsher conditions (Van de Peer et al., 2018). Such positive effects are
321 commonly attributed to differences in shade tolerance as species with rapid growth rates benefit from
322 a relaxation of intraspecific competition, which may or may not be accompanied by niche separation
323 favouring shade-tolerant species rapidly overtopped due to their lower height growth rate (Boyden et
324 al., 2009; Tobner et al., 2016). However, we evidenced that overyielding can be triggered by species
325 similarities in their shade tolerance. Mixture effect was not conditioned by different light acquisition
326 strategies but more probably by their unequal ability to both tolerate drought. The experimental
327 plantation was on sandy heathlands that experience intense drought episodes in summer, water
328 availability is an important limiting factor for tree growth, especially in silver birch, which has the
329 lowest drought tolerance. Maritime pine is able to maintain its stem growth during a longer period and
330 even to restart height grow in autumn (fast-growth evergreen species, (Heuret et al., 2006)). Silver
331 birch remains a species sensitive to interspecific competition at a young age, even in the Nordic
332 countries where temperature is a more limiting factor for growth than water (Jucker et al., 2020), but
333 it is likely that dry conditions further accentuate its competitive disadvantage.

334 Nonetheless effects that we observed 8 (7?) years after planting will change very quickly, the growing
335 gap in height between maritime pine and silver birch being detrimental to birch under current climatic
336 conditions, tree mortality will intensity (Morin et al., 2020). Long term simulations of pine and birch
337 stand showed a lasting overyielding due to the relaxation of intraspecific competition for pine over

338 time (Morin et al., 2020). Oaks species with their slower growth rates and varying drought and shade
339 tolerances will gradually establish into stands, leading to a stand stratification possibly suitable to
340 mixed stands, even though at this point, there is no consensus on the stage of forest development for
341 which the positive effect of diversity peak (Jucker et al., 2020; Taylor et al., 2020).

342 2§ TRANSGRESSIVE MIXTURE EFFECT WAS NOT SIGNIFICANTLY DIFFERENT FROM ZERO IN THE
343 ADDITION SCENARIO

344 We did not find any transgressive mixture effect in mixed birch-pine stand created by addition of the
345 two species. Conversely the substitutive approach caused a loss of mixed stand productivity compares
346 to pine monocultures due to the substitution of a high productive species (maritime pine) by a low
347 productive species (silver birch). These findings mirror what has been found in colder and more humid
348 sites for the same species that we studied (Frivold & Frank, 2002), more generally in mixed-forest
349 (Jactel et al., 2018) and in plant community where positive transgressive overyielding were rarely
350 reported (Cardinale et al., 2007).

351 At a medium stand density in the additive scenario the absence of any competition effect of silver birch
352 on maritime pine can be explained by two inseparable mechanisms: either, a purely neutral effect of
353 the addition of the least productive species due to an insufficient proximity of stems, or a facilitating
354 effect of birch on soil resource that compensates for a weak competitive constraint due to species
355 addition. Leaves of silver birch have a rate of decomposition higher than needles of Pinus species
356 (Palviainen et al., 2004) and depending on the stand structure, nutrient cycling can be higher in birch
357 regeneration than in pine regeneration (De Schrijver et al., 2009). Hence in the studied site, carbon
358 and nitrogen at an intermediate soil depth have been found higher in mixed stands than on
359 monospecific stands (Maxwell et al., 2020), even though there is no evidence on belowground
360 complementarity of fine roots (Altinalmazis-Kondylis et al., 2020).

361 These findings are also of great ecological relevance because they demonstrate that it is possible to
362 diversify pine monocultures with addition of birch at an early age and then benefit from ecosystem
363 services such as pest protection (Damien et al., 2016; Jactel et al., 2019) and increased diversity of
364 predatory insects (Jouveau et al., 2020) without compromising the wood production of the target
365 species (here maritime pine). Long-term simulations of pine and birch growth on the study sites
366 supported our results (Morin et al., 2020) showing that the ecosystem services associated with pine
367 monoculture diversification can persist as the stand ages.

368 3§ MIXTURE EFFECTS AND TRANSGRESSIVE MIXTURE EFFECTS DO NOT CHANGE WITH STAND DENSITY,
369 BUT TREE PRODUCTIVITY DOES.

370 In young stands, high stand densities usually speed up mixture effects (Tobner et al., 2016; Van de Peer
371 et al., 2018). In this study, we did not observe any intensification with stand density neither of the
372 mixture effect nor of transgressive mixture effect. However, an intensification of interactions with
373 stands density was observed at the tree level: at medium density, heterospecific addition did not affect
374 maritime pine trees (the most productive species) but silver birch trees (the least productive species).
375 At high density, the intensification of interspecific competition led to a reduction of productivity for
376 both species. Regarding species substitution, at medium density maritime pine (the most productive
377 species) benefit from mixture at the expense of silver birch (the least productive species). When stand
378 density increased, the difference between inter and intraspecific competition becomes narrower,
379 which might explain the absence of any effect of species substitution. This illustrates on the one hand
380 that the same response pattern in term of mixture effect can emerge from different mechanisms at
381 the individual levels and. On the other hand, it is consistent with what has been observed elsewhere
382 in young and dynamic stages with an intensification of competitive interactions (Boyden et al., 2009)
383 or at least a decrease in overyielding with density (Kweon & Comeau, 2019). Finally, these results
384 contrast with the intensification of the positive diversity productivity relationship observed as forest
385 stands become older (Huang et al., 2018) particularly when shade tolerant and shade intolerant species
386 are mixed (Brunner, 2020; del Rio & Sterba, 2009).

387 CONCLUSION

388 By controlling stand density and species identity, we have shown that selection effect is the main driver
389 of positive diversity – productivity relationships in the early stages of mixed species forests. This calls
390 for a careful choice of which tree species to associate when designing plantations of mixed species,
391 especially of fast-growing species. In addition, our results also showed that the addition of a pioneer
392 and low-demand species to a monoculture of a high productive species in young developmental stages
393 offers the opportunity to benefit from ecosystem services associated to mixed stands without affecting
394 the productivity of the target species. The addition of tree species is a promising way to promote
395 multifunctionality in mixed-species plantations and to preserve the harvest of a particular species for
396 timber production, thus circumventing two major obstacles in the implementation of mixed-species
397 forestry.

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402 AUTHORS' CONTRIBUTIONS

403 All authors contributed critically to conceived the ideas and designed methodology; HJ designed the
404 ORPHEE experiment; MT analysed the data; MT and CM led the writing of the manuscript. All authors
405 contributed critically to the drafts and gave final approval for publication.

406 DATA AVAILABILITY STATEMENT

407 Data will be available from the INRAE Digital Repository <https://data.inrae.fr/dataverse/biogeco>.

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