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

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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 and water availability gradient 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

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and diversification of vertical structure and tree morphology are caused by species identity (additive effects) but also by species interactions (multiplicative effects), and (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 (Fig. 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, e.g., by changing the CO_2-concentration of the air or the humidity (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 Fig. 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
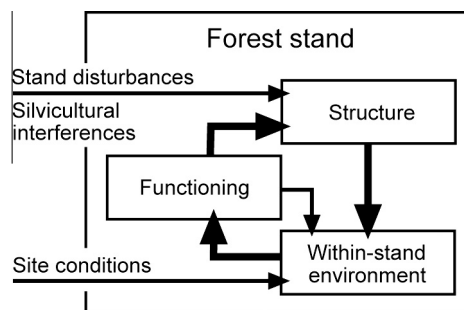
variability (Pretzsch, 2014) and the inequality of resource and growth distribution between the trees within a population (Binkley, 2004; Binkley et al., 2006).

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 homogenization (Wiedemann, 1951, p. 134). The mixing of species with differing ecological traits may enhance structural complexity above and below ground (Bauhus, 2009; Pretzsch, 2014) and this can increase stand productivity compared with monocultures (Forrester and Bauhus, 2016).

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, 2016; Río et al., 2014) and are likely to modify resource use and forest functioning in terms of stand productivity (Fig. 1). Therefore, multiplicative mixing effects on

Fig. 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).

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., 2015a,b; 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., 2015a,b). 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 the following questions:

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., 2015a,b). By locating the triplets along a productivity gradient (Fig. 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 (Fig. 2) in Europe and extend from Sweden to Bulgaria and from Spain to the Ukraine.

2.1. Material

2.1.1. 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 1175 mm (Fig. 2) and the elevation from 20 to 1290 m a.s.l. (Supplementary Table 1).

The natural distribution of Scots pine ranges from −3 to 10 °C mean temperature and 400–1250 mm yr^{-1} annual precipitation. European beech prefers warmer and moister conditions and occurs naturally between 3–13 °C and 450–1400 mm yr^{-1}. Analyses of the effects of environmental conditions on structure and growth require sampling over a broad range of site conditions. Fig. 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.

2.1.2. Triplet data

The study was based on 32 triplets. The triplets are sets of three rectangular plots including two monocultures 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. In order to exclude age effects and site differences from the comparison of mixed-species stands with monocultures we selected triplets were all three plots have similar stand ages and are located closely next to each other. In most cases Scots pine monocultures have been planted rather densely after clearcut (5000–15,000 trees per hectare) whereas European beech monocultures have been regenerated naturally or planted after clearing or under shelter (2500–10,000 trees per hectare). The mixed-species stands were mostly planted after clearing with plant numbers of 5000–15,000 in case of Scots pine and 5000–10,000 in case of European beech. For further plot-specific information including details about the initial stand situation see Supplementary Table 2. The plots were not thinned recently; thus, they 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). On average, the mixing proportions were close to 50:50, although they varied between 18% and 72% for Scots pine and consequently between 28% and 82% for European beech. In the Scots pine and European beech monocultures we tolerated up to 5% of other conifers (mainly *Larix*, *Picea*), and up to 5% of other broad-leaved tree species (mainly *Quercus*, *Betula*), respectively. In the mixed-species stands we accepted up to 10% of other species (mainly the same genera as in the monocultures). In the course of the evaluation we assigned all conifers to Scots pine and broad-leaved trees to European beech. 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., 2015a,b).

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 (Fig. 2). 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 3 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 randomly 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) mostly with BAF = 4 m^2 ha^{-1} (BAF = 1 m^2 ha^{-1} in case of triplet Bel_2, No. 1057). The stand basal area estimates resulting from the two angle count samples per tree were used as a measure of local stand density and therefore as a proxy for the competitive status of the individual trees. They were further used for calculating the stand basal area's coefficient of variation, CV$_{BA}$, which characterizes the variation of stand density within each plot (see Section 2.2.1 below). Tree coordinates were measured on 24 and crown radii on 21 out of the 32 triplets.

The mean stand age over all triplets was on average (±*SE*) 69 (±4) years and ranged between 40 and 135 years (Supplementary
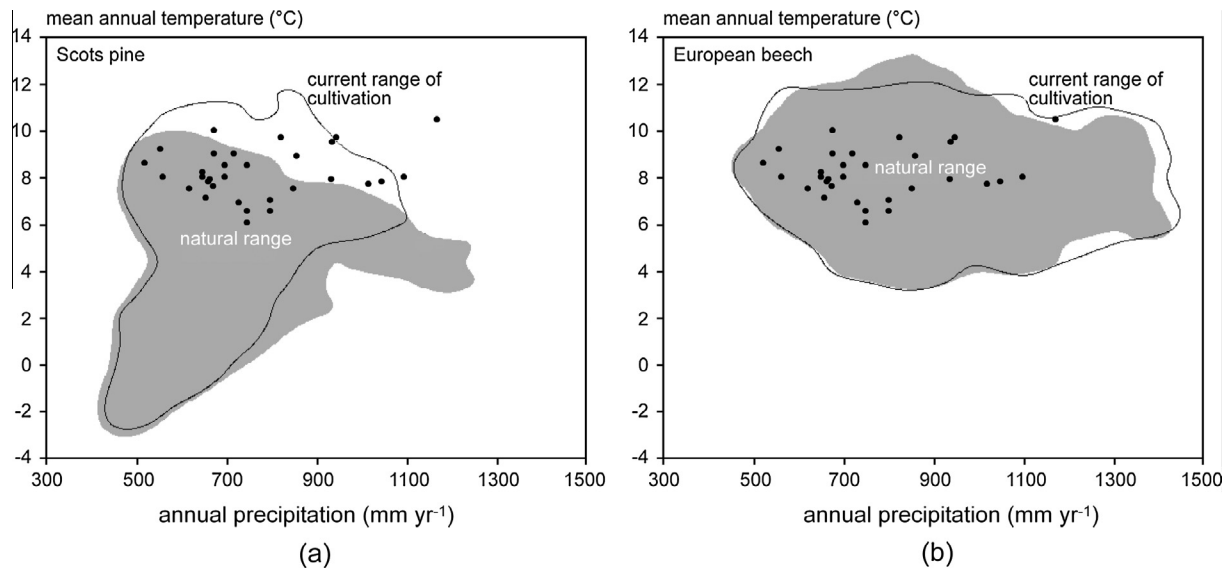
Fig. 2. Positioning of the 32 triplets (black circles) in the climate envelopes (see Kölling et al., 2009) in terms of mean annual precipitation (mm yr^{-1}) and mean annual temperature (°C) of the natural range (grey) and current range of cultivation (black line) of (a) Scots pine and (b) European beech.

Table 1). As the age of most of the triplets ranged between 40 and 60 years we used the top height (height associated with the quadratic mean diameter of the 100 largest trees per hectare), h_o, 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 h_o = 9.5–26.9 m and 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 834 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 4). For detailed information about how tree and stand variables were estimated in mixed and mono-specific plots see Pretzsch et al. (2015a,b).

2.2. Methods

2.2.1. 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 stand density we calculated the coefficient of variation of the stand basal area CV_{BA} based on the measurement of the at least 20 angle count samples per plot, taken at the positions of the cored sample trees. 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 monocultures 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, G_v = 0.0 means that all trees are equal in size. The higher the G 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

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			Reference
		Low	Medium	High	
Stand and canopy density					
N	Tree number	Sparse	Medium	Dense	Kramer (1988)
SDI	Stand density index	Sparse	Medium	Dense	Reineke (1933)
RCPA	Sum of crown area	Sparse	Medium	Dense	Pretzsch (2014)
RCC	Crown coverage	Sparse	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 and Schütze (2015)
$skew_h$	Skewness h	Left-skewed	Normal	Right-skewed	Pretzsch and Schütze (2015)
$skew_v$	Skewness v	Left-skewed	Normal	Right-skewed	Pretzsch and Schütze (2015)
$range_d$	Range d	Equal	Medium	Unequal	Pretzsch and Schütze (2014)
$range_h$	Range h	Equal	Medium	Unequal	Pretzsch and Schütze (2014)
G_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					
G_{iv}	Inequality iv	Equal	Medium	Unequal	Binkley et al. (2006)
GDC	Growth dominance	Low dom.	All equal	High dom.	Binkley (2004)

over diameter growth; so it indicates the slenderness of the stem and the mechanical stability of the tree. 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 G_v the coefficient for tree volume growth $G_{iv} = 0.0$ means that all trees are equal in volume growth. The higher the G_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.

2.2.2. 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 stem 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 one-sided transgression probability α) the differences can be considered as significant at the level $p \leqslant 0.05^*$, $p \leqslant 0.01^{**}$, or even $p \leqslant 0.001^{***}$ (Tables 2–4).

Notice, that in Tables 2–6 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 Fig. 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 (Fig. 3a 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 $m_2 = (1 - m_1)$ 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. The proportions m_1 and m_2 were calculated on the basis of the species' stand density indices weighted by equivalence coefficients in order to consider the species-specific growing space requirements (see Pretzsch et al., 2015a,b).

$\hat{D}_{1,2}$ represents the weighted mean of both monocultures (Fig. 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 Fig. 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.

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 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 (Fig. 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 (Fig. 3b) may be compared; analogously $D_{(1),2}$ may be compared with D_2 (Fig. 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 (Fig. 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 (Fig. 3d). For both comparisons the size distributions in mixture are scaled up to unit area of 1 ha 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 (Fig. 3f), and the differences between D_1 and $D_{1,(2)}$ (Fig. 3b) and D_2 and $D_{(1),2}$ (Fig. 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 ha) 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 ha) 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
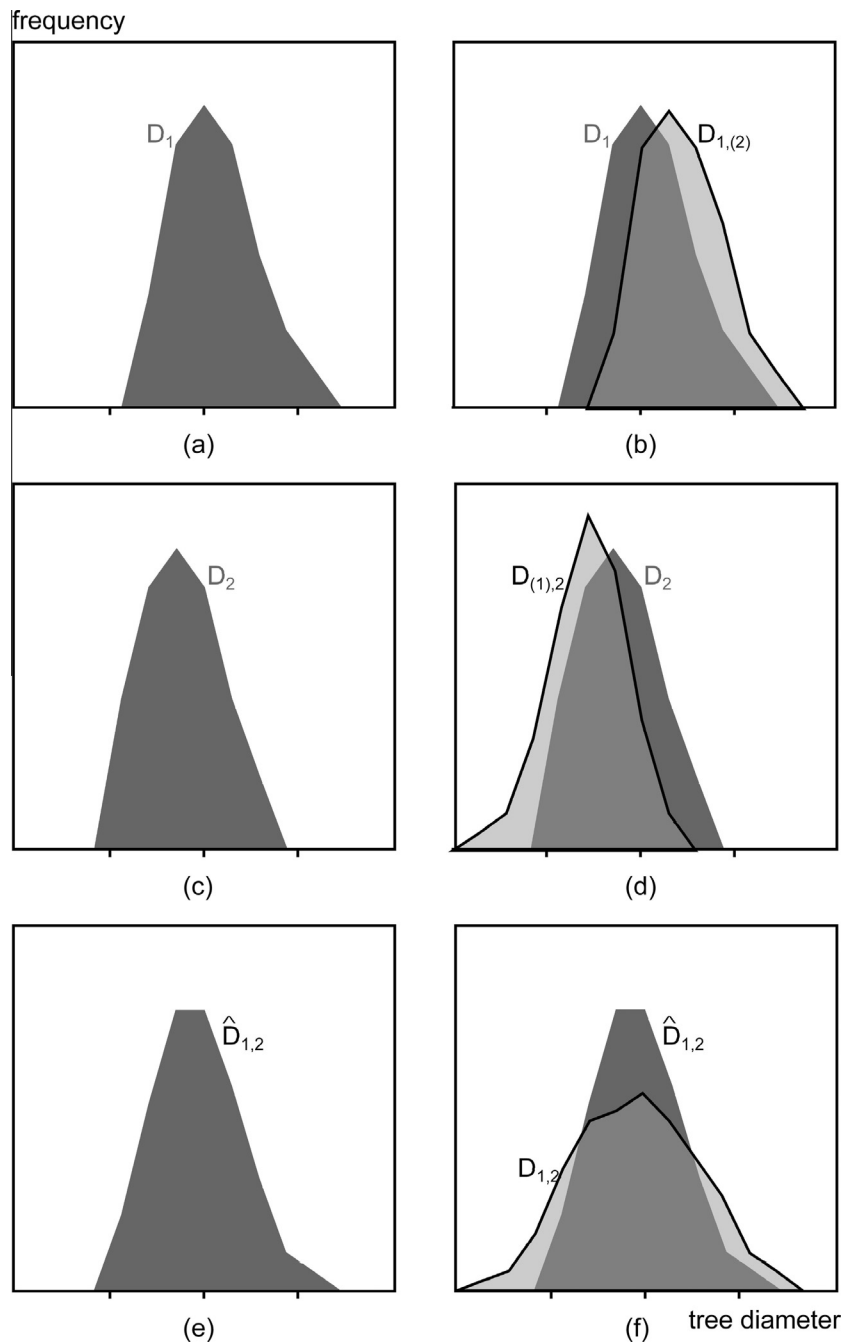
Fig. 3. Schematic representation of the comparison between monocultures and mixed-species stands' tree diameter distribution to quantify multiplicative effects (resulting from species interactions) as opposed to additive effects (resulting only from mixing species with different morphological or physiological 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 $\hat{D}_{1,2}$ (e and f). Differences between the reference distributions (a, c, and e) and the observed size distribution (b, d, and f) indicate inter-specific interactions and multiplicative mixing effects.

between $M = 28$–67 mm $°C^{-1}$ along the gradient due to the wide variation of precipitation (520–1175 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 (Fig. 2) and length of the growing season, this index appeared to be more appropriate than other indices that only consider annual pre-

cipitation 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 $\geqslant 3$ °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 tree, 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., 2015a,b). By calculating the standing volume in 2009 and 2013, as well as the removed volume, the periodic annual volume growth resulted as $PAIV_{2009-013} = (V_{2013} - V_{2009} + V_{removal})/5$. For further details of the applied evaluation algorithms see Pretzsch et al. (2015a,b).

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, and site index. Residuals were checked to assure normality. All calculations were carried out using the software package IBM SPSS Statistics (Version 22).

3. Results

Fig. 4 shows the height relationships between Scots pine and European beech in the monocultures and mixed-species stands of the 32 triplets. These height relationships indicate the competitive strength of both species and reveal which role they play in the mixture. They characterize the kind of stands the following analysis is based on and our results apply to.

On average, the mean heights of Scots pine and European beech are rather similar in both monocultures and mixed-species stands. European beech is just 10% higher than Scots pine in the monocultures (Fig. 4a) and Scots pine is by 10% higher than beech in the mixture (Fig. 4d). European beech is obviously slightly slowed down in height growth by Scots pine which is ahead of beech due to its fast growth during the early stand development phase. However, there is a strong variation around these mean height relationships because of the different site conditions prevailing on the triplets. Under a harsh continental climate, on dry sandy soils with poor nutrition, European beech is usually dominated by Scots pine and lower in height. On moist and fertile sites, and sites under a higher influence of the Atlantic climate, European beech is ahead of Scots pine (Bolte et al., 2007). For more detailed analyses of the stand characteristics see Pretzsch et al. (2015a,b).

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, G_v, 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 = 0.43 versus G_v = 0.28), 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
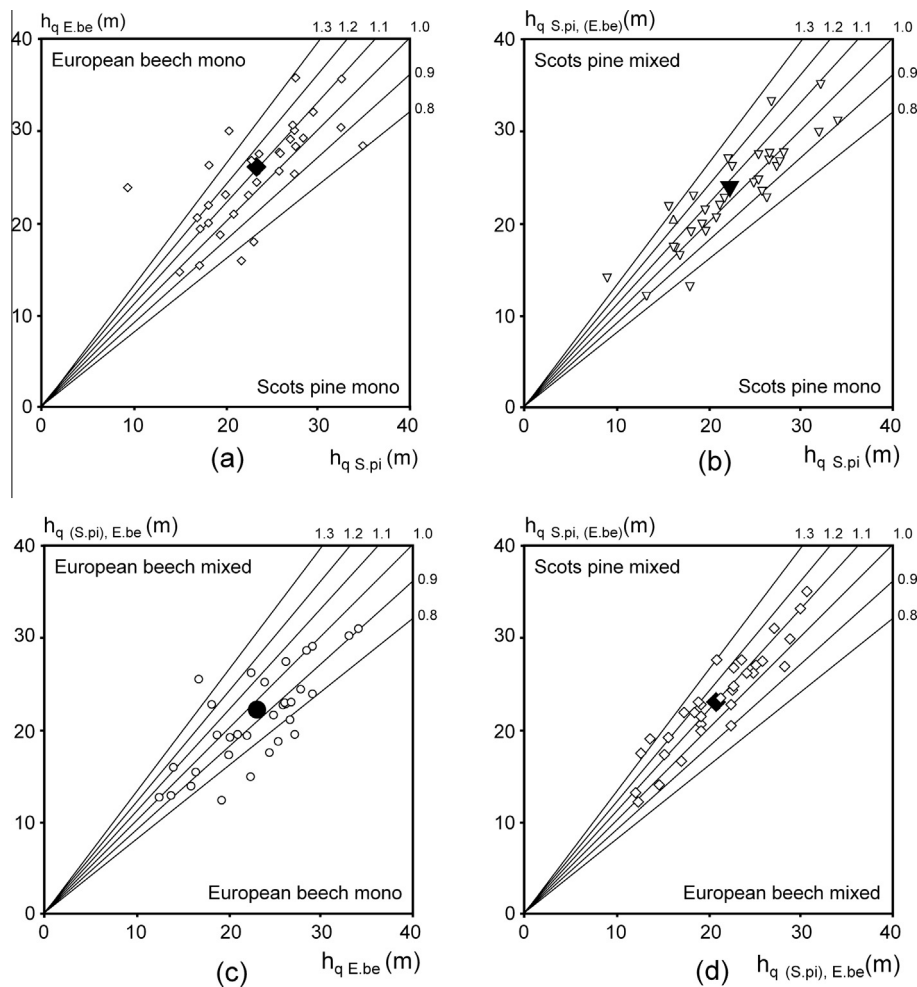
Fig. 4. Mean stand heights of Scots pine and European beech in the monocultures and mixed-species stands of the 32 triplets. The graphs compare the mean height of (a) European beech with Scots pine in the monocultures, (b) Scots pine in the mixed-species stand with Scots pine in the monoculture, (c) European beech in the mixed-species stand with European beech in the monoculture, and (d) Scots pine in the mixed stand with European beech in the mixed stand. The small symbols represent the observed values and the large symbols indicate the means across all triplets. Values on the bisector line indicate an equality of the compared groups.

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 G_v, 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, G_v 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

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.

(1) Stand structure indices	(2) Sample size, *n*	(3) Mono Scots pine Min	(4) Mean	(5) Max	(6) Mono E. beech Min	(7) Mean	(8) Max	(9) Mixed Sc. p + E. beech Min	(10) Mean	(11) Max	(12) Mixed vs. Sc. pi. mono	(13) Mixed vs. E. be. mono
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	**$1.18^{**} \pm 0.06$**
RCPA	25	0.55	1.15	1.83	0.68	1.29	2.15	1.51	2.23	3.69	**$2.02^{***} \pm 0.13$**	**$1.82^{***} \pm 0.12$**
RCC	25	0.46	0.73	0.98	0.44	0.74	0.97	0.73	0.89	0.98	**$1.27^{***} \pm 0.05$**	**$1.24^{***} \pm 0.06$**
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	**$1.53^{***} \pm 0.10$**	**$1.20^{***} \pm 0.06$**
$range_h$	32	3.00	12.93	28.60	2.80	13.80	25.50	7.80	17.10	31.10	**$1.68^{***} \pm 0.20$**	**$1.42^{*} \pm 0.17$**
$range_v$	32	0.31	1.42	4.80	0.48	2.39	7.87	0.29	2.31	6.27	**$1.98^{***} \pm 0.21$**	**$1.25^{*} \pm 0.13$**
G_v	32	0.12	0.28	0.46	0.29	0.43	0.62	0.22	0.44	0.64	**$1.74^{***} \pm 0.11$**	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	**$3.35^{***} \pm 0.63$**	**$2.14^{***} \pm 0.22$**
Morphological variation												
h/d	32	0.44	0.84	1.15	0.64	1.01	1.34	0.51	0.89	1.21	**$1.07^{*} \pm 0.03$**	**$0.90^{***} \pm 0.03$**
cl/h	32	0.22	0.36	0.60	0.40	0.54	0.79	0.28	0.45	0.66	**$1.29^{***} \pm 0.06$**	**$0.83^{***} \pm 0.03$**
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	**$1.30^{***} \pm 0.06$**	**$0.87^{***} \pm 0.03$**
cd^2/d^2	21	124	385	827	211	730	1507	247	593	948	**$1.88^{***} \pm 0.20$**	**$0.87^{*} \pm 0.06$**
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	**$1.66^{***} \pm 0.16$**	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

* Significant differences of mixed-species stand versus monoculture at the level $p < 0.05$ (bold).
** Significant differences of mixed-species stand versus monoculture at the level $p < 0.01$ (bold).
*** Significant differences of mixed-species stand versus monoculture at the level $p < 0.001$ (bold).

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 (column (5)). For European beech in mixed-species stands compared with monocultures the density, vertical structuring, crown ratio, and lateral crown 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.

The results of correlating the Martonne index with the structural ratios are shown in Fig. 5. No correlations between the

structural ratios and the Martonne index would indicate that the effects of species mixing on stand structure shown in Tables 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)).

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 ratios resulting from the pair-wise division of the group characteristics.

(1) Stand structure indices	(2) Sample size, n	(3) Scots pine mono	(4) European beech mono	(5) Sc. p vs. E. be	(6) S. pi + E. be weighted mean	(7) S. pi + E. be weighted mean vs. S. pi mono	(8) 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

[*] Significant differences of mixed-species stand versus monoculture at the level $p < 0.05$ (bold).
[**] Significant differences of mixed-species stand versus monoculture at the level $p < 0.01$ (bold).
[***] Significant differences of mixed-species stand versus monoculture at the level $p < 0.001$ (bold).

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. Although most correlations were rather weak they indicate important general trends.

4. Discussion

4.1. 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 (Bielak et al., 2014; Lei et al., 2009; Liang et al., 2007; Jucker et al., 2014; Pretzsch et al., 2013, 2015a,b; Río and Sterba, 2009), stability (Griess and Knoke, 2011; Jactel and Brockerhoff, 2007), reduced sensitivity to drought (Grossiord et al., 2014; Metz et al., 2013), 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 (Fig. 1), not only of monocultures but especially of mixed-species stands (Forrester and Pretzsch, 2015; Forrester and Bauhus, 2016; 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.

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.

(1) Stand structure indices	(2) Sample size, n	(3) Scots pine	(4)	(5)	(6) European beech	(7)	(8)	(9) Scots pine + E. beech	(10)	(11)
		Mono	Mixed	Mixed vs. mono	Mono	Mixed	Mixed vs. mono	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

* Significant differences of mixed-species stand versus monoculture at the level $p < 0.05$ (bold).

** Significant differences of mixed-species stand versus monoculture at the level $p < 0.01$ (bold).

*** Significant differences of mixed-species stand versus monoculture at the level $p < 0.001$ (bold).

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 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 (Pretzsch et al., 2015a,b). 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.

4.2. Additive and multiplicative 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 shade casting species, with high lateral crown plasticity and a slower
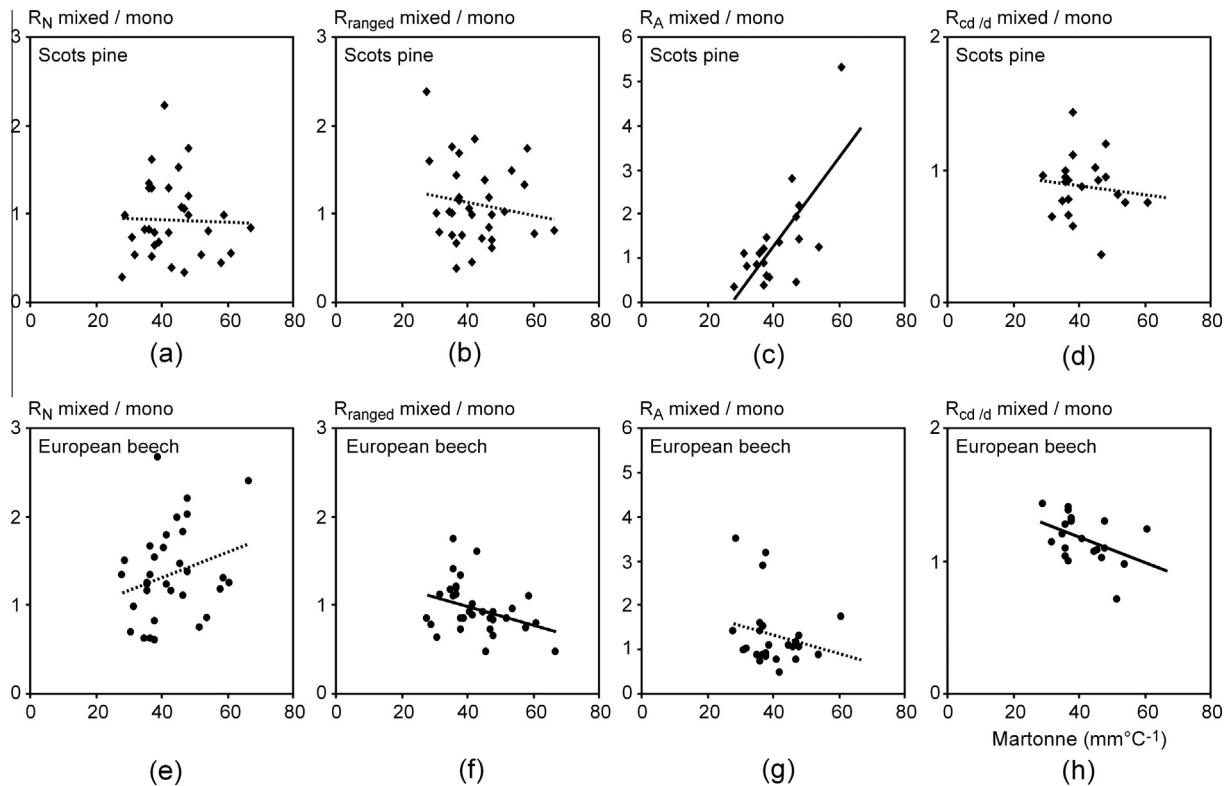
Fig. 5. Relationship between the Martonne index, M, and selected ratios (RN, Rrange$_d$, RA, and Rcd/d) indicating the multiplicative mixing effect at the species level for Scots pine and European beech. In particular, we show the results for ratios between the structure of Scots pine in mixture versus 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) $Rcd/d_{mix/mono,E.be.} = 1.57(\pm0.19) - 0.01(\pm0.004) \times M$, $n = 21$, $R^2 = 0.20$, $p < 0.05$.

Significant and non-significant relationships are indicated by continuous lines and dotted lines, respectively.

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 (*Tilia cordata*), Scots pine and red oak (*Quercus rubra*), or European larch (*Larix decidua*) and beech, larch and Norway spruce (*Picea abies*), silver birch (*Betula pendula*) and spruce, silver birch and silver fir (*Abies alba*), or red alder (*Alnus rubra*) and Douglas-fir (*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.

Mixing had just an additive effect on the horizontal variation of the stand density, indicated by CV$_{BA}$ (Table 6, columns (5) and (6)). Pine as a fast growing, early-successional species, is already in a more advanced, self-thinned, and homogenized stand development phase than the rather slow growing, late-successional beech. Therefore, local density varies more in mixed-species stands of

pine and beech than in already rather homogenized pine monocultures and less than in still rather heterogeneous beech monocultures. We expected also a multiplicative effect of mixing on CV$_{BA}$ because of the niche complementarity and denser packing of both species, but columns (7)–(9) in Table 6 show no multiplicative effects. Maybe CV$_{BA}$ might vary also with plot size (Supplementary Table 3) that was on average 30–40% larger in mixed-species than in monospecific stands. On the small plots the angle count samples may overlap in a way that they reduce CV, while on the larger plots they are less auto-correlated and may increase CV. However, statistical analysis yielded that plot size did not correlate significantly with CV$_{BA}$ and could be excluded as confounding factor.

The most interesting finding is that beyond this additive effect mixing triggers emergent properties, i.e., a multiplicative mixing effect (Table 6, columns (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 (columns (7) and (8)) and in recent studies on beech growing in mixtures with conifers (Metz et al., 2013, Pretzsch and Schütze, 2005). 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)).

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) Structure indices	(2) Unweighted	(3)	(4) Additive effect	(5)	(6)	(7) Multiplicative effect	(8)	(9)
Group 1 vs. group 2	Mixed obs vs. mono Sc.pi	Mixed obs vs. mono E.be	Mono Sc.pi vs. mono E.be	Mixed weighted vs. mono Sc.pi	Mixed weighted vs. mono E.be	Mixed Sc.pi vs. mono Sc.pi	Mixed E.be vs. mono E.be	Mixed observed vs. 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) Structure indices	(2) Unweighted	(3)	(4) Additive effect	(5)	(6)	(7) Multiplicative effect	(8)	(9)
Group 1 vs. group 2	Mixed obs vs. mono Sc.pi	Mixed obs vs. mono E.be	Mono Sc.pi vs. mono E.be	Mixed weighted vs. mono Sc.pi	Mixed weighted vs. mono E.be	Mixed Sc.pi vs. mono Sc.pi	Mixed E.be vs. mono E.be	Mixed observed vs. 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			−−−					

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 considered 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 monospecific plots, the larger range in the mixed plots could be partly an artefact 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., 2015a,b).

4.3. Change of mixing effects along the water availability gradient

We found a strong multiplicative mixing effect on stand density, crown morphology, and vertical structuring for both species (Table 6, columns (7) and (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 only weakly 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 al., 2015a,b). 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, columns (2) and (3)) as well as the analysis of the additive effect (columns (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 monoculture, 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 water availability 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.

4.4. 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. 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 (Barbeito et al., 2014; Seidel et al., 2013).

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. On the other hand, the high plasticity and increased light interception of beech in mixed stands compared with monospecific stands might result in a decrease in wood quality due to higher crown asymmetry and stem curvature in mixtures (Knoke and Seifert, 2008).

4.5. 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 of the 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).

The competitive relationship between Scots pine and European beech varies due to the broad range of covered site conditions (Fig. 4). In order to reduce the competition between both species, European beech may be allowed a temporal advantage by planting it earlier than Scots pine in particular harsh continental climate, on dry sandy soils with poor nutrition, where Scots pine is superior in height growth. In contrast, Scots pine may be supported by planting European beech some decades later under Scots pine under Atlantic climate, where European beech is superior in height growth velocity. Inter-specific competition can also be reduced by a continuous release of the inferior species by thinning (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 between both species which are the prerequisite for the increased light interception, productivity, and stand density.

Without such temporal or spatial uncoupling and inter-specific competition reduction by forest management, one of the two species would outcompete the other with proceeding stand development. On many sites European beech, as a late-successional species, would finally outcompete Scots pine. This can be avoided by harvesting Scots pine earlier than beech and result in a temporary mixture of both species.

A special challenge is the natural regeneration of Scots pine in mixed-species stands of Scots pine and European beech, as Scots pine needs bare mineral soil to take roots and ample light to grow up. Such conditions can only be established by strongly opening up the mature stands (e.g., by strong shelterwood cuts, gap cuts, or even small clearcuts) and may require soil preparation (e.g., by wounding of the soil, removal of any berry-shrub mat).

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., 2015a,b) 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).

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). Moreover, due to the observed positive additive and multiplicative mixing effects on structural heterogeneity as well as stand productivity, the conversion of common monocultures of Scots pine and European beech in Europe into mixture of both tree species could be a progressive contribution of forestry to higher carbon storage sequestration, and thus the mitigation of global warming effect. 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.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.04.043.

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. Can. J. For. Res. 41, 341–351.

Barbeito, I., Collet, C., Ningre, F., 2014. Crown responses to neighbor density and species identity in a young mixed deciduous stand. Trees 28, 1751–1765.

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*. Can. J. For. Res. 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. Ann. For. Sci. 66 (1), 1.

Bielak, K., Dudzińska, M., Pretzsch, H., 2014. Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. For. Syst. 23 (3), 573–589.

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. For. Ecol. Manage. 288, 5–13.

Binkley, D., 2004. A hypothesis about the interaction of tree dominance and stand production through stand development. For. Ecol. Manage. 190 (2), 265–271.

Binkley, D., Kashian, D.M., Boyden, S., Kaye, M.W., Bradford, J.B., Arthur, M.A., Fornwalt, P.J., Ryna, M.G., 2006. Patterns of growth dominance in forests of the Rocky Mountains, USA. For. Ecol. Manage. 236 (2), 193–201.

Bolte, A., Czajkowski, T., Kompa, T., 2007. The north-eastern distribution range of European beech – a review. Forestry 80 (4), 413–429.

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.

de Camino, R., 1976. Zur Bestimmung der Bestandeshomogenität. Allgem. Forst- und Jagdztg. 147, 54–58.

Chittagong, B., 2015. Climate to forest productivity: implication of Paterson's CVP index. Res. J. For. 9 (2), 27–34.

Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 35 (4), 445–453.

Condés, S., Río, M., 2015. Climate modifies tree in interactions 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. Perspect. Plant Ecol. Evol. Syst. 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 III, F.S., 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. For. Ecol. Manage. 295, 97–108.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For. Ecol. Manage. 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. For. Ecol. Manage. 328, 94–102.

Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity – productivity relationships in forests. Curr. Forest. Rep. 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 Struct. Funct. 26, 1203–1213.

Forrester, D.I., Pretzsch, H., 2015. Tamm review: on the strength of evidence when comparing ecosystem functions of mixtures with monocultures. For. Ecol. Manage. 356, 41–53.

von Gadow, K., 1998. Integrating environmental research into forest ecosystems planning. In: Environmental Forest Science. Springer, Netherlands, pp. 29–37.

von Gadow, 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. Nat. Commun. 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. Proc. Natl. Acad. Sci. 111 (41), 14812–14815.

Griess, V.C., Knoke, Th., 2011. Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. Can. J. For. Res. 41, 1141–1159.

Hari, P., 1985. Theoretical aspects of eco-physiological research. In: Tigerstedt, PMA., Puttonen, P., Koski, V. (Eds.), Crop Physiology of Forest Trees. Helsinki Univ Press, pp. 21–30 (336 p).

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London, New York.

Hattemer, H.H., 1994. Die genetische Variation und ihre Bedeutung für Wald und Waldbäume. J. For. Suisse 145 (12), 953–975.

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

Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol. Lett. 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. Ecol. Lett. 17 (12), 1560–1569.

Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct. Ecol. http://dx.doi.org/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. West. J. Appl. For. 11 (3), 90–96.

Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: The Ecology and Silviculture of Mixed-Species Forests. Kluwer, Dordrecht, pp. 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. West. J. Appl. For. 10 (1), 36–42.

Knoke, T., Seifert, T., 2008. Integrating selected ecological effects of mixed European beech–Norway spruce stands in bioeconomic modelling. Ecol. Model. 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. For. 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. For. Ecol. Manage. 243 (1), 116.

Martonne, de E., 1926. Une novelle fonction climatologique: L'indice d'aridité. La Météorologie 21, 449–458.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2005. Forest and woodland stand structural complexity: its definition and measurement. For. Ecol. Manage. 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. For. Ecol. Manage. 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? Curr. Opin. Environ. Sustain. 2, 75–79.

Neumann, M., Starlinger, F., 2001. The significance of different indices for stand structure and diversity in forests. For. Ecol. Manage. 145 (1), 91–106.

Niklas, K.J., Midgley, J., Rand, R.H., 2003. Tree size frequency distributions, plant density, age and community disturbance. Ecol. Lett. 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. Conserv. Biol. 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, E.C., 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. For. Ecol. Manage. 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. For. Ecol. Manage. 327, 251–264.

Pretzsch, H., Biber, P., 2016. Tree species mixing can increase maximum stand density. Can. J. For. Res. http://dx.doi.org/10.1139/cjfr-2015-0413.

Pretzsch, H., Schütze, G., 2005. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. Plant Biology 7 (6), 628–639.

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., Forrester, D.I., Rötzer, T., 2015a. Representation of species mixing in forest growth models. A review and perspective. Ecol. Model. 313, 276–292.

Pretzsch, H., Rais, A., 2016. Wood quality in complex forests versus even-aged monocultures. Review and perspectives. Wood Sci. Technol. http://dx.doi.org/10.1007/s00226-016-0827-z.

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., 2015b. 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. For. Res. 134 (5), 927–947.

Pretzsch, H., Schütze, G., 2014. Size-structure dynamics of mixed versus pure forest stands. For. Syst. 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. For. Res. 135 (1), 1–22.

Puettmann, K.J., Coates, K.D., Messier, C.C., 2012. A Critique of Silviculture: Managing for Complexity. Island Press.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.

Río, M., Condés, S., Pretzsch, H., 2014. Analyzing size-symmetric vs. size-asymmetric and intra-vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. For. Ecol. Manage. 325, 90–98.

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. Eur. J. For. Res. 135, 23–49. http://dx.doi.org/10.1007/s10342-015-0927-6.

Río, M., Sterba, H., 2009. Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. Ann. For. Sci. 66 (5), 1–11.

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, C.E., 1948. The mathematical theory of communication. In: Shannon, C.E., Weaver, W. (Eds.), The Mathematical Theory of Communication. Univ of Illinois Press, Urbana, 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.

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. For. Ecol. Manage. 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. f. d. g. Forstw. 98, 101–116.

Sterba, H., 1987. Estimating potential density from thinning experiments and inventory data. For. Sci. 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. J. Biogeogr. 31 (1), 79–92.

Vanclay, J.K., 1992. Assessing site productivity in tropical moist forests: a review. For. Ecol. Manage. 54 (1), 257–287.

Varga, P., Chen, H.Y.H., 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. In: Modelling the Effects of Competition between Individual Trees in Forest Stands. PhD Thesis. Unit of Forestry, Copenhagen, pp. 67–77 (Chapter 7).

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. J. D. Sauerländer's Verlag, Frankfurt, 346 p.

Zenner, E.K., Hibbs, D.E., 2000. A new method for modeling the heterogeneity of forest structure. For. Ecol. Manage. 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.