



## Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*-*Fagus sylvatica* mixtures across Europe

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1 **Species interactions increase the temporal stability of community productivity in *Pinus***  
 2 ***sylvestris-Fagus sylvatica* mixtures across Europe**

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57 Running headline:

58 Species interactions enhance stability in mixed forests

59

60 **Abstract**

61

62 1. There is increasing evidence that species diversity enhances the temporal stability of  
63 community productivity in different ecosystems, although its effect at population and tree  
64 levels seems to be negative or neutral. Asynchrony between species was found to be one of  
65 the main drivers of this stabilizing process. However, scarce research in this area has been  
66 undertaken in forest communities, so determining the effect of species mixing on the stability  
67 of forest productivity as well as the identity of the main drivers involved still poses a  
68 challenging task.

69 2. We investigate the way in which mixing species influences the temporal stability of  
70 productivity in *Pinus sylvestris* L. and *Fagus sylvatica* L. forests, and attempt to determine the  
71 main drivers. We used a network of 93 experimental plots distributed across Europe to  
72 compare the temporal stability of basal area growth over a 15-year period (1999-2013) in  
73 mixed and monospecific forest stands at different organizational levels, namely community,  
74 population and individual tree levels. Overyielding, asynchrony between species, and species  
75 interactions were explored as possible drivers of temporal stability of productivity.

76 3. Mixed stands showed a higher temporal stability of basal area growth than monospecific  
77 stands at community level, but not at population or individual tree levels. Asynchrony  
78 between species growth in mixtures was related to temporal stability, but neither overyielding  
79 nor asynchrony between species growth in monospecific stands were linked to temporal  
80 stability. Therefore, species interactions modify between-species asynchrony in mixed stands.  
81 Accordingly, temporal shifts in species interactions were related to asynchrony and to the  
82 mixing effect on temporal stability.

83 4. Synthesis. Our findings confirm that species mixing can stabilize productivity at  
84 community level whereas there is a neutral or negative effect on stability at population and  
85 individual tree level. The contrasting findings as regards the relationships between temporal  
86 stability and species asynchrony in mixed and monospecific stands suggest that the main  
87 driver in the stabilizing process is the temporal niche complementarity between species rather  
88 than differences in species specific responses to environmental conditions.

89

90 **Keywords**

91

92 Temporal variability; mixed-species forests; plant-plant interactions; overyielding;  
93 asynchrony; niche complementarity; organizational levels;

94

95 **Introduction**

96

97 Mixed-species stands are widely thought to provide many forest functions and services more  
98 effectively than monocultures (Hector & Baghi 2007; Gamfeldt *et al.* 2013; van der Plas *et*  
99 *al.* 2016). The superior level and stability of productivity in mixed forests is of interest for  
100 most functions and services, as well as being a precondition for the promotion of this

101 alternative in forestry practice. Much evidence exists that mixed-species stands often produce  
102 greater yields than monocultures (Piotto 2008; Paquette & Messier 2011; Vilà *et al.* 2013;  
103 Pretzsch *et al.* 2015; Liang *et al.* 2016) although contradictory findings of underyielding  
104 (Chen *et al.* 2003; Carvard *et al.* 2010) discourage generalization. Many studies show that  
105 mixing may improve different aspects related to the stability of productivity (Jucker *et al.*  
106 2014; Pretzsch, Schütze & Uhl, 2013; de Dios-García, Pardos & Calama, 2015; Metz *et al.*  
107 2016), but again, the findings of other research suggest the opposite (Grossiord *et al.* 2014;  
108 Merlin *et al.* 2015). Among the probable reasons for these varying and seemingly inconsistent  
109 findings are differences in the complementarity of the analyzed species assemblages (Toïgo *et al.*  
110 *et al.* 2015) as well as the underlying site conditions with their specific growth limiting factors  
111 (Forrester 2014). Findings may also differ depending on the level of analysis, as mixing  
112 effects in forest communities are frequently studied at stand, species, or individual tree level;  
113 the results not necessarily being the same (Forrester & Pretzsch 2015). The conservation and  
114 management of productive, stable, and resource-use efficient mixed-species stands requires an  
115 improved understanding of the mechanisms involved, which could also contribute towards  
116 theory development and greater generalization with regard to these forests.

117 The term ‘stability’ in ecosystems includes several concepts such as resistance, resilience or  
118 temporal stability of productivity, all of which address diversity-stability relationships  
119 (McCann 2000; Ives & Carpenter 2007). In the case of forests, temporal variability of  
120 community productivity is an important ecological property because stability of productivity  
121 is an indicator of sustainability of both forest functioning and the delivery of ecosystem  
122 services (Blüthgen *et al.* 2016). Temporal variability is usually measured by the coefficient of  
123 variation or its inverse, i.e temporal stability then depends on the mean and standard deviation  
124 (Tilman, Lehman & Bristow 1998). Different statistical and biological mechanisms have been  
125 identified as possible causes of increasing temporal stability as regards species diversity.  
126 These include overyielding, species asynchrony and species interactions (Hector *et al.* 2010,  
127 Loreau & Mazancourt 2013; Blüthgen *et al.* 2016). Overyielding means higher productivity in  
128 mixtures than in the corresponding monospecific systems, which may lead to a stabilizing  
129 effect by a higher mean if other factors remain constant (Tilman 1999). Species asynchrony  
130 exists when the temporal responses of the species are not perfectly positively correlated. Such  
131 increases in the variability of responses may result in a reduction in the community  
132 variability. Asynchrony of species-specific responses to environmental fluctuations has been  
133 reported as a key factor in temporal stability (Loreau & de Mazancourt 2008; Hector *et al.*  
134 2010), in accordance with the insurance hypothesis (Yachi & Loreau 1999). However, species  
135 interactions can also trigger species asynchrony by compensatory dynamics between species  
136 (Tilman, Lehman & Bristow 1998; Morin *et al.* 2014), which might result in less variation at  
137 community level (Loreau & de Mazancourt 2013). Species interactions may also involve  
138 temporal stability as a consequence of their effect on overyielding, and at the same time  
139 overyielding may be linked to species asynchrony (Allan *et al.* 2011). These direct and  
140 indirect relationships make it difficult to disentangle the key mechanisms and therefore the  
141 relative importance of the different mechanisms on the diversity-stability relationship is still  
142 poorly understood (Loreau & de Mazancourt 2013).

143 In general, diversity has been found to have a stabilizing effect on productivity at community  
144 level, but a destabilizing effect at population levels by increasing competitive interactions  
145 (Hector *et al.* 2010; Gross *et al.* 2014). However, contrasting results have been obtained at  
146 population level (Jiang & Pu 2009), even among the scarce studies undertaken in forest  
147 communities (Jucker *et al.* 2014; Morin *et al.* 2014). This trade-off between the effects at  
148 different organizational levels might be crucial in ecosystems with few species, where the  
149 species specific dynamic can be of major interest, as in many European temperate mixed  
150 forests comprising only two or three species.

151 Diversity-productivity relationships in forests have been found to depend on environmental  
152 gradients (Pretzsch *et al.* 2010; Toïgo *et al.* 2015; Jucker *et al.* 2016), since the result of the  
153 interactions among species changes depending on the growing conditions (Forrester, 2014;  
154 Forrester & Bauhus, 2016). The growth response of tree species to climatic conditions as well  
155 as temporal variation in climate-growth relationships also vary considerably among sites  
156 (Lloyd & Fastie 2002; Tardif *et al.* 2003). Therefore, differences in diversity-stability  
157 relationships might also be expected along ecological gradients, with the relative importance  
158 of different mechanisms varying along the gradients (Hallet *et al.* 2014; Xu *et al.* 2015).

159 The number of studies concerning the relationship between diversity and temporal stability of  
160 productivity based on empirical data in forests is far fewer than in grasslands communities.  
161 This is due to the inherent arduousness involved in carrying out experiments with tree species,  
162 due to their long life span, as well as the difficulties of conducting observational studies in  
163 natural ecosystems, where many often uncontrollable factors interact. In a recent study, Jucker  
164 *et al.* (2014) analysed several monospecific and mixed forests of 16 target species in Europe  
165 (Jucker *et al.* 2014) and found a positive effect of species diversity on the stability of wood  
166 productivity. However, a previous study found the opposite for conifer mixed forests in Sierra  
167 Nevada, California (DeClerck, Barbour & Sawyer 2006). Therefore, further research is  
168 required to elucidate the mixing effect on temporal stability of productivity and the  
169 underlying mechanisms for different forest species assemblages and sites.

170 In this study we focus on two tree species, *Pinus sylvestris* L. and *Fagus sylvatica* L., growing  
171 in mono-specific and mixed forests across a large range of their distribution. This design  
172 allows us to infer the general effect of this admixture on the temporal stability of productivity  
173 while considering the large spatial variability in site conditions across Europe. This mixture  
174 was selected because it includes a combination of species with highly complementary traits,  
175 including an early and a late-successional species, a light-demanding as opposed to a shade-  
176 tolerant species, and a conifer with a broad-leaved species. Actually, the mixture between *P.*  
177 *sylvestris* and *F. sylvatica* was found to shown significant mixing effects in terms of  
178 productivity and structural heterogeneity (Pretzsch *et al.* 2015, 2016). It may serve as a model  
179 system for other widespread species combinations of comparable spatial and temporal  
180 complementarity in traits.

181 The main hypotheses in this study are that: (i) temporal stability of productivity is higher in  
182 mixed than in mono-specific stands at community level but not at population and individual  
183 tree levels; (ii) in this model mixture, the dynamics of species interactions is one of the  
184 drivers in stabilizing productivity due to the complementary traits of these species; and (iii)

185 the mixing effect on temporal stability depends on site conditions. Our main objective is  
186 therefore to explore whether mixing species of contrasting traits increases the temporal  
187 stability of productivity at different organizational levels and if so, to elucidate the main  
188 underlying mechanisms in order to better understand the inter-specific dynamics of the  
189 *P.sylvestris* - *F.sylvatica* and comparable mixtures.

190

## 191 MATERIAL AND METHODS

### 192 Field data and study design

193 The study data come from a transect of plots in mixed and monospecific forest stands of *P.*  
194 *sylvestris* (Scots pine) and *F. sylvatica* (European beech) along an environmental gradient.  
195 The transect was established voluntarily and nationally-funded by members of the COST  
196 Action FP1206 EuMIXFOR (see [www.mixedforests.eu](http://www.mixedforests.eu)). The main aim of the initiative was  
197 to study the variability of over-yielding, structural properties and stability under different  
198 environmental conditions in monocultures and mixtures (see for example Pretzsch *et al.* 2015;  
199 2016). The study design was based on the ‘triplet’ concept (Pretzsch *et al.* 2014), i.e. at each  
200 location three plots were established, one in a mixed-species stand and two in the respective  
201 monocultures, with similar site conditions (soil and topographic conditions) in order to allow  
202 meaningful comparisons between mixtures and monocultures. A total of 31 triplets (93 plots)  
203 were set up across the main distribution area of this mixture in Europe (Fig. 1), covering a  
204 large environmental gradient, mainly determined by water supply. Climate data were gathered  
205 from all available meteorological stations in the proximity of each triplet (see Table S1 in  
206 Supporting Information for detailed information about climate and site conditions).

207 The three plots for each triplet were installed in even-aged, fully-stocked forest stands of  
208 similar age in which thinning treatments had not been recently applied (for details see Table  
209 S2 and Pretzsch *et al.* 2015, 2016). The mixed plots represent tree-wise mixtures with species  
210 proportions that range from 18% to 72 % of pine, although in most of them the proportion is  
211 around 50%. Plots are rectangular with varying sizes from 0.02 to 1.55 ha. In each plot, the  
212 tree species, tree diameter, height and height to the crown base were recorded for all trees. In  
213 a sub-sample of 20 trees per plot and species two increment cores were extracted at a stem  
214 height of 1.30 m for tree ring analysis. Annual growth series were cross-dated and the  
215 arithmetic means of the annual ring widths of the two cores were used for further analysis. A  
216 description of the main stand characteristics in mixed and monospecific stands are provided in  
217 Table S2.

### 218 Productivity data at different organizational levels

#### 219 *Community level*

220 As a proxy to represent community biomass productivity we use stand basal area growth per  
221 hectare, as it is closely linked to measured variables in the field. In contrast to other studies  
222 which focused on aboveground biomass growth when studying diversity-productivity and/or  
223 diversity-stability relationships (Paquette & Messier 2011; Jucker *et al.* 2014, 2016), we  
224 relied on basal area growth. Calculation of stand biomass growth would have required height-  
225 diameter functions and tree biomass allometric functions for all sites. However, it is well  
226 known that such calculations could lead to additional uncertainty at least in mixed stands  
227 (Toïgo *et al.* 2015) as the respective functions were derived from data of monospecific stands.  
228 Using these functions may have caused biased estimations of biomass growth as mixing tree  
229 species can modify tree allometry (Pretzsch 2014) as well as between-tree growth partitioning

230 (Binkley *et al.* 2003; Pretzsch & Schütze 2014), suggesting the need of specific functions for  
231 mixtures (Forrester & Pretzsch 2015; Río *et al.* 2016).

232 Our study focuses on the temporal stability and over-yielding during the 15 year period prior  
233 to the inventory (1999-2013). This period was chosen because it covers sufficient years to  
234 provide meaningful information on temporal variability in growth, whilst avoiding bias from  
235 unknown tree mortality or tree removal which could have interfered the results as mixing may  
236 change species-specific mortality rates (Zhao *et al.* 2006; Condés & Río 2015).

237 Stand basal area was calculated as the sum of the cross sectional area (at 1.3 m above ground  
238 level) of all the trees measured at a given time. Stand basal area increments per year were  
239 determined based on cored trees and non-cored trees. In the case of sampled trees, we used  
240 tree ring series to reconstruct tree diameters over bark for each of the 15 years of the study  
241 period. To estimate the diameter increments of non-cored trees we fitted diameter increment  
242 functions for each plot and species per year, based on diameter increments and tree diameters  
243 of cored trees (31 triplets \* 4 (two tree species in mixed and monospecific stand) \* 15 years =  
244 1980 functions for the studied period 1999-2013). We used log-log models ( $\ln(id)=a_0+a_1 \times$   
245  $\ln(d)$ ), where  $id$  is the tree diameter increment for that year ( $\text{cm year}^{-1}$ ) and  $d$  is the tree  
246 diameter at breast height (cm).

#### 247 *Population level*

248 To study the productivity at population level we additionally calculated the annual basal area  
249 increment (BAI) per species in mixed plots. In order to compare species behavior in mixed  
250 and monospecific stands we scaled up the species specific basal area increment series in  
251 mixed stands to one hectare using species basal area proportions. As species proportion can  
252 change from one year to another due to the different annual basal area increments between  
253 species we calculated species proportions per year through the estimated annual basal area per  
254 species.

#### 255 *Individual tree level*

256 At individual tree level we used the measured tree ring widths from cored trees transformed to  
257 individual tree basal area increments. As the tree growth response to variability in  
258 environmental conditions and to intra- and inter-competition level depends on tree social  
259 status (Martín-Benito *et al.* 2008; Zang, Pretzsch & Rothe 2012; Río, Condés & Pretzsch  
260 2014) we used only dominant and codominant trees (1691 trees), selected through the  
261 diameter and height distributions per species and plot.

### 262 **Data evaluation and analysis**

#### 263 *Temporal Stability at different organizational levels*

264 Temporal stability (TS) at the different organizational levels was calculated as the inverse of  
265 coefficient of variation for the 15 year study period, i.e. the ratio of mean basal area increment  
266 to its standard deviation. This measure is often preferred to the coefficient of variation, as the  
267 latter decreases with stability and when the stability increases it approaches zero (Lehman &  
268 Tilman 2000). Statistics of the mean, standard deviation and temporal stability of annual basal  
269 area increment at the different organizational levels are presented in Table S3.

270 The effect of mixing species on temporal stability of productivity at community and  
271 population level was analyzed using a mixed linear model including the species composition  
272 of the plot as a fixed factor. First we compared mixed vs monospecific stands, and in a second  
273 step we considered species identity of monospecific plots. Data were log-transformed to  
274 correct heteroscedasticity in residuals.



275 
$$\ln(\text{TS}_{ij}) = (a_0 + a_{0j}) + a_1 \cdot \text{composition} + \varepsilon_{ij} \quad \text{eqn 1}$$

276 where  $\text{TS}_{ij}$  is the temporal stability of the annual basal area increment for the plot  $i$  in the  
 277 triplet  $j$ ; composition is a dummy variable with two levels, mixed and monospecific, or three  
 278 levels, mixed, monospecific pine and monospecific beech;  $a_0$  and  $a_1$  are parameters to be  
 279 estimated. We included a random effect ( $a_{0j}$ ) due to the hierarchical structure of the data to  
 280 account for possible correlation of the three plots within a triplet. Covariates potentially  
 281 influencing TS included climatic attributes and their interaction with species composition  
 282 were tested. At tree level we fitted a similar model but taking also the effect of tree size on  
 283 temporal stability into account.

284 In order to study the effect of mixing on TS at different organizational levels we first defined  
 285 the mixing effect as the ratio of TS in mixed stands to TS in monospecific stands  
 286 ( $\text{TS}_{\text{mixed}}/\text{TS}_{\text{mono}}$ ) and then we analyzed the correlation between the ratios at community,  
 287 population and individual tree levels.

### 288 *Overyielding*

289 The over- or under-yielding values per triplet were estimated using the ratio of productivity  
 290 (RPP) (Harper, 1977),  $\text{RPP} = \sum P_{i,\text{mix}}/P_{i,\text{mono}}$ , where  $P_{i,\text{mix}}$  is the observed productivity (i.e. basal  
 291 area increment) of species  $i$  in the mixed stand and  $P_{i,\text{mono}}$  is the productivity of species  $i$  in  
 292 the monospecific stand. We estimated the RPP per year and triplet for the 15 year study  
 293 period and then averaged them per triplet.

294 To estimate the overyielding at population level we used the relative productivity per species  
 295 ( $\text{RP}_i$ ) (Pretzsch *et al.* 2013; Río *et al.* 2016), i.e. the ratio of the observed productivity of  
 296 species  $i$  in the mixed stand (up-scaled to one hectare) to the observed productivity of the  
 297 respective species in the monoculture,  $\text{RP}_i = (P_{i,\text{mix}}/m_i)/P_{i,\text{mono}}$ , where  $m_i$  is the species  
 298 proportion estimated by the proportion of species  $i$  in the stand basal area for a given year. As  
 299 for RPP,  $\text{RP}_i$  were estimated per year and later averaged for the 15 years in order to consider  
 300 the possible influence of temporal changes on species proportion. We tested whether the mean  
 301 RPP and  $\text{RP}_i$  were significantly different from one, i.e. significant over- or under-yielding,  
 302 using a t-student test, and the possible relationship between overyielding and temporal  
 303 stability at different levels through simple linear models. At community level we studied the  
 304 possible influence of RPP on the temporal stability in mixed stands ( $\text{TS}_{\text{mixed}}$ ) and on the  
 305 mixing effect ( $\text{TS}_{\text{mixed}}/\text{TS}_{\text{mono}}$ ). At population level we related the  $\text{RP}_i$  to the mixing effect, i.e.  
 306 ratio of TS at population level.

### 307 *Asynchrony*

308 To estimate the species asynchrony we used the coefficient of correlation between the growth  
 309 series of the two species growing in mixed stands ( $r_{\text{mixed}}$ ); a value of -1 means complete  
 310 asynchrony between species' growths and +1 indicates complete synchrony. This approach is  
 311 similar to that proposed by Gross *et al.* (2014), although in its simplest version of a mixture  
 312 composed of only two species. Additionally, we studied the correlation between the basal area  
 313 increment series of the two species growing in monocultures ( $r_{\text{mono}}$ ), as this correlation might  
 314 express the differences or the similarity in the dependence of the two species on inter-annual  
 315 environmental conditions, i.e. the asynchrony of the intrinsic response of each species to  
 316 environmental fluctuations (Loreau & de Mazancourt 2013). Species asynchrony was  
 317 estimated at the community level by stand basal area increment series of the two species. At  
 318 tree level it was studied by species specific mean tree basal area increment series.

319 We explored the role of species asynchrony in TS in a similar way than for overyielding, i.e.  
 320 by using linear models for relating  $\text{TS}_{\text{mixed}}$  and the ratios of  $\text{TS}_{\text{mixed}}/\text{TS}_{\text{mono}}$  to  $r_{\text{mixed}}$  and  $r_{\text{mono}}$  at

321 different levels. Furthermore, we tested whether there was any relationship between species  
322 asynchrony and overyielding.

### 323 *Temporal variation in species interactions*

324 To study the inter-annual variation in species interactions depending on annual growing  
325 conditions we used a similar approach to that used in Río, Schütze & Pretzsch (2014). We  
326 compared the annual productivity in mixed stands to the respective reference productivity.  
327 The latter reflects conditions where no mixing effect takes place, which is calculated as the  
328 sum of the productivities of the two species in monospecific stands times their proportion in  
329 the mixed stand ( $\sum P_i \cdot m_i$ ) (Pretzsch *et al.* 2013; Río *et al.* 2016). When the annual basal area  
330 increment in the mixed stand is higher than the reference basal area increment, there is a  
331 positive species interaction or overyielding; whereas if one year it is lower this indicates that  
332 there is negative interaction or underyielding. In this section, as the aim is to study the  
333 temporal variation in species interaction but not the net effect or overyielding, we  
334 standardized the observed and reference basal area increment series by dividing them by the  
335 mean and we built the respective basal area growth indices series (IBAI<sub>mixed</sub> and IBAI<sub>ref</sub>) to  
336 remove the net overyielding effect for the 15 year period (see Fig S1).

337 A year was considered to have favorable growing conditions when the IBAI was high and  
338 unfavorable when the IBAI was low. To test whether annual species interactions vary  
339 depending on growing conditions we fitted a linear model relating the two growth indices  
340 series (IBAI<sub>mixed</sub> = f(IBAI<sub>ref</sub>)). If the slope is not different from one, the temporal variation in  
341 species interaction does not depend on annual growing conditions (i.e variation is similar in  
342 good and bad years), whereas if the slope is different from one it means that the interactions  
343 depend on annual growing conditions (see Fig S1). As the two variables are assumed to be  
344 measured with the same error and we were interested in the slope value and not in predicting  
345 new IBAI values, we used a major regression to estimate the slope per triplet and then  
346 explored if the slope values were related to TS.

## 347 **RESULTS**

### 348 **Temporal stability at different levels: community, species and individual tree level**

#### 349 *Community level*

350 Temporal stability of annual stand basal area increment was lower in the monospecific stands  
351 than in the mixed stands ( $P = 0.010$ ), the observed mean being TS=5.14 and 6.08 respectively.  
352 When the composition of monospecific stand was considered the TS in monospecific  
353 European beech plots was lower than the mixed plots ( $P = 0.012$ ), whereas for Scots pine it  
354 was also lower although the difference was smaller ( $P = 0.052$ ) (Table S4). We tested the  
355 possible influence of climatic variables but found no significant relationships. When  
356 analyzing the mean and the standard deviation of stand BAI there were no statistical  
357 differences between compositions.

#### 358 *Population level*

359 There were no statistical differences between the TS of annual basal area growth in mixed  
360 (expanded to hectare) and in monospecific stands at population levels. For pine, both the  
361 mean of annual basal area increments and the standard deviation were significantly lower in  
362 mixed than in monospecific stands, whereas for beech the mean and the standard deviation  
363 were significantly higher in mixed than in monospecific stands. Climatic variables did not  
364 explain TS variability for either of the two species.

#### 365 *Individual tree level*

366 TS in annual tree basal area increment was significantly different between pure and mixed  
367 plots for pine ( $P < 0.001$ ), being greater in monospecific stands. The inclusion of the tree size  
368 or site covariates did not improve the basic model. The increase in TS in monospecific stands  
369 was due to a higher mean tree BAI, as the differences in the mean were significant between  
370 monospecific and mixed stand whereas in the case of the standard deviation they were not.  
371 For beech, there were no differences in tree TS between mixed and monospecific stands, but  
372 the tree size had a significant effect on tree TS (Table S4). Both the mean and the standard  
373 deviation were significantly higher in the mixed compared to the monospecific stands.

#### 374 *Overall effect*

375 The results showed that at community level the mixture leads to stability of productivity, but  
376 this effect disappears at population level while at tree level the opposite effect was observed  
377 in the case of pine. The stability is lower at population level than at community level,  
378 particularly for beech (Fig. 2a). The mean ratios  $TS_{\text{mixed}}/TS_{\text{mono}}$  at community level were 1.31  
379 and 1.28 for beech and pine respectively, whereas at population level they were not  
380 significantly different from one. There is a positive correlation ( $r$ ) between the mixing effect  
381 on stability at the two levels for both species ( $r = 0.763$   $P < 0.0001$  for pine and  $r = 0.716$   $P$   
382  $< 0.0001$  for beech). If we compare the mixing effect on stability at individual tree, population  
383 and community level we observe that there is no correlation between the effects of mixing on  
384 stability at tree level with the corresponding effects at the other two organizational levels (Fig.  
385 2b).

#### 386 **Overyielding**

387 The mean RPP of all triplets was 1.12 and it was statistically different from 1. This indicates  
388 that there was a general overyielding in stand basal area growth although the variability  
389 among triplets was large with some triplets showing underyielding (Fig S2). The RPP was not  
390 related to any of the site variables analyzed, nor to the TS in mixed stands. Accordingly,  
391 overyielding was not related to any of the mixing effects of TS at community level (ratio of  
392 TS in mixed stands to monospecific stands) (Fig. S2).

393 At population level we found overyielding in the case of beech (Relative productivity ( $RP_{\text{be}} =$   
394  $1.49$ ) and underyielding for pine ( $RP_{\text{pi}} = 0.87$ ), both significantly different from one (note that  
395 there was no correlation between the  $RP_i$  of the two species).  $TS_{\text{mixed}}/TS_{\text{mono}}$  ratio at  
396 population level (i.e. mixing effect on stability) was negatively related to the relative  
397 productivity by species ( $RP_i$ ). Thus, with increasing overyielding stability decreased in mixed  
398 stands (Fig 3). This suggests that at population level, under-yielding is linked to higher  
399 stability for pine, but it is important to highlight the absence of differences between mixed  
400 and monospecific stands in TS at this level.

#### 401 **Species asynchrony**

402 The mean coefficient of correlation between basal area increment series of beech and pine in  
403 the mixed stand ( $r_{\text{mixed}}$ ), or species synchrony at community level, was 0.37, but there was a  
404 high variability among triplets ranging from -0.62 to 0.89 (Fig. 4). The observed high  
405 negative values revealed the presence of a high species asynchrony at community level for  
406 some triplets. The respective mean correlation in monospecific stands ( $r_{\text{mono}}$ ) was similarly  
407 0.37 with a narrower range (-0.39 to 0.87), which indicates that in some triplets the two  
408 species use the annually available site resources differently whereas in other cases the  
409 response to the interannual fluctuations in environmental conditions is quite similar.  
410 However, it is important to highlight that the relationship between  $r_{\text{mixed}}$  and  $r_{\text{mono}}$  was not  
411 significant (Fig. S3), reflecting that the mixture changes the species-specific responses to

412 annual environmental conditions. No effect of any site characteristic on correlation between  
413 species' basal area increments was found.

414 The temporal stability of community productivity in mixed stands was partially explained by  
415 the species asynchrony in mixed plots (Fig. 4), following a quadratic model ( $R^2 = 0.40$ ;  
416  $P < 0.001$ ). For coefficients of correlation higher than 0.6 the  $TS_{\text{mixed}}$  decreases notably.  
417 Therefore, when the species asynchrony was lower, the stability in the mixture was lower.  
418 However, this relationship was not significant when considering the correlation in  
419 monocultures instead of in mixtures (Fig. S4). The mixing effect on stability at community  
420 level (ratio  $TS_{\text{mixed}}/TS_{\text{mono}}$ ) increased in the case of pine when the species asynchrony in  
421 mixed stands was higher ( $R^2 = 0.25$ ;  $P = 0.004$ ), but this effect was not significant for beech  
422 (Fig. S5).

423 At individual tree level the mean correlation between the mean tree basal area growth series  
424 of beech and pine was 0.41 in mixtures, varying between -0.65 to 0.91, whereas the respective  
425 mean correlation in monocultures was 0.32 with a narrower range (-0.35 to 0.77). In contrast  
426 to the results observed at community level, the coefficients of correlation in mixed and  
427 monospecific stands are correlated ( $r = 0.43$ ,  $P < 0.0161$ ). The coefficients of correlation at  
428 tree level and at community level are positively correlated in mixed stands ( $r = 0.58$ ,  $P <$   
429  $0.0005$ ) and in monocultures ( $r = 0.74$ ,  $P < 0.0001$ ). The asynchrony at tree level was not  
430 related to temporal stability at individual tree and species level.

431 The relationship between overyielding (RPP) and species asynchrony in mixed stands at  
432 community level was significant ( $R^2 = 0.20$ ;  $P = 0.011$ ), the overyielding increasing with the  
433 species asynchrony (Fig. 5). However, this relationship was not significant when relating RPP  
434 to the coefficient of correlation in monocultures. Therefore, the species asynchrony in mixed  
435 stands has an influence on the temporal variability and quantity of productivity at community  
436 level.

### 437 **Species interactions**

438 The results of the major regression per triplet, relating the observed and reference stand basal  
439 area growth indices, indicated that the slope was statistically different from one in 10 out of  
440 the 31 triplets ( $P < 0.05$ ), 5 having a slope higher than one and 5 with a slope lower than one.  
441 The relationship between the temporal stability in mixed stands ( $TS_{\text{mix}}$ ) and the slope values  
442 was negative ( $R^2 = 0.21$ ;  $P = 0.010$ ). Hence, higher temporal stability seems to be linked to  
443 slopes lower than one and lower stability to higher slopes. As with other variables, site  
444 characteristics were not significant.

445 Accordingly the slopes were also negatively related to the mixing effect on stability  
446 ( $TS_{\text{mixed}}/TS_{\text{mono}}$ ). In Fig. 6 it can be seen that lower slopes are linked to triplets where the TS  
447 is higher in mixed than in monospecific stands and this is particularly notable for pine ( $R^2 =$   
448  $0.32$ ;  $P = 0.001$  for beech; and  $R^2 = 0.53$ ;  $P < 0.001$  for pine). Thus, the reduction in temporal  
449 variation of productivity in mixed stands compared to monocultures is linked to a temporal  
450 variation in species interaction, this interaction being more positive in years with low growth  
451 rates and more negative in years with high growth rates. In triplets where the stability is  
452 higher in monospecific stands, the slopes tend to be greater than one, which means more  
453 positive interactions in years with high growth and more negative interactions in years with  
454 low growth rates.

455 The slopes explained part of the variability in the coefficient of correlation between basal area  
456 increment series of beech and pine in the mixed stand ( $r_{\text{mixed}}$ ) ( $R^2 = 0.16$ ;  $P = 0.027$ ). The  
457 positive relationships between them suggest that part of the asynchrony observed in mixed  
458 stands is due to temporal changes in species interactions.

459

460 **DISCUSSION**

461 Our findings show that species mixing can stabilize productivity at community level but not at  
462 population level. This stabilizing effect was mainly explained by species asynchrony in the  
463 mixed stands, which was influenced by the species interactions. This result along with the  
464 lack of any relationships between temporal stability and species asynchrony in monospecific  
465 stands suggests that the main driver in the stabilizing process was the temporal niche  
466 complementarity between species rather than differences in species-specific responses to  
467 environmental conditions. Overyielding was not linked to temporal stability but to species  
468 asynchrony in mixed stands, highlighting the important contribution of temporal niche  
469 complementarity to the level and stability of forest productivity.

470 **Drivers of temporal stability and the level of productivity**471 *Overyielding*

472 Overyielding was found to contribute to the stabilization of productivity in different types of  
473 communities (Hector *et al.* 2010; Isbell, Polley & Wilsey 2009, Jucker *et al.* 2014). Our  
474 analysis showed a significant overyielding at community level, but it was not linked to the  
475 temporal stability of productivity (Fig. S2). This result for our two species mixture is contrary  
476 to the findings of Jucker *et al.* (2014) for tree mixtures of 2-4 species. Based on long-term  
477 simulations, Morin *et al.* (2014) reported that temporal stability was weakly driven by  
478 overyielding, which is in line with our results. However, it is important to consider that the  
479 stabilizing effect of overyielding may increase with species diversity, and may therefore have  
480 a relatively small effect in two-species mixtures, such in our case (Hector *et al.* 2010).

481 *Asynchrony*

482 The important role of species asynchrony in community stability has been highlighted  
483 recently in many studies (Roscher *et al.* 2011; Blüthgen *et al.* 2016). The results from our  
484 study confirm that asynchrony in species growth is an important driver of temporal stability  
485 (Fig. 4). Asynchrony of temporal responses to varying environmental conditions between  
486 species has also been identified as a stabilizing factor (Loreau & de Mazancourt 2013).  
487 However, it should be noted that in our case, species asynchrony in monospecific stands was  
488 not related to stability (Fig. S4), indicating that intrinsic species-specific responses to  
489 environmental fluctuations observed in monospecific stands are not necessarily a good  
490 indicator of the stabilizing effect that emerges when species are mixed (Gross *et al.* 2014).  
491 The mixing of Scots pine and European beech therefore changes the intrinsic species  
492 responses to yearly environmental variations at community level in comparison to  
493 monospecific stands, and temporal shifts in species interactions linked to temporal niche  
494 complementarity seem to play a key role in this change. Previous studies concerning forests  
495 have reported changes in the growth response to extreme droughts between mixed and  
496 monospecific stands (Lebourgeois *et al.* 2013; Pretzsch *et al.* 2013), although the results  
497 depended on species composition (Merlin *et al.* 2015; Grossiord *et al.* 2014). Nevertheless,  
498 those studies were either mainly based on tree level growth analyses or made no attempt to  
499 link the tree and community level analyses. Our results indicate that the changes in species  
500 asynchrony between mixed and monospecific stands were considerably lower at tree than at  
501 community level, but also that the asynchronies at the two levels were correlated, the latter  
502 suggesting that differences in species specific responses to variability in environmental  
503 conditions may also affect temporal stability. These results underline the need for further  
504 studies at community level and the importance of linking both levels.

505 The asynchrony-overyielding relationship identified in this study (Fig. 5) suggests that  
506 temporal niche complementarity is one of the most important mechanisms driving  
507 overyielding in this mixture. These results contradict the hypothesis stated by Jucker *et al.*  
508 (2014), who argued that asynchrony might not influence overyielding because it would  
509 require a rapid response in forest dynamics to environmental conditions. However, our study  
510 assumed no diversity effect on mortality, although significant effects of mixing on tree  
511 mortality, self-thinning lines and stand density indices have been reported previously (Binkley  
512 1984, 2003; Condés & Río 2015; Pretzsch & Biber 2016; Woodall, Milles & Vissage 2005),  
513 and may influence overyielding as well as stability.

#### 514 *Species interactions*

515 We found the higher temporal stability in mixed stands to be linked to shifts in species  
516 interactions that influenced the growth response of a given species to inter-annual  
517 environmental conditions. That is, the temporal variation in niche complementarity between  
518 species, which results in compensatory dynamics between species, is one of the main factors  
519 underlying the increase in temporal stability. These results provide an empirical corroboration  
520 of the simulation-based findings of Morin *et al.* (2014), which pointed to the greater  
521 importance of species interactions as opposed to species-specific differences in responses to  
522 environmental conditions. However, the temporal scale and the compensatory dynamics  
523 considered in the simulations are not directly comparable to our approach.

#### 524 **Temporal stability and overyielding at different levels**

525 The different stabilizing effects of species mixing at different organizational levels are in  
526 accordance with theory-based expectations (Tilman 1999; Loreau & de Mazancourt 2013) and  
527 show that the general pattern found in diversity-temporal stability relationships at community  
528 level also occur in the case of mixed forests with two species. Generally, species diversity  
529 increases the temporal stability of productivity at community level, but a high variability in  
530 this effect was reported at population level (Jiang & Pu 2009). In our study, we found a  
531 stabilizing effect at community level, but a neutral effect at population level. This lack of any  
532 destabilizing effect at population level might be explained by the slower growth dynamics of  
533 forests along with the long periods that are often required before any change in relative  
534 species abundance occurs, this factor playing an important role in diversity-population  
535 stability (Roscher *et al.* 2011). Accordingly, a negative diversity effect on forest species  
536 stability was found by Morin *et al.* (2014) based on long-term simulations from a process-  
537 based succession model.

538 At population level, we found underyielding for pine and overyielding for beech when  
539 growing in the mixed stands. These changes in mean productivity in comparison to  
540 monospecific stands were also associated with comparable relative changes in the standard  
541 deviation, resulting in similar temporal stabilities. Nevertheless, mixing species resulted in a  
542 destabilizing effect on individual pines, mainly due to the lower mean productivity, whereas  
543 in the case of beech, a neutral effect was found. The differences between the population and  
544 individual-tree level responses for pine may be due to the fact that only dominant and  
545 codominant trees were explored at tree level. Temporal variation in tree growth is generally  
546 lower as tree size increases, as indicated by the increasing stability of beech with tree size,  
547 even within the dominant and codominant trees included in this study. Similarly, tree  
548 responses to drought can vary among trees of different social status within a stand (Martín-  
549 Benito *et al.* 2008).

550 Mixing effects that were evident at the mean tree or population levels do not necessarily have  
551 any far-reaching practical relevance at community level. Studies that apply an individual tree  
552 level approach may overlook any compensation effects at population or community levels and

553 lead to questionable predictions when the results from individual dominant trees were scaled  
554 up to community level responses. It is important to underline the possible mixing effect on  
555 size distributions (Pretzsch & Schütze 2014, 2015), which can be one cause of contrasting  
556 effects at different levels, and contribute to misleading results if not taken into account when  
557 up-scaling.

558 Our results clearly show that the behaviour of mixed species stands cannot be derived simply  
559 by assuming additive effects between the combined species (e.g., based on the traits or  
560 dynamics of the species in monocultures). Both the overyielding of mixed-species stands at  
561 community level and the differences in growth stability at the community, population, and  
562 individual tree levels point to a multiplicative character of mixing effects. Modelling  
563 approaches cannot derive mixed stand dynamics from the weighted mean of the respective  
564 monocultures and should be able to reproduce the spatial and temporal inter-specific  
565 interactions between the combined species (Pretzsch, Forrester & Rötzer 2015).

### 566 **Environmental drivers**

567 The experimental design of our study was originally developed to examine whether the  
568 temporal variability of productivity in monocultures and mixed species stands is higher at  
569 sites with lower mean water supply. Many dendrochronological studies suggest that trees at  
570 drought prone sites may frequently suffer water limitation and therefore present more distinct  
571 fluctuations between high- and low-growth years (Fritts 2001). However, we found no  
572 statistical effect of precipitation or de Martonne aridity index on the temporal stability of  
573 productivity. This finding may be due to the typical lack of *ceteris paribus* conditions in field  
574 experiments, such that many factors may change along the transect other than the water  
575 supply and humidity. These factors could modify the effect of water supply and confound any  
576 productivity-water relationship. Indeed, the high variability in species asynchrony observed in  
577 monospecific stands along the transect at both stand and mean tree levels (from negative  
578 values to almost one), suggests that different environmental factors might be influencing  
579 species-specific growth at the different sites. Similarly, species over- or under-yielding ( $RPP_i$ )  
580 were not correlated, indicating that different environmental factors influence the mixing effect  
581 for each species.

582 Few studies have quantified the effects of European beech and Scots pine interactions on  
583 water, light or nutrient availability, uptake or use-efficiencies. In the same plots as those used  
584 in this study, the RP for light absorption at stand level generally increased due to a  
585 combination of more stratified canopy structures, changes in diameter-crown allometric  
586 relationships and increases in mean tree size in the mixtures (Forrester *et al.* in prep). Water-  
587 related interactions may also play a role as a result of inter-specific differences in interception  
588 (Nihlgård 1970; Augusto *et al.* 2002; Gerrits, Pfister & Savenije. 2010; Staelens *et al.* 2006;  
589 Van Nevel 2015), the isohydric behavior of pine *vs.* the anisohydric behavior of beech  
590 (Hartman 2011) and contrasting vertical root distributions and litter layers (Bonnemann 1939;  
591 Heinsdorf 1999; Knapp 1991), which may influence the vertical profile of water availability  
592 and uptake. These differences could improve nutrient availability in the mixtures compared  
593 with the pine monocultures. The seasonality of resource-use by a given species can also be  
594 modified by mixing, as shown for transpiration and light (Forrester *et al.* 2010; Sapjanskas *et*  
595 *al.* 2014). Further studies on the water and nutrient pools and fluxes might be required to  
596 determine their contribution to the temporal niche complementarity effects in these pine and  
597 beech mixtures.

### 598 **Concluding remarks**

599 Spatial and temporal species' complementarity in structure or functioning seems to be  
600 essential to increase the level and stability of productivity in mixed compared with

601 monospecific stands. In our two-species mixture, species asynchrony in mixed stands  
602 improved the level and stability of productivity, while our results with regard to temporal  
603 shifts in species interactions highlight the role of temporal niche complementarity in the  
604 stabilizing process. This species assemblage may provide a model example for other  
605 widespread species combinations as regards the degree of spatial and temporal  
606 complementarity. Other common conifer-broadleaved mixtures of early and late successional  
607 species or shade intolerant and tolerant species may behave similarly in terms of level and  
608 stability of productivity. We found the stability of productivity to be superior at most of the  
609 sites, regardless of the water supply and humidity, suggesting that the stabilization results  
610 from various complementarity effects together.

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#### 616 **Data accessibility**

617 Data available from the Dryad Digital Repository

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802

### 803 **Supporting Information**

804 Additional Supporting Information may be found in the online version of this article:

805 **Table S1.** Overview of the 31 mixed *Pinus sylvestris-Fagus sylvatica* triplets included in this  
806 analysis

807 **Table S2.** Stand characteristics of monospecific and mixed-species stands of the triplets.

808 **Table S3.** Description of the mean, standard deviation and stability of the annual basal area  
809 increment at the different organizational levels observed in monospecific and mixed-species  
810 stands.

811 **Table S4.** Fixed effect results at stand level, species level and individual tree level for the  
812 prediction of temporal stability, mean and standard deviation of annual basal area increment.

813 **Figure S1.** Example of the process of standardization and analysis of temporal variation in  
 814 species interactions

815 **Figure S2.** Relationship between the mixing effect on stability and overyielding

816 **Figure S3.** Relationship between the coefficient of correlations of species stand basal area  
 817 increments at community level in mixed and monospecific stands

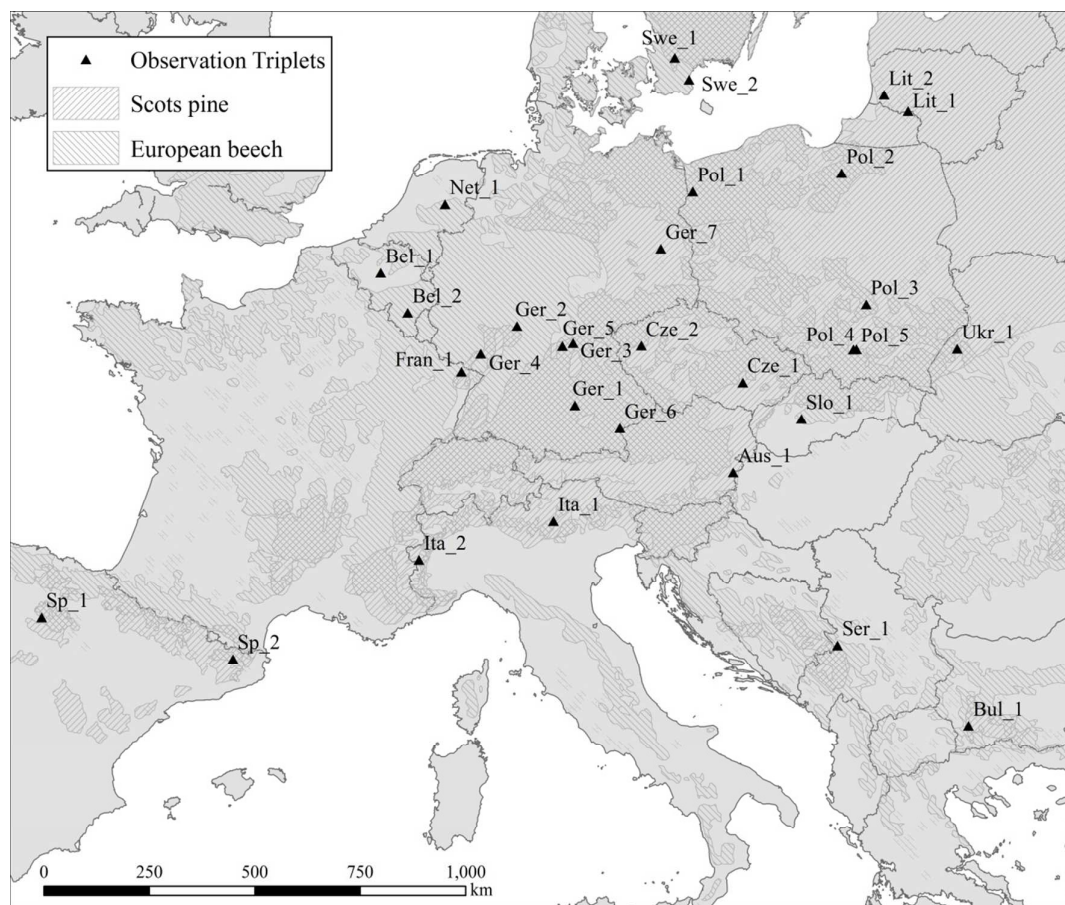
818 **Figure S4.** Relationships between temporal stability of stand basal area increment in mixed  
 819 stands and species asynchrony in mixed and monospecific stands

820 **Figure S5.** Relationship between the mixing effect on temporal stability at community level  
 821 and species asynchrony in mixed stands

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824 **Figures**

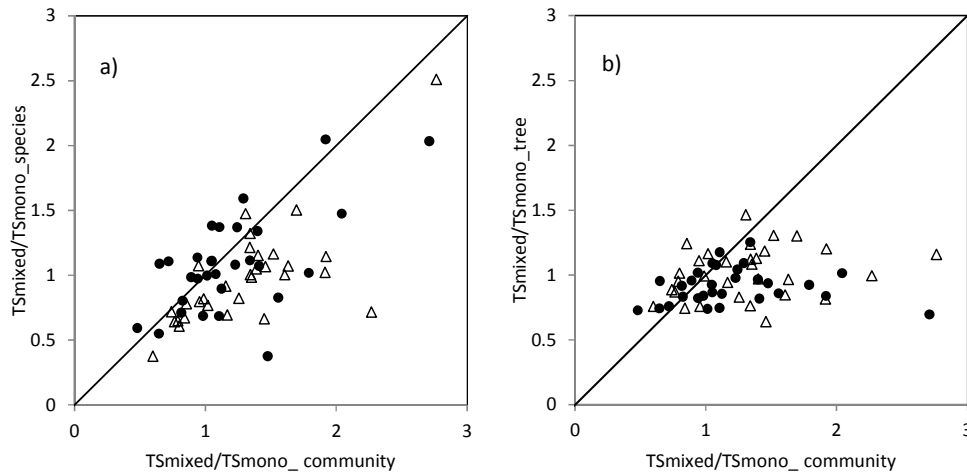


825

826 Fig 1. Location of the 31 triplets of monospecific and mixed stands of Scots pine and  
 827 European beech over the distribution of *Pinus sylvestris* and *Fagus sylvatica* according to  
 828 EUFORGEN (<http://www.euforgen.org/distribution-maps/>)

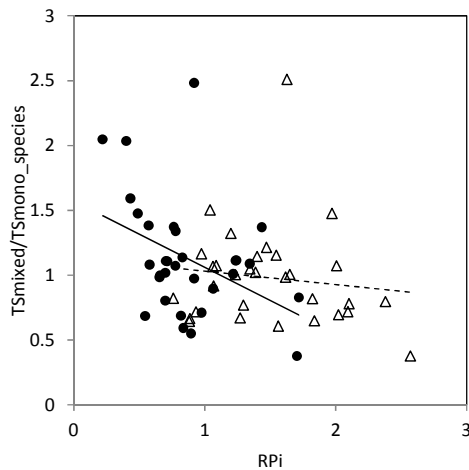
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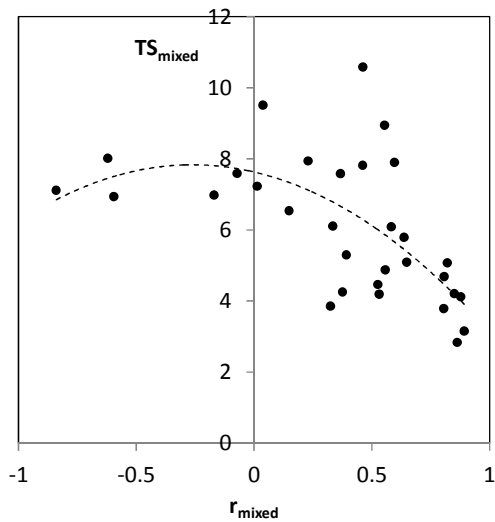
832 Fig 2. Relationship between mixing effects on temporal stability in basal area increment  
 833 ( $TS_{mixed}/TS_{mono}$ ) at different organizational levels for *F. sylvatica* (white triangles) and *P.*  
 834 *sylvestris* (black circles); a) species vs. community levels; b) individual tree vs. community  
 835 levels.



836

837 Fig. 3. Relationship between mixing effects on temporal stability in basal area increment at  
 838 species level ( $TS_{mixed}/TS_{mono}$ ) and relative productivity ( $RP_i$ ) for *F. sylvatica* (white triangles)  
 839 and *P. sylvestris* (black circles). Straight lines are the linear trend lines, dashed for *F.*  
 840 *sylvatica* (NS) and continue for *P. sylvestris* ( $R^2=0.17$ ;  $P=0.023$ )

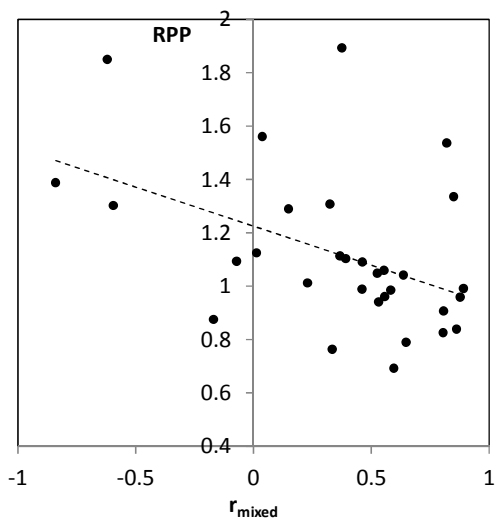
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841

842 Fig 4. Temporal stability in stand basal area increment ( $TS_{\text{mixed}}$ ) as a function of the  
 843 coefficient of correlation between species increments in mixed stands ( $r_{\text{mixed}}$ ) ( $R^2=0.40$ ;  
 844  $P<0.001$ ).

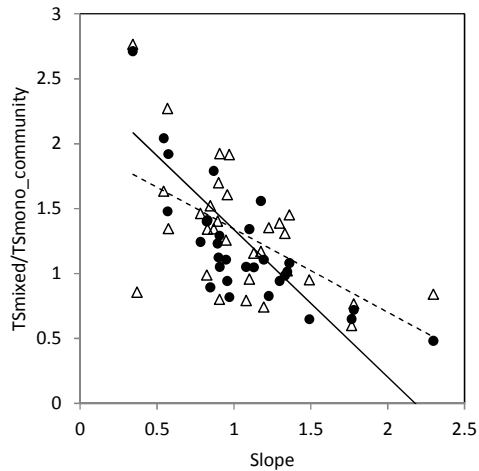
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846

847 Fig 5. Relationship between overyielding (RPP) and the coefficient of correlation between  
 848 species increments in mixed stands ( $r_{\text{mixed}}$ ) ( $R^2=0.20$ ;  $P=0.011$ ).





849

850 Fig. 6. Relationship between mixing effects on temporal stability in basal area increment  
 851 ( $TS_{\text{mixed}}/TS_{\text{mono}}$ ) at community level and slope of the major regression between observed and  
 852 reference stand basal area growth indices in mixed stands ( $IBAI_{\text{mixed}}=a+b \cdot IBAI_{\text{reference}}$ ; see text  
 853 and Fig. S1 for additional information) for *F. sylvatica* (white triangles) and *P. sylvestris*  
 854 (black circles). Straight lines are the linear trend lines, dashed for beech ( $R^2=0.32$ ;  $P=0.001$ )  
 855 and continue for pine ( $R^2=0.53$ ;  $P<0.001$ ).

## Supporting information

5 **Table S1.** Overview of the 31 mixed *Pinus sylvestris-Fagus sylvatica* triplets included in this analysis. Explanation of variables: Triplet identification code and number, ID and No, range of plot sizes (hectare), longitude, N, latitude, E, elevation above sea level, E a.s.l., mean annual temperature in the studied period (1999-2013),  $T_{(1999-2013)}$ , mean annual precipitation in the studied period,  $P_{(1999-2013)}$ , de Martonne index (1926) in the studied period,  $M_{(1999-2013)}$  ( $M$ =annual precipitation (mm)/(mean annual temperature °C +10)), substrate, inclination, I, exposition, Exp. For explanation of substrate see Arbeitskreis Standortkartierung (1985).

ID	No	Plot sizes (ha)	Geographic location		E. a.s.l. (m)	I (°)	Exp (°)	$T_{(1999-2013)}$ ° C	$P_{(1999-2013)}$ (mm yr <sup>-1</sup> )	$M_{(1999-2013)}$ (mm °C <sup>-1</sup> )	Substrate
			N	E							
Aus_1	1048	0-0.26-0.048	47°22'34.00"	16°23'20.00"	490	19	213	9.7	696	35	loamy sand
Bel_1	1057	0.065-0.101	50°01'48.00"	05°27'00.00"	530	8	180	10.9	873	42	stony loam
Bel_2	1063	0.080-1.298	50°45'06.10"	04°19'29.60"	120	0	315	8.0	1179	66	loam
Bul_1	1047	0.030-0.045	41°53'43.00"	23°21'03.00"	1150	20	0	9.9	669	34	loamy sand
Cze_1	1049	0.077-0.114	49°18'14.40"	16°36'08.78"	460	8	45	9.1	550	29	cambisol mezotrofic
Cze_2	1058	0.025-0.050	13°12'45.90"	49° 58' 02.5"	510	11	328	8.5	547	30	dystric and podzol cambisol
Fran_1	1040	0.090-0.180	48°58'41.80"	07°29'13.60"	275	20	315	10.1	993	49	sandstone sandy soil
Ger_1	1033	0.050-0.088	48°34'57.95"	11°14'12.49"	450	1	45	8.8	803	43	slightly loamy sand
Ger_2	1031	0.027-0.068	50°06'48.74"	09°03'54.36"	250	0	20	10.6	721	35	slightly loamy sand
Ger_3	1032	0.018-0.037	49°53'11.64"	10°58'13.12"	250	2	30	9.5	696	36	loamy sand
Ger_4	1071	0.027-0.050	49°24'57.77"	08°01'03.88"	400	1	60	9.7	633	32	loamy sand
Ger_5	1034	0.014-0.084	48°59'11.66"	08°10'48.58"	125	3	0	9.6	707	36	slightly loamy sand
Ger_6	1070	0.030-0.044	12°44'08.30"	48°11'12.47"	40	0	0	9.0	940	49	slightly loamy sand
Ger_7	1061	0.148-0.473	52°04'45.55"	13°37'06.05"	60	0	0	9.6	576	29	sandy
Ita_1	1055	0.056-0.180	46°04'02.93"	10°56'10.61"	1000	8	26	6.2	1339	83	cutanic luvisoil
Ita_2	1062	0.200-0.320	44°54'12.49"	07°03'53.30"	1250	25	315	6.7	983	59	inceptisol
Lit_1	1051	0.054-0.070	55°04'47.30"	22°24'24.01"	20	0	0	7.8	811	46	sand and slightly loamy sand
Lit_2	1052	0.041-0.077	55°27'02.08"	21°32'23.44"	25	0	0	7.8	791	44	sand and slightly loamy sand
Net_1	1043	0.032-0.056	52°25'40.55"	06°01'20.42"	34	2	0	10.1	828	41	coarse sand
Pol_1	1035	0.030-0.090	53°20'07.40"	14°36'17.51"	60	0	0	9.4	616	32	slightly loamy sand

2

Pol_2	1036	0.055-0.160	53°48'19.15"	19°54'42.27"	136	0	0	7.4	644	37	loamy sand and sand
Pol_3	1037	0.050-0.086	50°59'27.96"	20°41'08.90"	383	2	275	8.2	703	39	sandstone loamy sand/ loam
Pol_4	1044	0.080-0.158	50°01'27.60"	20°13'45.84"	210	0	0	9.0	710	37	slightly loamy sand
Pol_5	1045	0.070-0.180	50°01'36.00"	20°19'37.26"	225	0	0	9.0	706	37	loamy sand
Ser_1	1056	0.054-0.160	43°42'17.40"	19°37'30.00"	1090	20	0	8.3	1077	59	loam with a little sand
Slo_1	1046	0.025-0.150	48°33'09.18"	18°31'11.19"	500	15	90	9.2	682	36	cambisol
Sp_1	1042	0.050-0.058	42°05'57.00"	-03°-10'-19.00"	1290	14	0	8.8	731	39	sandy loam
Sp_2	1041	0.070-0.220	42°10'18.09"	02°15'44.23"	1130	30	0	9.8	870	44	loam slightly clay
Swe_1	1054	0.055-0.156	56°09'12.00"	13°35'35.00"	130	5	180	7.8	889	50	loamy sand
Swe_2	1053	0.040-0.187	55°42'33.00"	14°11'46.00"	110	17	135	8.5	686	37	sandy till
Ukr_1	1060	0.052-0.158	49°57'05.00"	23°39'44.00"	390	0	0	8.9	641	34	slightly loamy sand

10

To estimate the mean annual temperatures ( $T$ , °C) and the sum of annual precipitations ( $P$ , mm) for the studied period (1999-2013), we gathered climate data from all available meteorological stations located next to each triplet. We used monthly mean temperatures and sum of precipitations from the selected 1-5 stations. Finally, we spatially adjusted the above data to the location of each triplet by means of Inverse Distance Weighting (IDW) interpolation, according to the following formula:

15

$$T'(P') = \frac{\sum_{i=1}^n \frac{1}{D_i} \times T_i(P)_i}{\sum_{i=1}^n \frac{1}{D_i}}$$

$T'$ ,  $P'$  – temperature (°C) and precipitation (mm) to be estimated for the location of given triplet,

20

$T_i$  – temperature at „i” meteorological station,

$P_i$  – precipitation at „i” meteorological station,

$D_i$  – distance (km) between the given triplet and „i” meteorological station.

25

The minimal distance between the station and given triplet amounted on average to 11.91 km, while the maximal one was 24.62 km. For 5 triplets there were no available meteorological stations within the searching distance up to 30 km (Ita\_1 and Ita\_2) or just one or two, but at a considerably

different (>150 m) elevation (Sp\_1 and Sp\_2). Therefore, to compensate this shortcomings, we used gridded monthly climate data from the ERA-Interim gridded dataset for Italy (<http://www.ecmwf.int/en/research/climate-reanalysis/era-interim>) and the Digital Climatic Atlas of Spain ([http://montesdata.creaf.cat/MontesClima/clima/filtre.htm?idioma=es\\_ES](http://montesdata.creaf.cat/MontesClima/clima/filtre.htm?idioma=es_ES)). Finally, we computed the mean annual temperatures and the annual precipitations for the given triplet and each of 15 studied years. In the final step, based on the above results we calculated the average (1999-2013) mean annual temperature and precipitation (Table S1). Furthermore, for better characterizing the mean water supply at each triplet location we calculated the de Martonne index (1926) based on the formula:  $M = P / (T + 10)$  (M, mm °C<sup>-1</sup>). The higher the M index, the better the water supply for the plant growth (Table S1). Because of the minimal data requirement, this index has been widely used to describe the drought condition or aridity in a given region (Pretzsch et al., 2013; Quan et al., 2013; Bielak et al, 2014).

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45

**Table S2.** Stand characteristics of the triplets of monospecific and mixed-species stands. A total of 31 triplets were included consisting of 31 mixed-species stands and 62 neighbouring monospecific stands. Growth and yield stand characteristics are given for the mixed-species stands and the respective monocultures. Means of all 31 triplets are given in plain text and ranges (min-max) over all 31 triplets are given in italics (after Pretzsch et al. 2015, Table 1, triplet no. 1059 in Bosnia-Herzegovina excluded).

50

Tree number (trees ha<sup>-1</sup>), N, quadratic mean diameter (cm), d<sub>q</sub>, height of the quadratic mean diameter tree (m), h<sub>q</sub>, Stand density index, SDI (trees ha<sup>-1</sup>), stand basal area, BA (m<sup>2</sup> ha<sup>-1</sup>), standing volume V (m<sup>3</sup> ha<sup>-1</sup>), mean periodic annual basal area growth in the last 5 years, PAIBA (m<sup>2</sup> ha<sup>-1</sup> yr<sup>-1</sup>).

55

Composition	n	stand age (years)	N (trees ha <sup>-1</sup> )	d <sub>q</sub> (cm)	h <sub>q</sub> (m)	SDI (trees ha <sup>-1</sup> )	BA (m <sup>2</sup> ha <sup>-1</sup> )	V (m <sup>3</sup> ha <sup>-1</sup> )	PAIBA (m <sup>2</sup> ha <sup>-1</sup> yr <sup>-1</sup> )
Mixed	31	67 <i>40-149</i>	980 <i>250-2628</i>	27.0 <i>11.2-70.1</i>	21.9 <i>12.1-35.0</i>	814 <i>236-1631</i>	40.05 <i>11.51-77.94</i>	436 <i>122-956</i>	0.78 <i>0.29-1.80</i>
P. sylvestris_mono	31	67 <i>40-149</i>	974 <i>82-3200</i>	27.1 <i>13.7-45.5</i>	22.0 <i>8.7-33.9</i>	820 <i>155-1426</i>	39.97 <i>8.28-62.93</i>	400 <i>97-923</i>	0.71 <i>0.14-1.62</i>
F.sylvatica_mono	31	67 <i>40-149</i>	1026 <i>220-2745</i>	24.5 <i>12.0-47.7</i>	22.9 <i>12.4-34.1</i>	714 <i>219-1266</i>	33.75 <i>10.73-53.37</i>	398 <i>134-959</i>	0.76 <i>0.28-1.49</i>

### References

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K. et al. (2015) Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research*, **134**, 927–947.

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65 **Table S3.** Description of the mean (BAI\_m), standard deviation (BAI\_std) and stability (TS=BAI\_m/BAI\_std) in the 15 years period (1999-2013) of the annual basal area increment (BAI) at the different organizational levels (stand, species and individual tree) observed in monospecific and mixed-species stands. A total of 31 triplets were included consisting of 31 mixed-species stands and 62 neighbouring monospecific stands. Values are given for the mixed-species stands and the respective monocultures.

Level	Composition	N° data	BAI_m (m <sup>2</sup> ha <sup>-1</sup> yr <sup>-1</sup> )		BAI_std		TS	
			Mean	Std	Mean	Std	Mean	Std
Stand	Mixed	31	0.8818	0.3702	0.1658	0.0990	6.0778	1.9544
	<i>P. sylvestris</i> _mono	31	0.8576	0.3905	0.1830	0.1024	5.2457	1.7695
	<i>F. sylvatica</i> _mono	31	0.8401	0.2729	0.1993	0.1149	5.0336	1.9833
Species	<i>P. sylvestris</i> _mixed	31	0.6886	0.3850	0.1387	0.0842	5.4642	1.6759
	<i>F. sylvatica</i> _mixed	31	1.2172	0.4968	0.3023	0.1784	4.6474	1.9103
Individual tree	<i>P. sylvestris</i> _mono	448	0.0013	0.0007	0.0004	0.0002	3.8800	1.3232
	<i>F. sylvatica</i> _mono	419	0.0014	0.0007	0.0004	0.0002	3.5471	1.2141
	<i>P. sylvestris</i> _mixed	423	0.0017	0.0010	0.0005	0.0003	3.6745	1.3402
	<i>F. sylvatica</i> _mixed	401	0.0017	0.0010	0.0005	0.0003	3.6249	1.2617

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75 **Table S4.** Fixed effect results at stand level, species level and individual tree level for the prediction of temporal stability (lnTS), mean (lnBAI\_m) and standard deviation of annual basal area increment (lnBAI\_std) with species composition as factor (mixture is the reference level for all analysis). Variables were log-transformed for the analysis. Diameter at breast height (lnD) was used as a covariate in the analysis at individual tree level.

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**Stand level model: monospecific vs mixed**

variable	lnTS			lnBAI_m			lnBAI_std		
	Value	Std. error	p-value	Value	Std. error	p-value	Value	Std. error	p-value
Intercept	1.7744	0.0701	<0.0001	-0.2269	0.0818	0.0073	-2.0012	0.1203	<0.0001
Monospecific	-0.1675	0.0631	0.0101	-0.0577	0.0615	0.3513	0.1098	0.0878	0.2159

**Stand level model: monospecific pine/monospecific beech vs. mixed**

variable	lnTS			lnBAI_m			lnBAI_std		
	Value	Std. error	p-value	Value	Std. error	p-value	Value	Std. error	p-value
Intercept	1.7744	0.0704	<0.0001	-0.2269	0.0821	0.0075	-2.0012	0.1206	<0.0001
P. sylvestris_mono	-0.1899	0.0731	0.0117	-0.0260	0.0709	0.7149	0.1639	0.1010	0.1097
F. sylvatica_mono	-0.1450	0.0731	0.0516	-0.0894	0.0709	0.2123	0.0556	0.1010	0.5837

**Species level: pine monospecific vs. pine mixed**

variable	lnTS			lnBAI_m			lnBAI_std		
	Value	Std. error	p-value	Value	Std. error	p-value	Value	Std. error	p-value
Intercept	1.6982	0.0740	<0.0001	-0.5566	0.1037	<0.0001	-2.2549	0.1360	<0.0001
P. sylvestris_mono	-0.0689	0.0724	0.5874	0.2404	0.0800	0.0052	0.3093	0.1297	0.0234

**Species level: beech monospecific vs. beech mixed**

variable	lnTS			lnBAI_m			lnBAI_std		
	Value	Std. error	p-value	Value	Std. error	p-value	Value	Std. error	p-value
Intercept	1.4823	0.0760	<0.0001	0.0909	0.0719	0.2159	-1.3915	0.1136	<0.0001
F. sylvatica_mono	0.1021	0.0640	0.1208	-0.3438	0.0565	<0.0001	-0.4458	0.0946	<0.0001

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**Individual tree level: pine monospecific vs. pine mixed**

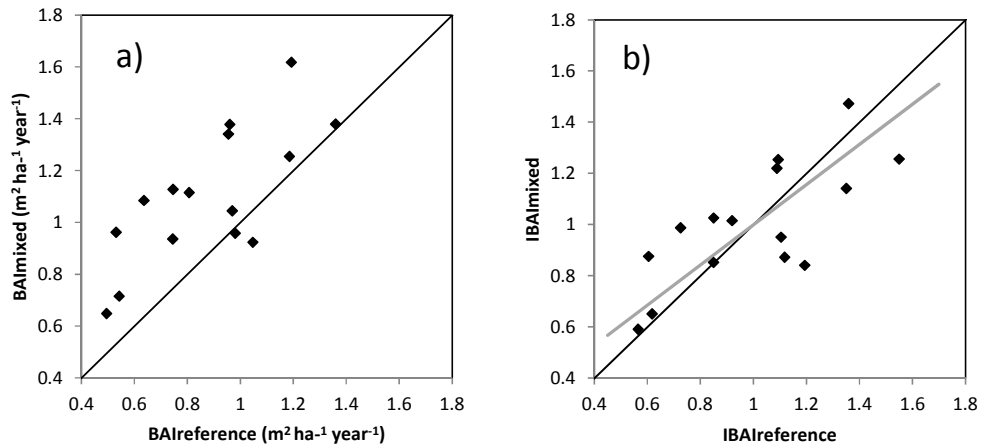
variable	lnTS			lnBAI_m			lnBAI_std		
	Value	Std. error	p-value	Value	Std. error	p-value	Value	Std. error	p-value
Intercept	0.9899	0.3678	0.0073	-	0.5256	<0.0001	-14.8206	0.5459	<0.0001
				14.1705					
P. sylvestris_mono	0.0967	0.0209	<0.0001	0.1011	0.0265	<0.0001	-0.0012	0.0281	0.9636
lnD	0.0382	0.0627	0.5425	1.2755	0.0891	<0.0001	1.1792	0.0928	<0.0001

**Individual tree level: beech monospecific vs. beech mixed**

variable	lnTS			lnBAI_m			lnBAI_std		
	Value	Std. error	p-value	Value	Std. error	p-value	Value	Std. error	p-value
Intercept	-0.4151	0.3090	0.1795	-17.8115	0.3267	<0.0001	-16.8475	0.3855	<0.0001
F. sylvatica_mono	-0.0056	0.0213	0.7915	-0.0968	0.0203	<0.0001	-0.0859	0.0251	0.0007
lnD	0.2920	0.0544	<0.0001	1.9991	0.0567	<0.0001	1.6097	0.0676	<0.0001

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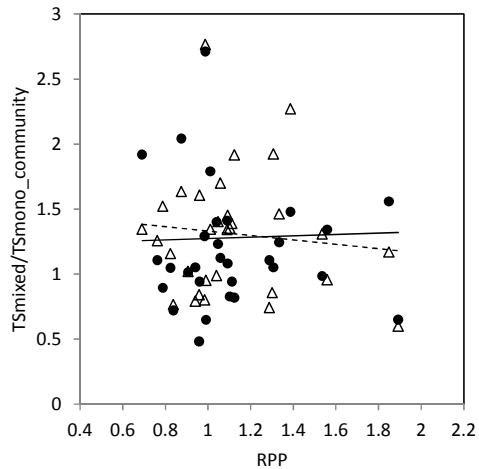


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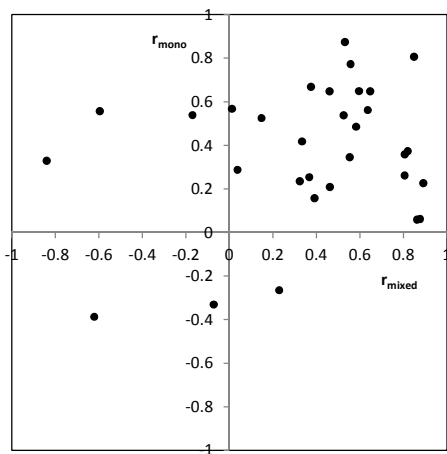
**Figure S1.** Example of the process of standardization and analysis of temporal variation in species interactions in triplet Sp\_1 (15 points indicate the respective values in the study period 1999-2013); a) annual basal area increments observed in mixed plot ( $BAI_{mixed}$ ) over the reference annual basal area increment assuming that there is not mixing effect ( $BAI_{reference}$ ). It can be seen that in this triplet there is a mean positive interaction or overyielding; b) similar relationship than in a) but using the standardized series ( $IBAI_{mixed}$  and  $IBAI_{reference}$ ), that removed the mean positive effect. The grey line in b) represents the relationships predicted by the major regression ( $IBAI_{mixed} = 0.215 + 0.784 \cdot IBAI_{reference}$ ), which indicates that in bad years (low IBAI) the species interactions are more positive than the mean interaction and in good years (high IBAI) species interactions are less positive than the mean. The standardization of BAI series was done by dividing of respective  $BAI_{(mixed/reference)}$  for a given year by the calculated mean of  $BAI_{(mixed/reference)}$  based on the study period of 15 years.

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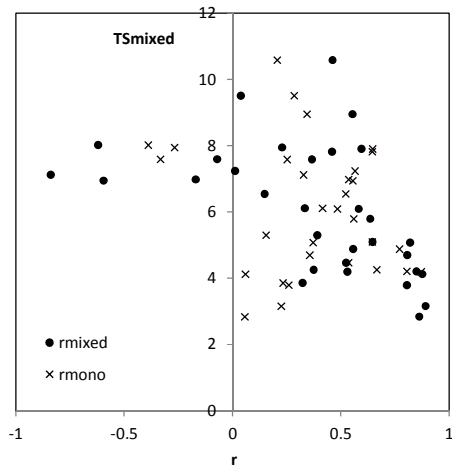




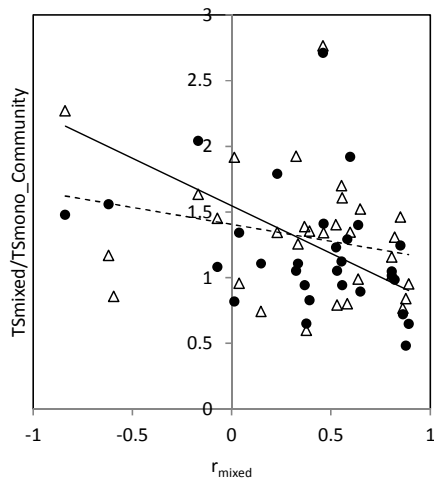
120 **Figure S2.** Relationship between the mixing effect (ratio of TS in mixed stands to monospecific stands) and overyielding (ratio of productivity, RPP) for *F. sylvatica* (white triangles) and *P. sylvestris* (black circles). Straight lines are the linear trend lines, dashed for beech (NS) and continue for pine (NS).



125 **Figure S3.** Relationship between the coefficient of correlations of species stand basal area increments at community level in mixed and monospecific stands.



130 **Figure S4.** Relationships between temporal stability of stand basal area increment in mixed stands ( $TS_{mixed}$ ) and the coefficient of correlation between species basal area increments at community level in mixed ( $r_{mixed}$ ) and monospecific stands ( $r_{mono}$ ).



135 **Figure S5.** Relationship between the mixing effect (ratio of TS in mixed stands to monospecific stands) and species asynchrony expressed by the coefficient of correlation between species increments ( $r_{mixed}$ ) for *F. sylvatica* (white triangles) and *P. sylvestris* (black circles). Straight lines are the linear trend lines, dashed for beech (NS) and continue for pine  
 140 ( $R^2=0.25$ ;  $P=0.004$ ).