Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with humidity

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Keywords:
additive mixing effect, multiplicative mixing effect, morphological variability, stand density, tree size unequality, overyielding

Highlights

- ► Scots pine and European beech monocultures differ significantly in structure
- ► Mixed stands of both have more heterogeneous structures than monocultures
- ► Stand density increases, vertical structure and tree morphology diversify
- ► Multiplicative mixing effects can further enhance additive effects on structure
- ► Superior heterogeneity over monocultures increases with humidity

Graphical abstract

…under development….

Triplets of stands of Scots pine and European beech (centre) have significantly higher structural heterogeneity than monocultures of Scots pine (left) and European beech (right). The superior heterogeneity of mixed stands over monocultures increases from dry to moist sites (from top to bottom).

Abstract

The mixing of tree species with complementary ecological traits may modify forest functioning regarding productivity, stability, or resilience against disturbances. This may be achieved by a higher heterogeneity in stand structure which is often addressed but rarely

quantified. Here, we use 32 triplets of mature and fully stocked monocultures and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) located along a productivity gradient and including dry to moist sites, through Europe to examine how mixing modifies the stand structure in terms of stand density, horizontal tree distribution pattern, vertical stand structure, size distribution pattern, and variation in tree morphology. We further analyze how site conditions modify these aspects of stand structure. For this typical mixture of a light demanding and shade tolerant species we show that (i) mixing significantly increases many aspects of structural heterogeneity compared with monocultures, (ii) mixing effects such as an increase of stand density and diversification of vertical structure and tree morphology are caused by species identity (additive effects) but also by species interactions (multiplicative effects), (iii) superior heterogeneity of mixed stands over monocultures can increase from dry to moist sites. We discuss the implications for analyzing the productivity, for modelling and for the management of mixed species stands.

1 Introduction

Quantification of structure is essential for understanding and predicting the functioning of forest stands and also for maintaining and managing their various functions and services. This applies for monocultures which dominated forestry in the past, but even more so for mixed-species stands which are currently receiving a lot of interest (Puettmann et al. 2012) since they can have a higher structural heterogeneity (Varga et al. 2005, Río et al. 2016) and positive effects on various ecosystems services (Gamfeldt et al. 2013).
By influencing the local environmental conditions within the stand (e.g., distribution of light and precipitation) the structure of the canopy and crowns is crucial for the feedback between structure→within-stand environment→functioning that drives stand dynamics (Figure 1). The trees within the stand can slowly modify their environment by changing their crown and canopy structure (feedback represented by bold arrows) or quickly modify their environment via functioning (thin arrows). The within-stand environment is influenced by the structure and in turn influences tree functioning, which feeds back to influence the development of tree and stand structure (Hari 1985, Pretzsch 2014). As a result of the slow but continual feedback between structure, within-stand environment and tree functioning and growth (bold arrows in Figure 1), the trees acclimate their morphology. The stand structure is therefore both a pivotal driver and a result of stand dynamics.

The significant role of structure has given rise to many methodological studies and reviews about how to measure and quantify various aspects of stand structure (Río et al. 2016, Zenner and Hibbs 2000). These include methods to quantify the horizontal tree distribution pattern (Clark and Evans 1954, Cox 1971), the vertical profile and size distribution (Pretzsch 1997, Wichmann 2002), stand density (Reineke 1933, Sterba 1981, 1987), different development stages (Zenner et al. 2015), species richness and diversity (Hattemer 1994, Shannon 1948, Sterba 2008), the pattern of species intermingling (Pielou 1977), the morphological tree variability (Pretzsch 2014) and the inequality of resource and growth distribution between the trees within a population (Binkley 2004, Binkley et al. 2006).
The few extensive studies of stand structure suggest that different indices of stand structure closely correlate with each other, so that analyses may be based on a relatively small number of variables that are most indicative (McElhinny et al. 2005, Neumann and Starlinger 2001, Pommerening 2002, Zenner and Hibbs 2000). In monospecific stands, shifting from spatially regular thinning to less regular but more intense harvest events or increasing the duration of the regeneration period may increase structural diversity throughout the whole rotation period

(Barbeito et al. 2011, Peck et al. 2014). Alternatively, species mixing could be used to enrich stand structure and heterogeneity (Pretzsch and Schütze 2014, 2015) but strong competitive superiority of one species may also cause structural homogenisation (Wiedemann 1951, p 134). The mixing of species with differing ecological traits may enhance structural complexity above and below ground (Pretzsch 2014, Bauhus 2009) and this can increase stand productivity compared with monocultures (Forrester and Bauhus, in press).

Comparing the structural traits of mixed-species stands with monocultures seems simple at the first glance but there are several aspects that are important to differentiate, just as there are with the more common comparison of productivity (Harper 1977, Kelty 1992). For example, structural characteristics such as the canopy density, size distribution or tree morphology of mixtures and neighbouring monocultures may indicate a higher structural heterogeneity in mixtures. If so, they show how decisions to favour species mixing modifies stand structure and forest functions and services, such as stability (Griess and Knoke 2011, Jactel and Brockerhoff 2007), habitat diversity (Tews et al. 2004), or aesthetic value (Schütz 2002, Stölb 2005).
Just as it is logical that mixing a low and highly productive species can result in a mixture with an intermediate productivity between the monocultures, it could be expected that the structure of a mixed-species stand deviates from the neighbouring monocultures as a result of differences in species structural traits. An interesting question is to what extent any differences between mixture and monoculture are just a weighted average of the monocultures, also referred to as an additive effect, or whether the mixture characteristics depart from the weighted average of the monocultures, sometimes referred to as non-linear or multiplicative effects (Kelty, 1992; Forrester and Pretzsch, 2015). The term “additive effect” underlines that this kind of mixing effect results from nothing more than selecting the species and adding up the characteristics of the monocultures (Forrester 2014, Kelty 1992).
A multiplicative effect is of particular relevance for analyzing, understanding, and predicting mixed stand dynamics and productivity. Multiplicative mixing effects on structure and the resulting outcomes such as productivity, stability, and resistance emerge from the species interactions and cannot be predicted by only studying the species in their monocultures. Many of the species interactions that occur in mixtures are at least partly the result of structural differences between mixtures and monocultures (Forrester and Bauhus, in press) and are likely to modify resource use and forest functioning in terms of stand productivity (Figure 1). Therefore, multiplicative mixing effects on structure may contribute to better understanding changes in forest functioning, which may cause overyielding, underyielding or even transgressive overyielding as detected for mixtures of Scots pine and European beech (Pretzsch et al. 2015; Seidel et al. 2013).

In order to analyse the effect of tree species mixing on stand structure we used 32 triplets of mature and fully stocked monospecific and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), located along a productivity and rainfall gradient through Europe. The mixing effects on growth have previously been presented (Pretzsch et al. 2015). In this study we examined how mixing modifies canopy density, horizontal and vertical tree distribution patterns, size distribution, tree species diversity, morphological variability, and how the site conditions modify these aspects of stand structure. Specifically, we examined
Q1 How does the stand structure of mixed Scots pine and European beech stands differ from their monocultures?
Q2 To what extent is the structure of mixed stands only an additive effect of combining species with different traits as opposed to a multiplicative effect resulting from inter-specific interactions?

Q3 How do the mixing effects on stand structure vary along an ecological gradient through Europe?

2 Material and methods

In order to achieve generalizable knowledge of the productivity of mixed versus monospecific stands of Scots pine and European beech we used a set of 32 triplets, each containing a mixed-species plot and monospecific plots of each species (Pretzsch et al. 2015). By locating the triplets along a productivity gradient (Figure 2, Supplementary Table 1) mainly determined by water supply, it is possible to examine the effect of site conditions on the species mixing effects. The voluntary and nationally-funded triplets were established by members of the COST Action FP1206 EuMIXFOR (see www.mixedforests.eu) and are spread over 16 countries. The 32 triplets represent a broad range of eco-physiographical conditions (Figure 2) in Europe and extend from Sweden to Bulgaria and from Spain to the Ukraine.

2.1 Material

Study area

The triplets are spread across most of the overlapping area of the natural range of Scots pine and European beech, with triplets at the northern border of Lithuania and the southern range in Bulgaria and Spain. The study covers the far southwest region in Spain and reaches to the eastern border of the Ukraine. The highest concentration of plots is in the central European area in Germany, Belgium, the Netherlands, the Czech Republic, and Poland, where mixed stands of Scots pine and European beech make up to 30 % of the forest area. For the triplets in the entire study region the mean annual temperature ranges from 6.0 to 10.5 °C, the annual precipitation from 520 to 1,175 mm (Figure 2) and the elevation from 20 to 1,290 m a. s. l. (Supplementary Table 1).
The natural distribution of Scots pine ranges from -3 to 10 °C mean temperature and 400 to 1,250 mm yr^{-1} annual precipitation. European beech prefers warmer and moister conditions and occurs naturally between 3 to 13 °C and 450 to 1,400 mm yr^{-1}. Analyses of the effects of environmental conditions on structure and growth require sampling over a broad range of site conditions. Figure 2 shows that the 32 triplets cover considerable parts of the natural and current range of cultivation of both species in terms of mean annual precipitation (mm yr^{-1}) and mean annual temperature (° C). For Scots pine in particular, the gradient from dry to moist sites is represented better than the gradient from cold to warm sites.

Triplet data

The study was based on 32 triplets (Figure 2). The triplets are sets of three rectangular plots including two moncultures of Scots pine and European beech and one mixed stand of these species. The plot size varies between 0.02 and 1.55 ha. All triplets represent more or less even-aged, fully stocked and mono-layered forest stands. The plots were not thinned recently and represent approximately the maximum stand density for the given sites. The mixtures are relatively intermingled mixtures (tree-by-tree as opposed to group-by-group). The mixing proportion of most plots was close to 50:50 although the mixing proportion of Scots pine varied between 18-72 % and the mixing proportion of European beech varied between 28-82

%. The mixing proportions were based on the species' stand density indices weighted by equivalence coefficients in order to consider the species-specific growing space requirements (see Pretzsch et al. 2015).

The plots within any given triplet have similar site conditions in terms of geographical location, topography, aspect, climate, soil substrate, and soil type. The monocultures are used as the reference for the mixed stands and for quantification of mixing effects in terms of over- or underyielding and structural heterogeneity. We inventoried the plots in order to derive the dendrometric state variables at the tree and the stand level. Supplementary Table 2 gives an overview of the field measurements and sampling of increment cores. On all 32 triplets we measured the stem diameters at breast height (1.3 m), tree heights, and heights to the crown base. For growth analysis at the tree and stand levels we sampled increment cores of at least 20 trees per plot and per species on all triplets. On 31 out of the 32 triplets the local density around those cored sample trees was measured by two angle count samples (on 30 cm east, one 30 cm west of the tree position) with BAF=4 m^2 ha^{-1}. Tree coordinates were measured on 24 and crown radii on 21 out of the 32 triplets. The triplets cover the structure and growth of monospecific and mixed stands of Scots pine and European beech across a range of site conditions never measured before (Figure 2). Additional measurements of light, nutrient, and water supply, of root structure and mycorrhiza, and wood density and quality are in progress in the EuMIXFOR project FP1206 (http://www.mixedforests.eu/).

The age of most of the triplets ranged between 40 and 60 years. Therefore we used the top height (height associated with the quadratic mean diameter of the 100 largest trees), ho, and the mean height (height associated with the quadratic mean diameter of all trees), h_q, at age 50 to characterize the variation between the triplets regarding their site quality. Top height of Scots pine at age 50 years ranges between ho= 9.5-26.9 m and quadratic mean height between h_q= 8.9-25.8 m. For European beech the respective values are h_o=11.7-27.6 and h_q= 9.4-25.9 m. This wide variation in stand height at age 50 years indicates the wide range of site conditions represented by the set of 32 triplets in different parts of Europe. The SDI is on average 824 trees ha^{-1} in the mixed stands; the shares of Scots pine and European beech to the mixed stand are, on average, 444 and 380 trees ha^{-1}, respectively. In the monoculture of Scots pine and European beech the mean SDIs are 833 and 724 trees ha^{-1}, respectively. The mean standing volume of the Scots pine/European beech mixed stands amounts to 444 m^3 ha^{-1}. The shares of Scots pine and European beech are, on average, 255 and 189 m^3 ha^{-1}, respectively. The range of stand characteristics was rather wide due to the broad variation of site quality (for details see Supplementary Table 3). For detailed information about how tree and stand variables were estimated in mixed and mono-specific plots see Pretzsch et al (2015).

2.2 Methods

Measures of stand structure

Table 1 summarizes the measures used to characterize stand structure in this study, explains what their values indicate, and lists reference for further information.
For quantifying the stand density we used the tree number per unit area, N, and the Stand Density Index, SDI. The SDI considers both tree number and size, eliminates size-dependent changes in tree number during stand development, and enables comparison of the density of stands with different ages as it relates their tree number to an index mean diameter of 25 cm (Reineke 1933). The relative sum of crown projection area, RCPA, and relative ground cover

by crowns, RCC, indicate different aspects of canopy space filling (Pretzsch 2014). RCPA is the ratio of the sum of the crown projection areas of a stand and the stand area; i.e., RCPA =1.0 would indicate that the sum of the crown projection areas and stand area are equal. RCPA =1.5 means that the sum of the crown projection areas is by 50 % higher than stand area and some parts of the stand have overlapping crowns. Relative crown coverage (RCC) indicates the ground area covered by crowns when looking down from above. RCC=1.0 would indicate that the stand area is completely covered by crowns, RCC=0.80 indicates that 20 % of the ground is not covered by crowns. Unlike RCPA, RCC cannot exceed 1.0.

For quantifying the horizontal variation of the stand density we calculated the coefficient of variation of the stand basal area CV_{BA} based on the measurement of 20 randomly distributed angle count samples per plot with a basal area factor 4 (BAF=4). $CV_{BA}=0$ would indicate equal stand density over the whole plot area. The higher the CV_{BA} values the more the stand density varies within the plot.

For analyzing any differences in the size distribution of mixed stands versus moncultures we used the skewness as 3rd potency moment (Bortz, 1993, pp 45-46) calculated for the tree diameters, heights, and volumes on the plots, $skew_d$, $skew_h$, and $skew_v$, respectively. In the case of a symmetric distribution skew = 0. If an observed size distribution includes many small or short trees and a low number of large or tall ones, it is right-skewed such that skew>0. If the distribution includes many tall trees, but small are rare, it is left-skewed and skew<0. The ranges of the tree diameter, height, and tree volume distribution, $range_d$, $range_h$, $range_v$ indicate the spread in terms of size distribution ($range_d = d_{max}-d_{min}$, $range_h=h_{max}-h_{min}$, $range_v=v_{max}-v_{min}$). As a measure of the size inequality we further calculated the coefficient by Gini based on the individual tree volumes on the plots (see de Camino, 1976, Cordonnier and Kunstler 2015, Kramer, 1988, p 82). A Gini coefficient, $GC_v=0.0$ means that all trees are equal in size. The higher the GC the more unequal the tree sizes.

Index A for quantifying the vertical stand structuring takes into account the presence of different species in different height zones of a forest stand. The more equal the species presence in all different height zones, the higher the A-value of a forest stand (Pretzsch 1998, Río et al. 2016).

For characterization of the morphological traits at the individual tree level we calculated the mean slenderness, h/d, crown ratio, cl/h, and concentricity of the crown r_{min}/r_{max} (Pretzsch 2014). The higher the h/d value is the more the trees favour height growth over diameter growth; so it indicates the slenderness of the stem. The higher the cl/h ratio is the longer the crown in relation to the tree height; cl/h=1.0 would indicate trees with a crown down to the bottom. The concentricity r_{min}/r_{max} of the crown projection area is quantified by the ratio between the minimum and maximum crown radius. The higher this value is, the more concentric the crown cross-sectional area around the stem. The crown projection ratio, cd/d, between crown diameter, cd, and stem diameter, d, and also the quotient of ground cover area cd^2/d^2 indicate how many times the crown width or crown projection area, respectively, is larger than the stem diameter and stem basal area (Assmann 1970 p 112). High ratios indicate a tree's or species' crown plasticity and its capacity spread into vacant canopy space (Assmann 1970). However, high ratios can also indicate wide crowns and long branches, which mean larger branch diameters and a reduction of wood quality (Pretzsch and Rais 2016).

The Gini coefficient of the stem volume growth, G_{iv}, indicates the inequality of the growth allocation between the trees within a stand (Binkley et al. 2006). For this purpose we calculated the mean periodic volume growth of all individual trees in the period 2009-2013. Analogous to GC_v the coefficient for tree volume growth $GC_{iv}=0.0$ means that all trees are equal in volume growth. The higher the GC_v, the stronger the inequality of resource availability and growth distribution between the individuals of the population. The Growth Dominance Coefficient, GDC, combines information about size distribution with the respective growth distribution among the trees in a stand (Binkley 2004, Binkley et al. 2006). It indicates how trees with different stem volume contribute to the stand growth; whether the contribution to stand growth is proportional to the stem volume of the trees (GDC=0), whether small trees contribute over-proportionally (GDC<0), or under-proportionally (GDC>0) in relation to their volume. Thus the GDC reflects whether the efficiency of tree volume investment is equal for trees of all size, or how it changes with tree size (Binkley et al. 2006).

Notice, that on some of the 32 triplets not all structural measures could be calculated, because of missing tree coordinates, height to the crown base, or measurement of just 4 crown radii. So, some sample sizes in Tables 2-4 are lower than 32.

Evaluations for answering questions Q1-Q3

Q1 How does the stand structure of mixed Scots pine and European beech stands differ from their monocultures?

To compare a given characteristic, x, of tree morphology and stand structure (e.g., tree number, skewness and Gini coefficients of tree volume, mean strem slenderness) between mixed-species stands (x_{mixed}) and monocultures (x_{mono}) we used ratios ($Rx=x_{mixed}/x_{mono}$) between these characteristics in mixed stands versus monocultures (Table 2, columns (12) and (13), Table 3, columns (5), (7), and (8), and Table 4, columns (5), (8), and (11)). The mean ratio $\overline{Rx}$ and its standard error, SE, provides a simple basis for testing whether the performance of mixed-species stands and monocultures differs. If 1.0 is beyond the confidence intervals $\overline{Rx} \pm t_{n-1,\alpha=0.05} \times SE$, $\overline{Rx} \pm t_{n-1,\alpha=0.01} \times SE$, $\overline{Rx} \pm t_{n-1,\alpha=0.001} \times SE$ (with t being the critical value of the t-distribution with n-1 degrees of freedom and a selected two-sided transgression probability α) the differences can be considered as significant at the level $p \le 0.05{*}$, $p \le 0.01{**}$, or even $p \le 0.001{***}$ (Tables 3-5).

Notice, that in the Tables 2-6 and Supplementary Tables 2-3 the columns ‘mean mixed’ and ‘mean mono’ display the arithmetic means of all n observations within the respective groups. The columns ‘mean mixed/mono’, in contrast, report the ratios resulting from the pair-wise division of the characteristic of the mixed stand by the respective value of the neighbouring monoculture. The mean of these ratios (mixed/mono) is not necessarily equal to the ratio of the means (mean mixed/mean mono). So, we report both the group-wise arithmetic means (mean mixed and mean mono) as well as the mean ratios of the pair-wise comparison (mixed/mono). The mean ratios of the pair-wise comparison (mixed/mono) were used for testing group differences. Our focus was on the relationships between neighbouring mixed-species stands and monocultures (reflected by their pair-wise comparison) rather than on their differences in general (reflected by their overall means).

Q2 To what extent is the structure of mixed stands only an additive effect of combining species with different traits as opposed to a multiplicative effect resulting from inter-specific interactions?

The different structural traits in mixed species stands compared with monocultures may be a simple additive effect or a multiplicative effect. We use the tree size distributions in Figure 3 to illustrate how to reveal both and to distinguish between them.

Suppose the tree size distribution D (D stands for frequency distribution) of species 1 and 2 in the monoculture are D_1 and D_2 (Figure 3, a and c), then the weighted mean of both distributions in the case of a mixture with m_1 as the proportion of species 1 and thus $1-m_1$ for the proportion for species 2, $\hat{D}_{1,2}$ represents the mean of D_1 and D_2, weighted by the proportions m_1 and $1-m_1$, respectively. $\hat{D}_{1,2}$ represents the weighted mean of both monocultures (Figure 3e). It represents the expected distribution under the assumption that mixing simply causes an additive effect, i.e., retains the structural traits of the species as they are in the monoculture. In our example $\hat{D}_{1,2}$ ($\hat{D}_{1,2} = D_1 \times m_1 + D_2 \times m_2$, where m_1 and m_2 are species proportions, 0.5 in Figure 3, differs clearly from the two monocultures D_1 and D_2 (compare the distributions shown in (e) with both (a) and (c)). Such differences between $\hat{D}_{1,2}$ and D_1 and D_2 are referred to as an additive effect because they are simply the effect of species identity.

In order to reveal any additive effect we first compared the structural traits of both monocultures. This showed differences in the species specific behaviour in monoculture. Then we compared the weighted mean structural traits of the two monocultures with both monocultures. This can reveal how the species selection alone may modify the mixed stand traits compared with the monocultures. The weight was made using the species proportions m_1 and m_2 estimated for each triplet based on stand density index (Pretzsch et al 2015).

Any differences between the structural traits of the two monocultures, between the weighted mean structure and Scots pine monoculture and the weighted mean and European beech monocultures indicate an additive effect and were tested based on the ratios ($Rx=x_{mixed}/x_{mono}$) introduced in the previous section (see *Q1*).

We then tested whether there is was a multiplicative mixing effect on top of the additive effect. In the following we explain this again based on the size distribution. At the whole stand level, this was done by comparing the observed distribution $D_{1,2}$ with the weighted mean distribution $\hat{D}_{1,2}$. If the observed size distribution $D_{1,2}$ of a 50:50 mixture of both species was equal to the weighted mean there would be just an additive effect, i.e., any differences between the observed and weighted means would just result from the selection of species with different traits and not from inter-specific interactions. In our example (Figure 3f) however, the differences between the observed size distribution $D_{1,2}$ (broader range, lower peak) and the weighted mean distribution $\hat{D}_{1,2}$ indicate a multiplicative mixing effect at the whole stand level. For a refined analysis of how the different species contribute to a multiplicative mixing effect the size distribution of a species in mixture, $D_{1,(2)}$, with its size distribution, D_1, in the monoculture (Figure 3b) may be compared; analogously $D_{(1),2}$ may be compared with D_2 (Figure 3d). In this model example the distribution of species 1 in the mixed stand is “ahead” of the monospecific stand but has a similar shape (Figure 3b). The size distribution of species 2, $D_{(1),2}$, in mixture is lagging behind and is wider than the distribution D_2 of the monospecific stand (Figure 3d). For both comparisons the size distributions in mixture are scaled up to unit area of 1 hectare using the species’ mixing portions (m_1 and m_2 assumed as 0.50 and 0.50 in this example). In this example the differences between $D_{1,2}$ and $\hat{D}_{1,2}$ show a multiplicative mixing effect at the whole stand level (Figure 3f), and the differences between D_1 and $D_{1,(2)}$ (Figure 3b) and D_2 and $D_{(1),2}$ (Figure 3d) show that the stand level reaction is underpinned by both species’ mixing reactions.

To summarize, the additive effect results from the structural differences of the combined species; it quantifies the potential heterogeneity in the case that both species retain the same structural behaviour in mixed stands they had in monocultures. The additive effect may be modified towards higher or lower heterogeneity by a multiplicative mixing effect; the multiplicative mixing effect may be the opposite for each species, and if they are opposing to the same magnitude there will be no multiplicative effect at the total stand level because they will counter balance each other.

This approach for comparing mixed with monospecific stands can be applied for various tree attributes, e.g., for crown projection area, crown length, individual tree growing area. One reason for using monocultures for this comparison is that mixed stands are often considered as alternative to monocultures, and the tree attributes yielded by mixtures compared with monocultures may be a basis for silvicultural decisions. Beyond these practical reasons monocultures as references may best reveal the effect of inter- versus intra-specific competition on tree structure and growth.

The weighted mean distributions ($\hat{D}_{1,2} = D_1 \times m_1 + D_2 \times m_2$) were calculated by multiplication of the monospecific stand distributions in such a way that the observed species mixing proportion of the mixed stand was reproduced. In the case of a mixing proportion of 1:1 between Scots pine and European beech, e.g., the monoculture's distributions (scaled up to 1 hectare) were simply added up. In the case of a mixing proportion of 3:1 between Scots pine and European beech the monoculture distribution of Scots pine (scaled up to 1 hectare) was tripled and added to the one-fold distribution of the European beech monoculture. The resulting weighted mean distributions served as a reference for calculating the ratios between the observed and expected distribution of the mixed stands. For this evaluation it is important to notice that the location and shape parameters of the distributions (e.g., skewness) are invariant to linear transformation, i.e., if the size distribution of a species occupying a certain portion of the mixed stand is scaled up to 1 ha or multiplied in order to reproduce a given mixing proportion, the location and shape parameters remain unchanged.

For testing any differences of the structural attributes of Scots pine and European beech by mixing analyzed at the species level or at the whole stand level we applied the ratios ($Rx = x_{mixed}/x_{mono}$) as introduced in the previous section (*Q1*).

Q3 How do the mixing effects on stand structure vary along a productivity gradient through Europe?

To test for any correlations between the mixing effects on the environmental conditions along the gradient through Europe we applied the ratios of the comparison between mixed stands and monocultures (see *Q1*) and the ratios for quantifying the additive and multiplicative mixing effects (see *Q2*).

We used the mean annual temperature and the annual precipitation as site variables (see Supplementary Table 1). We also used the Martonne index (1926) (M=annual precipitation (mm)/(mean annual temperature (°C) +10)) for characterizing the water supply at the 32 sites (see Supplementary Table 1). This index varied between M=28-61 mm $°C^{-1}$ along the gradient due to the wide variation of precipitation (520-1,175 mm yr^{-1}) and mean annual temperature (6-10.5 °C).

In addition we calculated the CVP index by Paterson (1956) which has been widely used (Benavides et al. 2009, Chittagong 2015, Vanclay 1992) for characterization of growing conditions. As our stands vary widely in latitude and altitude and represent a broad range of mean and amplitude of temperature, precipitation (Figure 2) and length of the growing season, this index appeared to be more appropriate than other indices that only consider annual precipitation and mean annual temperature. To calculate this index we used climate series of the last 20 years (1994-2013). The index $CVP = T_v / T_a \times P \times G / 12 \times E / 100$ is based on the T_v (mean temperature of the warmest month in °C), T_a (temperature amplitude calculated by the difference of the mean temperature of the warmest month minus mean temperature of the coldest month in °C), P (mean annual precipitation in mm), G (number of months out of twelve with mean temperature ≥ 3° C), and E (Evapotranspiration intensity as a function of the latitude read from a nomogramm (see Paterson 1956, p 74), where E % is given as a function of the geographical latitude in degrees). The resulting CVP values along the gradient ranged between 195 and 641 (mean value 328).

As a less specific indicator for the site conditions we also used the height of the quadratic mean diameter, h_q, of Scots pine and European beech in monocultures at an age of 50 years and 100 years (see Pretzsch, 2009, pp 200-203 for the definition and calculation of d_q; based on the quadratic mean diameter d_q, the height h_q was read off the diameter-height curves). The site index was referenced or extrapolated from yield tables by Wiedemann (1943) and Schober (1967) for Scots pine and European beech.

Finally we used the stand productivity in terms of the periodic annual volume growth in the period 2009-2013 ($m^3\ ha^{-1}\ yr^{-1}$) of the monoculture and mixed species stands as indicators of the environmental conditions. Stand characteristics such as mean tree dimensions, stand basal area (BA), and standing volume stock per hectare (V) for the survey in 2013 and also for 2009 were evaluated following DESER-Norm 1993 (Johann 1993, Pretzsch 2009, pp 181-222). The evaluation for 2009 required the reconstruction of the stand development over the last 5 years based on increment cores (for calculation see Pretzsch et al. 2015). By calculating the standing volume in 2009 and 2013, as well as the removed volume, the periodic annual volume growth resulted as $PAIV_{2009\text{-}2013}=(V_{2013}-V_{2009}+V_{removal})/5$. For further details of the applied evaluation algorithms see Pretzsch et al. (2015).

Using Pearson correlation coefficients and linear models we examined whether the variability of the mixing effects on structure was related to the site conditions represented by the above mentioned measures such as climatic data, productivity indices, site index etc. Residuals were checked to assure normality. All calculations were carried out using the software package IBM SPSS Statistics (Version 22).

3 Results

Q1 How does the stand structure of mixed Scots pine and European beech stands differ from their monocultures?

Table 2 presents differences in many structural attributes between mixtures and monocultures of Scots pine or European beech, including ratios of the mixture values relative to the monoculture values (columns 12 and 13), which are of interest for forest practice when determining the pros and cons of mixed-species stands.

The tree number and SDI values varied considerably due to the wide range in site conditions and the variation in stand age, although the stands represent fully stocked and almost unthinned conditions. The mixed stands of both species tended towards higher stand densities, SDI, crown projection areas, RCPA, and crown coverage, RCC. On average the stand area was more than 2-fold covered by tree crowns (RCPA=2.23) in the mixed stands compared with just about 1-fold (RCPA=1.15 and 1.29) in the monocultures. The relative crown cover (RCC=0.89) was also some 15 % higher in mixed compare with monospecific stands. However, even in the fully stocked mixed stands it was always below RCC=1.0, i.e., some of the stand area remained uncovered in terms of the vertical projection of crown coverage.

The coefficients of variation of the stand basal area (CV_{BA}=0.19, 0.23, 0.20) were rather low in all three types of stands, i.e., they were rather homogeneously stocked. We found no significant differences between monocultures and mixed-species stands.

The skewness of the size distributions in mixed stands did not significantly differ from the monocultures. However, the range of tree size distribution, range, the Gini coefficient, Gv, and the index A for vertical heterogeneity indicated a significantly higher structuring in mixed-species stands compared with both monocultures. The inequality of tree volumes was higher in monospecific beech than in monospecific pine stands (G_v=0.46 versus G_v=0.30), and the mixed stands were in between (G_v=0.44). Mixing of pine and beech increased the inequality compared with monospecific Scots pine stands, but not compared with monospecific beech stands.

We observed a significantly wider and more diverse distribution of trees along the vertical crown profile (index A) in mixed compared with monospecific stands, probably enabled by the complementary light ecology of both species.

The indicators of morphological variation at the tree level showed significantly higher values of h/d, cl/h, cd/d and cd^2/d^2 in mixed stands compared with Scots pine monocultures. Beech in the mixture increased the mean crown plasticity and extension. In contrast, compared with the European beech monoculture, the mixed stand showed a lower mean crown plasticity and extension.

The Gini-coefficient for stem volume growth (G_{iv}) indicated a stronger inequality of growth allocation in favour of the tall trees in mixed stands compared with the rather homogeneous pine monocultures. While the inequality in mixed stands was significantly higher compared with monospecific pine stands, mixed stands and monospecific beech stands were similar regarding G_{iv}.

Overall, this comparison reflected a considerable structural diversification by cultivating mixed-species stands instead of monocultures.

Q2 To what extent is the structure of mixed stands only an additive effect of combining species with different traits as opposed to a multiplicative effect resulting from inter-specific interactions?

We first compared both species concerning their structural traits in monocultures. Table 3, columns (3) and (4) list the structural variables (mean) of the two monocultures, and column (5) reflects the mean of the ratios between Scots pine and European beech values. Those ratios show that stand density, SDI, was higher in pine compared with beech stands. Skewness, range, and Gini coefficient of tree volume were significantly lower in pine stands, i.e., their size distribution was more normal, narrow, and equal compared with European beech. Consequently the vertical structuring, A, was significantly lower for pine. Regarding the morphological variation, pine trees had lower slenderness, shorter crowns, more concentric crowns, and a significantly shorter crown extension. Compared with beech the stem growth of pine was distributed more equally among the trees of different sizes, and the growth dominance was significantly lower than in beech stands. This comparison of monocultures shows that both species are endowed with complementary structural traits; Scots pine tends towards high densities, rather homogeneous size structure, and slim and narrow crowns, with rather equal growth partitioning within the population. European beech, in contrast, tends to be heterogeneous in terms of the horizontal and vertical stand structure, widely extending, plastic crowns, and strong inequality of size structure and with a growth distribution in favour of the dominating individuals. The next section examines how those traits are modified when both species are mixed.

The strong variation of both species structural traits suggests a considerable additive effect. This was quantified by comparing the weighted mean of the two monocultures with the monoculture of Scots pine (Table 3, column (7)) and European beech (column (8)), respectively. The many boldly printed ratios in those columns indicate a strong additive effect.

Compared with the Scots pine monoculture the mixed stand calculated as the weighted mean of both monocultures showed lower SDI and higher RCC values, i.e., beech reduced the tree number but increased the canopy coverage. Furthermore the size range, inequality Gv, and vertical layering, A, was increased by the beech. Also the h/d, cl/h, cd/d and cd_2/d_2 were increased by the component of beech in the weighted mean.

Compared with the European beech monoculture a mixture based on the weighted mean of both monocultures showed higher SDI and lower RCPA values. The range of the size distribution was significantly higher. However, Gv was lower, because pine caused a homogenization. The weighted mean ratios h/d and cl/h were lower than in the beech monoculture, i.e., pine reduced the weighted mean by its lower h/d-values and shorter crowns compared with beech.

The finding that the majority of weighted mean structural indices differed from the monocultures indicates an overwhelming additive effect. Both species were so different in terms of their structures that just by mixing these species there was a large increase in structural heterogeneity (regardless of the presence of any inter-specific interactions). This additive effect can potentially be enhanced or reduced by the species' acclimation to the inter-specific competition, as indicated by any multiplicative effect.

Table 4 reveals multiplicative mixing effects by comparing the attributes of each species in mixed stands versus monocultures. In addition we compared the mixed stand as a whole with the weighted mean of both monocultures. Table 4 shows how the rather low effect of mixing at the stand level (column 11) emerged from strongly contrasting patterns at the species level (columns (5) and (8)). Comparison of structural traits of Scots pine in mixtures with monocultures showed higher stand density, wider size range, and reduced crown ratio and lateral crown expansion (columns (5)). For European beech in mixed-species stands compared with monocultures the density, vertical structuring, and crown ration and lateral expansion were significantly higher. The two species enhanced each other regarding stand density and vertical structuring. However, the opposite occurred for the morphological response that cancelled each other's effects at the whole stand level. So, the rather invariant response pattern of the morphological traits at the stand level (column (11)) resulted from a species-specific, counterbalancing effect at the species level.

Q3 How do the mixing effects on stand structure vary along an ecological gradient through Europe?

From the set of site variables considered, the Martonne index (1926) was the only one that was correlated with the stand structure ratios between mixed-species stands and monocultures. The other site variables and site indicators such as the mean annual temperature, annual precipitation, CVP index by Paterson (1956), site index, and site productivity showed no clear statistical correlation with the structural mixing patterns. Therefore, the following results are confined to correlations between the Martonne index and the ratios of the non-weighted comparison, the additive effect, and the multiplicative mixing effect.

Figure 4 shows that correlations between the Martonne index and the ratios indicating multiplicative mixing effects were generally rather low, but were significant in some cases, and varied between species.

No correlations between the structural ratios and the Martonne index would indicate that the effects of species mixing on stand structure shown in Table 2-4 and summarized in Table 6 are distinct but site-invariant. However, Table 5 shows that the site conditions in terms of the Martonne index can modify the mixing effect as follows.

Table 5, columns (2) and (3) show how the unweighted ratios between the mixtures and monocultures of Scots pine and European beech were modified by environmental conditions. With improving water supply, indicated by the Martonne index, stand density, vertical structuring, and h/d values increase, while length and lateral extension of crowns decrease in mixed stands compared with Scots pine monocultures (column (2)). The ratio between mixed stands and European beech monocultures was less site-dependent. Crown area and h/d decreased while the share of small trees and the inequality of the size distribution increased (column (3)).

Column (4) shows how the structural relationships between the monocultures of Scots pine and monocultures of European beech change with environmental conditions. With improving water supply the stand density, canopy density, slenderness, and inequality of inter-individual growth distribution of Scots pine in relation to beech decreased, while crown length increased.

Columns (5) and (6) reflect the site dependency of the additive effect. The better the water supply, the more heterogeneous the weighted mean of both monocultures in relation to Scots pine monocultures, i.e., the stronger the structuring effect of beech in mixture (column (5)). The advantage of the weighted mean in relation to the European beech monoculture was less pronounced (column (6)).

Columns (7) and (8) reflect the site dependency of the multiplicative mixing effect at the species level. With improving water supply Scots pine decreased in terms of crown coverage and size range but increased in vertical structuring in mixed compared with monospecific stand conditions (column (7)). Beech increased in density and share of small trees but decreased in size range and lateral crown expansion (column (8)). The site dependency of the multiplicative effect at the whole stand level in column (9) showed only slight site-dependencies, probably because of the opposite sign of pine and beech regarding the site dependency.

A common tendency of the different levels of the site-dependency of mixing effects in Table 5 is the increase in different aspects of stand density and vertical structuring, and a decrease in crown length and lateral crown extension with improving water supply.

4 Discussion

Practical and scientific relevance of structural heterogeneity in mixed-species stands

Stand structure and species diversity affect most forest functions and services. Increases in species diversity and heterogeneity of other structural attributes can, e.g., stabilize and raise the productivity (Liang et al 2007, Lei et al 2009, Jucker et al. 2014, Pretzsch et al. 2013, 2015), stability (Griess and Knoke 2011, Jactel and Brockerhoff 2007), reduced sensitivity to drought (Grossiord et al. 2014, Metz et al. 2016), habitat diversity (Tews et al. 2004), plant and animal richness (Brunet et al. 2010, Ishii et al. 2004, Roth 1976), and the aesthetic value (Schütz 2002, Stölb 2005) of forest stands. On the other hand more heterogeneous structures can have a negative effect on some taxa (Paillet et al. 2010), on the wood quality (Pretzsch and Rais 2016), on the effort of forest inventory, planning, and management (von Gadow 1998, von Gadow et al. 2002), and on the costs of opening up the stands to harvest the timber (Keegan et al. 1995, Kellogg et al. 1996).

Forest science needs detailed information on stand structures to improve our understanding and modelling of stand dynamics (Figure 1), not only of monocultures but especially of mixed-species stands (Forrester and Pretzsch 2015, Forrester and Bauhus in press, Pretzsch 2014). A deeper insight into stand structure and its dependency on site conditions is also important for the further development of silvicultural guidelines for the management of mixed stands which may address multiple services (Río et al 2016). It may for instance reveal which species assemblages or site conditions allow for continuous structural within stand heterogeneity, and which lead inevitably to one-layered canopy closure and within stand homogeneity.

The very different physiological and morphological traits of Scots pine and European beech suggest a strong additive effect when cultivating them together. On top of this the mixed-species stands in this study had about 50 years to adapt to their inter-specific habitat; i.e., to develop multiplicative mixing effects. They widened their size distribution, the inequality of tree sizes, extended the canopy space occupation, increased the stand density, and extended and diversified the boundaries between crowns of different species.

Compared with the restriction in monocultures that can result when most trees occupy the same canopy or root layer, inter-specific neighbourhoods may trigger crown expansion and crown packing that result from inter-specific interactions as well as inter-specific differences in morphology. These responses that increase variability, which may also have developed from mutual co-evolution in the past are often undesired by foresters at present, and may even be unknown if the species are mainly only grown in monoculture. When crowns and roots are developing in inter-specific neighbourhoods they may develop a behaviour that is not predictable from monocultures but can be highly relevant for understanding, modelling and predicting mixed stand dynamics. The species-specific properties that only develop in inter-specific neighbourhoods may contribute the most to the heterogeneity of stand structure in mixed stands compared with monocultures.

Additive effects and multilicative effects of mixing on stand structure

An additive effect results from inter-specific differences in morphology and size distribution that are unaffected by any species interactions, while a multiplicative mixing effect reveals new structural and morphological aspects that result from the inter-specific environment. Ignoring the two effects of mixing may cause confusion and misinterpretation. The combination of both effects may be more relevant for practical purposes and decision support in relation to the pros and cons of mixtures versus monocultures, whereas the separation of the multiplicative mixing effect is clearly relevant for ecological theory and modelling. The multiplicative mixing effect is often referred to as an emergent property, because it cannot be predicted from the dynamics of the monocultures. It is likely to require long-term observation of tree development in inter- versus intra-specific neighbourhoods.

Table 6 (columns (2) and (3)) shows that when comparing mixtures with monocultures, without weighting the effects using mixing proportions, most of the structural characteristics measured indicate strong effects towards higher structural heterogeneity. There were a few exceptions such that, in comparison with beech monocultures, the mixed-species stand had a lower heterogeneity, e.g., lower slenderness, crown length, and lateral crown extension. This unweighted comparison and the increase in heterogeneity by mixing may be relevant for decision making in forest practice, because it shows that mixing both species can result in higher structural heterogeneity which might be an aim for providing the above mentioned forest functions and services. However, those differences provided very limited information about the emerging mixing effects.

The causes for strong additive effects of mixing Scots pine and European beech are clear when comparing the very different structural traits of both species in their monocultures. Most of the structural indices indicate that Scots pine is less variable, plastic, and multi-layered than beech (Table 6, column (4)). The structural differences between the monocultures of pine and beech are consistent with many other studies (Jucker et al. 2015, Kelty 1992, Pretzsch 2014). Scots pine represents a light demanding, rather crown-transparent and vertically oriented fast growing species with an early culminating course of growth (early successional species). European beech represents a shade tolerant, and shading species, with high lateral crown plasticity and a slower but more continuously and later culminating course of growth (late successional species). As a result of those species-specific traits the mixed stands of both species differ significantly from both monocultures, i.e., they show strong additive effects (Forrester and Pretzsch, 2015). Other common mixtures of early and late successional or shade intolerant and tolerant species such as Scots pine and lime tree, Scots pine and American oak, or European larch and beech, larch and spruce, silver birch and spruce, silver birch and silver fir, or Alnus rubra and Pseudotsuga menziesii may behave similarly.

Table 6 shows that because of the different structural traits the weighted mean of both monocultures differs, for many variables, significantly from the monoculture, and indicates a strong additive effect (columns (5) and (6)). This means that the differences found by the unweighted comparison result mainly from the morphological and structural differences between the selected species. The most interesting finding is that beyond this additive effect mixing triggers emergent properties, i.e., a multiplicative mixing effect (Table 6, column (7)-(9)). Analyses at the species level showed that stand density, size range, vertical layering, and morphological variation are enhanced by mixing. Scots pine becomes restricted and European beech is released in mixture, as shown at the species level (column (7) and (8)) and in recent studies on beech growing in mixtures with conifers (Pretzsch and Schütze 2005, Metz et al. 2013). However, due to the opposite sign of the reactions they compensate each other to some extent and so the multiplicative effects are less detectable at the whole stand level (column (9)).

As the size of the smallest and tallest tree in a stand as well as the size range are frequently used for indicating community structure (Niklas et al. 2003) they were included in the set of structural measures. However, it should be consider that the range may be a biased estimator for the variation as it depends strongly on sample size. The larger the sample size, the higher the probability of finding the rarer small and large values. Since our mixed-species plots were on average twice as large as the monocspecific plots, the larger range in the mixed plots could be partly an artifact of the design.

The primary multiplicative mixing effect is the higher morphological variability, crown extension, interlocking, and canopy space filling down to the lower canopy layers because of the different light ecology of both species. This may cause a higher crown density and stocking density, and finally a higher productivity and overyielding as shown for these triplets elsewhere (Pretzsch et al. 2015).

Change of mixing effects along the humidity gradient

We found a strong multiplicative mixing effect on stand density, crown morphology, and vertical structuring for both species (Table 6, column (7)-(8) and also at the whole stand level (column (9)). However, this multiplicative effect was usually only weakly correlated with the environmental conditions (Table 5, columns (7)-(9)). This means the multiplicative mixing effects, which might be mainly responsible for any overyielding or underyielding were not significantly related to the site variables that were included in the analysis. This is in line with our findings on the same triplets, that standing volume (+12 %), stand density (+20 %), basal area growth (+12 %), and stand volume growth (+8 %) were higher than the weighted mean of the neighbouring monocultures, but that the superiority of the mixed stands versus monocultures did not show a clear dependency of the site conditions (Pretzsch et a. 2015). This shows that both species can be maintained in mixtures along a broad range of site conditions and indicates that they are able to acclimate to the mixture, and to potentially use resources better than in monocultures thereby increasing both productivity and stand density.

Mixing increases many aspects of structural heterogeneity compared with monocultures. The unweighted comparison (Table 5, column (2) and (3)) as well as the analysis of the additive effect (column (4)-(6)) showed that mixed stands of Scots pine and European beech can simply be richer in structure because the two species have very different ecological traits and structural morphology. As both species develop differently in monocultures, e.g., in tree height growth and vertical structuring, when environmental conditions improve, the additive effect can also increase together with the Martonne index (see Table 5, columns (4)-(6)). However, the additive effect is rather a potential effect, derived from the characteristics of the species in the monoculture. The multiplicative mixing effect may also counteract the potential additive effect. This becomes obvious in Table 5, where the additive effect is highest (columns (4)-(6)) and indicates further differences that were not apparent when using the unweighted comparison (columns (2) and (3)). There is a counteracting multiplicative mixing effect behind this difference. This inter-specific interaction effect becomes obvious on productive sites where European beech may out-compete pine. That is, while both species have very complementary traits, on sites that are very favourable to beech the multiplicative mixing effects result in a restriction of Scots pine and a release of European beech to such an extent that in the long term the multiplicative mixing effect leads to a beech monocultures, thereby strongly reducing the structural heterogeneity.

This turnaround from a structure enhancing to a structure reducing multiplicative effect may occur when European beech obtains an upper hand in competition on better sites and at advanced stand ages simply because of its higher maximum height and crown plasticity. This may be indicated by negative correlations between the multiplicative mixing effect and increasing Martonne values (Table 5, columns (7)-(9)). This trend of more favourable conditions for beech in pine-beech mixtures when increasing the humidity agrees with the findings of Condés and Río (2015), who reported that the positive pine admixture effect on beech growth and mortality increased significantly with site precipitation.

Causal explanation

There is increasing evidence that functional diversity or the presence, abundance, distribution, and diversity of functional traits rather than species diversity per se control ecosystem functioning (e.g. Díaz et al. 2006, Nadrowski et al. 2010). This may be why the observed findings can be explained by the different functional traits of European beech and Scots pine. Obviously, because of its shade tolerance European beech can grow under the light transparent Scots pine crowns and thereby widen the size range in mixed stands compared with pine monocultures. At the same time, the light that penetrates the pine canopies can be absorbed by European beech to increase the total light absorption of the mixtures compared with the pine monocultures; while light intensity under beech canopies is only 1-2 % of above canopy light availability, it is 15 %, i.e., about tenfold, under Scots pine (Ellenberg and Leuschner, 2010, p 89). Combinations of high light-use efficient species with more shade tolerant species capable of high light absorption have been shown to increase light-use efficiency and light absorption of mixtures compared with monocultures (Kelty 1992, Binkley et al. 2013, Forrester et al. 2012). This may also explain the higher carrying capacity in terms of beech density in mixed plots (Pretzsch and Biber 2016), probably linked to lower mortality rates (Condés and Río, 2015), since beech tree mortality is often due to competition for light (Monserud and Sterba 1999, Ruíz-Benito et al. 2013).

The crown morphology in terms of the relationships between tree diameter and crown diameter, crown length and leaf area can differ between mixtures and monocultures (Pretzsch 2014). For instance, individuals of European beech growing in mixture with Norway spruce showed greater crown volumes when compared to those in monospecific stands (Bayer et al. 2013). Beech crown plasticity was also detected when growing with pine, with larger crown sizes than in monospecific stands (Dieler and Pretzsch 2013, Metz et al. 2013). These differences in crown morphology, as well as inter-specific differences in height, can result in a more efficient packing of tree crowns within the canopy space and an increased light absorption by individual tree crowns of a given species and size in mixtures compared with monocultures (Bauhus et al., 2004; Forrester and Albrecht, 2014). However, canopy space filling seems more affected by morphological properties of the species in the mixture rather than by species richness itself (Seidel et al. 2013, Barbeito et al. 2014).
The higher plasticity in canopy shape and volume in mixtures in response to changes in the local neighbourhood increases canopy occupation, maximizing light interception and thereby increasing productivity. The other hand, the high plasticity and increased light interception of beech in mixed stands compared with monospecific stands might be a decrease in wood quality due to higher crown asymmetry and stem curvature in mixtures (Knoke and Seifert 2008).

Consequences for silviculture

The strong species-specific multiplicative mixing effects on stand density (Table 6, columns (7)-(9)) are probably enhanced by the dense interlocking of both species, their morphological variability, and vertical structuring. Most mixed-species plots represent close to 50:50 mixing portions and a rather individual tree mixing pattern. This individual tree mixing enables the extension of the beech crowns in length and width at the expense of the pine crowns (Pretzsch 2014). As crown size is closely related to light absorption and hence productivity (Binkley et al. 2013) beech benefits from growing in pine neighbourhoods. Beech has a rather low self-tolerance in monocultures but competes strongly with pine, which is less plastic (Metz et al. 2013). The crown extension means longer and more branches and a reduction of wood quality of beech (Pretzsch and Rais 2016, Wiedemann 1951, p 135). Interference by beech can reduce the number of branches of Scots pine, which can improve timber strength and stiffness (Pretzsch and Rais 2016). However, in older stands the high plasticity of beech can suppress and eliminate pine in individual tree mixtures regardless of whether it is competing laterally or from below by pushing its crowns upwards into the pine crowns (Wiedemann 1951, p 134). This may be avoided by a continuous release of pines by thinning, by pine being additionally favoured through the greater positive mixing effect at lower stand densities (Condés et al 2013), or by a group or cluster mixing of both species where both can grow in intra-specific instead of inter-specific neighbourhoods (Spathelf and Ammer 2015). However, this may reduce the close vertical and horizontal interactions of both species which may be the main reason for the increased light interception, productivity, and stand density.
Mixed stands of Scots pine and European beech can carry more trees of a given size, and this effect increases with site productivity. The complementary light ecology of both species

(pine light demanding, beech shade tolerant) increases the light interception or light use efficiency to such an extent that not only stand productivity (Pretzsch et al. 2015) but also the carrying capacity is continuously higher than in monocultures (Pretzsch and Biber 2016). The finding that this tendency and vertical structuring increases with site productivity substantiates the assumption that greater light interception explains the increase in density and growth; on rich sites where water and nutrient supply are higher the light complementarity might become more effective than on poor sites, where other environmental conditions are limiting (Forrester and Albrecht 2014).

mixtures can carry more trees of a given size. Thus, the self-thinning relationships of mixed stands are assumed to differ from that of the respective monocultures. Future research is needed to reveal which of the two parameters of the self-thinning line (intercept and/or slope) are changed in mixed stands (Pretzsch and Biber, 2016). The knowledge about any increase in maximum stand density by species mixing is relevant for developing silvicultural guidelines. If thinning guidelines for mixed stands simply adopt the target curves for stand basal area or tree number developed for monocultures, this may result in suboptimal stand densities and thereby losses in stand productivity. The strong increase in density when mixing the ecologically very different Scots pine with European beech suggests that assemblages of complementary species may increase the supply, capture, or use efficiency of resources to such an extent that not only the growth rate but also the carrying capacity is higher than in monocultures. This finding is of special interest in terms of biomass production and carbon sequestration by forests; both of which are of increasing importance (Mund et al. 2015). Further research will be required to determine which resources become more efficiently used and how this depends on site conditions and stand age, particularly because the outcomes of such research will find direct application by forest management practices.

Acknowledgement

The networking in this study has been supported by COST Action FP1206 EuMIXFOR. All contributors thank their national funding institutions and the woodland owners for agreeing to establish, measure, and analyze data from the triplets. The first author also thanks the Bayerischen Staatsforsten (BaySF) for supporting the establishment of the plots, the Bavarian State Ministry for Nutrition, Agriculture, and Forestry for permanent support of the project W 07 ”Long-term experimental plots for forest growth and yield research“ (# 7831-22209-2013) and the German Science Foundation for providing the funds for the projects PR 292/12-1 ”Tree and stand-level growth reactions on drought in mixed versus pure forests of Norway spruce and European beech“.The second author thanks the COST Action FP1206 EuMIXFOR for funding the STSM FP1206-160714-045064, and the Spanish project AGL2014-51964-C2-2-R. Thanks are also due to Ulrich Kern for the graphical artwork, and to two anonymous reviewers for their constructive criticism.

References

Assmann E (1970) The principles of forest yield study. Pergamon Press, Oxford, New York, 506 p

Barbeito, I., LeMay, V., Calama, R., Cañellas, I. (2011) Regeneration of Mediterranean Pinus sylvestris under two alternative shelterwood systems within a multiscale framework. Canadian Journal of Forest Research 41:341-351.

Bauhus, J. (2009) Rooting patterns of old-growth forests: is aboveground structural and functional diversity mirrowed belowground? In Wirth C. et al. (Eds.), Old-growth Forests. Ecological Studies 207, 211-229.

Bauhus, J., van Winden, A.P., Nicotra, A.B. (2004) Above-ground interactions and productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*. Canadian Journal of Forest Research 34, 686-694.

Bayer, D., Seifert, S., Pretzsch, H. (2013) Structural crown properties of Norway spruce (Picea abies [L.] Karst.) and European beech (Fagus sylvatica [L.]) in mixed versus pure stands revealed by terrestrial laser scanning. Trees, 27(4), 1035-1047.

Benavides, R., Roig, S., Osoro, K. (2009) Potential productivity of forested areas based on a biophysical model. A case study of a mountainous region in northern Spain. Annals of forest science, 66(1), 1.

Binkley, D., Campoe, O. C., Gspaltl, M., Forrester, D. I. (2013) Light absorption and use efficiency in forests: Why patterns differ for trees and stands. Forest ecology and management, 288, 5-13.

Binkley D, (2004) A hypothesis about the interaction of tree dominance and stand production through stand development. Forest ecology and management, 190(2): 265-271.

Binkley D, Kashian DM, Boyden S, Kaye MW, Bradford JB, Arthur MA, Fornwalt PJ, Ryna MG, (2006) Patterns of growth dominance in forests of the Rocky Mountains, USA. Forest ecology and management, 236(2): 193-201.

Bortz, J., (1993) Statistik, Springer, Berlin, Heidelberg, New York, 753 p.

Brunet J, Fritz Ö, Richnau G (2010) Biodiversity in European beech forests–a review with recommendations for sustainable forest management. Ecol Bull 53:77–94

Camino R, de., 1976. Zur Bestimmung der Bestandeshomogenität. Allgemeine Forst- und Jagdzeitung 147: 54-58.

Chittagong, B. (2015) Climate to Forest Productivity: Implication of Paterson's CVP Index. Research Journal of Forestry, 9(2), 27-34.

Clark PJ, Evans FC (1954) Distance to nearest neighbour as a measure of spatial relationships in populations. Ecol 35 (4): 445-453

Condés S., Río M. (2015) Climate modifies tree in intereactions in terms of basal area growth and mortality in monospecific and mixed Fagus sylvatica and Pinus sylvestris forests. Eur J For Res 134, 1095-1108.

Condés, S., del Rio, M., Sterba, H., 2013. Mixing effect on volume growth of Fagus sylvatica and Pinus sylvestris is modulated by stand density. For Ecol Manage 292, 86-95.

Cordonnier, T., Kunstler, G. (2015). The Gini index brings asymmetric competition to light. Perspectives in Plant Ecology, Evolution and Systematics, 17(2), 107-115.

Cox F (1971) Dichtebestimmung und Strukturanalyse von Pflanzenpopulationen mit Hilfe von Abstandsmessungen. Mitt Bundesforschungsanst Forst- u Holzwirtschaft 87, Reinbek (Hamburg), 184 p

Díaz S, Fargione J, Chapin FS III, Tilman D (2006) Biodiversity loss threatens human well-being. PLoS Biol 4: e277.

Dieler, J., Pretzsch, H., (2013) Morphological plasticity of European beech (Fagus sylvatica L.) in pure and mixed-species stands. Forest Ecology and Management 295, 97-108.

Forrester, D. I. (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. Forest Ecology and Management, 312, 282-292.

Forrester, D. I., Albrecht, A. T. (2014) Light absorption and light-use efficiency in mixtures of Abies alba and Picea abies along a productivity gradient. Forest Ecology and Management, 328, 94-102.

Forrester, D.I., Bauhus, J., (2016) A review of processes behind diversity - productivity relationships in forests. Current Forestry Reports. 2, 45-61.

Forrester, D.I., Lancaster, K., Collopy, J.J., Warren, C.R., Tausz, M., (2012) Photosynthetic capacity of Eucalyptus globulus is higher when grown in mixture with Acacia mearnsii. Trees Structure and Function 26, 1203-1213.

Forrester, D. I., Pretzsch, H. (2015) Tamm Review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. Forest Ecology and Management, 356, 41-53.

Franz F. Bachler J, Deckelmann B, Kennel E, Kennel R, Schmidt A, Wotschikowsky U (1973) Bayerische Waldinventur 1970/71, Inventurabschnitt I: Großrauminventur Aufnahme- und Auswertungsverfahren. Forstl Forschungsber München 11, 143 p

Gadow von, K. (1998) Integrating Environmental Research into Forest Ecosystems Planning. In Environmental Forest Science (pp. 29-37). Springer Netherlands.

Gadow von, K., Nagel, J., Saborowski, J. (2002) Continuous cover forestry: assessment, analysis, scenarios (Vol. 4). Springer Science & Business Media.

Gamfeldt L., Snall T., Bagchi R., Jonsson M., Gustafsson L., Kjellander P., Ruiz-Jaen M.C., Froberg M., Stendahl J., Philipson C.D., Mikusinski G., Andersson E., Westerlund B., Andren H., Moberg F., Moen J. & Bengtsson J. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4, 1340.

Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Chećko, E., Scherer-Lorenzen, M. (2014). Tree diversity does not always improve resistance of forest ecosystems to drought. Proceedings of the National Academy of Sciences, 111(41), 14812-14815.

Griess, V. C. und Knoke, Th. (2011) Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. Canadian Journal of Forest Research 41:1141-1159.

Hari, P (1985) Theoretical aspects of eco-physiolocigal research. In: Tigerstedt PMA, Puttonen P, Koski V (eds) Crop physiology of forest trees. Helsinki Univ Press, pp 21-30 (336 p)

Harper JL (1977) Population Biology of Plants. Academic Press, London, New York

Hattemer HH (1994) Die genetische Variation und ihre Bedeutung für Wald und Waldbäume. J Forestier Suisse 145 (12): 953-975

Homeier, J., Breckle, S. W., Günter, S., Rollenbeck, R. T., & Leuschner, C. (2010) Tree Diversity, Forest Structure and Productivity along Altitudinal and Topographical Gradients in a species-Rich Ecuadorian Mountain Rain Forest. Biotropica, 42(2), 140-148.

Ishii, H. T., Tanabe, S. I., Hiura, T. (2004) Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. Forest Science, 50(3), 342-355.

Jactel, H., and Brockerhoff, E. G. (2007) Tree diversity reduces herbivory by forest insects. Ecology letters, 10(9), 835-848.

Johann, K., (1993) DESER-Norm 1993. Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwachstumskundlichen Dauerversuchen. Proc Dt Verb Forstl Forschungsanst, Sek Ertragskd, in Unterreichenbach-Kapfenhardt, pp 96-104.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D. A. (2014) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecology letters, 17(12), 1560-1569.

Jucker, T., Bouriaud, O., & Coomes, D. A. (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Functional Ecology, doi:10.1111/1365-2435.12428

Kellogg, L. D., Bettinger, P., Edwards, R. M. (1996) A comparison of logging planning, felling, and skyline yarding costs between clearcutting and five group-selection harvesting methods. Western Journal of Applied Forestry, 11(3), 90-96.

Kelty, M. J. (1992) Comparative productivity of monocultures and mixed-species stands. The ecology and silviculture of mixed-species forests. Kluwer, Dordrecht, 125-141.

Keegan, I. I. I., Charles, E., Fiedler, C. E., Stewart, F. J. (1995) Cost of Timber Harvest Under Traditional and "New Forestry" silvicultural prescriptions. Western Journal of Applied Forestry, 10(1), 36-42.

Knoke, T., Seifert, T. (2008). Integrating selected ecological effects of mixed European beech–Norway spruce stands in bioeconomic modelling. Ecological modelling, 210(4), 487-498.

Kölling, C., Knoke, T., Schall, P., Ammer, C. (2009) Überlegungen zum Risiko des Fichtenanbaus in Deutschland vor dem Hintergrund des Klimawandels. Forstarchiv, 80(2), 42-54.

Kramer H (1988) Waldwachstumslehre. Paul Parey, Hamburg, Berlin, 374 p

Lei X.D., Wang W.F., Peng C.H. (2009) Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. Can J Forest Res 39(10), 1835-1847

Liang J., Buongiorno J., Monserud R.A., Kruger E.L., Zhou M. (2007) Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. Forest Ecol Manag 243(1), 116

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J. (2005) Forest and woodland stand structural complexity: its definition and measurement. Forest Ecology and Management, 218(1), 1-24.

Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E. D., Ammer, C. (2013) Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra-and interspecific competition on tree growth. Forest Ecology and Management, 310, 275-288.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109-123

Mund M, Frischbier N, Profft I, Raacke J, Richter F, Ammer C (2015) Klimaschutzwirkung des Wald- und Holzsektors: Schutz- und Nutzungsszenarien für drei Modellregionen in Thüringen. BfN-Skripten 396: 1-168.

Nadrowski K, Wirth C, Scherer-Lorenzen M (2010) Is forest diversity driving ecosystem function and service? Current Opinion in Environmental Sustainability 2: 75–79.

Neumann, M., Starlinger, F. (2001) The significance of different indices for stand structure and diversity in forests. Forest ecology and Management, 145(1), 91-106.

Niklas, K. J., Midgley, J. J., Rand, R. H. (2003). Tree size frequency distributions, plant density, age and community disturbance. Ecology letters, 6(5), 405-411.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., BERNHARDT-RÖMERMANN, M. A. R. K. U. S., Kanka, R. (2010) Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conservation biology, 24(1), 101-112.

Paterson, S. S., (1956) The forest area of the world and its potential productivity, The Royal university of Göteborg, Sweden, Department of geography, Lerums Boktryckeri, Sweden, p 216

Peck, J.E., Zenner, E.K., Brang, P., Zingg, A. (2014) Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. Eur. J. For. Res. 133: 335-346.

Pielou EC (1977) Mathematical Ecology. John Wiley & Sons, New York, 385 p

Pommerening, A. (2002) Approaches to quantifying forest structures. Forestry, 75(3), 305-324.

Pretzsch H (1997) Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony, Forest Eco Mngt 97: 237-253

Pretzsch H (1998) Structural diversity as a result of silvicultural operations. Lesnictví-Forestry 44 (10): 429-439

Pretzsch, H. (2009) Forest dynamics, growth and yield. From measurement to model, Springer, Berlin, Heidelberg, 664 p.

Pretzsch, H. (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. Forest Ecology and Management, 327: 251-264.

Pretzsch, H., Biber, P. (2016) Tree species mixing can increase maximum stand density. Canadian Journal of Forest Research, DOI: 10.1139/cjfr-2015-0413

Pretzsch H., Bielak K., Block J., Bruchwald A., Dieler J., Ehrhart H-P., Kohnle U., Nagel J., Spellmann H., Zasada M., Zingg A. (2013) Productivity of pure versus mixed stands of oak (Quercus petraea (MATT.) LIEBL. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. Eur. J. For.Res. 132 (2), 263-280.

Pretzsch, H. Rais, A. (in revision): Wood quality in complex forests verus even-aged monocultures. Review and perspectives, Wood science and technology.

Pretzsch, H., del Río, M., Ammer, Ch., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D. I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A. (2015) Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. Eur J Forest Res, 134 (5): 927-947

Pretzsch, H., Schütze, G. (2014) Size-structure dynamics of mixed versus pure forest stands, Forest Systems, 23(3):560-572.

Pretzsch, H., Schütze, G. (2015) Effect of tree species mixing on the size structure, density, and yield of forest stands, Eur J Forest Res, DOI 10.1007/s10342-015-0913-z

Puettmann, K. J., Coates, K. D., Messier, C. C. (2012) A critique of silviculture: managing for complexity. Island Press.

Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agr Res 46: 627-638

Río M., Pretzsch H., Alberdi I., Bielak K., Bravo, F., Brunner A., Condés S., Ducey M.J., Fonseca T., von Lüpke N., Pach M., Peric S., Perot T., Souidi Z., Spathelf P., Sterba H., Tijardovic M., Tomé M., Vallet P., Bravo-Oviedo A. (2016) Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. European Journal of Forest Research, Eur J Forest Res, 135:23–49, DOI 10.1007/s10342-015-0927-6

Roth, R. R. (1976). Spatial heterogeneity and bird species diversity. Ecology, 773-782.

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A., 2013. Patterns and drivers of tree mortality in Iberian forests: climatic effects are modified by competition. PLoS One 8, e56843.

Shannon CE (1948) The mathematical theory of communication. In: Shannon CE, Weaver W (eds) The mathematical theory of communication. Urbana, Univ of Illinois Press, pp 3-91

Schober R (1967) Buchen-Ertragstafel für mäßige und starke Durchforstung, In: Schober R (1972) Die Rotbuche 1971. Schr Forstl Fak Univ Göttingen u Niedersächs Forstl Versuchsanst 43/44, JD Sauerländer's Verlag, Frankfurt am Main, 333 p

Schütz, J. P. (2002). Silvicultural tools to develop irregular and diverse forest structures. Forestry, 75(4), 329-337.

Schwinning S, Weiner S (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113: 447-455.

Seidel, D., Leuschner, C., Scherber, C., Beyer, F., Wommelsdorf, T., Cashman, M. J., Fehrmann, L. (2013) The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. Forest Ecology and Management, 310, 366-374.

Spathelf P, Ammer C (2015) Forest management of Scots pine (*Pinus sylvestris* L.) in northern Germany – A brief review of the history and current trends. Forstarchiv 86: 59-66

Sterba H (1981) Natürlicher Bestockungsgrad und Reinekes SDI. Cbl für das ges Forstwesen 98: 101-116

Sterba, H. (1987) Estimating Potential Density from Thinning Experiments and Inventory Data. Forest Science 33 (4) 1022-1034

Sterba, H. (2008) Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. Forestry, 81(5), 587-597.

Stölb, W. (2005) Waldästhetik: über Forstwirtschaft, Naturschutz und die Menschenseele. Kessel, 400 p

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of biogeography, 31(1), 79-92.

Vanclay, J. K. (1992) Assessing site productivity in tropical moist forests: a review. Forest Ecology and Management, 54(1), 257-287.

Varga P., Chen H.Y.H., and Klinka K. (2005) Tree-size diversity between single- and mixed-species stands in three forest types in western Canada. Can. J. For. Res. 35: 593–601.

Wichmann L (2002) Competition Symmetry. Chapter 7. In: Modelling the effects of competition between individual trees in forest stands. PhD Thesis, Unit of Forestry, Copenhagen. pp. 67-77

Wichmann L (2001) Annual Variations in Competition Symmetry in Even-aged Sitka Spruce. Annals of Botany 88: 145-151.

Wiedemann E (1943) Kiefern-Ertragstafel für mäßige Durchforstung, starke Durchforstung und Lichtung, In: Wiedemann E (1948) Die Kiefer 1948. Verlag M & H Schaper, Hannover, 337 p

Wiedemann, E. (1951) Ertragskundliche und waldbauliche Grundlagen der Forstwirtschaft. Frankfurt: J. D. Sauerländer‘s Verlag, 346 p.

Zenner, E. K., Hibbs, D. E. (2000) A new method for modeling the heterogeneity of forest structure. Forest ecology and management, 129(1), 75-87.

Zenner, E.K., Peck. J.E., Holbi, M., Commarmot, B. (2015) The dynamics of structure across scale in a primaeval European beech stand. Forestry 88: 180-189.

Figures and Tables

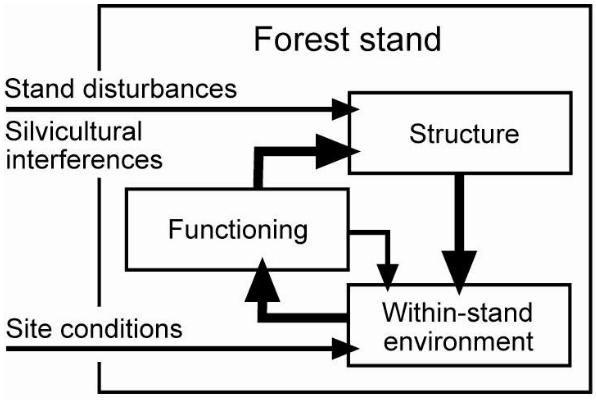

Figure 1 Schematic representation of the connections between within-stand environment, functioning and structure. The species within the stand can slowly modify their environment via structure (feedback circle represented by bold arrows) or quickly modify their environment via functioning (thin arrow). External factors, such as disturbances, silvicultural interferences and site conditions influence the structure and within-stand environment of the stand and thereby its functioning (Pretzsch 2014).

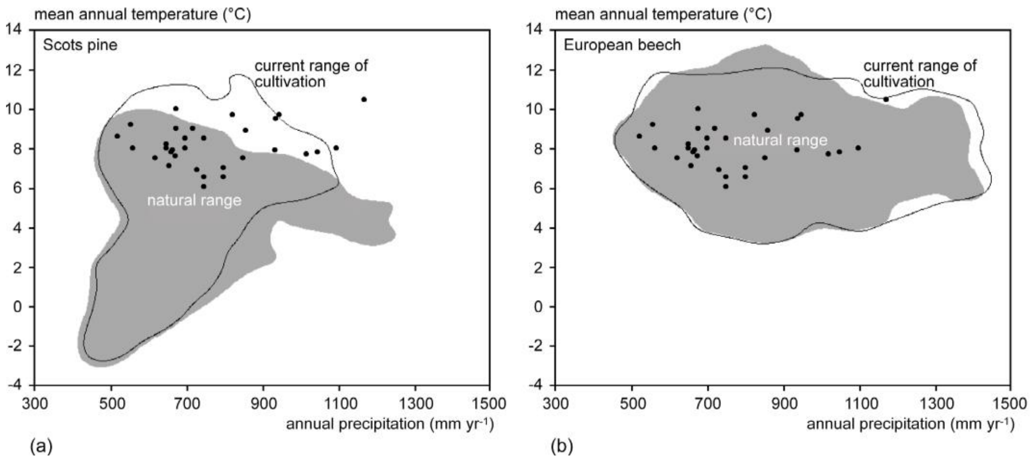

Figure 2 Positioning of the 32 triplets (black circles) in the climate envelopes (see Kölling et al. 2009) in terms of mean annual precipitation (mm yr^{-1}) and mean annual temperature (° C) of the natural range (grey) and current range of cultivation (black line) of (a) Scots pine and (b) European beech.

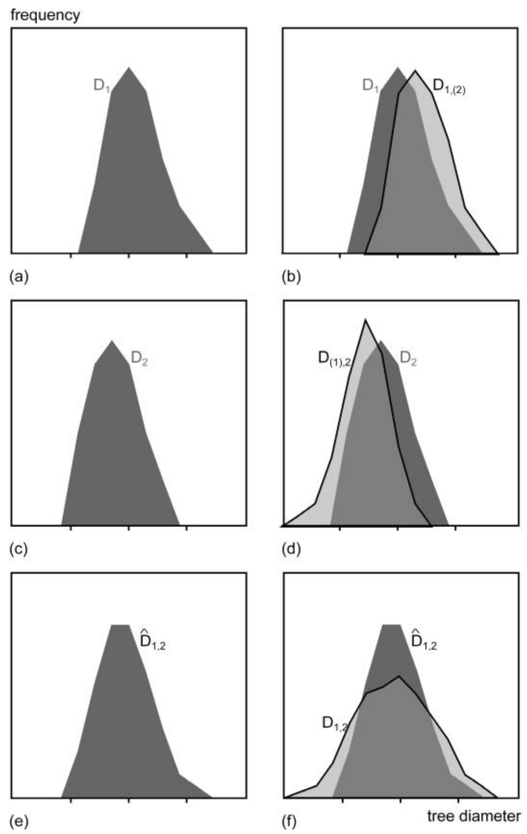

Figure 3 Schematic representation of the comparison between monocultures and mixed-species stands' tree diameter distribution to quantify multiplicative effects (resulting from species interactions) as opposed to additive effects (resulting only from mixing species with different morphological or physiological traits). At the species level, size distributions D_1 and D_2 in monospecific stands can be compared with the respective distributions $D_{1,(2)}$ and $D_{(1),2}$ in neighbouring mixed stands (a-d). For quantification of the mixing effect at the whole stand level the weighted mean of both monoculture distributions $\hat{D}_{1,2}$ can be compared with the observed whole stand distribution $D_{1,2}$ (e and f). Differences between the reference distributions (a, c, e) and the observed size distribution (b, d, f) indicate inter-specific interactions and multiplicative mixing effects.

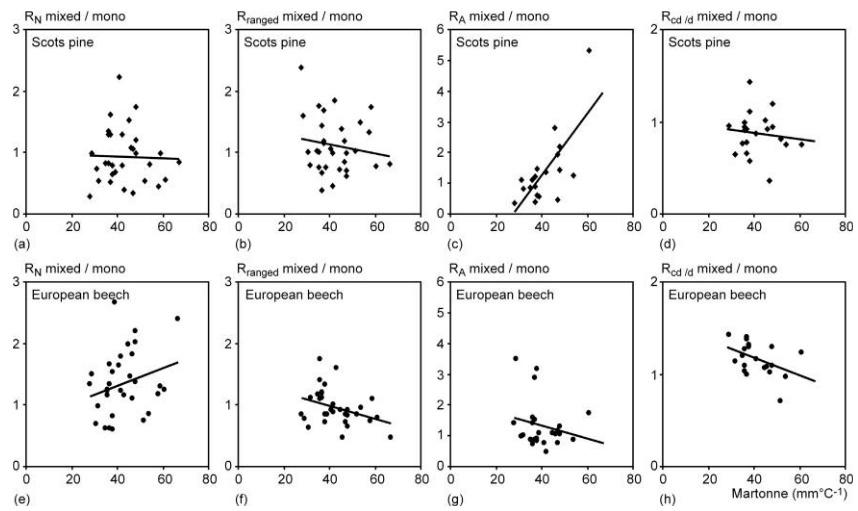

Figure 4 Relationship between the Martonne index, M, and selected ratios (RN, $Rrange_d$, RA, and Rcd/d) indicating the multiplicative mixing effect at the species level for Scots pine and European beech. In particular, we show the results for ratios between the structure of Scots pine in mixture versus Scots pine in the monoculture and European beech in mixture versus European beech in the monoculture for the structural variables (a and e) tree number, N, (b and f) range of stem diameter, $range_d$, (c and g) vertical species profile, A, and (d and h) crown projection ratio, cd/d. OLS regression analyses yielded

(a) $RN_{mix/mono,\ Sc.p.} = 1.00\,(\pm0.38) - 0.002\,(\pm0.009) \times M$, n=32, R^2=0.01, p<0.85

(b) $Rrange_{d\ mix/mono,\ Sc.p.} = 1.42\,(\pm0.38) - 0.01\,(\pm0.009) \times M$, n=32, R^2=0.02, p<0.41

(c) $RA_{mix/mono,\ Sc.p.} = -2.68\,(\pm0.97) + 0.10\,(\pm0.023) \times M$, n=19, R^2=0.52, p<0.001

(d) $Rcd/d_{mix/mono,\ Sc.p.} = 1.002\,(\pm0.27) - 0.003\,(\pm0.01) \times M$, n=21, R^2=0.01, p<0.63

(e) $RN_{mix/mono,\ E.be.} = 0.74\,(\pm0.42) + 0.02\,(\pm0.01) \times M$, n=32, R^2=0.07, p<0.15

(f) $Rrange_{d\ mix/mono,\ E.be.} = 1.43\,(\pm0.23) - 0.01\,(\pm0.005) \times M$, n=32, R^2=0.13, p<0.05

(g) $RA_{mix/mono,\ E.be.} = 2.17\,(\pm0.82) - 0.02\,(\pm0.02) \times M$, n=25, R^2=0.05, p<0.30

(h) $Rcd/d_{mix/mono,\ E.be.} = 1.57\,(\pm0.19) - 0.01\,(\pm0.004) \times M$, n=21, R^2=0.20, p<0.05

Table 1 Overview of the measures for characterization of different structural aspects used in this study, an explanation of what they indicate, and references.

Measure	structural aspect	Indication of index when its value is low	medium	high	reference
stand and canopy density					
N	tree number	thinly	medium	dense	Kramer 1988
SDI	stand density index	thinly	medium	dense	Reineke 1933
RCPA	sum of crown area	thinly	medium	dense	Pretzsch 2014
RCC	crown coverage	thinly	medium	dense	Assmann 1970
horizontal distribution pattern					
CV_{BA}	basal area	homogeneous	medium	heterogeneous	Bortz 1993
size distribution pattern					
$skew_d$	skewness d	left-skewed	normal	right-skewed	Pretzsch, Schütze 2015
$skew_h$	skewness h	left-skewed	normal	right-skewed	Pretzsch, Schütze 2015
$skew_v$	skewness v	left-skewed	normal	right-skewed	Pretzsch, Schütze 2015
$range_d$	range d	equal	medium	unequal	Pretzsch, Schütze 2014
$range_h$	range h	equal	medium	unequal	Pretzsch, Schütze 2014
GV_v	inequality of v	equal	medium	unequal	Binkley 2004
vertical structuring					
A	vertical species profile	monotonous	medium diverse	highly diverse	Pretzsch 1998
morphological variation					
h/d	slenderness	conical	medium	slender	Pretzsch 2014
cl/h	crown ratio	short crown	medium	long crown	Pretzsch 2014
r_{min}/r_{max}	crown concentricity	eccentric	medium	concentric	Pretzsch 2014
cd/d	crown projection ratio	slim crown	medium crown	wide crown	Assmann 1970
cd^2/d^2	Quotient ground cover area	slim crown	medium crown	wide crown	Assmann 1970
intra-individual growth allocation					
GV_{iv}	inequality iv	equal	medium	unequal	Binkley et al. 2006
GDC	growth dominance	low dom.	all equal	high dom.	Binkley 2004

Table 2 Minimum, mean, and maximum of the structural measures for monocultures of Scots pine and European beech and mixed-species stands of Scots pine and European beech. In the columns (12) and (13) we report the p-values for testing group differences between the mixed-species stands and the monocultures of Scots pine and European beech, respectively. Notice, that in columns (4), (7), and (10) we report the arithmetic means (unweighted by mixing proportions) of all n observations within the respective groups. In columns (12) and (13) we report the mean of the ratio resulting from the pair-wise division of the characteristic of the mixed-species stands by the respective value of the neighbouring monocultures. '*', '**', and '***' indicate significant differences of mixed-species stand versus monoculture at the level $p<0.05$, 0.01, and 0.001 (bold).

(1) Stand structure indices	(2) sample size	(3) mono Scots pine	(4)	(5)	(6) mono E. beech	(7)	(8)	(9) mixed Sc. p + E. beech	(10)	(11)	(12) mixed vs. Sc. pi. mono	(13) mixed vs. E. be. mono
	n	min	mean	max	min	mean	max	min	mean	Max		
stand and canopy density												
N	32	*82*	970	*3200*	*220*	1027	*2745*	*250*	990	*2628*	1.27±0.14	1.10±0.07
SDI	32	*215*	834	*1426*	*392*	724	*1266*	*337*	824	*1631*	1.06±0.07	**1.18**±0.06**
RCPA	25	*0.55*	1.15	*1.83*	*0.68*	1.29	*2.15*	*1.51*	2.23	*3.69*	**2.02***±0.13**	**1.82***±0.12**
RCC	25	*0.46*	0.73	*0.98*	*0.44*	0.74	*0.97*	*0.73*	0.89	*0.98*	**1.27***±0.05**	**1.24***±0.06**
horizontal distribution pattern												
CV_{BA}	31	*0.08*	0.19	*0.44*	*0.09*	0.23	*0.44*	*0.10*	0.20	*0.39*	1.06±0.08	0.90±0.07
size distribution pattern												
$skew_d$	32	*-2.13*	-0.11	*1.27*	*-1.15*	0.42	*2.21*	*-0.79*	0.37	*1.53*	0.65±3.92	-1.56±2.13
$skew_h$	32	*-3.84*	-1.11	*0.01*	*-3.54*	-0.68	*0.60*	*-1.36*	0.08	*3.63*	1.14±0.72	-0.21±0.90
$skew_v$	32	*-1.02*	0.58	*1.84*	*-0.12*	1.41	*4.56*	*-0.01*	1.19	*2.33*	1.37±0.67	0.85±0.30
$range_d$	32	*14.10*	27.42	*53.40*	*18.80*	34.30	*66.50*	*17.00*	38.48	*65.10*	**1.53***±0.10**	**1.20***±0.06**
$range_h$	32	*3.00*	12.93	*28.60*	*2.80*	13.80	*25.50*	*7.80*	17.10	*31.10*	**1.68***±0.20**	**1.42*±0.17**
$range_v$	32	*0.31*	1.42	*4.80*	*0.48*	2.39	*7.87*	*0.29*	2.31	*6.27*	**1.98***±0.21**	**1.25*±0.13**
G_v	32	*0.12*	0.28	*0.46*	*0.29*	0.43	*0.62*	*0.22*	0.44	*0.64*	**1.74***±0.11**	1.04±0.05
vertical structuring												
A	25	*0.00*	0.37	*0.90*	*0.17*	0.61	*1.08*	*0.68*	1.12	*1.34*	**3.35***±0.63**	**2.14***±0.22**
morphological variation												
h/d	32	*0.44*	0.84	*1.15*	*0.64*	1.01	*1.34*	*0.51*	0.89	*1.21*	**1.07*±0.03**	**0.90***±0.03**
cl/h	32	*0.22*	0.36	*0.60*	*0.40*	0.54	*0.79*	*0.28*	0.45	*0.66*	**1.29***±0.06**	**0.83***±0.03**
r_{min}/r_{max}	20	*0.29*	0.42	*0.55*	*0.27*	0.40	*0.51*	*0.30*	0.43	*1.00*	0.96±0.04	1.03±0.03
cd/d	21	*11.0*	17.2	*25.4*	*14.3*	25.5	*36.7*	*13.8*	21.7	*26.0*	**1.30***±0.06**	**0.87***±0.03**
cd^2/d^2	21	*124*	385	*827*	*211*	730	*1507*	*247*	593	*948*	**1.88***±0.20**	**0.87*±0.06**
intra-individual growth allocation												
G_{iv}	32	*0.08*	0.30	*0.51*	*0.31*	0.46	*0.68*	*0.28*	0.44	*0.57*	**1.66***±0.16**	0.98±0.04
GDC	32	*-0.20*	0.01	*0.13*	*-0.12*	0.01	*0.14*	*-0.33*	-0.07	*0.08*	-5.22±4.21	-0.86±1.37

Table 3 Analyzing the “additive effect” on the structural measures of Scots pine and European beech in mixed-species stands versus monocultures. In column (5) we test the group differences between monocultures of Scots pine and European beech. In columns (7) and (8) we report the p-values of testing group differences between the weighted mean (by mixing proportions) of the monocultures of Scots pine and European beech and the respective monocultures. Notice, that in columns (3), (4), and (6) we report the arithmetic means of all n observations within the respective groups. In columns (5), (7), and (8) we report the mean of the ratio resulting from the pair-wise division of the characteristic of the mixed-species stands by the respective value of the neighbouring monocultures. ‘*’, ‘**’, and ‘***’ indicate significant differences of mixed-species stand versus monoculture at the level $p<0.05$, 0.01, and 0.001.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Stand structure Indices	sample size n	Scots pine mono	European beech mono	Sc. p vs. E. be	S. pi + E. be weighted mean	S. pi + E. be weighted mean vs S. pi mono	S. pi + E. be weighted mean vs. E. be mono
stand and canopy density							
N	32	970	1027	1.12±0.15	975	1.06±0.06	1.00±0.04
SDI	32	833	724	**1.18***±0.05**	772	**0.94**±0.02**	**1.07**±0.02**
RCPA	25	1.15	1.29	0.92±0.04	1.21	**1.06*±0.03**	**0.95**±0.02**
RCC	25	0.73	0.74	1.00±0.04	0.73	1.01±0.02	1.00±0.02
horizontal distribution pattern							
CV_{BA}	29	0.19	0.23	0.91±0.07	0.21	**1.10*±0.04**	**0.93*±0.03**
size distribution pattern							
$skew_d$	32	-0.11	0.42	0.46±1.57	0.24	1.53±0.92	-3.86±3.98
$skew_h$	32	-1.11	-0.68	-0.14±1.20	-0.62	0.54±0.28	0.22±0.48
$skew_v$	32	0.58	1.41	**0.19***±0.23**	1.29	0.47±0.83	0.84±0.20
$range_d$	32	27.19	34.29	**0.87*±0.05**	37.25	**1.45***±0.10**	**1.11***±0.03**
$range_h$	32	12.93	13.79	1.05±0.12	17.40	**1.60***±0.15**	**1.36***±0.10**
$range_v$	32	1.42	2.39	**0.79*±0.08**	2.58	**2.21**±0.40**	**1.14**±0.05**
G_v	32	0.28	0.43	**0.64***±0.03**	0.41	**1.56***±0.07**	**0.94**±0.02**
vertical structuring							
A	32	0.37	0.61	**0.60**±0.13**	0.57	**1.70*±0.31**	1.09±0.11
morphological variation							
h/d	32	0.84	1.00	**0.85***±0.03**	0.91	**1.11***±0.02**	**0.92***±0.01**
cl/h	32	0.36	0.54	**0.68***±0.04**	0.45	**1.30***±0.04**	**0.84***±0.02**
r_{min}/r_{max}	20	0.42	0.40	**1.09*±0.04**	0.41	0.97±0.02	1.05±0.02
cd/d	21	17.2	25.5	**0.70***±0.04**	24.0	**1.41***±0.08**	0.95±0.05
cd^2/d^2	21	385	730	**0.61***±0.10**	826	**2.40***±0.28**	1.19*±0.13
intra-individual growth allocation							
G_{iv}	32	0.30	0.46	**0.67***±0.04**	0.44	**1.57***±0.09**	0.96±0.02
GDC	32	-0.01	0.01	**-0.94***±0.50**	-0.01	0.61±0.55	0.63±0.37

Table 4 Analyzing the “multiplicative mixing effect” on the structural measures of Scots pine and European beech in mixed-species stands versus monocultures. In column (5) and (8) we test the group differences between the species-specific behaviour in mixed stands versus monoculture. In column (11) we report the p-values of testing group differences between the observed mixed-species stand and the weighted mean of the monocultures of Scots pine and European beech. Notice, that in columns (3), (4), (6), (7), (9), and (10) we report the arithmetic means (unweighted means) of all n observations within the respective groups. In columns (5), (8), and (11) we report the mean of the ratio resulting from the pair-wise division of the characteristic of the mixed-species stands by the respective value of the neighbouring monocultures. ‘*’, ‘**’, and ‘***’ indicate significant differences of mixed-species stand versus monoculture at the level $p<0.05$, 0.01, and 0.001.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Stand structure indices	sample size n	Scots pine mono	mixed	mixed vs. mono	European beech mono	mixed	mixed vs. Mono	Scots pine + E. beech obs	weighted	obs vs. weighted
stand and canopy density										
N	32	970	786	0.93±0.08	1027	1214	**1.35***±0.09**	990	975	**1.14*±0.07**
SDI	32	833	887	**1.11*±0.06**	724	779	**1.11*±0.06**	824	772	**1.11*±0.06**
RCPA	25	1.15			1.29			2.23	1.21	**1.91***±0.11**
RCC	25	0.73			0.74			0.89	0.73	1.15±0.08
horizontal distribution pattern										
CV_{BA}	29	0.19	0.19	0.98±0.07	0.23	0.21	0.94±0.08	0.20	0.21	0.97±0.07
size distribution pattern										
$skew_d$	32	-0.11	0.01	-1.74±2.00	0.42	0.58	-2.17±2.93	0.37	0.24	1.72±1.02
$skew_h$	32	-1.11	-0.94	-1.20±2.46	-0.68	-0.41	**0.44*±0.27**	-0.64	-0.62	**-2.75*±1.76**
$skew_v$	32	0.58	0.60	**0.24*±0.33**	1.41	1.47	0.97±0.52	1.19	1.29	1.98±0.67
$range_d$	32	27.19	27.54	1.11±0.08	34.29	31.34	0.96±0.05	38.48	37.25	1.09±0.05
$range_h$	32	12.93	9.79	0.94±0.10	13.79	15.69	1.30±0.17	17.10	17.40	1.04±0.05
$range_v$	32	1.42	1.71	**1.51**±0.18**	2.39	1.81	0.93±0.12	2.31	2.58	1.11±0.11
G_v	32	0.28	0.27	1.03±0.06	0.43	0.45	1.07±0.04	0.44	0.41	**1.11*±0.05**
vertical structuring										
A	32	0.37	0.45	1.38±0.26	0.61	0.68	**1.31*±0.15**	1.12	0.57	**1.96***±0.03**
morphological variation										
h/d	32	0.84	0.78	**0.94*±0.03**	1.00	1.00	1.01±0.03	0.91	0.91	1.01±0.02
cl/h	32	0.36	0.32	**0.91*±0.04**	0.54	0.58	**1.08*±0.04**	0.47	0.45	1.04±0.03
r_{min}/r_{max}	20	0.42	0.44	0.99±0.04	0.40	0.42	0.99±0.04	0.40	0.41	0.99±0.03
cd/d	21	17.2	14.5	**0.87**±0.05**	25.5	29.4	**1.16***±0.04**	21.7	24.0	0.96±0.05
cd^2/d^2	21	385	242	**0.77*±0.10**	730	969	**1.39***±0.09**	593	826	0.91±0.11
intra-individual growth allocation										
G_{iv}	32	0.30	0.30	1.06±0.05	0.46	0.46	1.03±0.04	0.44	0.44	1.04±0.05
GDC	32	-0.01	0.00	0.44±1.13	0.01	-0.01	1.51±1.09	-0.07	-0.01	6.47±4.81

Table 5 Overview of the correlation between different kinds of mixing effects and the index of Martonne (1926) as an indicator of the environmental conditions prevailing along the ecological gradient through Europe. The black symbols +, ++, +++ and -, --, --- indicate significant (level p< 0.05, 0.01, and 0.001) positive and negative Pearson correlation, respectively. Grey symbols indicate weak correlation coefficients but with <-0.30 and >+0.30.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Structure indices	*unweighted*			*additive effect*		*multiplicative effect*		
group 1	mixed obs	mixed obs	mono Sc. pi	mixed weighted	mixed weighted	Mixed Sc.pi	mixed E.be	mixed observed
vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.
group 2	mono Sc.pi	mono E.be	mono E.be	mono Sc.pi	mono E.be	Mono Sc.pi	mono E.be	mixed weighted
stand and canopy density								
N	+		-	+	--		+	+
SDI	+			+				
RCPA	-	--	-	+				
RCC				+		-		
horizontal distribution pattern								
CV_{BA}					+			
size distribution pattern								
$skew_d$		+			+		+	
$skew_h$				+				
$skew_v$								
$range_d$							-	
$range_h$						-		
$range_v$								
G_v		+						+
vertical structuring								
A	++			++		++		+
morphological variation								
h/d	+	--	--	++	--			
cl/h	-		+	-				
r_{min}/r_{max}								
cd/d	-						-	
cd^2/d^2	-						-	-
intra-individual growth allocation								
G_{iv}			-	+				
GDC				-	+			

Table 6 Overview of the unweighted comparison of mixed-species stands, the additive effect and the multiplicative mixing effects. The symbols +, ++, +++ and -, --, --- indicate significantly higher and lower indices, respectively (level p< 0.05, 0.01, and 0.001) of group 1 versus group 2.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Structure indices	*unweighted*			*additive effect*		*multiplicative effect*		
group 1	mixed obs	mixed obs	mono Sc. pi	mixed weighted	mixed weighted	mixed Sc.pi	mixed E.be	mixed observed
vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.
group 2	mono Sc.pi	mono E.be	mono E.be	mono Sc.pi	mono E.be	Mono Sc.pi	mono E.be	mixed weighted
stand and canopy density								
N							+++	+
SDI		+++	+++	--	++	+	+	+
RCPA	+++	+++		+	--			++
RCC	+++	+++						
horizontal distribution pattern								
C&E			+			-		
CV_{BA}				+	-			
size distribution pattern								
$skew_d$								
$skew_h$							-	-
$skew_v$			---			-		
$range_d$	+++	+++	-	+++	+++			
$range_h$	+++	+		+++	+++			
$range_v$	+++	+	-	++	++	++		+
G_v	+++		---	+++	--			
vertical structuring								
A	+++	+++	--	+			+	+++
morphological variation								
h/d	+	---	---	+++	---	-		
cl/h	+++	---	---	+++	---	-	+	
r_{min}/r_{max}			+					
cd/d	+++	---	---	+++		--	+++	
cd^2/d^2	+++	-	---	+++		-	+++	
intra-individual growth allocation								
G_{iv}	+++		---	+++				
GDC			---					

Online Supplementary Material

Supplementary Table 1: Overview of the 32 mixed Scots pine-European beech observation plots included in this analysis. Explanation of variables: Triplet identification code and number, ID and No, stand age of the triplet (years), longitude, N, latitude, E, elevation above sea level, E a.s.l., mean annual temperature, T, annual precipitation, P, Martonne index (1926), M (M=annual precipitation (mm)/(mean annual temperature °C +10)), substrate, inclination, I, exposition, Exp. For explanation of substrate see Arbeitskreis Standortskartierung (1985).

ID	No	Stand age (years)	Geographic location N	Geographic location E	E. a.s.l. (m)	I (°)	Exp (°)	T ° C	P (mm yr^{-1})	M (mm $°C^{-1}$)	Substrate
Aus_1	1048	40	47°22'34.00"	16°23'20.00"	490	19	213	8.5	750	41	loamy sand
Bel_1	1063	115	50°45'06.10"	04°19'29.60"	120	0	315	7.5	852	49	loam
Bel_2	1057	150	50°01'48.00"	05°27'00.00"	530	8	180	10.5	1175	57	stony loam
BHe_1	1059	135	44°13'34.56"	18°29'56.12"	627	25	225	9.5	939	48	humus silicat soil-ranker
Bul_1	1047	65	41°53'43.00"	23°21'03.00"	1150	20	0	6	750	47	loamy sand
Cze_1	1049	45	49°18'14.40"	16°36'08.78"	460	8	45	7.5	620	35	cambisol mezotrofic
Cze_2	1058	55	13°12'45.90"	49° 58' 02.5"	510	11	328	7.1	656	38	dystric and podzol cambisol
Fran_1	1040	60	48°58'41.80"	07°29'13.60"	275	20	315	9.7	948	48	sandstone sandy soil
Ger_1	1033	57	48°34'57.95"	11°14'12.49"	450	1	45	8.5	700	38	slightly loamy sand
Ger_2	1031	55	50°06'48.74"	09°03'54.36"	250	0	20	9	720	38	slightly loamy sand
Ger_3	1032	47	49°53'11.64"	10°58'13.12"	250	2	30	8	650	36	loamy sand
Ger_4	1071	65	49°24'57.77"	08°01'03.88"	400	1	60	9	675	36	loamy sand
Ger_5	1034	57	48°59'11.66"	08°10'48.58"	125	3	0	10	675	34	slightly loamy sand
Ger_6	1070	65	12°44'08.30"	48°11'12.47"	40	0	0	8	560	31	slightly loamy sand
Ger_7	1061	80	52°04'45.55"	13°37'06.05"	60	0	0	8.6	520	28	sandy
Ita_1	1055	40	46°04'02.93"	10°56'10.61"	1000	8	26	7.8	1050	59	cutanic luvisoil
Ita_2	1062	55	44°54'12.49"	07°03'53.30"	1250	25	315	7.9	938	52	inceptisol
Lit_1	1051	90	55°04'47.30"	22°24'24.01"	20	0	0	6.5	750	45	sand and slightly loamy sand
Lit_2	1052	111	55°27'02.08"	21°32'23.44"	25	0	0	6.5	800	48	sand and slightly loamy sand
Net_1	1043	47	52°25'40.55"	06°01'20.42"	34	2	0	9.7	825	42	coarse sand

Pol_1	1035	55	53°48'19.15"	19°54'42.27"	136	0	0	7.9	666	37	loamy sand and sand
Pol_2	1036	81	53°20'07.40"	14°36'17.51"	60	0	0	9.2	556	29	slightly loamy sand
Pol_3	1037	76	50°59'27.96"	20°41'08.90"	383	2	275	7.8	662	37	sandstone loamy sand and loam
Pol_4	1044	57	50°01'27.60"	20°13'45.84"	210	0	0	8.2	650	36	slightly loamy sand
Pol_5	1045	55	50°01'36.00"	20°19'37.26"	225	0	0	8.2	650	36	loamy sand
Ser_1	1056	75	43°42'17.40"	19°37'30.00"	1090	20	0	7.7	1020	58	loam with a little sand
Slo_1	1046	55	48°33'09.18"	18°31'11.19"	500	15	90	6.9	730	43	cambisoil
Sp_1	1042	40	42°05'57.00"	-03°-10'-19.00"	1290	14	0	8.9	860	46	sandy loam
Sp_2	1041	50	42°10'18.09"	02°15'44.23"	1130	30	0	8	1100	61	loam slightly clay
Swe_1	1054	80	56°09'12.00"	13°35'35.00"	130	5	180	8	700	39	loamy sand
Swe_2	1053	65	55°42'33.00"	14°11'46.00"	110	17	135	7	800	47	sandy till
Ukr_1	1060	105	49°57'05.00"	23°39'44.00"	390	0	0	7.6	673	38	slightly loamy sand

Supplementary Table 2 Overview of the measurements on the 32 triplets of monospecific and mixed Scots pine and European beech observation plots included in this analysis. The symbols ‘x’ indicate the measurement of tree diameter, d, tree height, h, height to crown base, hcb, stem coordinates, coo, crown radii, crorad, angle count sampling with BAF=4 at the position of the cored trees, ACS, and increment coring of sample trees, core. The symbols ‘-’ indicate which variable were not measured.

name	no	d	h	hcb	coo	crorad	ACS	Core
Aus _1	1048	x	x	x	x	x	x	X
Bel_1	1063	x	x	x	-	-	x	X
Bel_2	1057	x	x	x	-	-	x	X
BHe_1	1059	x	x	x	x	x	x	X
Bul_1	1047	x	x	x	-	-	x	X
Cze_1	1049	x	x	x	x	x	x	X
Cze_2	1058	x	x	x	x	x	x	x
Fran_1	1040	x	x	x	-	-	x	x
Ger_1	1033	x	x	x	x	x	x	x
Ger_2	1031	x	x	x	x	x	x	x
Ger_3	1032	x	x	x	x	x	x	x
Ger_4	1071	x	x	x	x	x	x	x
Ger_5	1034	x	x	x	x	x	x	x
Ger_6	1070	x	x	x	x	x	x	x
Ger_7	1061	x	x	x	x	-	x	x
Ita_1	1055	x	x	x	-	-	-	x
Ita_2	1062	x	x	x	-	x	x	x
Lit_1	1051	x	x	x	x	x	x	x
Lit_2	1052	x	x	x	x	x	x	x
Net_1	1043	x	x	x	x	-	x	x
Pol_1	1035	x	x	x	x	x	x	x
Pol_2	1036	x	x	x	x	x	x	x
Pol_3	1037	x	x	x	x	x	x	x
Pol_4	1044	x	x	x	x	x	x	x
Pol_5	1045	x	x	x	x	x	x	x
Ser_1	1056	x	x	x	-	-	x	x
Slo_1	1046	x	x	x	-	-	x	x
Sp_1	1042	x	x	x	x	x	x	x
Sp_2	1041	x	x	x	x	x	x	x
Swe_1	1054	x	x	x	x	-	x	x
Swe_2	1053	x	x	x	x	-	x	x
Ukr_1	1060	x	x	x	x	x	x	x
total		32	32	32	24	21	31	32

Supplementary Table 3 Stand characteristics of the triplets of monospecific and mixed-species stands. A total of 32 triplets were included consisting of 32 mixed-species stands and 64 neighbouring monospecific stands. Growth and yield characteristics are given for the monospecific stands, for the species in the mixed stands and for the mixed stand as a whole. Means of all 32 triplets are given in plain text and ranges (min-max) over all 32 triplets are given in italics (see Pretzsch et a. 2015, Table 1).

Notice that this table shows the characteristics for the mixed stand in total and the share of both species.

Tree number (ha^{-1}), N, quadratic mean diameter (cm), d_q, height of the quadratic mean diameter tree (m), h_q, Stand density index, SDI (trees ha^{-1}), stand basal area, BA (m^2 ha^{-1}), standing volume V (m^3 ha^{-1}), mean periodic annual volume growth , PAIV (m^3 ha^{-1} yr^{-1}).

Species	n	stand age (years)	N (trees ha^{-1})	d_q (cm)	h_q (m)	SDI (trees ha^{-1})	BA (m^2 ha^{-1})	V (m^3 ha^{-1})	PAIV ($m^3 ha^{-1} yr^{-1}$)
Sc. pine + E. be.	32	70	990			824	40.65	444	13.6
		39-149	*250-2628*			*337-1631*	*15.85-77.94*	*134-956*	*5.1-31.2*
Sc. pine mixed	32	70	405	32.3	23.1	444	23.33	255	6.0
		39-149	*50-1529*	*14.0-70.1*	*12.1-35*	*87-838*	*4.35-43.48*	*44-658*	*1.7-13*
E. beech mixed	32	70	585	22.3	20.9	380	17.32	189	7.6
		39-149	*127-1733*	*11.2-46.8*	*12.2-30.8*	*216-884*	*9.61-36.78*	*56-392*	*3.0-18.2*
Sc. pine pure	32	69	970	27.6	22.1	833	40.92	413	11.3
		39-149	*82-3200*	*13.7-45.5*	*8.7-33.9*	*215-1426*	*13.29-62.93*	*162-923*	*2.7-21.9*
E. beech pure	32	69	1027	25.1	23.0	724	34.48	411	14.7
		39-149	*220-2745*	*12.0-49.4*	*12.4-34.1*	*392-1266*	*17.84-53.37*	*146-959*	*6.0-27.6*