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The final publication is available at:

<https://doi.org/10.1111/1365-2745.12803>

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1 Effects of crown architecture and stand structure on light absorption in
2 mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests
3 along a climate gradient through Europe

4
5 *Running head:* Light absorption in mixed-species forests

6
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44
45 *Keywords:* biodiversity, allometric equation, complementarity, Maestra model, plant–plant
46 interactions; stand structure, tree height

47

48 **Summary**

49

50 1. When tree-species mixtures are more productive than monocultures, higher light absorption
51 is often suggested as a cause. However, few studies have quantified this effect and even fewer
52 have examined which light-related interactions are most important, such as the effects of
53 species interactions on tree allometric relationships and crown architecture, differences in
54 vertical or horizontal canopy structure, temporal effects of deciduous species or the mixing
55 effects on tree size and stand density.

56

57 2. Measurements of tree sizes and stand structures were combined with a detailed tree-level
58 light model to examine the contribution of each light-related interaction on tree- and stand-
59 level light absorption in 21 triplets, each of which contained a mixture and monocultures of
60 *Fagus sylvatica* and *Pinus sylvestris* (63 plots). These triplets were distributed across the
61 current distribution of these species within Europe.

62

63 3. Averaged across all triplets, the light absorption of mixtures was 15% higher than the mean
64 of the monocultures. This mixing effect resulted from light-related interactions corresponding
65 to vertical canopy structure, stand density, deciduousness of *F. sylvatica*, and mixing effects
66 on tree size and allometric relationships between diameter and height, crown diameter and
67 crown length. Effects at the tree level often differed in magnitude to those at the stand level
68 and the mixing effects on each species were often in opposite directions. At the stand level,
69 the positive effects of mixing on light absorption increased as canopy volume or site
70 productivity increased.

71

72 4. The mixing effects on light absorption were only correlated with the mixing effects on *P.*
73 *sylvestris* growth, suggesting that the mixing effects on this species were driven by the light-

74 related interactions, whereas mixing effects on *F. sylvatica* or whole community growth were
75 probably driven by non-light-related interactions.

76

77 5. Synthesis. The overall positive effect of mixing on light absorption was the result of a
78 range of light-related interactions. However, the importance of these interactions varied
79 between sites and is likely to vary between species combinations and as stands develop.

80

81 **Introduction**

82

83 Greater absorption of photosynthetically active radiation (APAR) is often proposed as a
84 reason for greater productivity in mixed-species forests than in monocultures (Kelty, 1992,
85 Morin et al., 2011, Pretzsch, 2014, Forrester and Bauhus, 2016). However, positive mixing
86 effects on APAR have rarely been quantified (Binkley et al., 1992, Forrester et al., 2012, le
87 Maire et al., 2013, Forrester and Albrecht, 2014, Sapijanskas et al., 2014). It is therefore
88 difficult to determine which canopy structure or crown architectural characteristics are most
89 strongly influencing light-related complementarity effects in mixtures and how these effects
90 might differ between sites, species compositions and stand ages.

91

92 Complementarity effects in forests generally result from inter-specific differences in
93 physiology, phenology, or morphology or intra-specific differences (i.e. plasticity) that result
94 from interspecific interactions (Kelty, 1992, Ishii and Asano, 2010, Forrester and Bauhus,
95 2016). These effects may improve resource acquisition or support higher resource-use
96 efficiency. With regards to light-related interactions, there are several ways leaves can be
97 distributed more effectively in the canopies of mixtures than in monocultures. Seasonal
98 differences in competition for light can result from mixing evergreen and deciduous species,
99 or deciduous species that with contrasting phenology (Ishii and Asano, 2010, Sapijanskas et

100 al., 2014). Vertical stratification could enable the leaves of each species to be distributed in
101 complementary vertical profiles. This can result from contrasting height dynamics, ages and
102 physiology including shade tolerance (Kelty, 1992, Forrester et al., 2004, Valladares and
103 Niinemets, 2008, Ishii and Asano, 2010, Niinemets, 2010). Even when different species have
104 similar crown positions, the vertical distribution of foliage may still be superior to
105 monocultures if the species distribute their foliage at different positions within their crowns,
106 such that the vertical distribution of one species is skewed towards the top while the other is
107 skewed towards the bottom (Binkley, 1992, Niinemets, 2010, Guisasola et al., 2015).

108

109 Contrasting tree allometric relationships in mixtures compared with monocultures can also
110 influence APAR. For a given tree diameter, the crown sizes (width, length, leaf area), shapes
111 or height of a given species can be different in mixtures compared with monocultures
112 (Binkley, 1992, Forrester and Albrecht, 2014, Pretzsch, 2014, Forrester et al., in press). These
113 allometric differences can add to the effects of stratification when it allows crowns to expand
114 sideways at different levels in the canopy, or upwards or downwards away from other species
115 (Binkley, 1992).

116

117 Horizontal stand structure can also influence light absorption. For example, a higher number
118 of trees or a greater mean tree size could increase the stand density in terms of leaf area and
119 hence APAR (Forrester et al., 2013). While mixtures are not necessarily more productive than
120 monocultures, those that are more productive are likely to have greater stand densities and
121 lower mortality rates; as indicated by higher intercepts of self-thinning lines (Binkley, 1984,
122 Binkley et al., 2003, Reyes-Hernandez et al., 2013, Pretzsch et al., 2015, Pretzsch and Biber,
123 2016).

124

125 Most of these stand structural effects are not restricted to mixed-species forests and could also
126 result in differences in APAR between monocultures with different levels of structural
127 diversity, such as a result of contrasting levels of size class differentiation or in uneven-aged
128 monocultures compared with even-aged monocultures (Forrester and Bauhus, 2016, Ligot et
129 al., 2016). In monocultures, greater structural diversity has been associated with reduced
130 productivity (Binkley et al., 2010, Aspinwall et al., 2011, Bourdier et al., 2016, Soares et al.,
131 2016). In these stands, APAR, light-use efficiency (LUE) and growth of the more dominant
132 trees increases with structural diversity but this positive effect is outweighed by an even
133 greater reduction in APAR, LUE and growth of the smaller and intermediate trees (Binkley et
134 al., 2010). Therefore while greater structural diversity might increase the APAR of some
135 mixtures, these monospecific studies show that structural diversity can also reduce
136 productivity.

137

138 This study aimed to determine how stand structure and crown architecture affect APAR by
139 examining how individual tree APAR is influenced by tree size, crown architecture,
140 deciduous competitors, stand density and vertical canopy structure. A second aim was to
141 examine how these tree-level effects are expressed at the stand level for each individual
142 species (species population level) or for the whole community (community level). These
143 dynamics are likely to vary between sites, even for the same species combination, because
144 different resource availability along site gradients will influence stand density and could also
145 influence biomass partitioning and allometric relationships (Litton et al., 2007, Forrester et al.,
146 in press). Therefore this study was done at 21 sites across Europe for one of the most widely
147 distributed European species combinations (*Pinus sylvestris* and *Fagus sylvatica*) (Fig. 1).

148

149 We hypothesised that (i) the complementarity effect on growth that was reported by Pretzsch
150 et al. (2015) was caused by light-related interactions; (ii) these interactions relate to crown

151 and tree architecture, in terms of allometric relationships, that vary between mixtures and
152 monocultures for each species; (iii) they also relate to the horizontal canopy structure (e.g.,
153 leaf area index) and vertical canopy structure (e.g., canopy stratification), which vary between
154 mixtures and monocultures; (iv) these differences in canopy structure and crown architecture
155 all influence APAR at the tree and the stand levels and (v) these effects change with site
156 characteristics.

157

158 **Materials and methods**

159 **Site description and experimental design**

160 Tree allometry, canopy structure and light absorption were examined at 21 sites along a
161 productivity and rainfall gradient through Europe. The most southern sites are located in
162 Spain and Bulgaria and the most northern sites are in Sweden. They are spread across a large
163 proportion of the overlapping area of the distributions of *P. sylvestris* and *F. sylvatica* (Fig. 1).
164 The mean annual precipitation ranges from 520 to 1100 mm, the mean temperature from 6 to
165 10 °C and the elevation from 40 to 1340 m a.s.l. The aridity of each site was also quantified
166 using the de Martonne (1926) index (= annual precipitation in mm / (mean annual temperature
167 in °C+ 10)). More detail about the climatic and edaphic conditions of each site is provided in
168 Table S1 of Supporting Information.

169

170 At each site a triplet of plots was established, which includes a monoculture of each species
171 and a mixture. The plot sizes ranged from 0.011 to 0.41 ha and were generally rectangular in
172 shape. The criteria used when selecting the plots were that they were as close as possible to
173 even-aged, that they had not been thinned for at least ten years and that the trees were mostly
174 mixed on a tree-by-tree basis as opposed to groups of individuals of one species mixed with
175 groups of the other species. The even-aged criterion also, importantly, resulted in relatively
176 mono-layered forest stands, such that while the mean heights of each species were often

177 different, there was still some vertical overlap of the crowns of each species and therefore
178 direct interacting within the canopy. Additional criteria were that for a given triplet, all three
179 plots were on a similar soil substrate, aspect and slope.

180

181 The 63 plots within the 21 triplets covered a wide range of stand structures. In the mixtures,
182 the percent of basal area that was *F. sylvatica* ranged from 23% to 77% and the percent of
183 LAI ranged from 71% to 94%. A site productivity index (SI) was also calculated for each site,
184 using the monocultures of each species, to indicate the combined effect of all climatic,
185 edaphic and management conditions on productivity. This SI was the height of the 100
186 largest-quadratic-mean-diameter trees per hectare at age 50 years (Pretzsch et al., 2015). The
187 basal area ranged from 16 to 72 m² ha⁻¹, the number of trees per hectare from 211 to 4059 and
188 the stand age from 39 to 105 years.

189

190 **Data collection**

191

192 The diameters at 1.3 m of all trees were measured in each plot and their positions were
193 mapped as x-y coordinates. The heights, height to the crown base and crown diameters were
194 also measured for all trees within the plots or for a sample of trees (usually at least 10
195 randomly selected trees per species per plot; see Table S2). At least two crown diameters per
196 tree were measured (minimum and maximum) and for some plots four crown diameters per
197 tree were measured. Measurements were done between autumn 2013 and spring 2014. The
198 crown diameters, heights and live-crown lengths of the trees that were not measured were
199 predicted using site- and species-specific allometric equations (described below and in Table
200 S2).

201

202 **Basal area growth**

203 Growth was quantified in terms of basal area growth. Biomass growth was not used to avoid
204 additional errors associated with the need to have different biomass equations for each plot;
205 biomass equations can vary due to species interactions, climatic or edaphic factors and age
206 (Wirth et al., 2004, Laclau et al., 2008). Tree growth during 2013 was calculated using the
207 increment cores that were collected from at least 20 trees per species per plot covering the
208 diameter range for the given species and plot. The diameter increments of all non-cored trees
209 were calculated by fitting diameter increment functions for each plot and species (for the year
210 2013), where diameter increment was a linear function of diameter at 1.3 m and both were ln-
211 transformed. More detail is provided in Pretzsch et al. (2015).

212

213 **Calculations of stand canopy and structural variables**

214

215 To examine whether structural diversity influenced APAR, tree-diameter and -height diversity
216 were quantified using Shannon's index (Shannon, 1948) based on the basal area of each i^{th} 2-
217 cm diameter or 2-m height class within a plot (BA_i) and the total plot basal area (BA_T), using
218 Equation 1.

219

$$220 \text{ Diameter or height diversity} = - \sum_{i=1}^n \frac{BA_i}{BA_T} \ln \left(\frac{BA_i}{BA_T} \right) \quad (1)$$

221

222 The leaf area index ($\text{m}^2 \text{m}^{-2}$) was predicted using the general allometric leaf area equations in
223 Appendix S1. The canopy volume ($\text{m}^3 \text{ha}^{-1}$) was calculated as the sum of all crown volumes in
224 the plot and expressed per ha. Crown volumes were calculated assuming a half-elliptical
225 crown shape with a length equal to the live-crown length and a diameter equal to the crown
226 diameter. The canopy depth (m) is the height of the tallest tree in the plot minus the lowest
227 height to the live crown in the plot. Two variables were used to quantify the canopy density.
228 One was the canopy leaf-area density ($\text{m}^2 \text{m}^{-3}$), which is the leaf area ($\text{m}^2 \text{ha}^{-1}$) divided by the

229 canopy volume ($\text{m}^3 \text{ha}^{-1}$). The second was the proportion of canopy space that was filled with
230 tree crowns. This was calculated as the canopy volume divided by the total canopy space (m^3 ;
231 canopy depth $\times 10\,000 \text{m}^2$).

232

233 **Estimation of the absorption of photosynthetically active radiation**

234

235 Direct measurement of the absorption of photosynthetically active radiation (APAR) by
236 individual trees within a forest canopy is labour intensive and difficult in mature stands where
237 trees can be more than 30 m tall. Therefore, the light absorption by each tree within the plots
238 was predicted using a detailed 3D tree-level model, Maestra (Grace et al., 1987, Wang and
239 Jarvis, 1990, Medlyn, 2004, Duursma and Medlyn, 2012). The stand APAR of a given species
240 or the whole community was calculated as the sum of the APAR of all trees within the given
241 plot and expressed per hectare. Depending on the hypotheses, light absorption was expressed
242 as either APAR (GJ ha^{-1} or GJ tree^{-1}) or as the fraction (f) of PAR that was absorbed. The use
243 of f removes some of the effects that latitude could have on APAR. Maestra predicts the
244 APAR of individual trees using information about crown architecture (crown width and
245 length, leaf area and leaf angle distributions) and also accounts for shading from neighbouring
246 trees by representing the canopy as an array of tree crowns whose positions are defined by x
247 and y coordinates. The slope and aspect of a site are accounted for in both the x and y
248 directions.

249

250 The crown dimensions (height, crown length, crown radius and leaf area) were obtained using
251 the direct measurements or allometric equations. The Maestra model also requires solar
252 radiation data. However, there were often no weather stations that recorded solar radiation
253 close to the sites. Therefore the ERA-Interim reanalysis was used to provide daily
254 photosynthetically active radiation (PAR) data with a spatial resolution of

255 0.125° latitude × 0.125° longitude, ≈10 km × 10 km, depending on the latitude (Dee et al.,
256 2011). This is the latest global atmospheric reanalysis dataset produced by the European
257 Centre for Medium-Range Weather Forecasts. This PAR data was highly correlated ($R^2 > 0.7$)
258 with the three sites where solar radiation was available. More detail about the Maestra model
259 and the parameterisation for this study is provided in Appendix S2.

260

261 APAR predictions were not used for any trees that were along the outer edge of the plot to
262 avoid edge effects. That is, trees must have been far enough from the plot edge that they were
263 being buffered by a least one other tree that was closer to the plot edge but still inside the plot.
264 To ensure that the buffer was wide enough to avoid overestimating APAR, an additional 25-
265 m-wide buffer was simulated around each plot. The buffer for each plot contained the average
266 tree spacing, species composition and tree dimensions of the given plot. Individual tree APAR
267 (GJ year^{-1}) was calculated from the beginning to the end of 2013.

268

269 APAR predictions at the stand level from Maestra ($\text{APAR}_{\text{Maestra}}$) were validated using
270 predictions obtained by analysing hemispherical photos ($\text{APAR}_{\text{Hemispherical photos}}$) (Appendix
271 S3). The $\text{APAR}_{\text{Hemispherical photos}}$ and $\text{APAR}_{\text{Maestra}}$ were correlated ($R^2 = 0.67$) and indicated that
272 $\text{APAR}_{\text{Maestra}}$ predictions were on average 8% lower than $\text{APAR}_{\text{Hemispherical photos}}$ estimates. This
273 level of accuracy is expected given that (i) the plots covered a wide range of stand structures
274 and LAI, (ii) the hemispherical photos are another indirect estimate of APAR and (iii)
275 Maestra is a process-based model that does not require any assumptions about leaf area
276 density or light extinction coefficients. The Maestra model is therefore considered to provide
277 realistic predictions of APAR for this study, as has also been found in other Maestra
278 validation studies (Wang and Jarvis, 1990, Charbonnier et al., 2013, le Maire et al., 2013).

279

280 Eight Maestra model runs were used to examine how tree and stand APAR were influenced
281 by allometry, deciduousness of *F. sylvatica* and the mixing effects on tree size and stand
282 density. The first run was used to predict the APAR and f from the measured stand structures
283 and tree sizes as described above (run 1). For the other runs, the Maestra inputs were changed
284 to examine the effects of allometry, deciduousness of *F. sylvatica*, and the mixing effects on
285 tree size and stand density. Four runs (runs 2-5) were used to examine the effect of allometry
286 on APAR or f , such that the heights, live-crown lengths, crown diameters or all three of these
287 variables were replaced for all trees in the mixtures with values predicted using the allometric
288 equations obtained from the monocultures for the given species and site. A sixth run (run 6)
289 was done where the leaves of the *F. sylvatica* trees were not lost in winter to examine how
290 much additional light *P. sylvestris* obtains by growing with this deciduous species.

291

292 The mean heights, live-crown lengths and crown diameters of mixtures were sometimes
293 different to those in monocultures due to differences in size distributions and allometric
294 relationships (Table S2). Therefore, the effect of these tree size differences on stand-level
295 APAR or f was examined using a seventh comparison (run 7a and 7b, only for summer). This
296 time, a run (7a) was done where all trees in the mixed plot were given the mean dimensions
297 for the given species in the mixed plot (height, live-crown length, crown diameter, leaf area).
298 This was compared with a run (7b) where the trees in the mixed plots were given the mean
299 dimensions of the given species in its monoculture. Both runs (7a and 7b) retained the
300 horizontal positioning of all the trees in the mixture.

301

302 The stand density also varied between mixtures and monocultures in some of the triplets
303 (Pretzsch et al., 2015). Therefore an eighth comparison (run 8) was used to examine whether
304 this mixing effect on density influenced stand-level APAR. To do this, new mixtures were
305 created that used the mean tree spacing (in terms of trees per ha) from either the *F. sylvatica*

306 or *P. sylvestris* monocultures, such that trees were positioned at a regular spacing (on a square
307 grid) and with the same mixing proportions that were measured in the mixtures. In these
308 synthetic mixtures, the tree sizes were the mean measured sizes of each species in the
309 mixtures of the given triplet. For all runs where the live-crown lengths were changed, the
310 heights to the live crowns were changed simultaneously. Also, APAR was usually only
311 calculated for the growing season, which was defined by foliated period of *F. sylvatica* (Table
312 S1). However, for *P. sylvestris* or the whole community, whole year APAR was used when
313 examining relationships with annual growth or the effects of *F. sylvatica* leaf fall on APAR.

314

315 **Data analyses**

316

317 The effects of species composition on height (h), live-crown length (lcl) or crown diameter
318 (cd) were examined using Equation 2.

319

$$320 Y = b_0 + b_1 \ln(d) + b_2 M + b_3 \ln(d) \times M + \varepsilon \quad (2)$$

321

322 where Y is h , lcl or cd (all in metres), d is the stem diameter at 1.3 m (cm) and $\varepsilon \sim N(0, \sigma)$. M
323 is a dummy variable to define the mixing treatment and is either monoculture or mixture. For
324 some triplets the cd or lcl were ln-transformed to linearize relationships and to reduce
325 heteroscedasticity. When this transformation was used, the correction factor required when
326 back-transforming the Y-variables was calculated as the ratio of measured to (back-
327 transformed) predicted values (Snowden, 1991). A separate equation was fitted for each
328 species in each triplet.

329

330 **Tree-level APAR**

331 The effects of tree and stand variables on the fraction of PAR absorbed (f) were examined
332 using linear mixed models fitted to the Maestra estimates of APAR that were converted to f
333 (Equations 3 to 6). The random effects of each of these equations were plot nested within
334 triplet, or only triplet for equations 5 and 6, which were only used for mixtures. In equations 3
335 to 6, $\varepsilon \sim N(0, \sigma)$, and $\beta_k = \alpha_k + a_{k,ij}$ where α_k is the fixed part of the parameter β_k and a_k is
336 the random component, $a_{k,ij} \sim N(0, \sigma_k)$, at the level of the triplet i and plot j .

337

338 Equation 3 was used to examine the effect of species mixing (M) on the relationship between
339 individual tree f and crown size, in terms of leaf area (la , m^2), and whether this mixing affect
340 varied with site variables (S) such as site productivity index, precipitation, de Martonne index
341 and canopy volume.

342

$$343 \ln(f) = \beta_0 + \beta_1 \ln(la) + \beta_2 M + \beta_3 S + \beta_4 \ln(la) \times M + \beta_5 \ln(la) \times S + \beta_6 M \times S + \varepsilon \quad (3)$$

344

345 Equation 4 was then used to divide the mixing effect into a horizontal component quantified
346 as the plot leaf area index (LAI) and a vertical component quantified as the relative height, rh ,
347 which is the height of the target tree divided by the mean height of all trees in the plot. The M
348 was retained in the model to account for any mixing effect that was not accounted for by rh or
349 LAI.

350

$$351 \ln(f) = \beta_0 + \beta_1 \ln(la) + \beta_2 rh + \beta_3 LAI + \beta_4 M + \beta_5 \ln(la) \times M + \beta_6 rh \times M + \beta_7 LAI \times M + \varepsilon \quad (4)$$

352

353 Focusing only on the mixtures, the effect of allometry was examined by comparing f predicted
354 (by Maestra) using the measured h , lcl and cd , with f predicted using the allometric equations
355 developed for the monocultures of the given triplet (runs 2-5). This was examined by
356 replacing the M in equation 4 with a dummy variable, A , which defines whether allometric

357 relationships from monocultures or mixtures were used to predict h , lcl or cd . The resulting
358 equation 5 was only applied to mixtures. In some triplets there was no mixing effect on some
359 of the allometric equations so there will be no effect on f in those instances. The variable A ,
360 includes four levels to define whether only one variable (h , lcl or cd) was predicted using the
361 equations from monocultures, or all of these variables were predicted using the equations
362 from the monocultures.

363

$$364 \ln(f) = \beta_0 + \beta_1 \ln(la) + \beta_2 rh + \beta_3 LAI + \beta_4 A + \beta_5 \ln(la) \times A + \beta_6 rh \times A + \beta_7 LAI \times A + \varepsilon \quad (5)$$

365

366 Equation 6 was used for *P. sylvestris* in the mixtures to test how much individual tree f
367 changed if the *F. sylvatica* trees retained their leaves all year (run 6). The D is a dummy
368 variable that defines whether the *F. sylvatica* retain their leaves or not.

369

$$370 \ln(f) = \beta_0 + \beta_1 \ln(la) + \beta_2 rh + \beta_3 LAI + \beta_4 D + \beta_5 \ln(la) \times D + \beta_6 rh \times D + \beta_7 LAI \times D + \varepsilon \quad (6)$$

371

372 Initially all fixed effect candidate predictors were included in the models in equations 2 to 6,
373 before all non-significant ($P > 0.05$) variables were removed in order of decreasing P -value.
374 Residual and normal quantile plots were visually assessed to ensure that the residuals were
375 centred at zero, approximately normally distributed, with constant variance.

376

377 **Stand-level APAR**

378

379 Linear regression was also used to examine relationships between growth, APAR and LUE, as
380 well as how stand-level f and mixing effect on f for a given species or the whole community
381 were influenced by site and stand characteristics (e.g., mean annual precipitation, basal area,
382 canopy volume). At the stand level, the mixing effect on f was quantified using the relative

383 productivity equation (RP), which was calculated using equation 7 at the community level and
384 equation 8 at the species population level (Forrester and Pretzsch, 2015).

385

$$386 \quad RP_{total\ community\ f} = \frac{f_{1,2}}{m_1 f_1 + m_2 f_2} \quad (7)$$

387

$$388 \quad RP_{species\ f} = \frac{f_{1,(2)}}{m_1 f_1} \quad (8)$$

389

390 where $f_{1,2}$ is the f of the whole mixed community and $f_{1,(2)}$ is the f of species 1 in a
391 mixture with species 2. f_1 and f_2 are the f of species 1 and species 2 in their respective
392 monocultures. The m_1 and m_2 are the mixing proportions. These m_i were calculated in
393 terms of LAI because it is considered most representative of the species contributions to
394 light dynamics and species proportions by leaf area have been shown to provide
395 realistic estimates of species proportions on an area-basis (i.e. per hectare; Dirnberger
396 and Sterba, 2014). When $RP = 1$ the f of the mixtures is exactly as expected based on
397 the monocultures (i.e. an additive effect), and indicates no complementarity effect. RP
398 > 1 or $RP < 1$ indicate overyielding and underyielding effects on f , respectively.

399

400 In contrast to the effects on tree-level f , which were examined using Equations 3-6, the stand-
401 level effects on f (for a given species or the whole community) were examined using linear
402 models between the f predicted using actual tree dimensions and stand structure, as a function
403 of the f predicted after changing the Maestra inputs to the allometry, deciduousness, size and
404 stand density treatment. A slope significantly different to 1, indicates a significant treatment
405 effect on stand f . All statistical analyses were carried out using R 3.2.1 (R Core Team, 2015),
406 including the *nlme* package for fitting the mixed models (Pinheiro et al., 2013).

407

408 **Results**

409

410 **Mixing effects on tree allometry and stand structure**

411

412 Mixing often had a significant effect on relationships between diameter and height, live-
413 crown length or crown diameter (Table S2, Fig. 2). These mixing effects were very variable
414 and ranged from decreases to increases in all variables, for a given diameter, for each species.
415 Often the more common response to mixing for *P. sylvestris* was the opposite to the most
416 common response of *F. sylvatica*. Mixing was more likely to increase the height (for a given
417 diameter) of *P. sylvestris* and decrease the height for *F. sylvatica*. In contrast, mixing was
418 more likely to decrease the live-crown length or crown diameter of *P. sylvestris* and increase
419 them for *F. sylvatica*.

420

421 At the stand level, these differences in allometric equations and the mixing effects on mean
422 tree sizes (Table S5) and stand density (Table S6), resulted in stand structures where *P.*
423 *sylvestris* was likely to occupy a higher position in the canopy than *F. sylvatica* (Fig. 3).

424 While the expected vertical overlap in leaf area index based on the monocultures was about
425 21%, the changes in stand structure in the mixtures led to higher crown segregation
426 (stratification) and an actual overlap of only 7%, averaged across all triplets.

427

428 The predicted LAI of *F. sylvatica* monocultures (8.4) were significantly higher than the
429 mixtures (6.5) and *P. sylvestris* monocultures (2.2) due to the difference between the
430 allometric leaf area equations for these species (Appendix S1). The canopy depth, the total
431 stand canopy volume, the proportion of canopy space that was filled with tree crowns and the
432 canopy leaf-area density were usually higher in the mixtures and the *F. sylvatica*
433 monocultures than in the *P. sylvestris* monocultures (Table S6). The basal areas of the

434 mixtures and *P. sylvestris* monocultures (both 45 m² ha⁻¹) were higher than *F. sylvatica*
435 monocultures (33 m² ha⁻¹) (Table S6).

436

437 Despite the differences in horizontal (LAI, basal area or trees per ha) and vertical structures,
438 there was no significant difference in structural diversity between the mixtures and
439 monocultures, in terms of Shannon's index (Table S6). That is, the differences in mean
440 diameters and heights, or their distributions between mixtures and monocultures were large
441 enough to influence vertical and horizontal canopy structure, but not the structural diversity,
442 in terms of stem diameter and height diversity.

443

444 **Tree level - Fraction of PAR absorbed**

445

446 The predicted fraction of PAR absorbed (f) by *P. sylvestris* trees in monocultures was higher
447 than that in mixtures, for a given individual tree leaf area (Fig. S3; Table S7). For *F. sylvatica*
448 trees, predicted f was very similar or slightly lower in monocultures than mixtures when
449 individual tree leaf area was lower than about 300 m² (> 90% of the trees in these plots).

450

451 Higher stand densities, in terms of predicted LAI, had no significant effect on f of *P. sylvestris*
452 trees but reduced the APAR of individual *F. sylvatica* trees (Fig. S4; Table S7). For both
453 species, individual tree f increased with increasing relative height (Fig. S4; Table S7). This
454 effect was influenced by mixing such that for a given relative height, predicted f of *F.*
455 *sylvatica* trees was higher in mixture, because they were then competing with *P. sylvestris*,
456 which are less competitive for light when at the same level in the canopy. In contrast, the
457 APAR of *P. sylvestris*, for a given relative height, was lower in mixture because it is then
458 competing for light with *F. sylvatica* (Fig. S4; Table S7), which is a stronger competitor for
459 light at any given level within the canopy. The relationships between individual tree leaf area

460 and f were not influenced by any other site or canopy variables such as site productivity index,
461 climatic variables, canopy volume or leaf-area density.

462

463 **Stand level – production ecology and the fraction of PAR absorbed**

464

465 The stand level basal area growth of each species and the whole community were positively
466 correlated with APAR, however this relationship was much stronger for *P. sylvestris* and was
467 not significant for the whole community (Fig. 4). The light-use efficiency was also positively
468 correlated with growth in all treatments. The relationship between the mixing effects on
469 APAR (RP_{fAPAR}) and the mixing effects on growth (RP_{Growth}) were used to indicate whether
470 the light complementarity could be causing the growth complementarity. This relationship
471 was only significant for *P. sylvestris* (Fig. S5). The species were also regressed against each
472 other for RP_{Growth} , RP_{fAPAR} and their site productivity indices to indicate whether there was
473 any similarity in the sites that they performed well vs. poorly on. There were significant
474 positive correlations between the RP_{Growth} of each species and also between the site
475 productivity indices of each species (Fig. S6), however, the RP_{fAPAR} of each species were not
476 correlated.

477

478 **Stand level – fraction of PAR absorbed**

479

480 *P. sylvestris* generally occupied a higher position in the canopy than *F. sylvatica*. Therefore
481 the mixing effect (RP_{fAPAR}) for *F. sylvatica* usually increased as its contribution to the stand
482 increased, in terms of its total canopy volume, basal area, and the total canopy depth, which
483 usually increased in the presence of *F. sylvatica* (Fig. S7). Many stand-level correlations are
484 listed in Table 1. In contrast, the RP_{fAPAR} of *P. sylvestris* generally increased as its
485 contribution to the stand decreased and hence competition within the upper canopy decreased

486 (where *P. sylvestris* was more likely to occur). That is, the RP_{fAPAR} of *P. sylvestris* increased
487 as the proportion of *F. sylvatica* LAI increased and as the LAI of *P. sylvestris* decreased (Fig.
488 S8). The RP_{fAPAR} of *P. sylvestris* also increased as Shannon's index (based on height classes)
489 increased (Fig. S8b), probably also because that meant that there was more *F. sylvatica* trees
490 in the stand. The RP_{fAPAR} of *P. sylvestris* was always greater than that of *F. sylvatica* because
491 (i) *P. sylvestris* occupied a more favourable position within the canopy of the mixtures, and
492 (ii) for a given diameter, *P. sylvestris* has a much lower leaf area and contributed a lower
493 proportion of LAI to the stand than *F. sylvatica* (for the same basal area), which reduced the
494 *F. sylvatica* RP_{fAPAR} by increasing the mixing proportion of *F. sylvatica* in Equation 8.
495 Despite the different patterns for each species, the RP_{fAPAR} of *F. sylvatica* was not correlated
496 with that of *P. sylvestris* (Fig. S6b).

497

498 At the whole community level, RP_{fAPAR} increased with total crown volume, canopy depth and
499 site productivity index (Fig. 5). It was not related to the proportion of canopy space that was
500 filled with tree crowns and only weakly to the canopy leaf-area density (Fig. 5). There were
501 positive relationships between predicted community f and LAI, canopy volume and the
502 proportion of canopy space filled with crowns (Fig. S9).

503

504 The predicted f of *P. sylvestris* increased as its LAI increased and when its canopy volume
505 increased (Fig. S10a,b). However, *P. sylvestris* f decreased as the proportion of *F. sylvatica*
506 (by LAI) increased or as the proportion of canopy space filled with crowns increased (Fig.
507 S10c,d). This resulted because as these variables increased, the LAI or canopy volume of *P.*
508 *sylvestris* was likely to decrease. The predicted f of *F. sylvatica* increased as its LAI increased
509 and as its relative height increased (Fig. S11). It also increased within increasing community
510 leaf area-density ($P = 0.016$), increasing proportions of *F. sylvatica* LAI ($P > 0.001$). The f of

511 *F. sylvatica*, *P. sylvestris* or the whole community were not correlated with the site
512 productivity index, the de Martonne index or precipitation ($P > 0.05$).

513

514 **Effects of allometry, deciduousness, mean tree size and mean stand density on f**

515

516 The contrasting allometric relationships between the mixtures and monocultures contributed
517 to the greater predicted f of the mixtures. When all the actual measurements (or allometric
518 equations of mixtures for unmeasured trees) were used in the mixtures, a significantly higher
519 tree-level f was predicted for *P. sylvestris* (16.5%) but a lower f for *F. sylvatica* (5.8%) (Fig.
520 6, Table S7) compared with when the allometric equations from monocultures were used for
521 the mixtures. At the stand level, the effects were small and insignificant; actual dimensions
522 (or allometry from mixtures) resulted in a slightly greater predicted f for *P. sylvestris* (1.5%)
523 and the community (1.1%) but a lower f for *F. sylvatica* (3.7%) compared with when all the
524 monospecific allometric equations were used (Fig. 7). Each variable had different effects on f .
525 The greatest changes resulted from changes in crown diameter or live-crown length (which
526 includes changes in height to the live crown), and the smallest changes resulted from changes
527 in allometric height relationships. For a given tree diameter, equations that predicted larger
528 crown diameters or heights often resulted in greater predicted f at the tree and stand levels,
529 and vice versa. In contrast, increases in live-crown length (and associated changes in height to
530 the live crown) reduced f , probably because this extended the crowns towards the same
531 canopy level of the other species and intensified competition. The differences in allometric
532 equations between mixtures and monocultures also influenced the effect of relative height on
533 individual tree f (Fig. S12). The use of monospecific allometric relationships for live-crown
534 length reduced the effect of relative height for both species.

535

536 The predicted f for *P. sylvestris* was increased by 9.2% at the tree level and 4.9% at the stand
537 level due to the deciduousness of *F. sylvatica* (Figs 6, 7 and S13). The difference in stand
538 density, in terms of trees per ha, had no influence on stand level f because differences in trees
539 per ha were not large enough. At the tree level, the predicted f for *P. sylvestris* was not
540 influenced by stand density (in terms of LAI) but the lower LAI of mixtures compared with *F.*
541 *sylvatica* monocultures increased tree-level f for *F. sylvatica* in mixtures by 8.9% (Figs 6 and
542 S4). The mean tree sizes of *P. sylvestris* were larger in mixtures than in monocultures, while
543 those of *F. sylvatica* were usually not significantly different (Table S5). This mixing effect on
544 *P. sylvestris* sizes (h , cd , lcl , la) resulted in a 19.8% higher individual tree f compared with
545 when the mean tree sizes of monocultures were used in the mixtures, while retaining the tree
546 positioning of the mixture (Fig. 6). The mixing effects on *F. sylvatica* sizes were often
547 insignificant and also had no significant effect on individual tree f (Fig. 6).

548

549 **Discussion**

550 Averaged across all triplets, mixtures had 15% higher predicted annual APAR than
551 monocultures of *F. sylvatica* or *P. sylvestris* even though the mean leaf area index of mixtures
552 was 29% lower than that of the deciduous *F. sylvatica* monocultures (Table S6). Even during
553 the growing season the mixtures had a similar APAR to the *F. sylvatica* monocultures despite
554 their lower leaf areas. Species mixing also increased APAR in other temperate or tropical
555 stands (Binkley et al., 1992, Forrester et al., 2012, le Maire et al., 2013, Sapijanskas et al.,
556 2014). The greater APAR of the mixtures in this study was largely due to a higher than
557 expected APAR of *P. sylvestris* in all triplets (Fig. S8; mean $RP_{fAPAR} = 3.1$), whereas the
558 response of *F. sylvatica* was more varied, and was often lower in the mixtures than expected
559 from monocultures (Fig. S7; mean $RP_{fAPAR} = 0.83$).

560

561 It is critical to note that complementarity effects on APAR do not mean that greater APAR
562 caused the growth complementarity. For example, many studies have used production ecology
563 or mass balance approaches to show that a process that was occurring in a mixture (e.g.,
564 symbiotic nitrogen fixation) was not causing any complementarity effect on growth or
565 resource uptake by the associated species (Binkley et al., 1992, Forrester and Pretzsch, 2015).
566 In this study, the complementarity effect on *P. sylvestris* growth (RP_{Growth}) was positively
567 correlated with the complementarity effect on APAR (RP_{fAPAR}), indicating that light-related
568 interactions contributed to the growth complementarity for *P. sylvestris*. In contrast, this was
569 not the case for *F. sylvatica* or the whole community suggesting that in those treatments
570 water- or nutrient-related interactions may play a greater role in the growth complementarity
571 effect than light-related interactions. This contrasting importance of the light complementarity
572 for these species occurred despite them both favouring similar sites; the site productivity
573 indices of each species were correlated, as were their RP_{Growth} (Fig. S6). These findings
574 should not imply that light-related interactions are not also benefiting *F. sylvatica* or that non-
575 light related interactions are not benefiting *P. sylvestris*, it only indicates that they are not the
576 dominating effects for the given species, respectfully.

577

578 The overall mixing effect on APAR was driven by a range of different mixing effects on
579 crown architecture and canopy structure, which included a seasonal effect caused by the
580 deciduous *F. sylvatica*, a dominating effect of *P. sylvestris* relating to the vertical canopy
581 stratification, the effects of allometry (crown diameter, height and live-crown length), stand
582 density (LAI) and mixing effects on mean tree sizes. Feedbacks between these different
583 effects meant that mixing effects on the tree-level APAR often differed from those at the
584 stand level, as also found for the growth dynamics of the same plots (del Río et al., in review).

585

586 **Mixing effects on tree allometry and stand structure**

587

588 Allometric relationships for trees can change in response to inter-specific interactions
589 (Pretzsch, 2014, Forrester et al., in press) and this influences the vertical and horizontal
590 distribution of leaves within the canopy. For a given diameter, *F. sylvatica* crowns in mixtures
591 tended to widen and extend downwards, which is indicative of a reduction in competition (for
592 light) in the mixtures (Lines et al., 2012, Dieler and Pretzsch, 2013, Forrester et al., in press).
593 In contrast, crowns of *P. sylvestris* were more likely to become narrower with shorter lengths
594 but higher above the ground, suggesting more intense competition for light in the mixtures
595 encouraging height growth more than crown expansion (Figs 2 and 3).

596

597 Despite this general pattern, there were also triplets that showed departures from these
598 allometric responses. Therefore, both the magnitude and direction of a change in any given
599 allometric relationship can vary, even within a single species combination. This reflects the
600 wide range in canopy structures across the 21 mixed-species plots but also indicates that
601 biased predictions of mixing effects can result from assuming that allometric relationships do
602 not vary across stands with different structures (Forrester and Pretzsch, 2015, Forrester et al.,
603 in press).

604

605 Consistent with the changes in allometry, the vertical stratification of the stands became more
606 distinct in the mixtures than was expected from the monocultures. The *P. sylvestris* were taller
607 in the mixtures, while the *F. sylvatica* were shorter in the mixtures, relative to their respective
608 monocultures, and this reduced the proportion of vertical leaf area overlap in mixtures from
609 an expected 21% to only 7% (Fig. 3). This shift is consistent with mixing effects on the
610 vertical structure of other species combinations (Binkley, 1992, Kelty, 1992, Bauhus et al.,
611 2004, Forrester et al., 2004). The degree of leaf area overlap was not related to tree age or any
612 site conditions and while it was probably influenced by species interactions, it was probably

613 also influenced by previous management. Even though the stands have not been (or only
614 minimally) managed for several decades, management during the first few decades probably
615 actively prevented *F. sylvatica* from dominating *P. sylvestris*.

616

617 **Mixing effects on absorbed PAR**

618 *Vertical canopy structure and crown positioning*

619

620 At the tree level, the predicted fraction of PAR absorbed (f) by individuals of both species
621 increased with relative height (Fig. S4). This was reflected at the stand level, such that the f of
622 *F. sylvatica* increased with its relative height (Fig. S11a). While stratification is often
623 observed in mixtures and is assumed to affect APAR, the effect is rarely quantified. In this
624 study, stratification (relative height) had a positive effect on the predicted f of *F. sylvatica* as
625 it became more dominant, but not on *P. sylvestris*, which was generally already in a dominant
626 position in the mixtures. Stratification was also not correlated with total community APAR
627 because both species cannot dominate the other simultaneously. Therefore, while the
628 development or management of stratification is clearly important in mixtures, there are other
629 factors that can have an even greater effect on APAR, such as encouraging long crowns,
630 especially for *P. sylvestris*.

631

632 It is important to note that the RP is based on species proportions in terms of LAI because this
633 is considered most appropriate when examining APAR. The use of species proportions based
634 on other variables, such as basal area, will result in different RP_{fAPAR} values. This is because
635 the species contrast in their stem diameter-leaf area relationships, and this difference
636 determines how the species proportions will differ when calculated based on diameters (i.e.
637 basal area) compared with leaf areas.

638

639 ***Allometry***

640

641 The allometric equations of the mixed stands contributed to their greater predicted f . Changes
642 in allometric equations that resulted in larger crown diameters for a given diameter, resulted
643 in a greater f at the tree or stand levels, and vice versa. In contrast, increases in live-crown
644 length reduced f , possibly because this extended the crowns towards the same level of the
645 other species and intensified competition. Changes in live-crown length also had a greater
646 effect on individual tree APAR than crown width in mixtures of *P. abies* and *A. alba*
647 (Forrester and Albrecht, 2014), but since both species occupied a similar level in the canopy
648 the increase in live-crown length increased the APAR. A reason for the larger effects of live-
649 crown length than other variables could be because there is less space to move sideways than
650 vertically; a different pattern may occur in more widely spaced mixtures. Similarly, by
651 predicting light availability above individual tree crowns, differences in allometric equations
652 were also predicted to change stand APAR in tropical mixtures (Sapijanskas et al., 2014).

653

654 It is important to note that a weakness of our study is that allometric leaf area equations could
655 not be developed by sampling in these plots, which may have introduced bias into the Maestra
656 model runs. However, this bias is expected to be minor because APAR predictions in *P. abies*
657 and *A. alba* mixtures showed that changes in individual tree leaf area of 10% resulted in
658 changes in predicted APAR of only 2%, compared with about 10-15% for changes live-crown
659 length and 4-5% for crown diameter (Forrester and Albrecht, 2014).

660

661 ***Effect of the deciduousness of F. sylvatica***

662

663 Seasonality of leaf area can temporarily reduce competition for light (Ishii and Asano, 2010,
664 Sapijanskas et al., 2014). The leaf loss by *F. sylvatica*, compared with the Maestra run where

665 its leaves were retained all year, resulted in a 10% increase in *P. sylvestris* APAR at the tree-
666 level (Fig. 6) and about 5% at the stand level (Fig. 7). Even though this seasonality of
667 competition for light was significant, the effects on growth are probably even lower because it
668 occurs during the winter. The effect is also relatively small because *P. sylvestris* was
669 generally taller than *F. sylvatica*, so greater effects are likely where deciduous species occupy
670 a more dominant canopy position (e.g., *Quercus robur*, *Q. petraea*, *Fraxinus excelsior*). For
671 example, the effect of seasonal foliage loss in young tropical plantations was found to have a
672 larger effect on light availability than factors such as crown shapes and crown openness
673 (Sapijanskas et al., 2014). This is because the deciduous species in that tropical plantation
674 were not necessarily the shortest species within the mixture.

675

676 *Tree size, stand density and mixing*

677

678 For a given crown leaf area, *P. sylvestris* trees in monocultures had greater predicted f than
679 those in mixtures (Fig. S3). The *P. sylvestris* probably experience more competition for light
680 at the tree level in mixtures due to the higher predicted LAI than *P. sylvestris* monocultures
681 because even though the *P. sylvestris* trees are often taller, there are many *F. sylvatica* crowns
682 intermingling at the same level as the *P. sylvestris*. Nevertheless, there was no LAI effect on
683 individual *P. sylvestris* f , probably because despite the presence of some *F. sylvatica* amongst
684 the *P. sylvestris* crowns, the LAI was still relatively low in the upper canopy layer containing
685 the *P. sylvestris*. This contrasts with the strongly positive mixing effect on stand-level *P.*
686 *sylvestris* APAR (RP_{IPAR}) because the minor tree level reduction was more than compensated
687 for by a greater mean tree size in the mixtures.

688

689 Mixing had a much smaller effect on the predicted *F. sylvatica* f , for a given crown leaf area.

690 Similarly, mixing had no effect on relationships between leaf area and APAR for *P. abies*

691 with *A. alba*, and actually increased APAR for a given leaf area for *A. alba* on productive
692 sites (Forrester and Albrecht, 2014). For *F. sylvatica*, the stand structure was a more
693 important determinant of tree level APAR than the species composition *per se*. The horizontal
694 structure, in terms of increasing stand LAI, basal area or canopy volume, resulted in a lower
695 individual tree f , but higher stand mixing effect (RP_{fAPAR} ; Fig. S8) for *F. sylvatica*.

696

697 In addition to stand density *per se*, trees optimise space occupation by shifting the position of
698 their crowns horizontally away from the point directly above the stem base, as well as
699 modifying the shapes of their crowns (Longuetaud et al., 2013, Lee and García, 2016). The
700 ability to reposition crowns can vary between species (Longuetaud et al., 2013). This factor,
701 which can reduce the horizontal overlap of neighbouring crowns, and therefore potentially
702 also APAR, was beyond the scope of this study. Similarly, the species were generally mixed
703 on a tree-by-tree based rather than coarser mixtures composed of small monospecific
704 neighbourhoods. The effect of a more coarse spatial distribution on APAR was not examined
705 in this study and is likely to reduce the size of most of the effects that were examined.

706

707 **Site factors**

708

709 Within the single species combination of *P. sylvestris* and *F. sylvatica* the factors examined in
710 this study varied along the site gradient and are likely to vary at least as much within a single
711 stand as it develops. Larger canopy volumes, LAI and hence competition for light, are likely
712 to develop along gradients of increasing soil resource availability (Smethurst et al., 2003).
713 Therefore, species interactions that increase APAR are likely to have an increasingly positive
714 effect on growth as soil resource availability increases (Forrester, 2014). This is consistent
715 with the increasing mixing effect on *P. sylvestris* growth with increasing site productivity
716 index that was found using the same plots (Pretzsch et al., 2016). While the mixing effects on

717 *F. sylvatica* APAR also increased with canopy volume or canopy depth, there was no
718 evidence to suggest that these mixing effects on APAR made any contribution to the mixing
719 effects on growth (Fig. S5).

720

721 **Conclusions**

722

723 Tree APAR often increases with individual tree leaf area (Binkley et al., 2013) and in this
724 study it also increased with relative height, for both species. However, the effects of allometry
725 and stand density on tree f were less consistent because the f -leaf area relationships are
726 subject to feedbacks between tree allometry/physiology/phenology/morphology and stand
727 structural characteristics. That is, the relative importance of allometry, phenology, vertical or
728 horizontal stand structure and tree size on tree f and stand f are therefore likely to vary, not
729 only due to these feedbacks but also in response to the characteristics of the admixed species,
730 site conditions and stand management.

731

732 Tree and stand f were influenced by all factors examined, however the relative sizes of these
733 effects and the direction of their effect sometimes differed between the tree and stand levels.
734 Similarly, mixing effects on growth variability also varied between the tree, species and
735 community levels in the same plots (del Río et al., in review). Therefore, while the effects on
736 one level cannot be used to predict the effects on another, information about each level was
737 complementary and helped to explain the patterns at the other level. This also indicates a
738 trade-off between silvicultural management to achieve higher individual tree APAR or to
739 achieve higher stand APAR, consistent with the trade-off between tree- and stand-level
740 growth (Long, 1985). In *P. sylvestris* and *F. sylvatica* mixtures, individual tree APAR can be
741 increased by reducing stand density (LAI or canopy volume) and increasing the relative

742 height, particularly for *P. sylvestris*. However, stand APAR could be increased by increasing
743 stand basal area and probably also by ensuring that *P. sylvestris* dominates *F. sylvatica*.

744

745 **Acknowledgements**

746

747 This article is based upon work from COST Action EuMIXFOR, supported by COST
748 (European Cooperation in Science and Technology). Funding for the Czech Republic triplet
749 was provided by the Ministry of Education, Youth and Sports" Effect of mixture on the
750 development of tree species composition, structure and biomass" (COST CZ - LD14063). All
751 contributors thank their national funding institutions and the forest owners for agreeing to
752 establish the triplets and to measure and analyse data from the triplets. We are also very
753 grateful to Patrick Schleppi and Josephine Haase who provided advice about using the
754 Hemisfer software. The first author was funded by a Heisenberg Fellowship (FO 791/4-1)
755 from the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG).

756

757 **Data accessibility**

758 Data available from the Dryad Digital Repository

759

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Table 1. The significance and direction of linear relationships between the mixing effect (RP_{fAPAR}) or the fraction of PAR absorbed (f) and stand or site characteristics. Positive and negative correlations are indicated with + and -, respectively. All blank cells were not significant ($P>0.05$). * indicates $0.01 < P < 0.05$, ** indicates $0.001 < P < 0.01$ and *** indicates $P < 0.001$.

Explanatory variables	<i>F. sylvatica</i>	<i>P. sylvestris</i>	Community	Relevant figures
Mixing effect in terms of the fraction of PAR absorbed (RP_{fAPAR})				
Canopy depth (m)	***		+	S4d
Canopy leaf area density ($m^2 m^{-3}$)			-	4c
Proportion of canopy space filled (proportion)				
Shannon's index for heights		***		S5b
Basal area of <i>F. sylvatica</i> ($m^2 ha^{-1}$)	***			S4c
Basal area of <i>P. sylvestris</i> ($m^2 ha^{-1}$)				
Stocking (trees ha^{-1})	- **			S4f
LAI of <i>F. sylvatica</i> ($m^2 m^{-2}$)				
LAI of <i>P. sylvestris</i> ($m^2 m^{-2}$)		- *		4b,S5d
Proportion (LAI) <i>F. sylvatica</i>		+		S5a
Canopy volume of <i>F. sylvatica</i> ($m^3 ha^{-1} \times 10^{-3}$)	***		+	S4a
Canopy volume of <i>P. sylvestris</i> ($m^3 ha^{-1} \times 10^{-3}$)				
Community canopy volume ($m^3 ha^{-1} \times 10^{-3}$)	***		+	4a,S4b
Fraction PAR absorbed <i>F. sylvatica</i> ($GJ ha^{-1} day^{-1}$)	***			S4e
Fraction PAR absorbed <i>P. sylvestris</i> ($GJ ha^{-1} day^{-1}$)	- *			
Site productivity index (<i>F. sylvatica</i>)				
Site productivity index (<i>P. sylvestris</i>)			+	
Fraction of PAR absorbed (f)				
Relative height	***		+	S8a
Canopy depth (m)				S6d,S7d
Canopy leaf area density ($m^2 m^{-3}$)	+	- ***	+	S6a
Proportion of canopy space filled (proportion)		- ***	+	S7e
Community basal area ($m^2 ha^{-1}$)	- *			S6b
LAI of <i>F. sylvatica</i> ($m^2 m^{-2}$)	***	- ***	+	S8b
LAI of <i>P. sylvestris</i> ($m^2 m^{-2}$)	- ***	+	-	S7b
Proportion (LAI) <i>F. sylvatica</i>	***	- ***	+	S7c
Canopy volume of <i>F. sylvatica</i> ($m^3 ha^{-1} \times 10^{-3}$)		- ***	+	
Canopy volume of <i>P. sylvestris</i> ($m^3 ha^{-1} \times 10^{-3}$)	- ***	+	-	S7a
Site productivity index (<i>F. sylvatica</i>)				
Site productivity index (<i>P. sylvestris</i>)				S6c
Mean annual precipitation (mm)				S6f,S7f,S8d
de Martonne Index				S6e,S8c

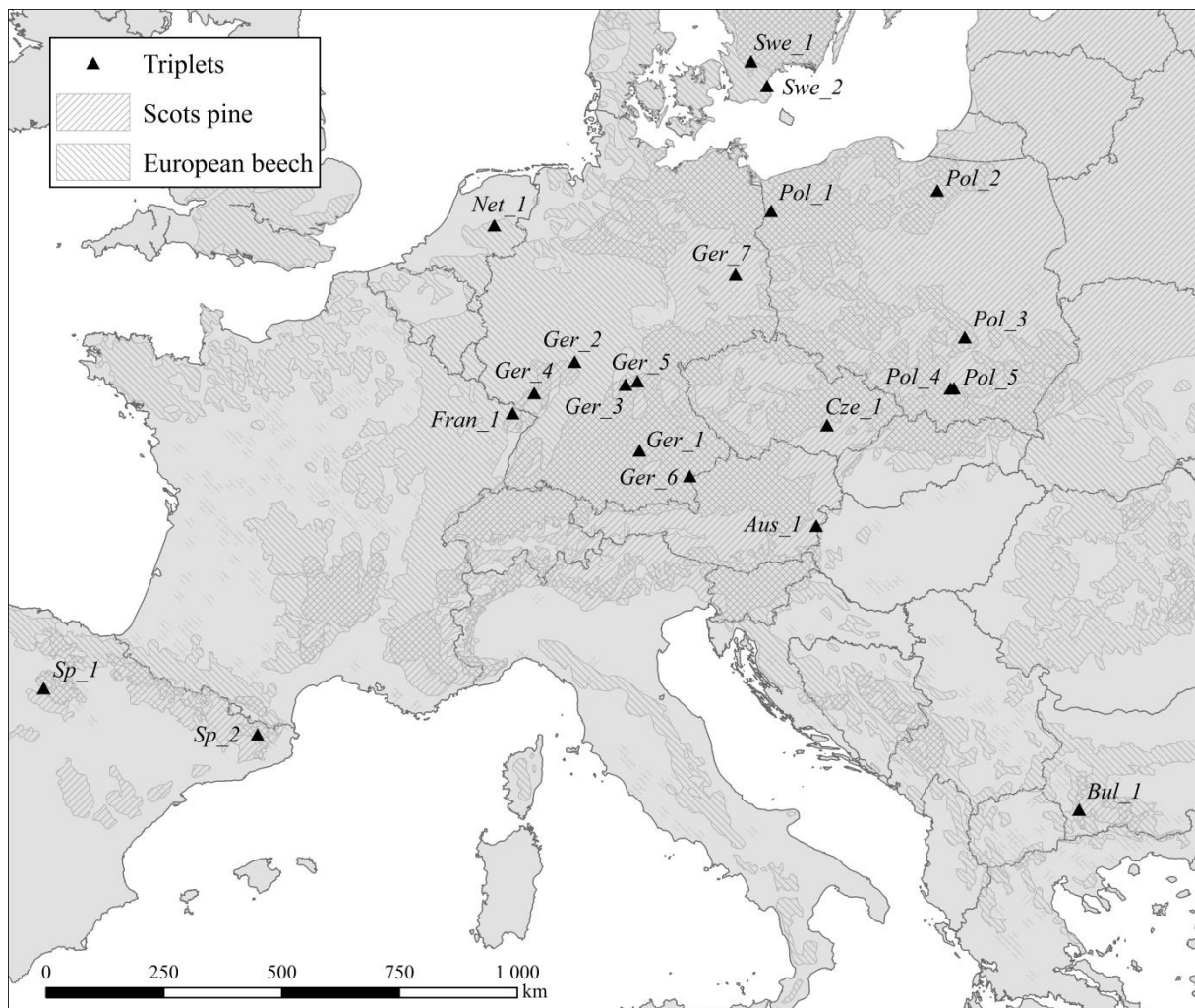


Figure 1. The locations of the 21 triplets of *Pinus sylvestris* (Scots pine) and *Fagus sylvatica* (European beech) in relation to their current distributions according to EUFORGEN (<http://www.euforgen.org/distribution-maps/>).

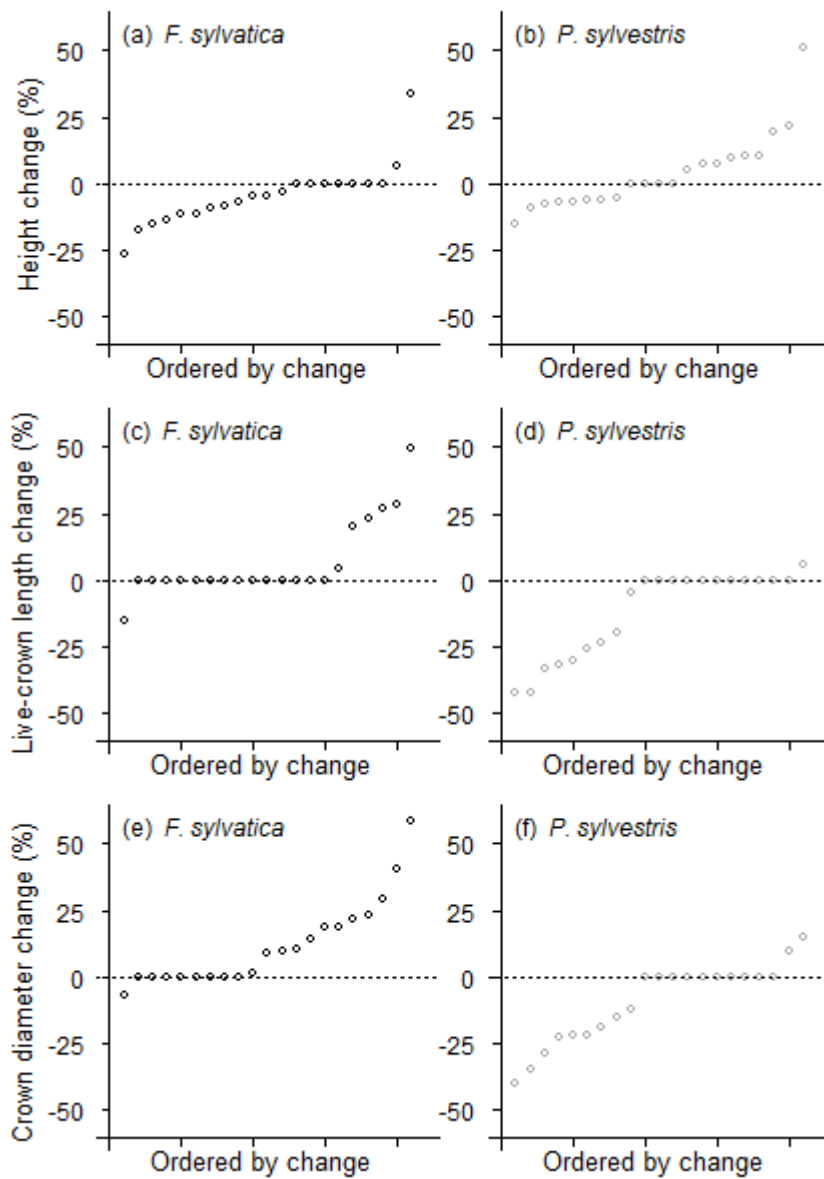


Figure 2. The change (%) in height, live-crown length or crown diameter, for a given diameter, when using the allometric equations (Equation 2, Table S2) from the mixtures compare with the equations for the monocultures for all 21 triplets. Points greater than zero indicate a larger height, live-crown length or crown diameter predicted using the mixture equations than the monoculture equation, for a given diameter. To remove any size affects, the diameter used for a given species and triplet was the mean diameter for that species in the given triplet.

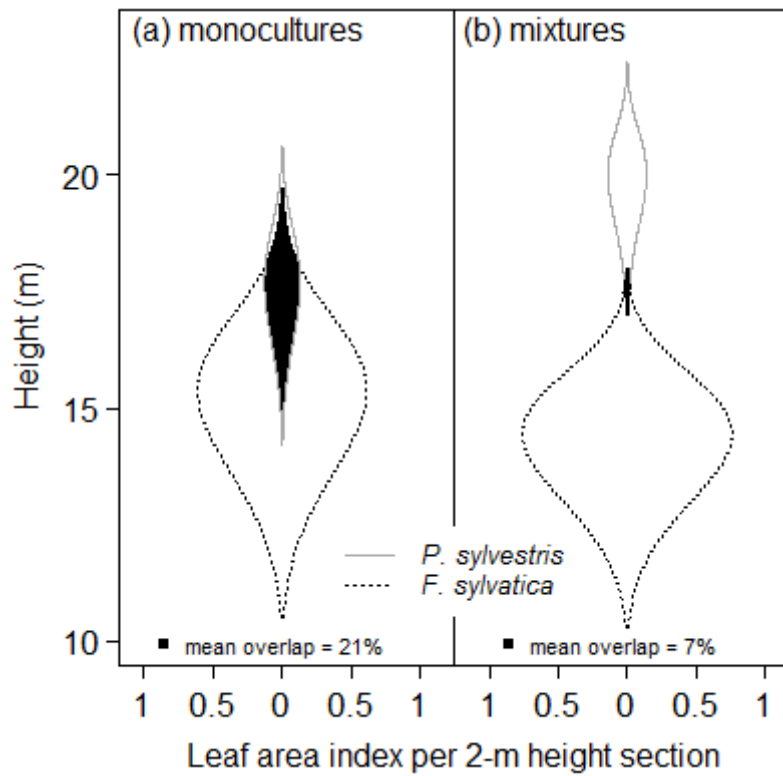


Figure 3. The vertical distribution of predicted leaf area index of each species in the monocultures and the mixtures. These leaf area distributions were created by placing the leaf area of each given tree into the 2-m layer of the canopy corresponding to its crown midpoint (halfway between the height to its live crown and its tree height). This distribution of leaf area was then fitted to a 2-parameter Weibull distribution.

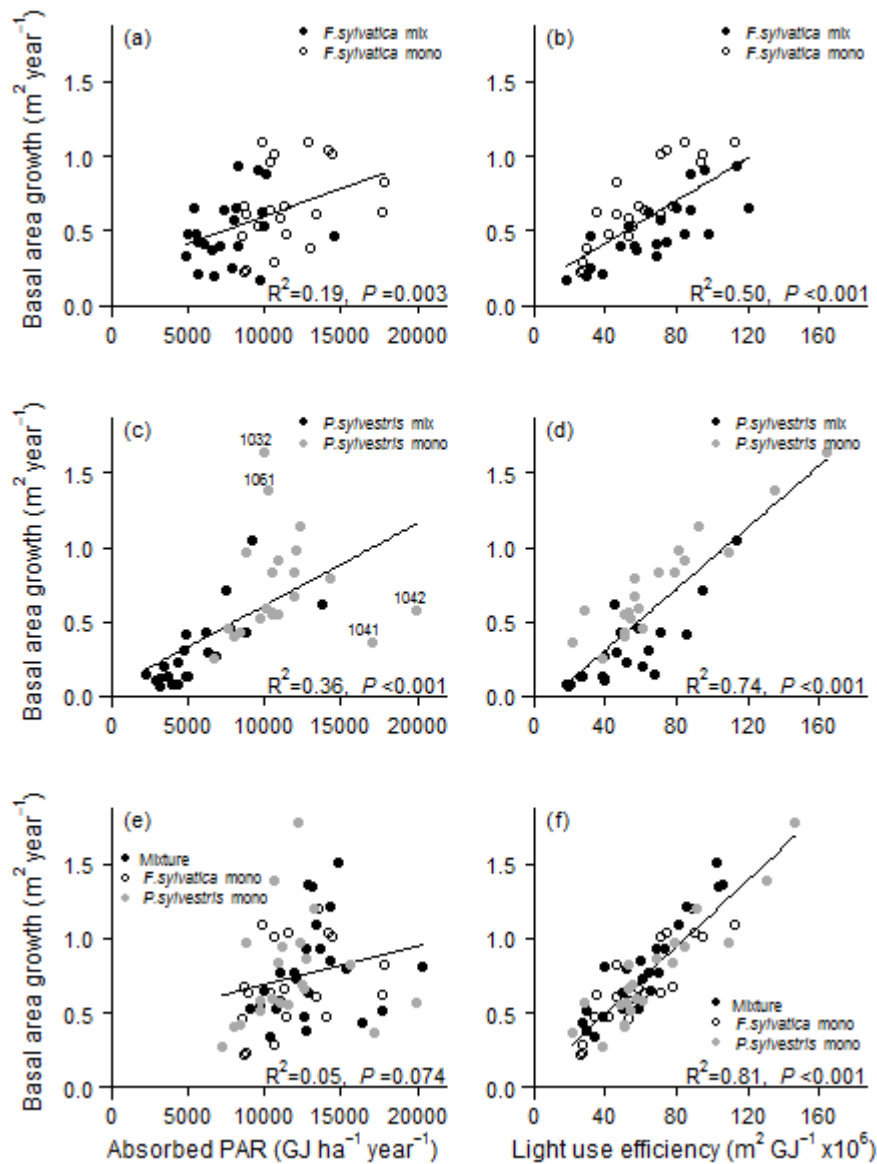


Figure 4. The relationship between stand basal area growth and the absorbed PAR (a,c,d) or the light-use efficiency in terms of basal area growth per unit APAR (b,d,f) for *F. sylvatica* (a,b), *P. sylvestris* (c,d) and the whole community (e,f). APAR was predicted for the whole year for *P. sylvestris* and for the growing season for *F. sylvatica*. The four labels in 2c indicate the triplet number from Table S1.

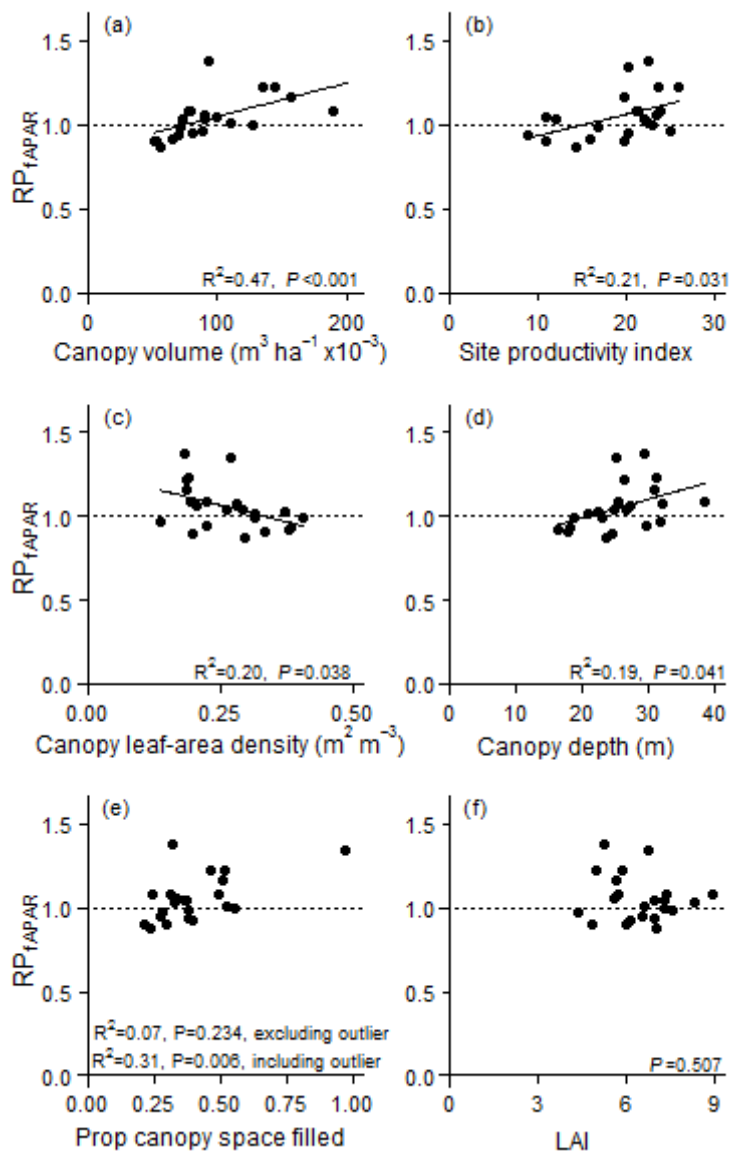


Figure 5. The relationships between the mixing effect on the fraction of PAR absorbed by the community (quantified as growing season RP_{fAPAR} ; Equation 7) and the total community canopy volume (a), the site productivity index for *P. sylvestris* (b), the canopy leaf-area density (c), canopy depth (d), the proportion of canopy space filled by crowns (e) and LAI (f).

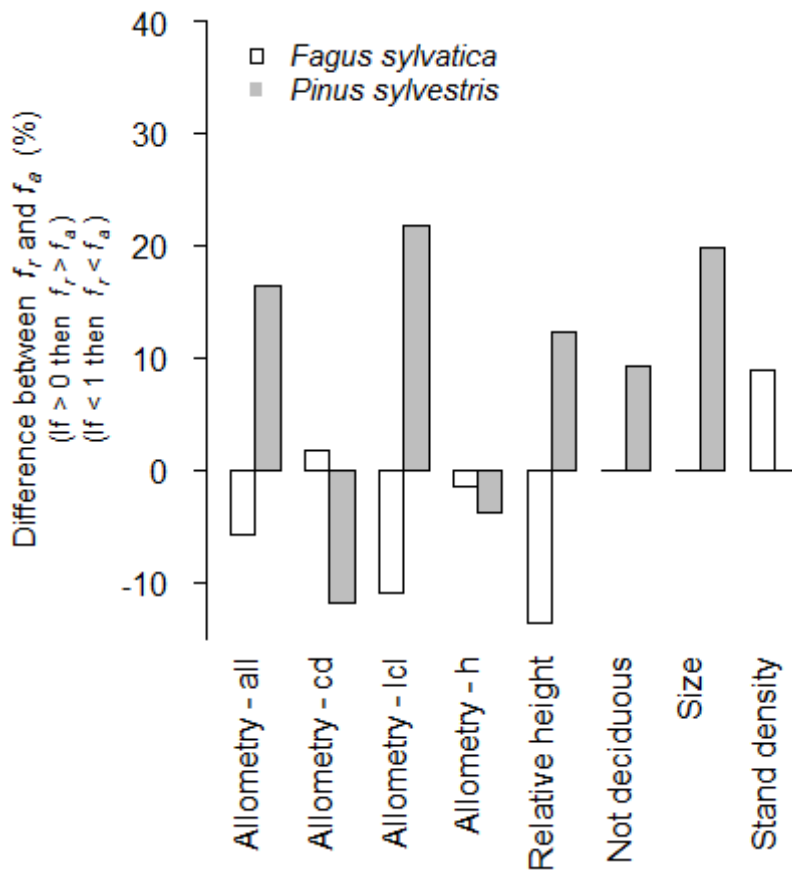


Figure 6. The effect of each factor (x-axis variables) on predicted tree-level fraction of PAR absorbed for each species. Effect sizes were calculated using the regression Equations 3-6, while using the means for the given species of all other variables. All effects that are not zero were significant in the regression equations ($P < 0.05$, Table S7). “Allometry - all” applied all the allometric equations from monocultures to the trees in the mixtures, while the other “Allometry” runs only use the monospecific allometric equations for the variables indicated; *cd* is crown diameter, *lcl* is live-crown length but also includes the effect of height to the live-crown, and *h* is height. “Not deciduous” is a run where the *F. sylvatica* do not lose their leaves in winter. The “Size” compares predicted fraction of PAR for trees with the mean tree leaf area (m^2) in the mixture to those with the mean tree leaf area in the monocultures. The “Stand density” compares the effects of density in terms of the mean LAI in mixtures and monocultures.

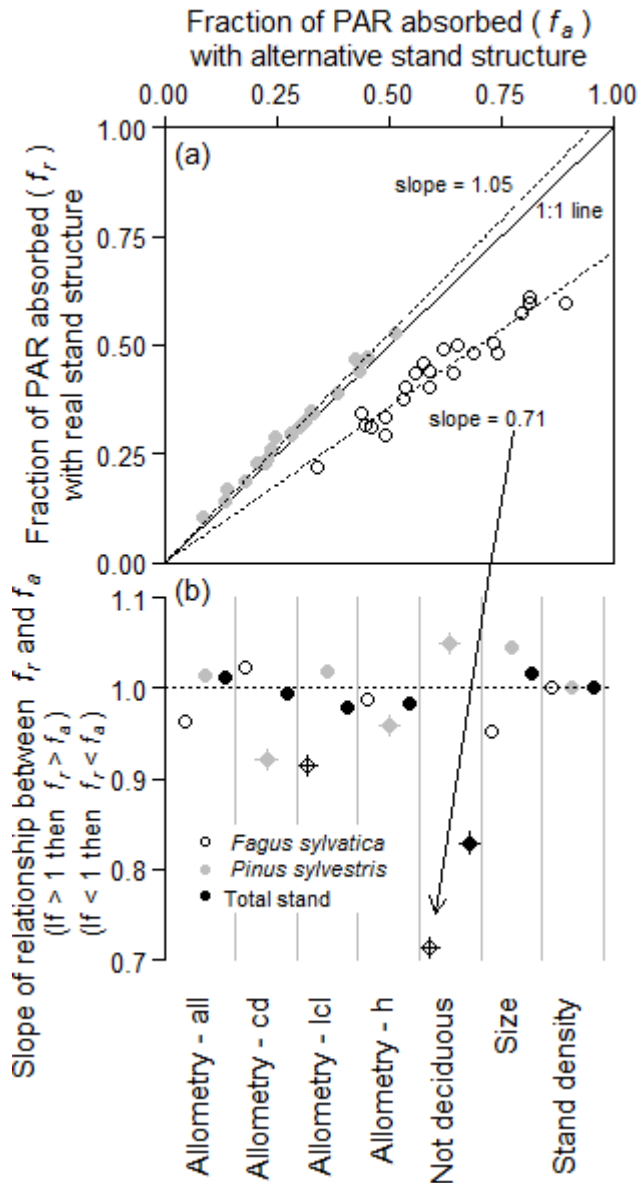


Figure 7. Part (a) shows the relationship between the fractions of PAR absorbed (f) by *P. sylvestris* or *F. sylvatica* trees in the real situation where *F. sylvatica* is deciduous versus a situation where they are not deciduous. The slopes of these relationships are shown and provide a measure of the effect size, which is then plotted in part (b). Part (b) shows the effect sizes of several stand-level effects, which are indicated on the x-axis. The x-axis values are as described in Fig. 6, except for the Size and Density effects. The “Size” compares predicted f for the mixtures when using the measured mean tree sizes of the mixture (height, crown diameter, live-crown length and leaf area) with runs where those mean sizes are replaced with the mean sizes measured in the monocultures. The Density compares a run using the actual stand density, with runs where the density (spacing between the trees) of the respective

monoculture is used (but the mean tree sizes and species proportions of the mixture are retained). The slopes that were significantly different to 1 are indicated with crosses.