

Effect of forest structure on stand productivity in Central European forests depends on developmental stage and tree species diversity

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ABSTRACT

Recently, many studies have found positive biodiversity–productivity relationships in forests. In contrast, different types of correlations have been identified in the analyses of tree diversity–structure–productivity relationships. We suspect that these conflicting conclusions might result from the different developmental stages of the investigated forest stands. We therefore analyzed the development of tree diversity–structure–productivity relationships at the stand level and individual tree level in 192 long-term experimental plots in Central Europe. As a measure of stand productivity, we analyzed stand volume growth ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$). Tree species diversity was quantified by the Shannon index and structural heterogeneity was represented by the Gini coefficient of basal area. For a more detailed analysis at the tree level using a smaller portion of the dataset, the tree position-dependent indices, diameter differentiation index, and aggregation index were used. Whether the effect of structural heterogeneity on stand productivity was positive or negative depended on the stand development stage. In early developmental stages, high structural heterogeneity lowered productivity. In later developmental stages, however, stand structural heterogeneity had a positive effect on productivity. Our study might provide insights regarding the mechanisms underlying the contradictory findings obtained in recent studies dealing with tree diversity–structure–productivity relationships. This knowledge is vital for the adaptation of forest management to meet future demands on forest ecosystems.

1. Introduction

Nowadays, it is expected that forests should not only produce a high amount of wood but also fulfill various ecosystem functions simultaneously and at the same stand. Therefore, the influence of forest structure and particularly the effect of tree species diversity on forest stand productivity has been examined in various studies. These studies show positive (Danescu et al., 2016; Liang et al., 2016; Morin et al., 2011; Paquette and Messier, 2011), negative (Jacob et al., 2010), neutral, or site-dependent (Pretzsch, 2013) biodiversity–productivity relationships and positive (Danescu et al., 2016) or negative effects (Bourdier et al., 2016; Soares et al., 2016) of stand structure on forest productivity. Others have found that neither compositional nor structural diversity had strong effects on productivity (Long and Shaw, 2010). Some studies have found that the stability of productivity (del Río et al., 2017; Jucker et al., 2014) or even the overall resilience (Morin et al., 2018) and stability of the plant community (De Boeck et al., 2018) over time can be enhanced by biodiversity. Additionally, species mixing is considered to bring further benefits, including a lower

risk of climate-induced damage (Neuner et al., 2015) through drought, windthrow, and pests (Bauhus et al., 2017) while still ensuring high growth values (Dieler et al., 2017; Griess and Knoke, 2011; Roessiger et al., 2013). Other researchers have discovered that stand structural heterogeneity, more than species diversity, can determine forest productivity (Bohn and Huth, 2017; Danescu et al., 2016; Ercanli, 2018) and stability (Díaz-Yáñez et al., 2017).

The large number of studies on tree diversity or biodiversity–structure–productivity relationships and their conflicting results reflect the increasing interest in the topic in recent years and the need for further clarification. These studies are commonly based on simulated forest stand data (Bohn et al., 2018; Silva Pedro et al., 2017) or inventory data. The trend of globalizing forest inventory data is vital for research in global forest ecosystem dynamics and management (Liang et al., 2016; Serra-Diaz et al., 2017). However, studies using inventory data (Danescu et al., 2016; McIntyre et al., 2015; Young et al., 2017) are often based on measurements from only one or two points in time (Zeller et al., 2018). This approach does not completely show how forest stand dynamics change over time. When the results are

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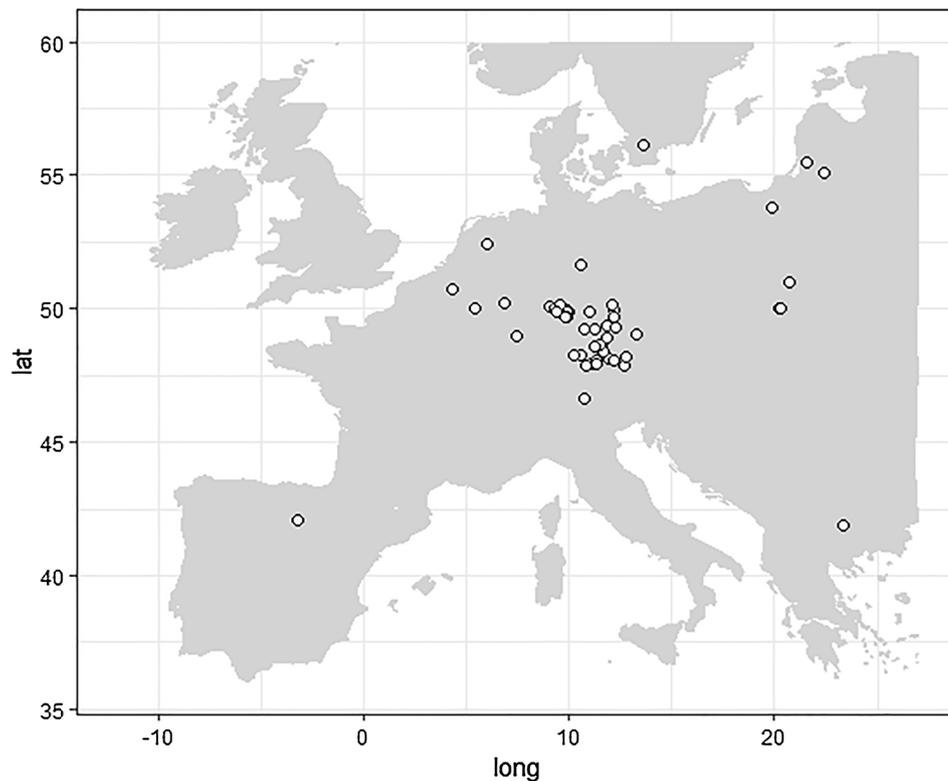


Fig. 1. Location of long-term experimental plots in Europe analyzed in this study. Long longitude, lat latitude.

compared, they can show contradictory tree diversity–structure–productivity relationships as these might depend on the context (Vanhellemont et al., 2018) and in particular, we suspect, on the developmental stage of the analyzed forest stand.

Therefore, the present analysis of structural traits in stands of different tree species composition over time shall complement the global overview. We tried to cover most of the expected context-related effects on stand productivity ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) by using data collected in a consistent way from well-known, long-term experimental plots (Pretzsch et al., 2013b) including stands at different stages of development and with different mixtures of tree species.

The most common species in the long-term experimental plots of this study were European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), sessile oak (*Quercus petraea*), Scots pine (*Pinus sylvestris*), Douglas fir (*Pseudotsuga menziesii*), silver fir (*Abies alba*), European larch (*Larix decidua*), and some hardwood deciduous tree species. Silver fir and Douglas fir are potential surrogates for the sensitive Norway spruce as they are believed to be more resistant to biotic and abiotic stress (Netherer et al., 2015; van der Maaten-Theunissen et al., 2013; Vitali et al., 2017). Scots pine and sessile oak are known to be drought-resistant and therefore show great potential for a future in which the frequency and intensity of droughts may increase under climate change (Lévesque et al., 2013; Pretzsch et al., 2013a). European beech, beyond its natural ranges, is also of particular interest as it is expected to become more competitive than Norway spruce under climate change (Bolte et al., 2010), except in lowlands with severe drought events (Weigel et al., 2018). In Central Europe, an admixture of European beech is commonly used to reduce the risk of bark beetle attacks (Jactel and Brockerhoff, 2007) and to increase the productivity of Norway spruce stands (Ammer et al., 2008; Knoke et al., 2008). European beech might even expand further to the north, making this mixture more interesting in Scandinavian countries.

In particular, the interactions between neighboring trees (Fichtner et al., 2018) and their functional traits can affect the productivity of mixed-species stands (Ammer, 2018) due to inter- and intraspecific

competition or facilitation. We therefore used tree position-based indices to complete the analysis at individual tree level. Tree species diversity, structural heterogeneity, and stand productivity contribute to multiple ecosystem goods and services. Knowledge of their interactions and trade-offs is thus particularly relevant to forest management (Ammer et al., 2018; Schall et al., 2018).

The present research paper aims to provide further insight into tree diversity–structure–productivity relationships by answering the following questions:

1. Does the effect of structural heterogeneity on stand productivity dependent on tree species diversity?
2. Does the effect of structural heterogeneity on stand productivity change over the course of development of a forest?

Based on these questions, we developed the following hypotheses to be tested in our analysis:

- H1.** The effect of structural heterogeneity on stand productivity does not depend on tree species diversity.
- H2.** The effect of structural heterogeneity on stand productivity remains unchanged over the course of development of a forest.

2. Material & methods

2.1. Material

2.1.1. Data

Most of the experimental plots analyzed in this study are located in Central Europe, with some areas, e.g., Bavaria, Germany, being over-represented due to the unique availability of long-term experimental plots in those areas (Pretzsch et al., 2013b). Some of the experimental plots are located in close proximity to each other (Fig. 1). In the analysis, they were treated separately, with spatial autocorrelation being accounted for in the statistical model. All plots included in this study

Table 1
Summary of experimental plots (all plots).

	n meas.	n species	dbh (cm)	dq (cm)	ba (m ² ha ⁻¹)	h (m)	h100 (m)	vol (m ³ ha ⁻¹)	ivol (m ³ ha ⁻¹ year ⁻¹)
Mean	1.5	2.31	27.81	30.82	31.20	25.39	29.18	508.77	15.70
sd	1.79	1.25	10.16	10.78	13.25	6.47	6.53	222.11	6.27
min	1.00	1.00	8.36	8.43	5.11	7.63	9.70	35.00	2.60
max	10.00	6.00	61.39	64.10	70.80	45.85	53.30	1388.00	44.96
Total meas.	291								
n plots	192								

Mean mean value, sd standard deviation, min minimum value, max maximum value, meas. measurement, n number, dbh diameter at breast height, dq quadratic mean diameter, h height, h100 height of 100 largest trees, vol volume, ivol volume increment.

(Fig. 1) were designed and artificially regenerated but unmanaged with the intention of examining the natural development of stand density, competition, and facilitation between tree species. All included plots were fully stocked. In total, 291 measurements were taken in 192 different plots over time between 1927 and 2014 (Fig. A.1a). Plots were measured between 1 and 10 times and, in plots where multiple measurements were taken, on average every seven years. Each plot contained up to six species groups in different compositions (Table 1). Other species representing less than 1% of total trees were added to one of the six species groups according to their functional traits. Primary variables measured in the plots were diameter at breast height (dbh), tree height, crown height, and location of each tree, which were used to derive further variables at the plot level such as mean values and sums according to the DESER standard (Johann, 1993). The experimental plots used in the present study included stands with a range of tree species diversity, or more precisely, from monocultures up to a Shannon index value (based on individuals) of about 0.4 (Table 3). All measurements (291) were treated as separate plots, while repeated measurements were accounted for by the random error term, which also covered the remaining unexplained variation that was not accounted for by the explaining variables. The data distribution, which showed a high frequency of very low and very high Shannon index values, allowed for a representative model covering a large span of possible mixtures. Monocultures and mixed plots were evenly represented in the different regions; thus, a purely location-related effect on stand productivity in pure or mixed stands can be excluded.

While multiple studies face the problem of overrepresentation of monospecific stands, we aimed to use sample plots including the whole range of tree species diversity. The detailed measurements conducted in those plots enabled the calculation of structural indices based on dbh, height, and partly on individual tree positions.

Stands including European beech were checked for thinning operations as we suspected the potential release of other species. Special fostering of certain species in mixed stands including European beech can be excluded; the share of drop-outs per plot and species, which was more random than selective, showed only self-thinning without special fostering of one species or another. If any slight thinning operations were conducted, they would only have caused very slight reductions in stand volume growth (Franklin et al., 2009; Skovsgaard, 2009) and were therefore considered irrelevant.

For the second part of the analysis, we used only a subset of the experimental plots. The tree positions of all trees in each plot were used to examine the structural traits of forest stands at the individual tree level. The dataset for this analysis covered 142 plots and 199 measurements in total (Fig. A.1b). The number of measurements and measurement intervals were comparable to those of the whole dataset. (Table 2). The Shannon index ranged from 0.14 to 0.35 (Table 4).

The variables used in this study to quantify stand structure and tree species diversity were selected with the aim of using standardized, commonly-used indices that can be applied easily to other data, thus making different analyses comparable (del Río et al., 2015).

2.1.2. Climate and site conditions

The long-term experimental plots analyzed are located in Central Europe, where the altitude ranged from 20 m a.s.l. to around 1730 m a.s.l. The mean annual temperature ranged from about 5.5 °C to 10.5 °C and the annual precipitation ranged between 550 mm and 1350 mm (Table 5). The smaller dataset including tree positions covered a similar climatic range (Table 6).

2.2. Methods

2.2.1. Indices

Productivity was calculated as volume growth of stems and branches (> 7 cm at thinnest ending) per hectare and year (m³ ha⁻¹ year⁻¹) based on dbh, height, and form factors following the DESER standard (Johann, 1993). Stand age for a whole forest stand, in which age may not be consistent throughout, is usually difficult to deduce. After identifying a clear relationship between standing volume and estimated forest age in our data (Fig. A.2), we used standing volume as an indicator of the developmental stage of forest stands. Since the experimental plots were only slightly thinned or even unmanaged, standing volume represents the mass accumulation and maturity of a forest stand and serves as a determinant for volume growth, further referred to as productivity. Stand density index (SDI), defined by Reineke (1933), was included in the model to account for the potential effect of stand density on productivity. To describe forest stand structure, we selected the Gini coefficient of basal area as suggested by Lexerød and Eid (2006), Binkley et al. (2006), and Kramer and Gussone (1988) to represent a whole group of indices showing the same trends (coefficient of variation of basal area, Gini coefficient of dbh, coefficient of variation of dbh). For the second part of the analysis, using solely the dataset including tree positions, we calculated structural indices using nearest neighbor distances for the plots for which the coordinates of all individual trees were available (Table 7). Nearest neighbor distance-based indices are commonly used to describe horizontal patterns of tree distribution (del Río et al., 2015); in our case, they were used to calculate the diameter differentiation index and aggregation index to explain the structural effects observed at the stand level. Due to the lack of existing coordinates of tree positions, only ~70% of the whole dataset was used to determine tree level indices (Figs. 2, 4, and Fig. A.1b). The experimental plots were not divided categorically into pure and mixed stands. Tree species diversity was accounted for by the continuous variable Shannon index to consider the effect of diversity on the structure–productivity relationship.

2.2.2. Linear mixed model

We set up a linear mixed model in order to examine the interactive effect of tree species diversity and structural heterogeneity on stand productivity. The logarithmic function of standing volume enabled us to determine the linear relationship between stand development and productivity (volume growth). Since several measurements were

Table 2
Summary of experimental plots (plots incl. tree positions).

	n meas.	n species	dbh (cm)	dq (cm)	ba (m ² ha ⁻¹)	h (m)	h100 (m)	vol (m ³ ha ⁻¹)	ivol (m ³ ha ⁻¹ year ⁻¹)
Mean	1.40	2.20	28.77	31.54	32.60	25.85	29.83	539.60	16.59
sd	1.40	1.18	10.64	10.95	13.14	6.35	6.25	221.74	6.14
min	1.00	1.00	8.41	8.70	10.00	13.21	14.60	108.00	5.30
max	10.00	6.00	61.39	64.10	70.80	45.85	53.30	1388.00	44.96
Total meas.	199								
n plots	142								

Mean mean value, sd standard deviation, min minimum value, max maximum value, meas. measurement, n number, dbh diameter at breast height, dq quadratic mean diameter, h height, h100 height of 100 largest trees, vol volume, ivol volume increment.

Table 3
Structure and mixing (all plots).

	shan	SDI	ba.gini	ba.cv	dbh.gini	dbh.cv	agg	ddif
Mean	0.14	744.28	0.37	0.70	0.21	0.38	1.08	0.29
sd	0.13	293.63	0.12	0.26	0.08	0.14	0.13	0.10
min	0.00	155.21	0.12	0.22	0.06	0.11	0.54	0.09
max	0.36	2276.15	0.76	1.85	0.47	1.04	1.41	0.48

Mean mean value, sd standard deviation, min minimum value, max maximum value, shan Shannon index, ba.gini Gini coefficient of basal area, ba.cv coefficient of variation of basal area, dbh.cv coefficient of variation of diameter at breast height, agg aggregation index, ddif diameter differentiation index.

Table 4
Structure and mixing (plots incl. tree positions).

	shan	SDI	ba.gini	ba.cv	dbh.gini	dbh.cv	agg	ddif
Mean	0.14	770.59	0.36	0.68	0.20	0.37	1.08	0.29
sd	0.13	283.37	0.12	0.26	0.08	0.14	0.13	0.10
min	0.00	217.48	0.12	0.22	0.06	0.11	0.54	0.09
max	0.35	2276.15	0.70	1.74	0.41	0.85	1.41	0.48

Mean mean value, sd standard deviation, min minimum value, max maximum value, shan Shannon index, ba.gini Gini coefficient of basal area, ba.cv coefficient of variation of basal area, dbh.cv coefficient of variation of diameter at breast height, agg aggregation index, ddif diameter differentiation index.

Table 5
Climate and site conditions (all plots).

	Mean annual temperature (°C)	Annual precipitation (mm)	Elevation (m a.s.l.)
Mean	7.5	924	528
sd	1.3	219	270
min	5.5	552	20
max	10.5	1350	1734

Mean mean value, sd standard deviation, min minimum value, max maximum value, m a.s.l. meters above sea level.

Table 6
Climate and site conditions (plots incl. tree positions).

	Mean annual temperature (°C)	Annual precipitation (mm)	Elevation (m a.s.l.)
Mean	7.5	916	486
sd	1.1	229	232
min	5.5	560	20
max	9.7	1350	1290

Mean mean value, sd standard deviation, min minimum value, max maximum value, m a.s.l. meters above sea level.

conducted over time and multiple plots were in one location, measurement year and location were treated as random effects, accounting for potential autocorrelation. The chosen model [Eq. (1)] showed the highest significances for all explaining variables relative to other

models, including more, fewer, or other explaining variables with different interaction terms. This was achieved through backward elimination of non-significant variables. Eq. (1) was set as the final model.

$$\log(ivol_i) = a + \log(f_1(vol_i)) * (f_2(str_i) + f_3(SDI_i)) * f_4(shan_i) + \varepsilon_i \quad (1)$$

where *ivol_i* is the productivity (volume increment) per ha and year on plot *i*. The standing volume *vol_i* represents the developmental stage of stand *i*. The structural index *str_i* is the Gini coefficient *GC_i* of basal area, representative of other indices yielding the same results (Gini coefficient *GC_i* of dbh, variation coefficient *CV_i* of basal area or variation coefficient *CV_i* of dbh). The stand density index *SDI_i* and Shannon index *shan_i* are explaining variables, whereas the random error term *ε_i* contains all the remaining unexplained information due to repeated measurements and the spatial proximity of some of the experimental plots. The interaction terms indicated by asterisks ensure that the interdependencies between stand developmental stage, structural heterogeneity *str_i*, and tree species diversity *shan_i* were considered in the model.

2.2.3. Additional analysis based on tree positions

In order to further explore the relationship between stand structure, the degree of mixing, and stand productivity, we used the part of the dataset including tree positions for quantifying stand structure based on nearest neighbor distances. Similar to Eqs. (1) and (2) was set up. The structural component *str_i* was replaced by the tree position-dependent diameter differentiation index *ddif_i* [Eq. (2)].

$$\log(ivol_i) = a + \log(f_1(vol_i)) * (f_2(ddif_i) + f_3(SDI_i)) * f_4(shan_i) + \varepsilon_i \quad (2)$$

Additionally, the aggregation index *agg_i* (Clark and Evans, 1954) over time was examined in a simple regression model to explain the development of stand structure in more detail (Fig. 4).

For the calculation of the nearest neighbor-based indices *ddif_i* and *agg_i*, the four nearest neighbors of each tree were used. The border effect was addressed by reflecting trees from inside the plot to the outside (Monserud and Ek, 1974; Radtke and Burkhart, 1998). All reflected trees up to 7 m outside of the plot border were included to calculate indices for all trees inside the original plot.

For the application of linear mixed-effects models, we used the lme function of the nlme package in R (Pinheiro et al., 2018; R Core Team, 2014).

3. Results

We found that the effect of stand structure on stand productivity was modified by both the species diversity (Hypothesis 1) and the developmental stage (Hypothesis 2) of a forest. No climatic or other site-dependent effects on productivity were found and thus these were excluded from the model function, leaving unexplained variation between the experimental plots to the random error term.

Other indices based on plot level (*GC_i* of basal area, *GC_i* of dbh, *CV_i* of basal area, *CV_i* of dbh) yielded similar results as the *GC_i* of ba and were therefore not treated separately but represented by the *GC_i* of basal area as the structural component *str_i* (Tables 8 and 9).

Table 7
Non-spatial and spatial structural indices.

Level	Code	Name	Equation	Description
Non-spatial	GC	Gini coefficient of ba	$GC_{ba} = \frac{1}{2N} \sum_{i=1}^N ba_i - ba_j $	GC_{ba} (Dorfman, 1979) quantifies the heterogeneity of tree sizes at plot level based on ba
	CV	Coefficient of variation coefficient of individual tree ba	$CV_{ba} = \frac{sd}{ba}$	CV_{ba} (Brown, 1998, pp. 155–157) relates the standard deviation sd to the mean ba . It measures tree size heterogeneity in each plot based on ba or dbh.
	shan	Shannon index	$shan = -\sum_{i=1}^s p_i \cdot \ln p_i$	Shan (Shannon, 1948) is the species diversity in a plot, calculated by multiplying the proportion of species i by its logarithm. Rare species are weighted overproportionally
	SDI	Stand density index	$SDI = N \cdot \left(\frac{2.5}{dq}\right)^{-1.605}$	SDI by Reineke (1933), uses total stem number per ha, $N_p = \sum_{i=1}^N n_i$, and dq . SDI enables the comparison of forest stands of different ages
Spatial	agg	Aggregation index	$agg = \frac{\bar{r}_{observed}}{r_{expected}}$	Agg uses four nearest neighbors and describes the ratio of observed mean distance to nearest neighbor tree $\bar{r}_{observed}$ and the expected mean distance in a random horizontal distribution $r_{expected}$ (Clark and Evans, 1954)
	ddif	Diameter differentiation	$ddif = \frac{1}{n} \sum_{j=1}^{n-4} \left(1 - \frac{\min(d_i, d_j)}{\max(d_i, d_j)}\right)$	$ddif$ by Gadov and Fuldner (1995) measures the size heterogeneity of each tree and its four nearest neighbors

3.1. Stand level indices

Structural heterogeneity str_i , represented by Gini coefficient of basal area, had a negative effect on stand productivity in early developmental stages for pure stands as well as for all types of mixed stands (Fig. 2a). The more species-diverse a forest stand, the higher the productivity and the stronger the negative effect of structural heterogeneity. In older stages, however, structural heterogeneity had a positive effect on productivity, which was equally strong in pure and tree species-diverse stands (Fig. 2d and e). All experimental plots, from monocultures to the highest tree species diversity measured, are shown between the dotted line (pure stands) and the dashed line (highest Shannon index) in Fig. 2. The developmental stages of the analyzed experimental plots are presented according to the standing volume per plot (Fig. 2). The model functions represent the data points per developmental stage. The model function considers random effects and interaction terms, which explain the visual deviation from the original data points when plotted together. The youngest experimental plots (Fig. 2a) with the lowest standing volume ($< 200 \text{ m}^3 \text{ ha}^{-1}$) showed that structural heterogeneity had a negative effect on productivity; this effect was stronger in mixed stands than in pure stands. Stands of average age ($200\text{--}400 \text{ m}^3 \text{ ha}^{-1}$) are presented in Fig. 2b. At $334 \text{ m}^3 \text{ ha}^{-1}$, the effect of structural heterogeneity on productivity in pure stands was zero (dotted line) and switched from negative to positive. The model function showed a turning point at a standing volume of $450 \text{ m}^3 \text{ ha}^{-1}$ in species-diverse stands (Fig. 2c) of average age ($400\text{--}600 \text{ m}^3 \text{ ha}^{-1}$), where the effect of structural heterogeneity on productivity switched from negative to positive (dashed line); this happened at a later developmental stage than in the pure stands. The more species-diverse a forest stand, the later the structural effect changed from negative to positive. In the developmental stage of $600\text{--}800 \text{ m}^3 \text{ ha}^{-1}$, the effect of structural heterogeneity on productivity became clearly positive (Fig. 2d) and no difference between pure and mixed stands was found. In the oldest experimental plots, characterized by a standing volume $> 800 \text{ m}^3 \text{ ha}^{-1}$, the positive effect of structural heterogeneity on productivity was even more pronounced and was equally strong in both pure and mixed stands (Fig. 2e).

The development of mean productivity (straight line) over the course of the development of the examined forest stands (Fig. 2) matched the trend described by Pretzsch (2009, p. 58), as expected. The highest productivity of up to $20 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ was found in young stands (Fig. 2a). It then decreased throughout the developmental stages (Fig. 2b–d) until it reached $\sim 10 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ in the oldest plots (Fig. 2e). The results of the linear mixed-effects model applied at the stand level are shown in Table 8.

3.2. Tree position-based indices

For a more detailed exploration of the tree diversity–structure–productivity relationship, we analyzed the sample plots in terms of individual tree position–dependent structural indices.

By setting up Eq. (2) containing the diameter differentiation index $ddif_i$ as a structural component at the tree level, additional information on the structural effects on stand productivity was gained. While the effect of structural heterogeneity in terms of $ddif_i$ between each tree and its four nearest neighbors on stand productivity was negative in very young forest stands, it became more positive in pure and mixed stands over time and therefore supported the findings at the stand level.

The youngest experimental plots (Fig. 3a) with the lowest standing volume ($< 200 \text{ m}^3 \text{ ha}^{-1}$) are represented by the model function at their mean standing volume of $140 \text{ m}^3 \text{ ha}^{-1}$ (Fig. 3a). Here the effect of structural heterogeneity on productivity was negative. Average-aged stands in the developmental stage of $200\text{--}400 \text{ m}^3 \text{ ha}^{-1}$ including the model function at their mean standing volume of $320 \text{ m}^3 \text{ ha}^{-1}$ (Fig. 3b) still showed a negative effect of structural heterogeneity on productivity. The turning points of the effect of structural heterogeneity on

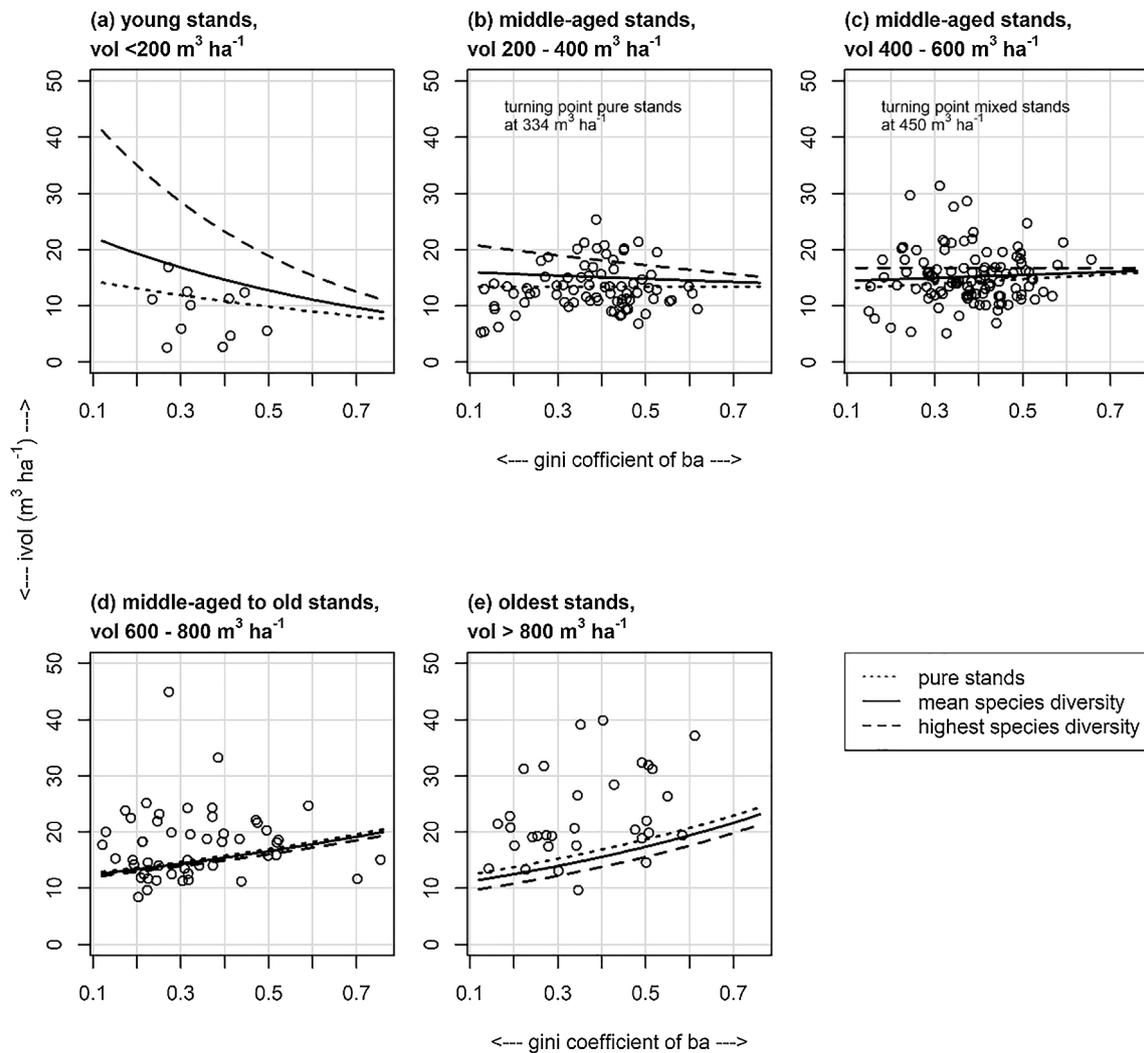


Fig. 2. Effect of structural heterogeneity at the stand level on stand productivity in various developmental stages (a)–(e). Structural heterogeneity at the tree level quantified by the Gini coefficient of basal area. Developmental stages (a)–(e) were quantified by standing volume (m³ ha⁻¹). Ivol stand volume increment (m³ ha⁻¹ year⁻¹), dotted line pure stands, dashed line highest tree species diversity, solid line mean tree species diversity. Tree species diversity was quantified by the Shannon index. Gini coefficient of basal area increasing with increasing tree size heterogeneity. Each graph shows data points of developmental stage and model function at the mean standing volume for each developmental stage.

Table 8
Results of linear mixed-effects model; structural indices at the stand level.

	value	std. error	p-value	Sig.
Intercept	6.13	0.25	0.0000	*
f ₁ (log(vol))	-0.67	0.04	0.0000	*
f ₂ (str)	-5.67	0.32	0.0000	*
f ₃ (SDI)	0.00	0.00	0.0000	*
f ₄ (mix)	-12.61	1.76	0.0000	*
f ₅ (log(vol) × str)	0.98	0.05	0.0000	*
f ₆ (log(vol) × SDI)	0.00	0.00	0.0000	*
f ₇ (log(vol) × mix)	2.25	0.29	0.0000	*
f ₈ (str × mix)	-11.85	3.05	0.0001	*
f ₉ (SDI × mix)	0.03	0.00	0.0000	*
f ₁₀ (log(vol) × str × mix)	1.81	0.49	0.0002	*
f ₁₁ (log(vol) × SDI × mix)	-0.01	0.00	0.0000	*

log logarithmic function, *vol* standing volume in m³ ha⁻¹, *str* structure quantified by the Gini coefficient of basal area, *SDI* stand density index, *mix* mixing quantified by the Shannon index. × interaction between variables. Sig. Significance values: 0 “*”. R² of the model was 0.914.

Table 9
Results of linear mixed-effects model; structural indices at the tree level.

	value	std. error	p-value	Sig.
Intercept	9.34	0.33	0.0000	*
f ₁ (log(vol))	-1.00	0.05	0.0000	*
f ₂ (str)	-4.31	0.68	0.0000	*
f ₃ (SDI)	-0.01	0.00	0.0000	*
f ₄ (mix)	9.55	2.08	0.0000	*
f ₅ (log(vol) × str)	0.69	0.10	0.0000	*
f ₆ (log(vol) × SDI)	0.00	0.00	0.0000	*
f ₇ (log(vol) × mix)	-1.71	0.33	0.0000	*
f ₈ (str × mix)	-143.49	5.13	0.0000	*
f ₉ (SDI × mix)	0.08	0.00	0.0000	*
f ₁₀ (log(vol) × str × mix)	22.88	0.77	0.0000	*
f ₁₁ (log(vol) × SDI × mix)	-0.01	0.00	0.0000	*

log logarithmic function, *vol* standing volume in m³ ha⁻¹, *str* structure quantified by diameter differentiation, *SDI* stand density index, *mix* mixing quantified by Shannon index. × interaction between variables. Sig. Significance values: 0 “*”. R² of the model was 0.938.

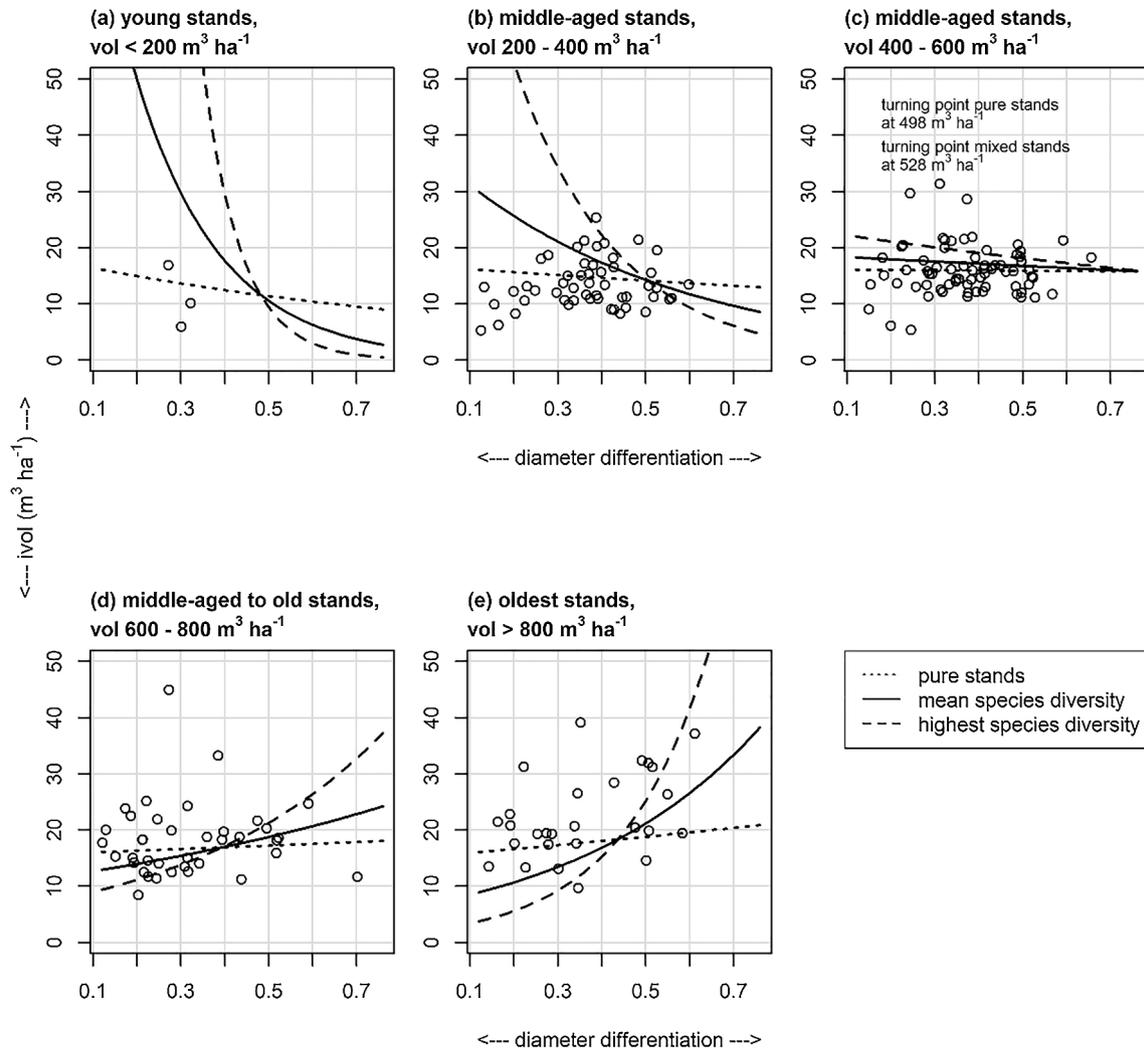


Fig. 3. Effect of structural heterogeneity at tree level on stand productivity between developmental stages (a)–(e). Structural heterogeneity at tree level quantified by diameter differentiation. Developmental stages (a)–(e) were quantified by standing volume (m³ ha⁻¹). Ivol stand volume increment (m³ ha⁻¹ year⁻¹). Dotted line pure stands, dashed line highest tree species diversity, solid line mean tree species diversity. Tree species diversity was quantified by the Shannon index. Diameter differentiation increasing with increasing tree size heterogeneity. Each graph contains data points of developmental stage and model function at mean standing volume of developmental stage.

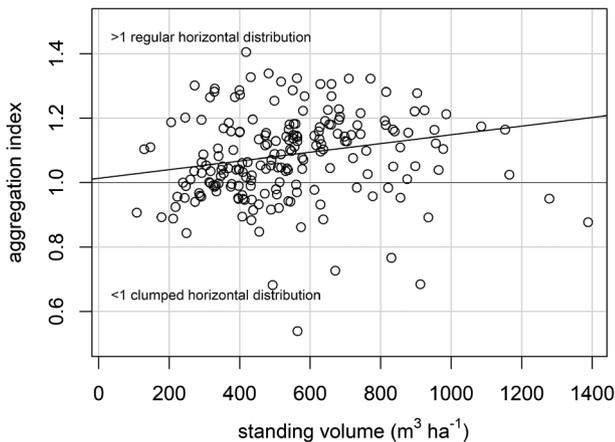


Fig. 4. Aggregation index over stand development. Horizontal distribution of trees quantified by mean aggregation index per measurement over stand development [standing volume (m³ ha⁻¹)]. Aggregation index > 1.0 regular distribution, 1.0 random distribution, < 1.0 clumped distribution.

productivity from negative to positive lay in the developmental stage of stands of average age (400–600 m³ ha⁻¹), more precisely at 500 m³ ha⁻¹ for pure stands and at 528 m³ ha⁻¹ for mixed stands. The model function in Fig. 3c represents this developmental stage, including the model function at its mean standing volume (498 m³ ha⁻¹). On stands of average to old age (600–800 m³ ha⁻¹), the structural effect was positive, especially in mixed stands (Fig. 3d), and became more pronounced in the developmental stage of the oldest stands (> 800 m³ ha⁻¹) (Fig. 3e). The negative structural effect measured at tree level in young stands and the positive structural effect in old stands, were stronger in mixed (dashed line) compared to pure stands (dotted line) (Fig. 3).

The development of mean productivity (straight line) over the developmental stages of the examined forest stands (Fig. 3) matched the trend described by Pretzsch (2009, p. 58), as expected. The results of the linear mixed-effects model applied at the stand level are shown in Table 9.

3.3. Horizontal distribution over time

For analyzing the development of stand structure over time, the

horizontal arrangement of trees was quantified by the nearest neighbor distance-based aggregation index *agg*. The aggregation index showed that the horizontal distribution of trees in the analyzed sample plots became more regular with ongoing stand development (aggregation index > 1 and increasing) (Fig. 4).

4. Discussion

Structural heterogeneity is thought to foster various ecosystem functions such as the biodiversity of flora and fauna (Dieler, 2013; McElhinny et al., 2005). Yet, studies often examine either species diversity or forest structure, but not the interdependencies between the two.

In the present study, Hypothesis I, which stated that the effect of structural heterogeneity on stand productivity does not depend on tree species diversity, was partly rejected. When analyzing stand structure on stand level, the negative effect of structural heterogeneity on stand productivity in young stands was stronger in mixed than in pure stands. In older stands the structural effect was equally strong in pure and mixed stands. At tree level, the effect of structural heterogeneity on stand productivity was stronger in mixed stands than in pure stands regardless of stand age.

Hypothesis II, stating that the effect of structural heterogeneity remains unchanged over the course of the development of a forest, could clearly be rejected. Our approach shows that an increase in structural heterogeneity led to a lower stand productivity in young stands, even more so in cases of high tree species diversity. In advanced developmental stages, however, structural heterogeneity had a positive effect on stand productivity in both monocultures and species-diverse stands (Figs. 2 and 3). This finding might help to explain the diverse and partly conflicting relationships among those variables in different studies (Bourdier et al., 2016; Danescu et al., 2016; Zeller et al., 2018) after excluding other potential context-related effects (Vanhellemont et al., 2018).

The turning point beyond which the effect of structural heterogeneity changed from negative to positive was later in species-diverse stands than in monocultures. We suspect that mixed stands may benefit from structural heterogeneity later than mixed stands due to higher interspecific competition up to a certain developmental stage.

Lei et al. (2009) found that structural heterogeneity can have positive effects on stand productivity throughout all developmental stages due to niche complementarity. Depending on the site conditions and competition, however, niche complementarity might not occur in all types of forest stands at all developmental stages (Pretzsch, 2013). According to Jactel et al. (2018), overyielding in mixed stands increases with increasing water supply, potentially due to a complementary light use. In case of a limited water or nutrient supply, trees might not be able to exploit a potential complementary light use. The experimental plots analyzed in our study were located on rather productive sites where competition for water or nutrients would be uncommon. If trees on our experimental plots experienced any kind of competition or complementarity it would thus be for light (Pretzsch and Biber, 2010; Schwinning and Weiner, 1998).

The smallest trees in young stands, while creating higher structural heterogeneity, are expected to be rather inefficient in their light use (Gspaltl et al., 2013) or resource use in general (Assmann, 1961, p. 34; Assmann, 1961, pp. 119–123; Binkley et al., 2010). Vertical diversification for a better use of niches might not yet be possible because the trees are still only occupying the lowest forest layers. High competition in young mixed forests between shade-tolerant species and light-demanding species (Vanhellemont et al., 2018), and the potential negative effect of small trees on larger trees (Mainwaring and Maguire, 2004) might have intensified the negative effect of structural heterogeneity on stand productivity in the sample plots of this study.

In contrast, large trees are known to use light more efficiently than small trees (Binkley et al., 2013), at least up to a certain age. In older

forest stands, after inefficient trees have dropped out—and have released nutrients (Rothe and Binkley, 2001) if not removed from the stand—gaps and niches left behind might be filled again by small trees, also shown in a more regular horizontal distribution of trees in older developmental stages (Fig. 4). Those do not directly compete with the largest trees due to vertical and horizontal stratification and their different sizes and shapes, but they can contribute additional productivity to the whole stand due to a more complete use of resources on the plot in later developmental stages (Silva Pedro et al., 2017). Not only spatial, but also temporal niche complementarity can consequently be an important determinant of forest growth (del Río et al., 2014; Sapjanskas et al., 2014).

When pursuing the idea of niche facilitation of functional groups of tree species in mixed stands, increased stand productivity due to structural diversification may result from one or more layers of shade-tolerant species below the canopy layer. Even though shade tolerance might not be the (only) reason for a positive effect of stand structure on stand growth (Bourdier et al., 2016), e.g. if both species are light-demanding (Riofrío et al., 2017), interactions between species due to their special traits can lead to facilitation and enhanced stand growth (Morin et al., 2011; Sapjanskas et al., 2014). Vanhellemont et al. (2018) discovered a positive influence of structural heterogeneity in close proximity for the growth of large oak trees and suspects crown plasticity to be the reason for that effect. Additionally, the occupation of space belowground and differences in rooting depth can play an important role in facilitation (Bolte et al., 2013), separate from the aboveground distribution of resources and space. Potential facilitation of different tree species due to spatial, temporal, or species-specific complementarity is also of considerable interest as it can foster other ecosystem services, such as carbon storage (Ruiz-Jaen and Potvin, 2010), biomass production (Callaway, 1998; Cardinale et al., 2007; Gómez-Aparicio et al., 2011), resistance (Dhôte, 2005; Pretzsch et al., 2013a; Schütz et al., 2006), and resilience (Silva Pedro et al., 2015). Structure must therefore be addressed not only horizontally or vertically, but in a three-dimensional way to cover all aspects of niche occupation in the structure–productivity relationship, especially crown dimensions and canopy space filling (Juchheim et al., 2017; Pretzsch, 2014; Sumida, 1995), which can play an important role in competition and facilitation processes.

With this study, we intended to include an additional factor in the analysis of diversity–structure–productivity relationships—stand age. The effect of the developmental stage of forest stands on tree diversity–structure–productivity relationships has rarely been investigated. Silva Pedro et al. (2017), contributing one of the few studies considering the effect of developmental status, found a positive effect of structural heterogeneity on stand growth for all examined developmental stages (100–500-year old stands). The growth-enhancing effect of structure became even more important over time, while the effect of species diversity on stand growth was stronger in younger stands. As our data comes from a range of stands between ~25 and ~150 years old, the positive effect of structure on productivity matches the trend found in our experimental plots in later developmental stages. Particularly in terms of continuous cover forestry (Pommerening, 2006), which is currently pursued in Germany and other European countries, later developmental stages in forests beyond a conventional rotation period of 80–120 years in clearcut forestry become relevant. Continuous cover forestry is practiced as it has various advantages over clearcutting in terms of economics (Knoke, 2012), risk reduction (Brang et al., 2014), carbon balance (Pukkala, 2014), stability (Gardiner et al., 2005), ecology (Nordström et al., 2013; Chaudhary et al., 2016), and aesthetics (Hockenjos, 1999; Hoffman and Palmer, 2018). It can therefore also make use of the positive structural effect on stand productivity found in later developmental stages. The fulfillment of various ecosystem goods and services at the same time and place might benefit from structural heterogeneity in older forest stands. The concept of seeing stand structure purely as mechanistic precondition (Forrester

et al., 2018) for the production of energy in trees through the arrangements of stems, branches and leaves, can thus be expanded by interactions with tree species diversity, functional traits and the developmental stage of a forest.

The second part of the analysis examining structural effects at tree level on stand productivity was in line with the analysis at stand level. Diameter differentiation index based on tree positions, describing the size heterogeneity of each tree and its four nearest neighbor trees, was clearly positively correlated with structural heterogeneity at stand level (Fig. 3). On the one hand, a higher tree-to-tree heterogeneity in diameters in young forest stands might be rather counterproductive due to increased competition (Vanhellemont et al., 2018) and inefficient resource use of suppressed, small trees (Assmann, 1961, p. 34; Waring, 1987). On the other hand, a vertical stratification in older forests might lead to enhanced stand productivity, which seems valid for stand structure measured both at the stand and the individual tree level. Yet, the positive effect of structural heterogeneity among neighbor trees on stand productivity in the older experimental plots was even stronger in species-diverse stands than in monocultures. This could be an indicator of even higher niche facilitation in species-diverse stands if structural heterogeneity is provided not only at the stand level but also at the tree level.

Additionally, more insight was gained from analysis of the horizontal distribution of trees over time. Aggregation index was positively correlated with the development of standing volume, which means that the horizontal distribution of trees became more regular with stand development. We suspect that this is because small trees can fill gaps that appear over time. In a more regular horizontal distribution, they might contribute to overall stand productivity, especially in mixed stands, by exploiting unused space and light (De Boeck et al., 2006). A potential explanation for this is that young trees that are too clumped experience higher competition or even die out, especially those standing too close to a strong neighbor. On the other hand, an individual tree in a good position will remain in the stand and suppress weaker, less efficient neighbors (Vanhellemont et al., 2018).

Unlike in other studies (Pretzsch and Biber, 2016; Pretzsch and Schütze, 2016), we did not find a higher stand density in mixed-species stands. Possible reasons for this could be the highly productive and densely-packed monocultures that formed part of the experimental plots. Comparing versions of the linear mixed-effects model including and excluding stand density index as variable yielded similar results. We therefore concluded that stand density could have only marginal effects on tree diversity–structure–productivity relationships. The potential effects of stand density were most likely already accounted for by standing volume as a fixed effect in the model.

When examining competition and complementarity in traits as important drivers for stand productivity, climate and site conditions can also play a role. Madrigal-González et al. (2016) state that at colder sites, small trees seemed to benefit more from complementarity, whereas at warmer sites, complementarity was rather found among large trees. Small trees even experienced a reduction in growth at warm sites. Tree size distribution might therefore lead to different outcomes when analyzing mixing effects or structural effects at the tree level. Mean annual temperature and annual precipitation did not show any significant effects in the present study and were therefore eliminated from the model function.

The long-term experimental plots in this study covered a broad range of tree species diversity from monocultures up to a Shannon index of 0.4. In particular, monocultures and very diverse forest stands were represented by a large number of sample plots. Also, the coverage of different developmental stages was given (Fig. A.1). The aim of our

study was to set up a straightforward model including variables that were suspected to account for the most probable structural effects on stand productivity. Similar studies using other data can easily be conducted if dbh for each tree is available. The second part of the analysis on a subset of the data using position-based indices did endorse the findings of our study. A similar analysis using other data would be more difficult to conduct in many cases due to the necessity of coordinates of tree positions. Our study demonstrates the advantage of long-term experimental plots that allow for analysis of the effect of time under *ceteris paribus* conditions, unlike inventory data, in which the sample plots are chronologically static and might therefore be more useful for broader analyses of spatial differences than time effects.

5. Conclusions

The main result of our analysis is that stand developmental stage can be a strong predictor of tree diversity–structure–productivity relationships. Our analysis can thus help to explain why many studies find different relationships between forest structure, tree species diversity, and productivity, and that they are not necessarily contradictory. Often, structural parameters are not considered in large-scale national inventories due to small plot sizes or low funds for detailed sampling. Also, biodiversity–productivity relationships are more often examined than structure–productivity relationships; the effect of stand development in particular has often been ignored. Consideration of the developmental stage of forest stands in future studies would thus allow for a more complete evaluation of tree diversity–structure–productivity relationships.

We conclude that the overarching analysis of tree diversity–structure–productivity relationships in long-term experimental plots and at different spatial scales (Chisholm et al., 2013; Whittaker, 2010) seems promising for the future elaboration of forest management and the understanding of the different findings of recent studies. Particularly in terms of climate change, the currently-applied or planned mixing and restructuring of European forests toward multifunctionality and continuous cover forestry could benefit from considering such interdependencies.

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Authors contributions

HP and LZ elaborated the idea for the study. HP provided the data of long-term experimental plots. LZ conducted the statistical analysis and drafting of the manuscript. Both authors contributed to the interpretation and discussion of results.

Appendix A

See Figs. A1 and A2.

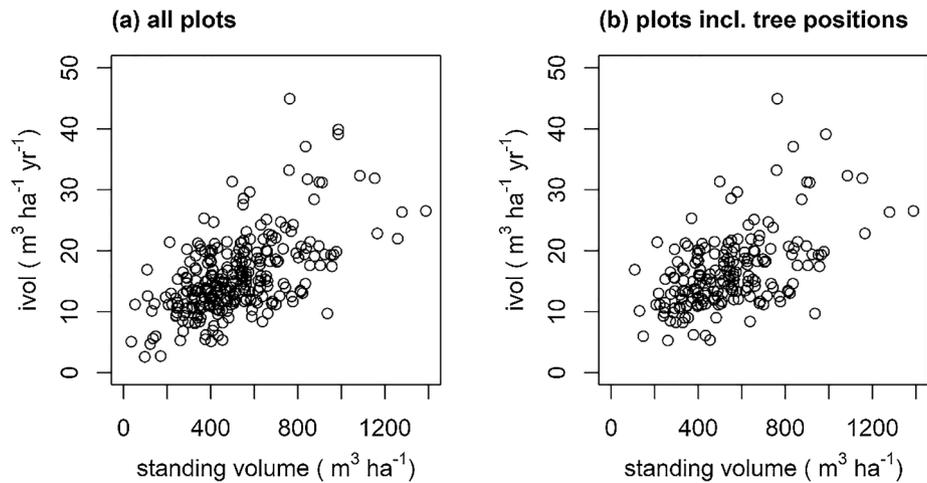


Fig. A.1. Data points (measurements) used in the first part [all plots (a)] and the second part [plots including tree positions (b)] of the study. *Ivol* volume increment.

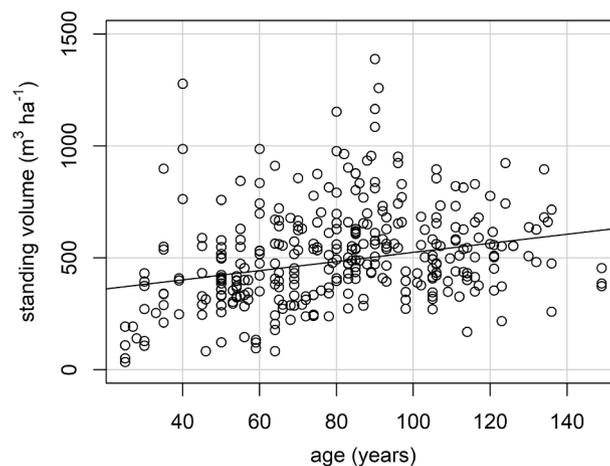


Fig. A.2. Standing volume over estimated stand age of all measurements in experimental plots.

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