

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

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Abstract

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

2. In this study, measurements of tree sizes and stand structures were combined with a detailed tree-level light model (Maestra) to examine the contribution of each light-related interaction on tree- and stand-level light absorption at 21 sites, each of which contained a triplet of plots including a mixture and monocultures of *Fagus sylvatica* and *Pinus sylvestris* (63 plots). These sites were distributed across the current distribution of these species within Europe.
3. Averaged across all sites, the light absorption of mixtures was 14% higher than the mean of the monocultures. At the whole community level, this positive effect of mixing on light absorption increased as canopy volume or site productivity increased, but was unrelated to climate. At the species population or individual tree levels, the mixing effect on light absorption resulted from light-related interactions involving vertical canopy structure, stand density, the presence of a deciduous species (*F. sylvatica*), as well as the effects of mixing on tree size and allometric relationships between diameter and height, crown diameter and crown length.
4. The mixing effects on light absorption were only correlated with the mixing effects on growth for *P. sylvestris*, suggesting that the mixing effects on this species were driven by the light-related interactions, whereas mixing effects on *F. sylvatica* or whole community growth were probably driven by non-light-related interactions.
5. *Synthesis.* The overall positive effect of mixing on light absorption was the result of a range of light-related interactions. However, the relative importance of these interactions varied between sites and is likely to vary between other species combinations and as stands develop.

KEYWORDS

allometric equation, biodiversity, complementarity, Maestra model, plant–plant interactions, resource availability, tree height

1 | INTRODUCTION

Greater absorption of photosynthetically active radiation (APAR) is often proposed as a reason for greater productivity in mixed-species forests than in monocultures (Forrester & Bauhus, 2016; Kelty, 1992; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Pretzsch, 2014). However, mixing effects on APAR have rarely been quantified (Binkley, Dunkin, DeBell, & Ryan, 1992; Forrester & Albrecht, 2014; Forrester, Lancaster, Collopy, Warren, & Tausz, 2012; Le Maire et al., 2013; Sapjanskas, Paquette, Potvin, Kunert, & Loreau, 2014). It is therefore difficult to determine which canopy structure or crown architectural characteristics are most strongly influencing light-related mixing effects and how these effects might differ between sites, species compositions and stand ages.

Mixing effects on forest productivity, sometimes referred to as complementarity, generally result from interspecific differences in physiology, phenology or morphology or intraspecific differences (i.e. plasticity) that result from interspecific interactions (Forrester & Bauhus, 2016; Ishii & Asano, 2010; Kelty, 1992). These effects may improve resource acquisition or support higher resource-use efficiency. With regard to light-related interactions, there are several ways foliage

can be distributed more effectively in the canopies of mixtures than in monocultures. Seasonal differences in competition for light can result from mixing evergreen and deciduous species, or deciduous species with contrasting phenology (Ishii & Asano, 2010; Sapjanskas et al., 2014). Vertical stratification could enable the foliage of each species to be distributed in complementary vertical profiles (Ishii & Asano, 2010; Ishii, Reynolds, Ford, & Shaw, 2000; Parker & Brown, 2000). This can result from contrasting height dynamics, ages and physiology, including shade tolerance (Forrester, Bauhus, & Khanna, 2004; Ishii & Asano, 2010; Kelty, 1992; Niinemets, 2010; Valladares & Niinemets, 2008). Even when different species have similar crown positions, the vertical distribution of foliage may still be superior to monocultures if the species distribute their foliage at different positions within their crowns, such that the vertical distribution of one species is skewed towards the top while the other is skewed towards the bottom (Binkley, 1992; Guisasola, Tang, Bauhus, & Forrester, 2015; Niinemets, 2010).

Contrasting tree allometric relationships in mixtures compared with monocultures can also influence APAR. For a given tree diameter, the crown sizes (width, length, surface area, leaf area), shapes or height of a given species can be different in mixtures compared with monocultures (Binkley, 1992; Forrester & Albrecht, 2014; Forrester,

Benneter, Bouriaud, & Bauhus, 2017; Metz et al., 2013; Pretzsch, 2014). These allometric differences can add to the effects of the vertical foliage distribution when it allows crowns to expand sideways at different levels in the canopy, or upwards or downwards away from other species (Binkley, 1992).

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

This study aimed to determine how stand structure and crown architecture affect APAR by examining how the APAR of individual trees and of the stand in terms of each individual species (species population level) or for the whole community (community level) is influenced by vertical canopy structure, tree allometry, deciduous competitors, tree size and stand density. Tree APAR was predicted using direct measurements of tree positions and dimensions as inputs for the tree-level model Maestra. These dynamics are likely to vary between sites, even for the same species combination, because different resource availability along site gradients will influence stand density and could also influence biomass partitioning and allometric relationships (Forrester et al., 2017; Litton, Raich, & Ryan, 2007). Therefore, this study was done at 21 sites across Europe for one of the most widely distributed European species combinations (*Pinus sylvestris* and *Fagus sylvatica*) (Figure S1).

We hypothesized that (1) the mixing effect on growth that was reported by Pretzsch et al. (2015) was caused by light-related interactions; these interactions relate to (2) the vertical canopy structure (e.g. vertical leaf area distribution and overlap between species); (3) crown and tree architecture, in terms of allometric relationships, which vary between mixtures and monocultures for each species; (4) the presence of a deciduous competitor; (5) mean tree size and stand density [e.g. leaf area index (LAI)] which vary between mixtures and monocultures; and (6) that these effects change with site characteristics.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

Tree allometry, canopy structure and light absorption were examined at 21 sites along a productivity and rainfall gradient through Europe. The southernmost sites are located in Spain and Bulgaria and the northernmost sites are situated in Sweden. They are spread across a large proportion of the overlapping area of the distributions of *P. sylvestris* and *F. sylvatica*. The mean annual precipitation ranges from 520 to 1,100 mm, the mean surface air temperature from 6 to 10°C and the elevation from 40 to 1,340 m a.s.l. The aridity of each site was also quantified using the de Martonne (1926) index (= annual precipitation

in mm/(mean annual temperature in °C + 10)). More detail about the climatic and edaphic conditions of each site is provided in Table S1.

At each site a triplet of plots was established, which included a monoculture of each species and a mixture. The plot sizes ranged from 0.014 to 0.473 ha and were generally rectangular in shape. The criteria used when selecting the plots were that they were as close as possible to even-aged, that they had not been thinned for at least 10 years and that the trees were mostly mixed on a tree-by-tree basis as opposed to groups of individuals of one species mixed with groups of the other species. The even-aged criterion also, importantly, resulted in relatively mono-layered forest stands, such that while the mean heights of each species were often different, there was still some vertical overlap of the crowns of each species and therefore direct species interactions within the canopy. Additional criteria were that for a given site, all three plots were on a similar soil substrate, aspect and slope.

The 63 plots within the 21 sites covered a wide range of stand structures. In the mixtures, the per cent of basal area that was *F. sylvatica* ranged from 23% to 77% and the per cent of LAI ranged from 71% to 94%. A site productivity index (SI) was also calculated for each site, using the monocultures of each species, to indicate the combined effect of all climatic, edaphic and management conditions on productivity. This SI was the height of the 100 largest-diameter trees per hectare at age 50 years (Pretzsch et al., 2015). The basal area ranged from 16 to 72 m²/ha, the number of trees per hectare from 211 to 4,059 and the stand age from 39 to 105 years.

2.2 | Data collection

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

2.3 | Basal area growth

Growth was quantified in terms of basal area. Biomass growth was not used to avoid additional errors associated with the need to have different biomass equations for each plot; biomass equations can vary due to species interactions, climatic or edaphic factors and age (Laclau et al., 2008; Wirth, Schumacher, & Schulze, 2004). Tree growth during 2013 was calculated using increment cores collected from at least 20 trees per species per plot covering the diameter range for the given species and plot. The diameter increments of all non-cored trees were calculated by fitting diameter increment functions for each plot and species (for the year 2013), where diameter increment was

a double logarithmic function of diameter at 1.3 m and both were ln-transformed. More detail is provided in Pretzsch et al. (2015).

2.4 | Calculations of stand canopy and structural variables

The LAI (m^2/m^2) was predicted using the general allometric leaf area equations in Appendix S1. The canopy volume (m^3/ha) was calculated as the sum of all crown volumes in the plot and expressed per ha. Crown volumes were calculated assuming a half-elliptical crown shape with a length equal to the live crown length and a diameter equal to the crown diameter. The canopy depth (m) is the height of the tallest tree in the plot minus the lowest height to the live crown in the plot. Two variables were used to quantify the canopy density. One was the canopy leaf area density (m^2/m), which is the leaf area (m^2/ha) divided by the canopy volume (m^3/ha). The second was the proportion of canopy space that was filled with tree crowns. This was calculated as the canopy volume divided by the total canopy space (m^3 ; canopy depth $\times 10,000 \text{ m}^2$).

2.5 | Estimation of the APAR

Direct measurement of the APAR by individual trees within a forest canopy is labour intensive and difficult in mature stands where trees can be more than 30 m tall. Therefore, the light absorption by each tree within the plots was predicted using a detailed 3D tree-level model, Maestra (Duursma & Medlyn, 2012; Grace, Jarvis, & Norman, 1987; Medlyn, 2004; Wang & Jarvis, 1990). The stand APAR of a given species or the whole community was calculated as the sum of the APAR of all trees within the given plot and expressed per hectare. Depending on the hypotheses, light absorption was expressed as either APAR (GJ/ha or GJ per tree) or as the fraction (f) of PAR that was absorbed, which was calculated as the tree (GJ per tree) or stand (GJ/ha) APAR divided by the total plot PAR (GJ/ha). The use of f removes some of the effects that latitude could have on APAR. Maestra predicts the APAR of individual trees using information about crown architecture (crown width and length, leaf area and leaf angle distributions), species-specific differences in leaf optical properties and leaf area density distributions and also accounts for shading from neighbouring trees by representing the canopy as an array of tree crowns whose positions are defined by x and y coordinates. The slope and aspect of a site are accounted for in both the x and y directions. The parameterization, validation and use of the Maestra model is described in Appendix S2.

Individual tree APAR (GJ/year) was calculated from the beginning to the end of 2013. APAR was usually only calculated for the growing season, which was defined by the foliated period of *F. sylvatica* (Table S1). However, for *P. sylvestris* or the whole community, whole year APAR was used when examining relationships with annual growth or the effects of *F. sylvatica* leaf fall on APAR.

Absorption of photosynthetically active radiation predictions at the stand level from Maestra (APAR_M) were validated using predictions obtained by analysing hemispherical photos (APAR_H) (Appendix S3).

The APAR_H and APAR_M were correlated ($R^2 = .67$) and indicated that APAR_M predictions were on average 8% lower than APAR_H estimates. This level of accuracy is expected given that (1) the plots covered a wide range of stand structures and LAI, (2) the hemispherical photos are another indirect estimate of APAR and (3) Maestra is a process-based model that does not assume that all trees of a given species have the same light extinction coefficients. The Maestra model is therefore considered to provide realistic predictions of APAR for this study, as has also been found in other Maestra validation studies (Charbonnier et al., 2013; le Maire et al., 2013; Wang & Jarvis, 1990).

2.6 | Tree allometry

The effects of species composition on height (h), live crown length (lcl) or crown diameter (cd) were examined using Equation 1.

$$Y = b_0 + b_1 \ln(d) + b_2 M + b_3 \ln(d) \times M + \varepsilon \quad (1)$$

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 is a dummy variable to define the mixing treatment and is either monoculture or mixture. For some sites the cd or lcl were ln-transformed to linearize relationships and to reduce heteroscedasticity. When this transformation was used, the correction factor required when back-transforming the Y -variables was calculated as the sum of the measured values divided by the sum of the (back-transformed) predicted values (Snowden, 1991). A separate equation was fitted for each species at each site.

2.7 | Tree-level f

The effects of tree and stand variables on the fraction of PAR absorbed by individual trees (f_{tree}) were examined using linear mixed models fitted to the Maestra estimates of APAR that were converted to f (Equations 2, 3, 6 and 7). The random effects of each of these equations were plot nested within site, or only site for Equations 4 and 5, which were only used for mixtures. In Equations 2–5, $\varepsilon \sim N(0, \sigma)$.

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

$$\ln(f_{tree}) = \beta_0 + \beta_1 \ln(la) + \beta_2 M + \beta_3 S + \beta_4 \ln(la) \times M + \beta_5 \ln(la) \times S + \beta_6 M \times S + \varepsilon \quad (2)$$

Equation 3 was then used to divide the mixing effect into a horizontal component quantified as the plot LAI and a vertical component quantified as the relative height, rh , which is the height of the target tree divided by the mean height of all trees in the plot. The M was retained in the model to account for any mixing effect that was not accounted for by rh or LAI.

$$\ln(f_{tree}) = \beta_0 + \beta_1 \ln(la) + \beta_2 rh + \beta_3 LAI + \beta_4 M + \beta_5 \ln(la) \times M + \beta_6 rh \times M + \beta_7 LAI \times M + \varepsilon \quad (3)$$

2.8 | Stand-level APAR and f

Linear regression was used to examine relationships between growth, APAR and light use efficiency (LUE). LUE (m^2/GJ) was calculated as the basal area growth ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$) per APAR ($\text{GJ ha}^{-1} \text{year}^{-1}$). Linear regression was also used to examine how stand-level f and the mixing effect on f for a given species or the whole community were influenced by site and stand characteristics (e.g. mean annual precipitation, basal area, canopy volume). At the stand level, the mixing effect on f was quantified using the relative productivity equation (RP), which was calculated using Equation 4 at the community level and Equation 5 at the species population level (Forrester & Pretzsch, 2015).

$$\text{RP}_{\text{total community } f} = \frac{f_{1,2}}{m_1 f_1 + m_2 f_2} \quad (4)$$

$$\text{RP}_{\text{species } f} = \frac{f_{1,(2)}}{m_1 f_1} \quad (5)$$

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

In contrast to the effects on tree-level f , which were examined using Equations 2 and 3, the stand-level effects on f (for a given species or the whole community) were examined using linear models between the f predicted using actual tree dimensions and stand structure, as a function of the f predicted after changing the Maestra inputs to the allometry, foliated period of *F. sylvatica*, size and stand density treatment. A slope significantly different to 1, indicates a significant treatment effect on stand f .

2.9 | Effects of allometry, competition from a deciduous species, mean tree size and mean stand density on f

To disentangle the effects of allometry, mixing deciduous and evergreen species, and the mixing effects on tree size and stand density on tree f and stand f , eight Maestra model runs were used. The first run was used to predict the APAR and f from the measured stand structures and tree sizes as described above (run 1) and fitted to Equations 2 and 3. Four runs (runs 2–5) were used to examine the effect of allometry on APAR or f , such that the heights, live crown lengths, crown diameters or all three of these variables were replaced for all trees in the mixtures with values predicted using the allometric equations obtained from the monocultures for the given species and

site. A sixth run (run 6) was done where the leaves of the *F. sylvatica* trees were not lost in winter to examine how much additional light *P. sylvestris* obtains by growing with this deciduous species.

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

The stand density also varied between mixtures and monocultures in some of the sites (Pretzsch et al., 2015). Therefore, an eighth comparison (run 8) was used to examine whether this mixing effect on density influenced stand-level APAR. To do this, new mixtures were created that used the mean tree spacing (in terms of trees per ha) from either the *F. sylvatica* or *P. sylvestris* monocultures, such that trees were positioned at a regular spacing (on a square grid) and with the same mixing proportions that were measured in the mixtures. In these synthetic mixtures, the tree sizes were the mean measured sizes of each species in the mixtures of the given site. For all runs where the live crown lengths were changed, the heights to the live crowns were changed simultaneously.

The f obtained from runs 2–5 were then analysed using linear regression. Focusing only on the mixtures, the effect of allometry was examined by comparing f predicted (by Maestra) using the measured h , lcl and cd (run 1), with f predicted using the allometric equations developed for the monocultures of the given site (runs 2–5). This was examined by replacing the M in Equation 3 with a dummy variable, A , which defines whether allometric relationships from monocultures or mixtures were used to predict h , lcl or cd . The resulting Equation 6 was only applied to mixtures. The variable A , includes four levels to define whether only one variable (h , lcl or cd) was predicted using the equations from monocultures, or all of these variables were predicted using the equations from the monocultures.

$$\ln(f) = \beta_0 + \beta_1 \ln(la) + \beta_2 rh + \beta_3 \text{LAI} + \beta_4 A + \beta_5 \ln(la) \times A + \beta_6 rh \times A + \beta_7 \text{LAI} \times A + \varepsilon \quad (6)$$

Equation 7 was used for *P. sylvestris* in the mixtures to test how much individual tree f changed if the *F. sylvatica* trees retained their leaves all year (run 6). The D is a dummy variable that defines whether the *F. sylvatica* retain their leaves or not.

$$\ln(f) = \beta_0 + \beta_1 \ln(la) + \beta_2 rh + \beta_3 \text{LAI} + \beta_4 D + \beta_5 \ln(la) \times D + \beta_6 rh \times D + \beta_7 \text{LAI} \times D + \varepsilon \quad (7)$$

Initially all fixed effect candidate predictors were included in the models in Equations 1–3, 6 and 7, before all non-significant ($p > .05$) variables were removed in order of decreasing p -value. Residual and

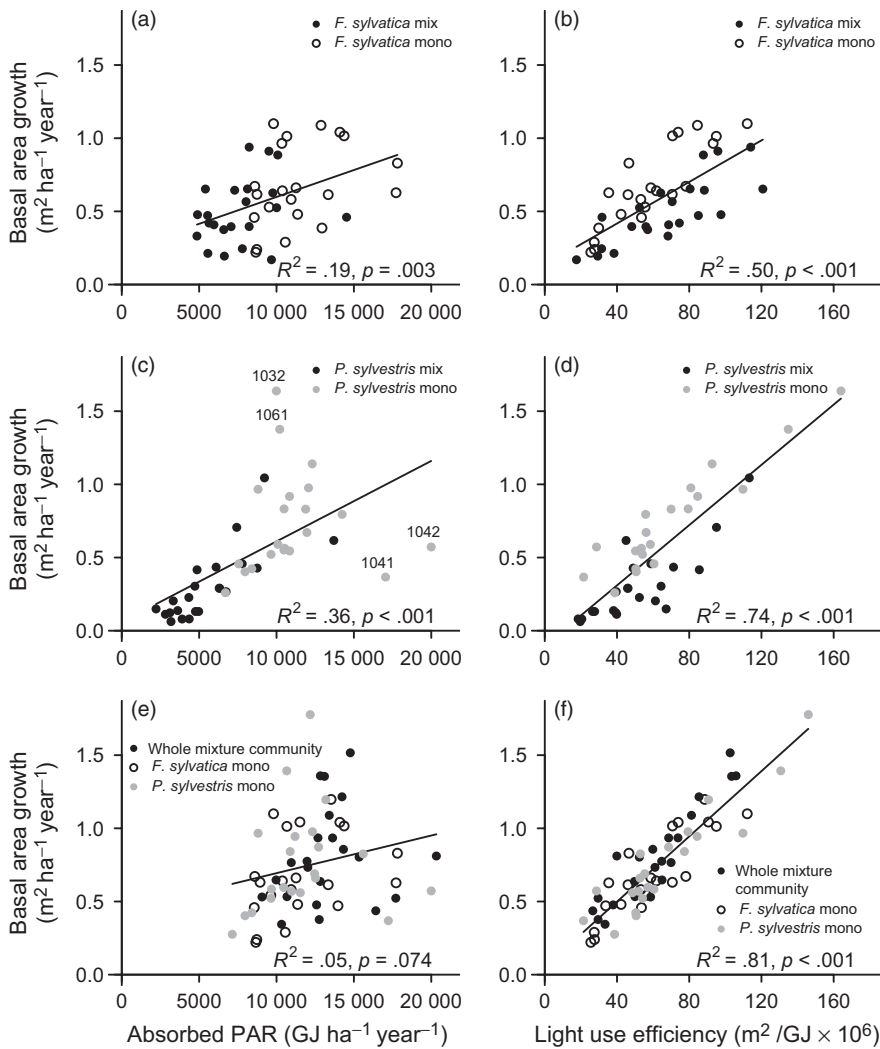


FIGURE 1 The relationship between stand basal area growth and the absorbed PAR (a, c, e) or the light use efficiency in terms of basal area growth per unit APAR (b, d, f) for *Fagus sylvatica* (a, b), *Pinus sylvestris* (c, d) and the whole community (e, f). APAR was predicted for the whole year for *P. sylvestris* or the whole community and for the growing season for *F. sylvatica*. The four labels in c indicate the site number from Table S1

normal quantile plots were visually assessed to ensure that the residuals were centred at zero, approximately normally distributed, with constant variance. All statistical analyses were carried out using R 3.2.1 (R Core Team 2015), including the *nlme* package for fitting the mixed models (Pinheiro, Bates, DebRoy, & Sarkar, 2013).

3 | RESULTS

3.1 | Production ecology—growth, light absorption and LUE

The stand-level basal area growth of each species and the whole community were positively correlated with APAR, however, this relationship was much stronger for *P. sylvestris* and was not significant for the whole community (Figure 1). The LUE was also positively correlated with growth in all treatments. The relationship between the mixing effects on light absorption (RP_{fAPAR}) and the mixing effects on growth (RP_{Growth}) were used to indicate whether the light complementarity could be causing the mixing effect on growth. This relationship was only significant for *P. sylvestris* (Figure 2). The species were also regressed against each other

for RP_{Growth} , RP_{fAPAR} and their site productivity indices to indicate whether there was any similarity in the sites that they performed well vs. poorly on. There were significant positive correlations between the RP_{Growth} of each species and also between the site productivity indices of each species (Figure S8), indicating that they favoured similar sites and benefited from mixing on similar sites. In contrast, RP_{fAPAR} of each species were not correlated indicating mixing effects on APAR occurred on different sites for *P. sylvestris* than those for *F. sylvatica*.

3.2 | Mixing effects on tree allometry and stand structure

Mixing often had a significant effect on relationships between diameter and height, live crown length or crown diameter (Figure 3, Table S2). These mixing effects were very variable and ranged from decreases to increases in all variables, for a given diameter, for each species. Often the more common response to mixing for *P. sylvestris* was the opposite to the most common response of *F. sylvatica*. Mixing was more likely to increase the height (for a given diameter) of *P. sylvestris* and decrease the height for *F. sylvatica*. In contrast, mixing was

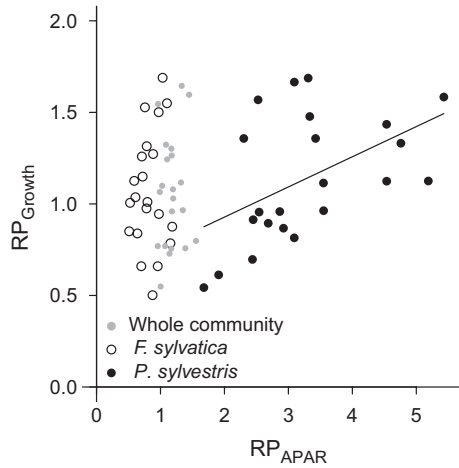


FIGURE 2 The relationship between the mixing effect on stand basal area growth (RP_{Growth}) and the mixing effect on the fraction of light absorbed ($RP_{f\text{APAR}}$) for *Pinus sylvestris*, *Fagus sylvatica* and the whole community. The fitted line is the relationship for *P. sylvestris* ($R^2 = .24$, $p = .020$). This relationship was not significant for *F. sylvatica* ($p = .799$) or the whole community ($p = .875$)

more likely to decrease the live crown length or crown diameter of *P. sylvestris* and increase them for *F. sylvatica*.

At the stand level, these differences in allometric equations and the mixing effects on mean tree sizes (Table 1) and stand density (Table 2), resulted in stand structures where *P. sylvestris* was likely to occupy a higher position in the canopy than *F. sylvatica* (Figure 4). While the expected vertical overlap in LAI based on the monocultures was about 21%, the differences in stand structure in the mixtures led to higher crown segregation (stratification) and an actual overlap of only 7%, averaged across all sites (Figure 4).

The predicted LAI of *F. sylvatica* monocultures (8.4) were significantly higher than the mixtures (6.5) and *P. sylvestris* monocultures (2.2) (Table 2) due to the difference between the allometric leaf area equations for these species (Appendix S1) but were all within the LAI range reported for these species (Leuschner, Voß, Foetzki, & Clases, 2006; Konôpka, Pajčík, Marušák, Bošel'a, & Lukac, 2016; Poyatos et al., 2007). The canopy depth, the total stand canopy volume, the proportion of canopy space that was filled with tree crowns and the canopy leaf area density were usually higher in the mixtures and the *F. sylvatica* monocultures than in the *P. sylvestris* monocultures (Table 2). In contrast to the LAI, the basal areas of the mixtures and *P. sylvestris* monocultures (both $45 \text{ m}^2/\text{ha}$) were higher than *F. sylvatica* monocultures ($33 \text{ m}^2/\text{ha}$) (Table 2).

3.3 | Climate and mixing effects on PAR absorption

Climate, in terms of the de Martonne index or precipitation, was not correlated with the mixing effect on light absorption ($RP_{f\text{APAR}}$) or the f for either species or the whole community ($p > .05$).

The $RP_{f\text{APAR}}$ for each species and the whole community generally increased with variables that quantify the size of the canopy (LAI, canopy volume, canopy depth) or site productivity index (Figures 5, S9

and S10). In contrast, the $RP_{f\text{APAR}}$ was not correlated, or was negatively correlated with the density of the canopy in terms of leaf area density and the proportion of space filled with crowns (Figure 5). For each species and the whole community, the predicted f increased as their respective LAI increased (Figures S11–13).

3.4 | Effects of allometry, competition from a deciduous competitor, mean tree size and mean stand density on f

The contrasting allometric relationships between the mixtures and monocultures contributed to the greater predicted f of the mixtures. When all the actual measurements (or allometric equations of mixtures for unmeasured trees) were used in the mixtures, a significantly higher tree-level f was predicted for *P. sylvestris* (16.5%) while that of *F. sylvatica* was lower (5.8%) (Figure 6, Table S6; Equation 6) compared with predictions based on the allometric equations from monocultures. At the stand level, the effects were small and insignificant; actual dimensions (or allometry from mixtures) resulted in a slightly greater predicted f for *P. sylvestris* (1.5%) and the community (1.1%) but a lower f for *F. sylvatica* (3.7%) compared with when all the monospecific allometric equations were used (Figure 7). Each variable had different effects on f . The greatest changes resulted from changes in crown diameter or live crown length (which includes changes in height to the live crown), and the smallest changes resulted from changes in allometric height relationships. For a given tree diameter, equations that predicted larger crown diameters or heights often resulted in greater predicted f at the tree and stand levels, and vice versa. In contrast, increases in live crown length (and associated changes in height to the live crown) reduced f , probably because this extended the crowns towards the same canopy level of the other species and intensified competition. The differences in allometric equations between mixtures and monocultures also influenced the effect of relative height on individual tree f (Figure S6). The use of monospecific allometric relationships for live crown length reduced the effect of relative height for both species.

The predicted f for *P. sylvestris* was increased by 9.2% at the tree level and 4.9% at the stand level by growing with a deciduous species (Figures 6 and 7 and S7). The difference in stand density, in terms of trees per ha, had no influence on stand level f because differences in trees per ha were not large enough. At the tree level, the predicted f for *P. sylvestris* was not influenced by stand density (in terms of LAI) but the lower LAI of mixtures compared with *F. sylvatica* monocultures increased tree-level f for *F. sylvatica* in mixtures by 8.9% (Figures 6 and S5). The mean tree sizes of *P. sylvestris* were larger in mixtures than in monocultures, while those of *F. sylvatica* were usually not significantly different (Table 1). This mixing effect on *P. sylvestris* sizes (h , cd , lcl , la) resulted in a 19.8% higher individual tree f compared with when the mean tree sizes of monocultures were used in the mixtures, while retaining the tree positioning of the mixture (Figure 6). The mixing effects on *F. sylvatica* sizes were often insignificant and also had no significant effect on individual tree f (Figure 6).

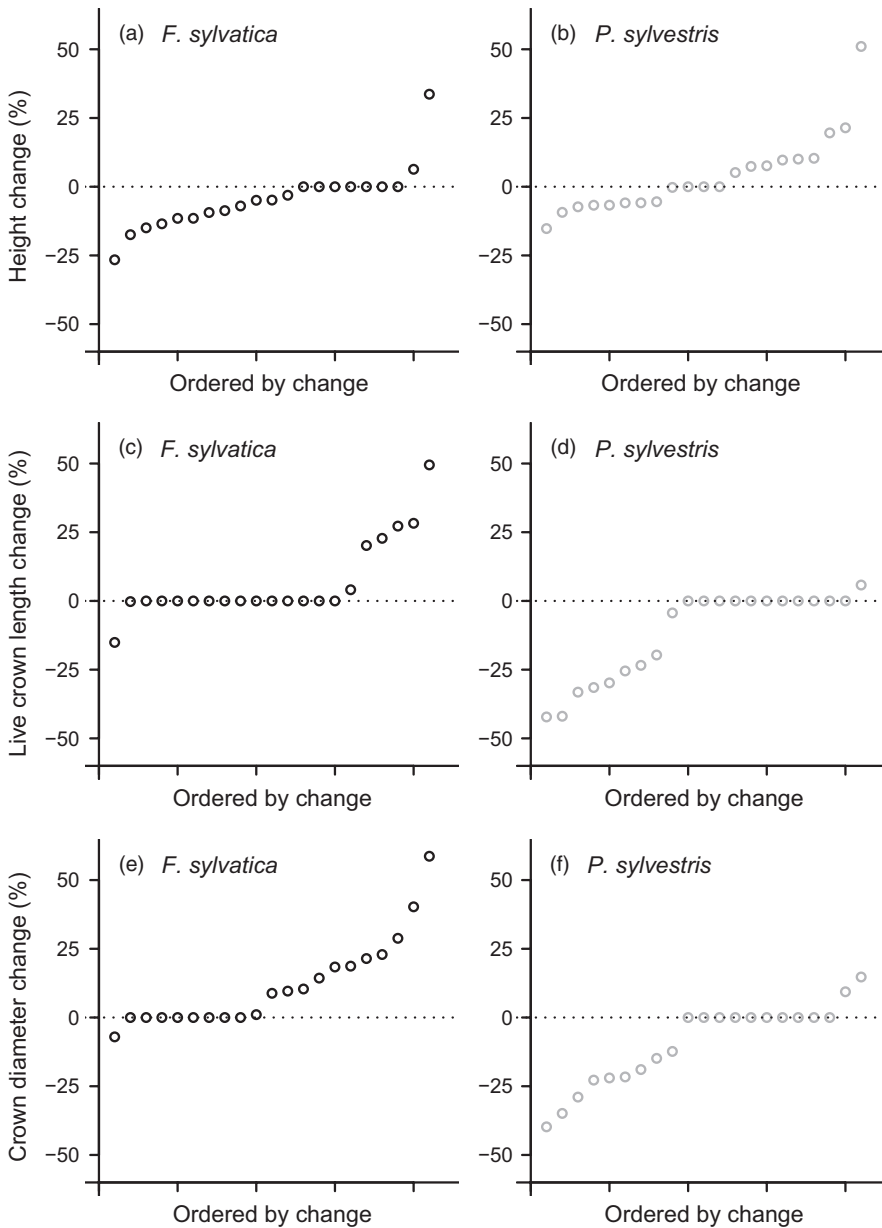


FIGURE 3 The change (%) in height, live crown length or crown diameter, for a given diameter, when using the allometric equations (Equation 1, Table S2) from the mixtures compared with the equations for the monocultures, for all 21 sites. Points greater than zero indicate a larger height, live crown length or crown diameter predicted using the mixture equations than the monoculture equation, for a given diameter. To remove any size effects, the diameter used for a given species and site was the mean diameter for that species at the given site

4 | DISCUSSION

Averaged across all sites, mixtures had 14% higher predicted annual APAR than monocultures of *F. sylvatica* or *P. sylvestris* even though the mean LAI of mixtures was 29% lower than that of the deciduous *F. sylvatica* monocultures (Table 2). Species mixing also increased APAR in other temperate or tropical stands (Binkley, Dunkin et al., 1992; Forrester et al., 2012; Le Maire et al., 2013; Sapjanskas et al., 2014). The greater fraction of PAR absorbed by the mixtures in this study was largely due to higher than expected values for *P. sylvestris* at all sites (Figure S10), whereas those of *F. sylvatica* were more variable, and were often lower in the mixtures than expected from monocultures (Figure S9).

It is critical to note that mixing effects on APAR do not mean that greater APAR is contributing to mixing effects on growth. For

example, many studies have used production ecology or mass balance approaches to show that a process occurring in a mixture (e.g. symbiotic nitrogen fixation) was not causing any mixing effect on growth or resource uptake by the associated species (Binkley, Sollins, Bell, Sachs, & Myrold, 1992; Forrester & Pretzsch, 2015). In this study, the mixing effect on *P. sylvestris* growth (RP_{Growth}) was positively correlated with the mixing effect on APAR (RP_{fAPAR}), indicating that light-related interactions contributed to the mixing effect on growth for *P. sylvestris*. This was not the case for *F. sylvatica* or for the whole community, suggesting that in those treatments water- or nutrient-related interactions may play a greater role in the mixing effect on growth than light-related interactions. These findings should not imply that light-related interactions are not also benefiting *F. sylvatica* or that non-light-related interactions are not benefiting *P. sylvestris*, it only indicates that they are not the dominating effects for the given species.

TABLE 1 Mean tree characteristics in mixtures and monocultures for each species across all sites. For a given row, values in bold font are significantly different ($p < .05$)

Variable	Monoculture	Mixture	<i>p</i> -value
<i>Fagus sylvatica</i>			
Diameter (cm)	17.25	16.78	.570
Height (<i>h</i> ; m)	20.27	18.76	.083
Crown diameter (<i>cd</i> ; m)	4.28	4.58	.186
Height to the live crown (<i>h_{lc}</i> ; m)	10.11	8.22	.019
Live crown length (<i>lcl</i> ; m)	10.13	10.49	.294
Leaf area (<i>la</i> ; m ²)*	70.17	61.28	.220
Crown volume (m ³)	58.71	69.46	.181
Relative height (<i>rh</i>)	1.01	0.95	<.001
Fraction of PAR absorbed (<i>f</i> × 10 ⁴)*	3.85	4.34	.043
APAR (GJ per tree)*	4.77	5.39	.429
<i>Pinus sylvestris</i>			
Diameter (cm)	22.4	25.73	.013
Height (<i>h</i> ; m)	20.93	22.41	.032
Crown diameter (<i>cd</i> ; m)	3.24	3.36	.565
Height to the live crown (<i>h_{lc}</i> ; m)	14.25	15.83	.006
Live crown length (<i>lcl</i> ; m)	6.67	6.57	.812
Leaf area (<i>la</i> ; m ²)*	16.88	24.67	.003
Crown volume (m ³)	28.6	30.73	.690
Relative height (<i>rh</i>)	1.05	1.13	.007
Fraction of PAR absorbed (<i>f</i> × 10 ⁴)	5.26	6.56	.043
APAR (GJ per tree)*	6.52	8.13	.104

*LAI was calculated using the allometric equations in Appendix S1 and APAR was predicted for the growing season using the Maestra model with inputs of measured crown dimensions and tree spatial positions.

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

4.1 | Mixing effects on tree allometry and stand structure

For a given diameter, *F. sylvatica* crowns in mixtures tended to widen and extend downwards, which is indicative of a reduction in competition for light in the mixtures (Dieler & Pretzsch, 2013;

Forrester et al., 2017; Lines, Zavala, Purves, & Coomes, 2012). In contrast, crowns of *P. sylvestris* were more likely to become narrower with shorter lengths but higher above the ground, suggesting more intense competition in the mixtures (Figures 3 and 4). However, despite these general patterns, both the magnitude and direction of a change in any given allometric relationship varied between sites. This reflects the wide range in canopy structures across the 21 mixed-species plots and shows that biased predictions of mixing effects result from assuming invariant allometric relationships across stands with different structures (Forrester & Pretzsch, 2015; Forrester et al., 2017).

The *P. sylvestris* were taller in the mixtures, while the *F. sylvatica* were shorter in the mixtures, relative to their respective monocultures, and this reduced the proportion of vertical leaf area overlap in mixtures from an expected 21% to only 7% (Figure 4). This shift is consistent with mixing effects on the vertical structure of other species combinations (Bauhus, van Winden, & Nicotra, 2004; Binkley, 1992; Forrester et al., 2004; Kelty, 1992). The importance of vertical canopy position was also illustrated by the strong positive relationships between individual tree *f* and relative height (Figure S5). Relative height is also one of the strongest predictors of crown length for many European species (Forrester et al., 2017). While canopy stratification is notoriously difficult to quantify (Parker & Brown, 2000), the relative height variable is useful for quantifying how the vertical position of trees within a canopy determines their crown architecture and APAR.

4.2 | Mixing effects on absorbed PAR

4.2.1 | Allometry

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

It is important to note that a weakness of our study is that allometric leaf area equations could not be developed by sampling in these plots, which may have introduced bias into the Maestra model simulations. However, this bias is expected to be minor because APAR predictions in *P. abies* and *A. alba* mixtures showed that changes in

Stand-level variable	<i>Fagus sylvatica</i> mono	<i>Pinus sylvestris</i> mono	Mixture	p-value
Trees per ha	992	1,055	1,104	.702
Basal area (m ² /ha)	32.7a	45.6b	45.2b	<.001
Leaf area index (LAI)*	8.4a	2.2c	6.5b	<.001
Shannon's Index from 2-cm diameter classes	1.87	1.77	1.71	.696
Shannon's Index from 2-m height classes	1.27	1.14	1.19	.653
Canopy depth (m)	23.3ab	21.8a	25.6b	.004
Canopy Volume (m ³ /ha × 10 ⁻³)	85.2a	41.0b	94.6a	<.001
Proportion of canopy space filled (m ³ /m ³)	0.37a	0.20b	0.38a	<.001
Canopy leaf area density (m ² /m ³)	0.35a	0.10c	0.26b	<.001
Fraction of PAR absorbed during the growing season*	0.91a	0.67b	0.89a	<.001
Fraction of PAR absorbed during the year*	0.65a	0.65a	0.75b	<.001
APAR during growing season (GJ/ha × 10 ⁻³)*	11.6a	8.4b	11.4a	<.001
Annual APAR (GJ/ha × 10 ⁻³)*	11.6a	11.7a	13.3b	<.001
Annual light use efficiency (m ² /GJ × 10 ⁻⁶)*	59.4	67.1	60.7	.266

TABLE 2 Differences between the mixtures and monocultures across all sites. For a given row, values with different letters (and bold font) are significantly different ($p < .05$)

*LAI was calculated using the allometric equations in Appendix S1 and APAR was predicted using the Maestra model with inputs of measured crown dimensions and tree spatial positions.

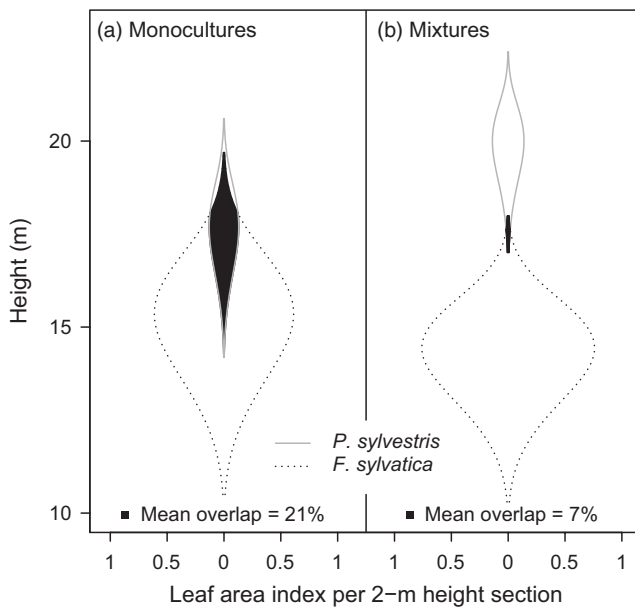


FIGURE 4 The vertical distribution of predicted leaf area index of each species in the monocultures and the mixtures. These leaf area distributions were created by placing the leaf area of each given tree into the 2-m layer of the canopy corresponding to its crown mid-point (halfway between the height to its live crown base and its tree height). This distribution of leaf area was then fitted to a two-parameter Weibull distribution

individual tree leaf area of 10% resulted in changes in predicted APAR of only 2%, compared with about 10–15% for changes live crown length and 4–5% for crown diameter (Forrester & Albrecht, 2014).

4.2.2 | Effect of a deciduous neighbour

Seasonality of leaf area can temporarily reduce competition for light (Ishii & Asano, 2010; Sapjanskas et al., 2014). The leaf loss by *F. sylvatica*, compared with the Maestra run where its leaves were retained all year, resulted in a 10% increase in *P. sylvestris* APAR at the tree level (Figure 6) and about 5% at the stand level (Figure 7). Even though this seasonality of competition for light was significant, the effects on growth may be lower because it occurs during the winter. The effect is also relatively small because *P. sylvestris* was often taller than *F. sylvatica*. Greater effects are likely where deciduous species occupy a more dominant canopy position (e.g. *Quercus robur*, *Quercus petraea*, *Fraxinus excelsior*). For example, the effect of seasonal foliage loss in young tropical plantations was found to have a larger effect on light availability than factors such as crown shapes and crown openness (Sapjanskas et al., 2014). This is because the deciduous species in that tropical plantation were not necessarily the shortest species within the mixture.

4.2.3 | Tree size, stand density and mixing

While mixtures had higher stand densities than the monocultures (Pretzsch et al., 2015), the simulations where density effects, in terms of trees per hectare, were separated from tree size effects, indicated that mixing effects on density were not causing any change in predicted species or community f . Instead, the mixing effect on individual tree sizes (e.g. *P. sylvestris* trees were larger in mixtures but vice versa for *F. sylvatica*) resulted in greater f in mixtures for *P. sylvestris*, lower

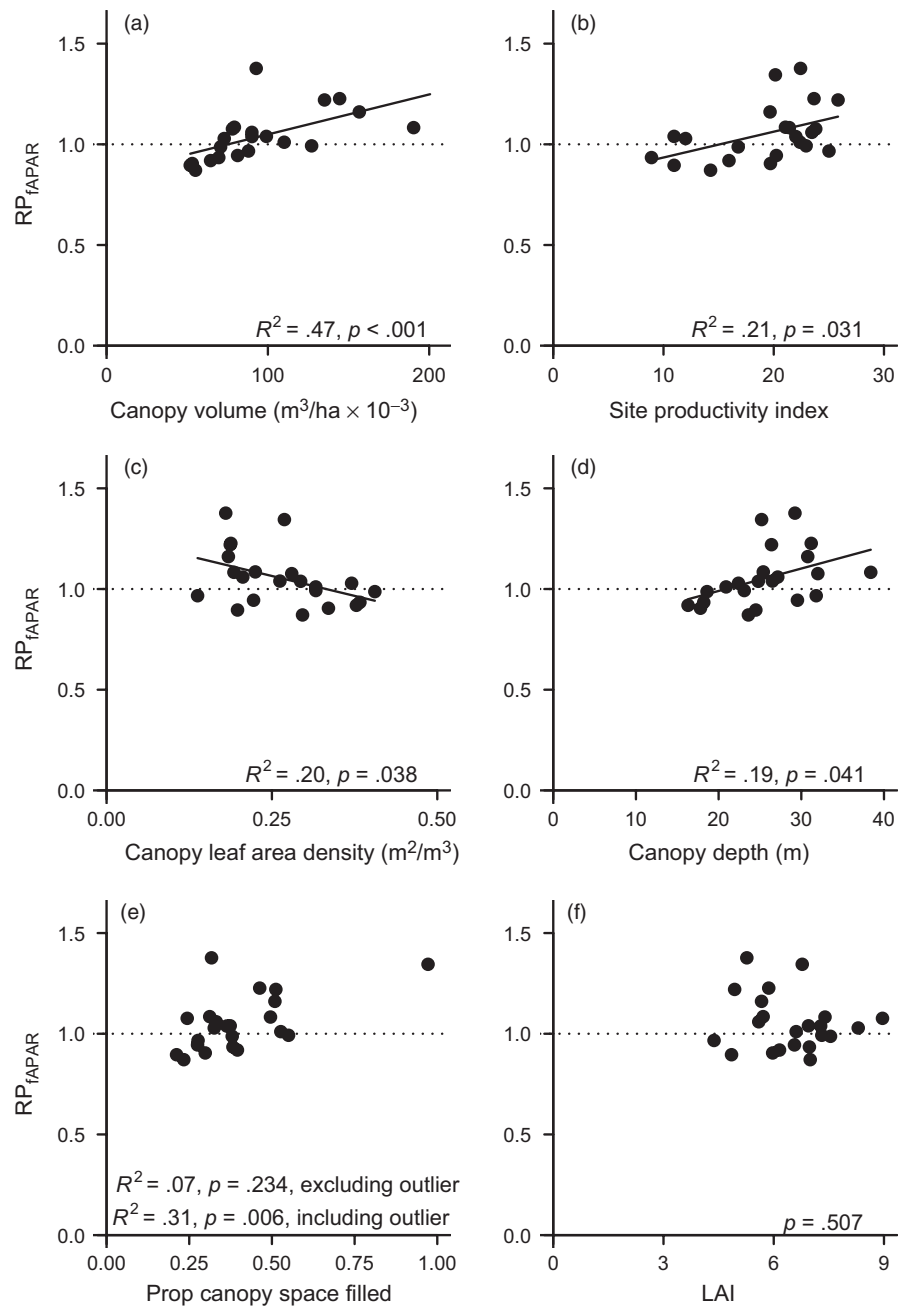


FIGURE 5 The relationships between the mixing effect on the fraction of PAR absorbed by the community (quantified as growing season RP_{fAPAR} ; Equation 4) and the total community canopy volume (a), the site productivity index for *Pinus sylvestris* (b), the canopy leaf area density (c), canopy depth (d), the proportion of canopy space filled by crowns (e) and LAI (f)

f for *F. sylvatica* and a minor increase for the whole community (when stand density was kept constant).

In addition to stand density per se, trees optimize space occupation by shifting the position of their crowns horizontally away from the point directly above the stem base, as well as modifying the shapes of their crowns (Brisson, 2001; Lee & García, 2016; Longuetaud, Piboule, Wernsdörfer, & Collet, 2013; Umeki, 1997). The ability to reposition crowns can vary between species (Longuetaud et al., 2013). This factor, which can reduce the horizontal overlap of neighbouring crowns, and therefore potentially increase APAR, was beyond the scope of this study. Similarly, the species were generally mixed on a tree-by-tree basis rather than coarser mixtures composed of small monospecific neighbourhoods. The effect of a more coarse

spatial distribution on APAR was not examined in this study and is likely to reduce the size of most of the effects that were examined.

4.3 | Site factors

Within the single species combination of *P. sylvestris* and *F. sylvatica* the factors examined in this study varied along the site gradient and are likely to vary at least as much within a single stand as it develops. Larger canopy volumes, LAI and hence competition for light, are likely to develop along gradients of increasing soil resource availability (Smethurst, Baillie, Cherry, & Holz, 2003). Therefore, species interactions that increase APAR are likely to have an increasingly positive effect on growth as soil resource availability increases (Forrester, 2014).

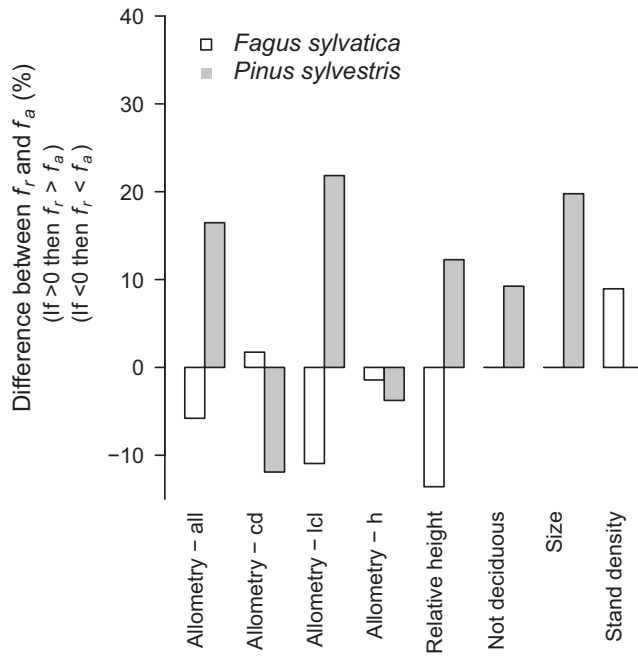


FIGURE 6 The effect of each factor (x-axis variables) on predicted tree-level fraction of PAR absorbed for each species. Effect sizes were calculated using the regression Equations 2, 3, 6 and 7, while using the means for the given species of all other variables. All effects that are not zero were significant in the regression equations ($p < .05$, Table S5). '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 *Fagus sylvatica* did not lose their leaves in winter. The 'Size' compares the 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

This is consistent with the increasing mixing effect on *P. sylvestris* growth with increasing site productivity index that was found using the same plots (Pretzsch et al., 2016). While the mixing effects on *F. sylvatica* APAR also increased with canopy volume or canopy depth, there was no evidence to suggest that these mixing effects on APAR made any contribution to the mixing effects on growth (Figure 2).

5 | CONCLUSIONS

This study showed that the mixing effects on community APAR differ greatly between sites for a given species combination. While the APAR of mixtures was on average 14% greater than that of monocultures, the magnitude of this mixing effect was positively correlated with site productivity, canopy volume and canopy depth, but not with climatic variables.

These patterns were a combination of several factors. Tree APAR was strongly correlated with individual tree leaf area (i.e.

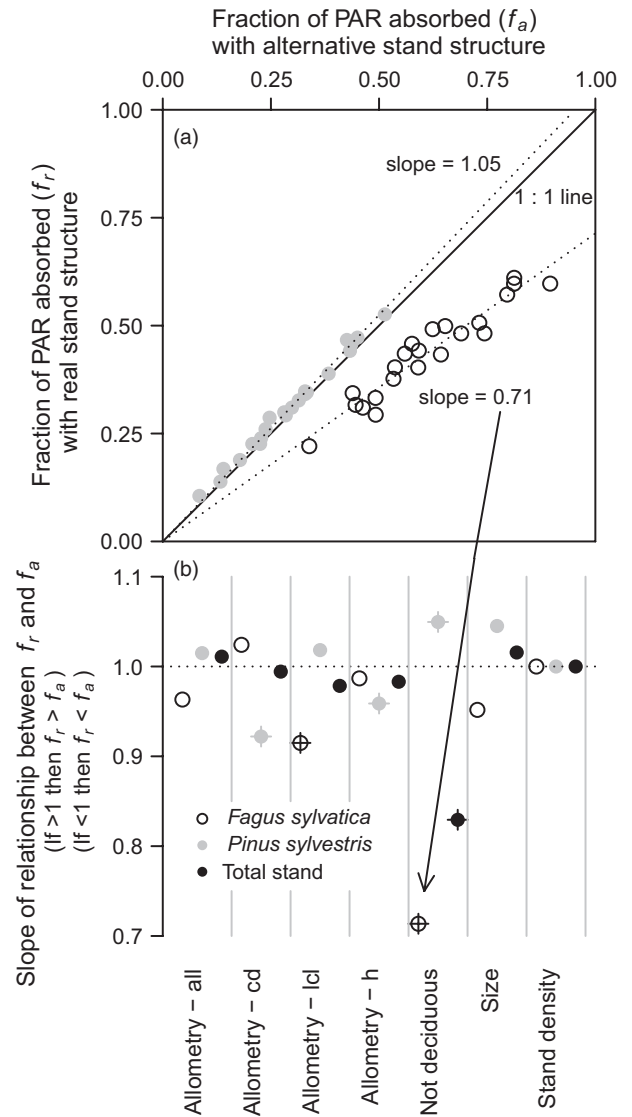


FIGURE 7 (a) The relationship between the fractions of PAR absorbed (f) by *Pinus sylvestris* or *Fagus sylvatica* trees in the real situation where *F. sylvatica* is deciduous versus a situation where they are not deciduous. The slopes of these relationships are shown and provide a measure of the effect size, which is then plotted in (b). (b) The effect sizes of several stand-level effects, which are indicated on the x-axis. The x-axis values are as described in Figure 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

tree size), as often observed in forests (Binkley, Campoe, Gspaltl, & Forrester, 2013), but it also increased with relative height, for both species. Mixing effects on allometry and the presence of a deciduous competitor caused 10–20% increases or decreases in f at the

tree level but smaller changes at the stand level. The direction of the change was positive, for a given species, when mixing increased tree size or the change in allometry improved the dominance of that species.

While the magnitude and ranking of the factors that influenced f (e.g. allometry, relative height, tree size, deciduous competitor) will clearly differ in other forests, the patterns observed in this study are likely to be common to many forest types, such as relationships between f and relative height or the way allometry influenced f by changing the position and dimensions of the crowns within the canopy.

Lastly, although mixing effects on f at the tree level cannot be used to predict stand-level effects or vice versa, information about each level was complementary and helped to explain the patterns at the other level. This also indicates a trade-off between silvicultural management to achieve higher individual tree APAR or to achieve higher stand APAR, consistent with the trade-off between tree- and stand-level growth (Long, 1985). In *P. sylvestris* and *F. sylvatica* mixtures, individual tree APAR can be increased by reducing stand density (LAI or canopy volume) and increasing the relative height, particularly for *P. sylvestris*. However, stand APAR could be increased by increasing LAI to about 6 and by ensuring that *P. sylvestris* occupies a different vertical layer to *F. sylvatica*.

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AUTHOR CONTRIBUTIONS

D.F. conceived the ideas and designed the light modelling methodology, analysed the data and led the writing of the manuscript; all authors, except D.F., contributed to data collection. All authors contributed to the results interpretation and discussion. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <http://datadryad.org/resource/doi:10.5061/dryad.8v04m> (Heym et al., 2017) and described in Heym et al. (in press).

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