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Interactions between forest stand structure, tree species composition, and stand productivity in spatial, temporal, and silvicultural context

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List of abbreviations

ba	basal area (m ²)
cm	centimeter
CVd (= dbh.cv)	coefficient of variation of dbh
d (= dbh)	diameter at breast height (1.3 m)
dbh (= d)	diameter at breast height (1.3 m)
dbh.cv (= CVd)	coefficient of variation of dbh
dq	quadratic mean diameter
GAM	Generalized additive model
GAMM	Generalized additive mixed model
ha (= h)	hectare
h (= ha)	hectare
h100	height of 100 largest trees
ivol	volume increment (m ³ ha ⁻¹ yr ⁻¹)
lme	linear mixed model
m	meter
MD	mean tree ring wood density
mm	millimeter
P	stand productivity (m ³ ha ⁻¹ yr ⁻¹)
R	species richness, number of tree species
RW	mean tree ring width
SDI	Stand density index
Vol	standing volume (m ³ ha ⁻¹)
yr	year

Abstract

More and more, forest ecosystems are expected to provide not only wood products, but other ecosystem functions and services. Combining the classical research on stand productivity with forest stand structure and tree species composition is a promising approach to promote the understanding of forest ecosystems. This thesis is based on different types of data and addresses the interdependencies between forest stand structure, tree species composition and stand productivity in a broad context.

First, a comparison between pure and mixed stands concerning stand productivity and wood quality, in terms of tree ring width and wood density was conducted. A higher tree ring width of Scots pine (*Pinus sylvestris* L.) in mixed stands with European beech (*Fagus sylvatica* L.) and a lower tree ring wood density of both species in mixed stands were found. Since mixed stands usually differ from pure stands in their stand structure and the influence of forest structure in detail is often still unclear, the subsequent parts of the thesis focused on the role of stand structure.

Forest stand structure has only lately gotten more attention when analyzing biodiversity-productivity relationships. National forest inventory data from the USA and Germany were used for this thesis to analyze the interactions between stand structure, tree species composition and productivity on a broader geographical range. The effect of structural heterogeneity on stand productivity was found to be positive in the USA and negative in Germany. A higher number of tree species could partly mitigate the negative effect in Germany. This result led to the question why the effect of stand structural heterogeneity on stand productivity can be contrary. It was expected that the influence of time, meaning stand development, can have a vital effect on the interactions between forest structure, tree species composition, and stand productivity.

For analyzing the effect of stand structural heterogeneity in different developmental stages, long-term experimental plots based in Central Europe were used. The stand productivity was found to be negatively influenced by a high structural heterogeneity in young stands, but positively in old forest stands. Both the negative effect in young stands and the positive effect in old stands was found to be stronger in mixed stands. As most forests in Europe are managed, silvicultural management has the chance to control forest structure in a way to use its beneficial effects while fostering a provision of multiple forest ecosystems functions and services. Even

though long-term experimental plots are very useful for analyzing forest development over time, estimating the effect of different approaches of silvicultural management on forest structure and productivity in the future is often difficult.

Consequently, a simulation study was developed to gain further insight into how the structural heterogeneity and its trade-off with stand productivity is modified by different management scenarios and at different spatial scales. By virtually designing forest stands, consisting of forest types representative for forests in Central Europe, comparable initial situations were set up. A multifunctional, a production-orientated, and a set-aside scenario were then applied to the stands through simulation over a time of span of 100 years. In uneven-aged stands, a production-oriented scenario led to a decrease in structural heterogeneity per unit of productivity, whereas in the age-class stands, the production-oriented scenario was able to maintain a high structural heterogeneity per unit of productivity over time. A high wood production and a high structural heterogeneity at stand scale were thus best covered in a mosaic of age-class forest stands. This study can help to estimate the effect of silvicultural management on the trade-off between structural heterogeneity and productivity before applying it to real forests.

This doctoral thesis provides new insights into the complex interactions between forest stand structure, tree species composition and stand productivity in temperate forest ecosystems. It contributes to the knowledge needed for understanding and managing multifunctional forests sustainably in the long-term.

Zusammenfassung

Das Ökosystem Wald soll zunehmend nicht nur Holzprodukte, sondern auch andere Ökosystemfunktionen und -dienstleistungen erfüllen. Durch eine übergreifende Analyse von Bestandesstruktur, Baumartenzusammensetzung und Bestandesproduktivität können Waldökosysteme besser auf zukünftige Herausforderungen angepasst werden. Die vorliegende Dissertation basiert auf verschiedenenartigen Daten und untersucht die Zusammenhänge zwischen Bestandesstruktur, Baumartenzusammensetzung und Bestandesproduktivität in einem übergreifenden Kontext. Zuerst wurden Bestandesproduktivität und Holzqualität, in Form von Jahrringbreite und Holzdicke in Rein- und Mischbeständen untersucht. Die WaldKiefer (*Pinus sylvestris* L.) zeigte hierbei in den Mischbeständen breitere Jahrringe als in den Reinbeständen. Rotbuche (*Fagus sylvatica* L.) und Waldkiefer hatten jedoch in den Mischbeständen eine geringere Holzdicke als in den jeweiligen Reinbeständen. Da Mischbestände in der Realität meist auch eine andere Bestandesstruktur ausweisen als Reinbestände, stand in den nachfolgenden Studien, die im Rahmen dieser Thesis durchgeführt wurden, die Bestandesstruktur im Mittelpunkt.

Die Bestandesstruktur blieb in der Vergangenheit oft unbeachtet und wurde erst in den letzten Jahren verstärkt in die Erforschung von Artendiversität und Produktivität mit einbezogen. Für eine geographisch breit angelegte Analyse der Zusammenhänge zwischen Bestandesstruktur, Baumartenzusammensetzung und Produktivität wurden in dieser Thesis Daten der Waldinventuren aus den USA und Deutschland verwendet. In den USA war der Effekt einer höheren Strukturheterogenität auf die Bestandesproduktivität positiv, in Deutschland negativ. Eine höhere Baumartenanzahl konnte jedoch den negativen Effekt der Strukturheterogenität in Deutschland abmildern. Dieses Ergebnis führte zu der Frage, warum der Effekt der Strukturheterogenität so verschieden ausfallen kann. Eine Vermutung war dabei der Einfluss des Bestandesalters auf die Beziehungen zwischen Bestandesstruktur und Produktivität. Zeitreihendaten, die auf langfristigen Versuchsflächen basieren, wurden deshalb herangezogen, um den Einfluss des Bestandesalters auf die Beziehung zwischen Bestandesstruktur und Bestandesproduktivität in verschieden stark gemischten Beständen zu untersuchen. In jungen Beständen führte eine hohe Strukturheterogenität zu einer niedrigeren, in älteren Beständen hingegen zu einer höheren Bestandesproduktivität. Da die meisten Wälder in Europa bewirtschaftet werden, hat das waldbauliche Management die Möglichkeit, die Bestandesstruktur so zu steuern, dass ihre Vorteile

für eine Multifunktionalität des Waldes genutzt werden können. Obwohl sich langfristige Versuchsflächen für die Untersuchung der bisherigen Bestandesentwicklung eignen, sind waldbauliche Effekte in der Zukunft oft schwer abzuschätzen.

In der letzten Studie dieser Thesis wurden deshalb vergleichbare virtuelle Bestände geschaffen, die typische Waldarten in Mitteleuropa repräsentieren. Auf diesen Beständen konnte so, *ceteris paribus*, untersucht werden, wie sich das Trade-off zwischen einer hohen Bestandesstruktur und einer hohen Bestandesproduktivität unter verschiedenen Managementszenarien und auf verschiedenen räumlichen Ebenen entwickelt. Ein multifunktionales, ein produktionsorientiertes und ein Stilllegungsszenario wurden ausgewählt, um die Bestandesentwicklung über einen Zeitraum von 100 Jahren zu untersuchen. In den Plenterwaldartigen Beständen führte das produktionsorientierte Szenario mit der Zeit zu einem Rückgang der Strukturheterogenität pro Einheit Produktivität. Im Altersklassenwald konnte auf Bestandesebene eine hohe Strukturheterogenität pro Einheit Produktivität erreicht werden und gleichzeitig das Ziel einer hohen Produktivität verfolgt werden.

Die vorliegende Arbeit liefert somit neue Erkenntnisse über die Beziehung zwischen Bestandesstruktur, Baumartenzusammensetzung und Bestandesproduktivität in Waldökosystemen. Managemententscheidungen können so unterstützt werden, um die Multifunktionalität des Waldes nachhaltig und langfristig sicher zu stellen.

1 Introduction

Forests are complex ecosystems that interact with multiple factors. Humankind discovers and appreciates more and more the importance of forest ecosystems and their far reaching potential. The common objective of multifunctional forest ecosystems (Manning et al., 2018) requires an understanding of biodiversity-structure-productivity relationships as well as the long-term effects of forest management. Since the demand for wood products in Europe is expected to increase in the coming years (Reid, 2005), forests will be commercially used for wood production also in the future. At the same time, other ecosystem functions and services need to be provided (Sikkema et al., 2017). An overarching analysis of forest biodiversity, structure and productivity and the potentially conflicting relationships between the different interests (Felipe-Lucia et al., 2018; Seidl et al., 2007) is therefore necessary. An approach to see and manage forests as complex adaptive systems including multiple interactions was also described by Messier et al. (2013). Considering different aspects that influence the interactions between forest structure, tree species composition and productivity is one step in the direction towards sustainable forest management that can maintain and enhance the multifunctionality of forest ecosystems in the long-term. In Germany (Ammon, 1951; Knoke, 2012) and other European countries (Boncina, 2011; Buongiorno et al., 1994; Buongiorno et al., 1995), commercially used forests are supposed to be managed under the goal of multifunctionality (Häusler and Scherer-Lorenzen, 2001).

Species mixing is generally considered to be an important factor when aiming at multifunctional forest ecosystems (del Río et al., 2017; Hector and Bagchi, 2007; Schnabel et al., 2019; Schwaiger et al., 2018). Throughout Europe, a transition of monocultures to mixed-species stands has been pursued in the last decades (Ammer, 2008; Felton et al., 2010). Positive relationships between tree species richness and forest productivity were found on a global scale (Liang et al., 2016) and on long-term mixed-species experimental plots (Pretzsch et al., 2015) and on national forest inventory plots in Germany (Zeller et al., 2018). Both the total above-ground biomass (Pretzsch et al., 2010) and stem biomass growth (Thurm et al., 2016) can be higher in mixed stands compared to monocultures. Others state a more continuous productivity over time with increasing tree species richness as different species react differently to disturbances and can therefore level out drops in productivity (Morin et al., 2014). Admixing broad-leaved tree species to pure coniferous forest stands can therefore lead to a lower financial risk (Knoke et al., 2008). Species mixing is further considered to bring along benefits, such as a

lower risk of damage due to climate events (Neuner et al., 2015) or pest insects (Bauhus et al., 2017), a higher overall biodiversity (Felton et al., 2016), a stabilizing function for the water use (Felton et al., 2016) and nutrient cycles (Forrester et al., 2005), a higher value for recreation (Grilli et al., 2016), and further ecosystem functions and services (Gamfeldt et al., 2013). On the contrary, tree species mixing can compromise wood density (Zeller et al., 2017). A lower wood density means a lower wood quality, which depends on the morphological plasticity of the species and the stand structural heterogeneity in mixed stands (Pretzsch and Rais, 2016). Considering not only tree species composition, but also stand structural heterogeneity when examining the performance of forests is therefore important.

The role of forest stand structure has been discussed more and more in the recent years. Both positive (Danescu et al., 2016; Zeller et al., 2018) and negative effects (Bourdier et al., 2016; Soares et al., 2016; Zeller et al., 2018) of stand structural heterogeneity on wood production have been found. The mechanical stability (Gardiner et al., 2005; Mason, 2002) and resilience (O'Hara and Ramage, 2013) can be higher in structurally complex forest stands. Further, a mostly positive effect of a high structural heterogeneity on biodiversity (Lindenmayer et al., 2000) was discovered. Since stand structure depends on tree species composition, climatic conditions (Zeller et al., 2018), stand development (Zeller and Pretzsch, 2019), spatial scale and silvicultural management (Maleki et al., 20xx; Zeller et al., 20xx), it has to be investigated in a broad context.

Climatic conditions can modify the competition or facilitation between species in mixed stands (Madrigal-González et al., 2016; Morin et al., 2018). Facilitation can result from niche complementarity (Bolte et al., 2013) with consequently higher stand resource-use efficiency (Forrester and Bauhus, 2016) and can be the reason for beneficial mixing effects in terms of biomass production (Callaway, 1998), resistance (Dhôte, 2005) and resilience (Morin et al., 2018; Silva Pedro et al., 2015) carbon storage (Ruiz-Jaen and Potvin, 2010). In favorable growing conditions, competition was found to be high, whereas in poor growing conditions, tree growth of both species seemed to benefit from niche complementarity and facilitation (del Río et al., 2014). Site conditions are therefore important to be considered when investigating biodiversity-structure-productivity relationships. In general, the stand structure in mixed stands differs from that in monocultures, with a usually higher stand structural heterogeneity in mixed stands (Riofrío et al., 2017).

In which way forest ecosystem functions and services are influenced by tree species mixing and stand structure further depends on the stand developmental phase (Zeller and Pretzsch, 2019). Stand structural heterogeneity has been found to increase stand growth in 100-500-year old stands (Silva Pedro et al., 2017). In young stands, however, the interactions between tree species composition, stand structure and productivity can be different. Negative effects of a high structural heterogeneity on stand productivity have often been found in plantations (Soares et al., 2016) that have shorter rotation periods and do not reach the old growth phase. Most studies on the effect of forest structure on productivity cover only a part of the stand development, which might explain the sometimes contradicting results.

Furthermore, the spatial scale can determine the outcome of analyses of biodiversity-structure-productivity relationships (Leimgruber et al., 2002; Stein et al., 2014; Zeller et al., 20xx). If the provision of a high biodiversity or structural heterogeneity is necessary on a small or larger spatial scale depends on the purpose of a forest (Saab, 1999; van der Plas et al., 2016). For biodiversity in general, a high structural heterogeneity was found to be especially important at a larger spatial scale (Schall et al., 2017).

Over the last decades, the previously established even-aged, mostly monospecific stands in Europe have been more and more transferred to multifunctional forests (Nyland, 2003; Salek and Sivacioğlu, 2018; Sterba and Zingg, 2001) focusing on more than only high yields (Puettmann et al., 2015). In Germany, even-aged management and continuous cover forestry are the most common management strategies (Burschel and Huss, 2003). Even-aged management has been criticized for its altered forest structure and biodiversity (Paillet et al., 2010) and for being “unnatural”. When pursuing the goal of multifunctional forests, especially continuous cover forestry is known for its benefits (Seedre et al., 2018) and comes along with species mixing and a higher stand structure compared to even-aged stands. The potential negative effect of a high structural heterogeneity on stand productivity found in some cases (Soares et al., 2016; Zeller et al., 2018) can lead to conflicting trade-offs between a high structural heterogeneity and wood production (Dieler et al., 2017; Felipe-Lucia et al., 2018; Zeller et al., 20xx). Since most forests in Europe have been or are now managed (Sabatini et al., 2018; Schelhaas et al., 2018), silvicultural management has the chance to control and modify interactions and trade-offs in a sensible way to fulfil the long-term goals (MCPFE). This also means shaping the competition between tree species (Maleki et al., 20xx). Considering the changing environment and the long time span between implication of silvicultural interventions and their result, the management

of multifunctional forest ecosystems remains a challenge that needs constant improvement (Reich, 2009).

The aspects wood density, geographical location, stand development, spatial scale, and silvicultural management, that are related to and influence the interactions between forest structure, tree species composition and productivity (Figure 1), were covered in the present thesis based on different types of data. For an overarching analysis of the role of forest structure, triplet data (Zeller et al., 2017), long-term experimental plot data (Zeller and Pretzsch, 2019), national forest inventory data (Zeller et al., 2018), and simulated stand data (Zeller et al., 20xx) were utilized.

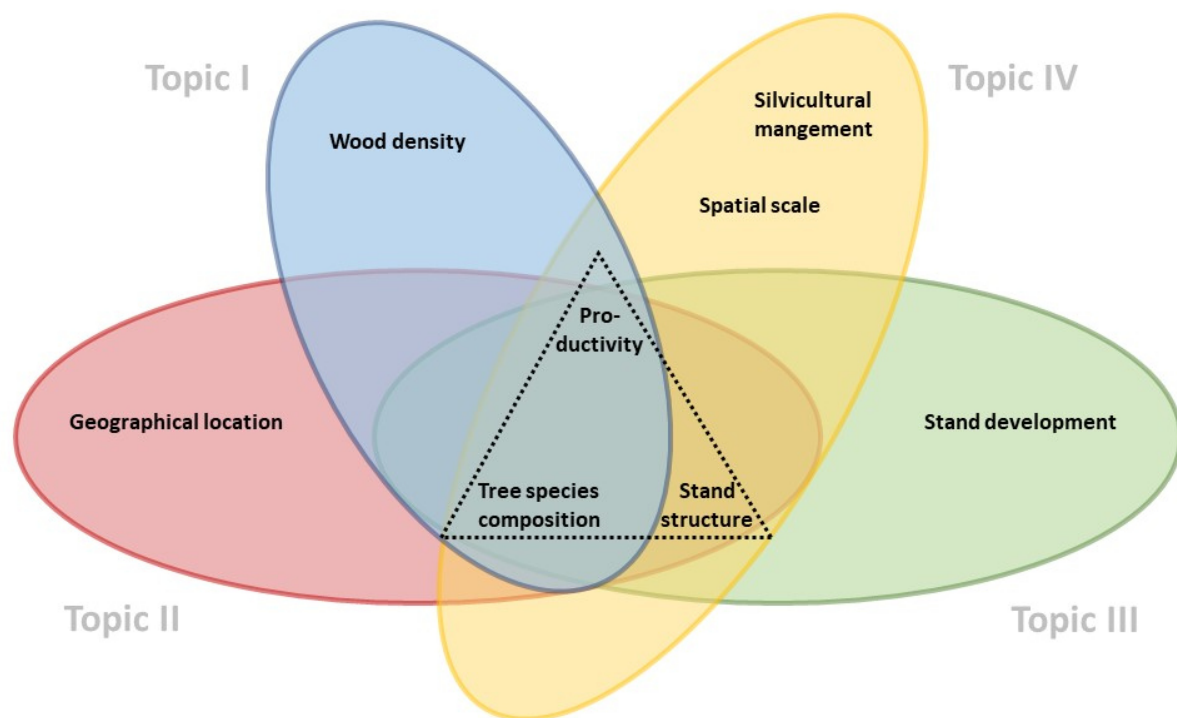


Figure 1: Overview of the topics I-IV to analyze the interactions between tree species composition, stand structure and productivity.

First, one aspect of forest structure was examined, the species composition and its effect on an important aspect of wood production, volume and wood quality in terms of tree ring width and tree ring wood density (Zeller et al., 2017). Wood density determines carbon storage, stability, the contained energy and the types of plant and animal species that depend on a certain type of

wood. Also it can define the volume overyielding found in mixed stands more precisely (Pretzsch et al., 2015).

When approaching the role of stand structure in biodiversity-structure-productivity relationships on a larger scale, national forest inventory data provides the basis for analyzing differences on a geographical range. National forest inventory data from the USA and Germany were used to determine an interactive effect of forest stand structure and tree species diversity on productivity (Zeller et al., 2018).

Since national forest inventories mostly do not date back in time for much more than one or two points in time, long-term experimental plots were used to examine the effect of time, i.e. the developmental status of a forest stand in biodiversity-structure-productivity relationships (Zeller and Pretzsch, 2019).

As most forests in Europe are commercially used in one way or another (Eurostat, 2011, p. 22), the effect of different silvicultural management on the relation between structural heterogeneity and stand productivity was examined based on simulated age-class and uneven-aged forest stands and at different spatial scales (Zeller et al., 20xx).

For all studies conducted within the scope of this thesis, linear models, linear mixed models, generalized additive models, and commonly used structural indices were applied. The utilized models and indices are easy to replicate and can serve as examples for further studies expanding the topic.

Four main research questions guide the course of this thesis. Each one of the overall questions QI - QIV led to a research article:

QI: Are stand productivity and wood quality in terms of tree ring width and tree ring wood density different in pure and mixed stands?

QII: How do tree species richness, tree size heterogeneity, mean annual temperature and precipitation influence forest productivity?

QIII: Does the effect of structural heterogeneity on stand productivity depend on tree species richness and the forest developmental stage?

QIV: How does stand structural heterogeneity in age-class vs. uneven-aged stands develop over time and spatial scale in different management scenarios?

2 Materials and Methods

2.1 Materials

2.1.1 Triplet data

The data was sampled at the five locations Alzenau, Bamberg, Steigerwald, Teupitzer Forst in Germany and in Huerta de abajo in northern Spain (Table 1).

Each location is a triplet, which consists of a pure stand of both Scots pine and European beech and one mixed stand of both species. The similarity in stand characteristics enables the comparison between pure and mixed stands (Table 2). In recent years, all triplets were unmanaged and the Stand density index (SDI) close to the maximum (Pretzsch et al., 2015). Tree ring width and wood density of 163 and 159 tree cores of Scots pine and European beech, respectively, were sampled. All tree rings of the years 1950 to 2014 were examined.

Table 1: Geographical information about the triplets (Zeller et al., 2017)

Name	Code	Latitude N	Longitude E	Altitude a.s.l. (m)	Precipitation (mm year ⁻¹)	Temperature (°C)	Geological substrate
Alzenau	Ger 2	50°06'48.74"	09°03'54.36"	250	720	9.0	slightly loamy sand
Bamberg	Ger 3	49°53'11.64"	10°58'13.12"	250	650	8.0	loamy sand
Steigerwald	Ger 5	10°38'10.10"	49°47'55.91"	125	713	9.5	slightly loamy sand
Teupitzer Forst	Ger 7	52°04'45.55"	13°37'06.05"	60	520	8.6	sandy
Huerta de abajo	Sp 1	42°05'57.00"	-03°-10'-19.00"	1290	860	8.9	sandy loam

Reference period for climate data: 1994–2013.

Table 2: Stand characteristics of pure and mixed stands of Scots pine and European beech (Zeller et al., 2017)

Triplet	Species	n	Stand age (years)	N (trees ha ⁻¹)	d _q (cm)	h _q (m)	SDI (ha ⁻¹)	V (m ³ ha ⁻¹)	IV (m ³ ha ⁻¹ year ⁻¹)
Ger 2	Sc p. mono	22	55	1461	21.21	25.28	1122	581	21.90
	Sc p. mixed	22	55	471	26.83	27.39	528	329	10.50
	E. be. mono	21	55	2022	16.46	22.39	1034	474	21.50
	E. be. mixed	20	55	604	21.94	25.98	490	300	13.73
Ger 3	Sc p. mono	21	47	2054	16.81	20.69	1086	407	19.99
	Sc p. mixed	13	47	1529	15.56	20.59	714	255	12.97
	E. be. mono	19	47	2090	14.22	20.95	845	334	16.87
	E. be. mixed	13	47	1099	13.49	19.29	408	144	7.19
Ger 5	Sc p. mono	19	57	1324	22.31	22.43	1103	517	17.69
	Sc p. mixed	19	57	346	29.55	26.15	452	256	7.27
	E. be. mono	14	57	1635	17.48	23.88	921	482	22.50
	E. be. mixed	16	57	489	21.07	24.99	372	219	8.76
Sp 1	Sc p. mono	9	40	1667	20.24	16.20	1188	399	12.40
	Sc p. mixed	6	40	1082	21.32	17.33	838	310	11.65
	E. be. mono	6	40	2542	12.75	16.38	862	248	15.34
	E. be. mixed	5	40	1477	11.20	15.22	407	99	5.23
Ger 7	Sc p. mono	16	80	1579	13.75	15.49	605	162	7.77
	Sc p. mixed	6	80	82	25.94	21.79	87	44	1.94
	E. be. mono	18	80	300	29.54	24.40	392	266	9.36
	E. be. mixed	20	80	327	21.17	17.31	250	105	5.04

Five triplets were included consisting of one mixed-species stand and two mono-specific stands each. Sc. P. = Scots pine; = E. be. = European beech.; mono = monocultures; mixed = mixed-species stands; N = tree number (trees ha⁻¹); d_q = quadratic mean diameter (cm); h_q = height of the tree with quadratic mean diameter (m); SDI = stand density index; V = standing volume (m³ ha⁻¹); IV = periodic annual volume increment (m³ ha⁻¹ year⁻¹).

2.1.2 National forest inventory data

The national forest inventories

For the analysis of the interactive effects of forest structure and productivity on a large spatial scale, 56,000 plots form the national forest inventory of Germany (Bundesministerium für Ernährung und Landwirtschaft BMEL, 2014) (Table 3) and about 576,000 plot of the national forest inventory of the USA (O'Connell et al., 2014) (Table 4) were used. The data represented different growing conditions along a climatic gradient on both the North American and the European continent. The German inventory was conducted based on a grid size of 4 km x 4 km, with a smaller grid in some regions (2.83 km x 2.83 km). The data from the USA was sampled on a hexagonal grid, where each inventory plot represents 2428 ha of forested land (O'Connell et al., 2014).

Productivity

Forest productivity ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$) for Germany was calculated using the second and third German national forest inventory. Forest productivity for the USA was derived from the periodic annual increment on plots where more than one inventory was conducted (Liang et al., 2016).

Climate data

Annual precipitation and mean annual temperature of Version 2 of the WorldClim data from 1970-2000 were used with a resolution of 2.5 min (Fick and Hijmans, 2017) .

Tree and stand characteristics

For characterizing and analyzing the inventory plots in Germany (Table 3) and the USA (Table 4), the mean diameter d , the quadratic mean diameter d_q , the coefficient of variation of diameter CV_d , the species richness R (Pretzsch, 2009), and Stand density index (SDI) by Reineke (1933) were used.

Table 3: Descriptive data of inventory plots (Germany) (Zeller et al., 2018)

	R	d	dq	CVd	SDI	Temp.	Precip.	P
mean	2.02	27.14	28.59	0.32	1158.02	8.32	842.12	12.24
sd	1.06	12.2	12.18	0.19	603.3	0.93	250.52	8.96
se	0	0.05	0.05	0	2.54	0	1.05	0.04
min	1	7	7	0	38.67	0.31	467	0
max	9	165	165	1.46	5375.02	10.83	1984	103.59
n	56449							

R = number of species, d = diameter at breast height (cm), dq = quadratic mean diameter (cm), CVd = coefficient of variation of diameter, SDI = stand density index, Temp. = mean annual temperature, Precip. = annual precipitation, P = stand productivity ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$).

Table 4: Descriptive data of inventory plots (USA) (Zeller et al., 2018)

	R	d	dq	CVd	SDI	Temp.	Precip.	P
Mean	4.67	19.91	21.97	0.44	522.63	11.56	1055.95	6.22
Sd	2.82	8.17	8.81	0.19	464.31	5.6	357.02	0.64
Se	0	0.01	0.01	0	0.61	0.01	0.47	0
Min	1	7.11	7.11	0	0.16	-2.88	56	4.01
Max	21	169.93	169.93	1.9	4998.34	24.57	3353	8.02
N	576415							

R = number of species, d = diameter at breast height (cm), dq = quadratic mean diameter (cm), CVd = coefficient of variation of diameter, SDI = stand density index, Temp. = mean annual temperature, Precip. = annual precipitation, P = stand productivity ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$).

2.1.3 Long-term experimental plot data

Long-term experimental plot data

The unique and well-studied set of long-term experimental plots (Pretzsch et al., 2013) used for exploring the effect of development stage on structure-productivity relationships were located mostly in Central Europe, with a high number of them being based in Bavaria, Germany. The plots were artificially regenerated, unmanaged and fully stocked. Between 1927 and 2014, 291 measurements were conducted on average every 7 years in the 192 different plots (Table 5). The plots contain six different species groups in different compositions with a range of tree species diversity (Shannon index) between 0 and 0.4. The plots are located in a climatic range of a mean annual temperature between 5.5 °C and 10.5 °C with an annual precipitation range of 550 mm and 1350 mm.

Table 5: Summary of experimental plots (Zeller and Pretzsch, 2019)

	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.

2.1.4 Virtual forest stand data

Based on the German National Forest Inventory a stratification was conducted leading to real forest types that occur in Bavaria and are representative for large parts of European forest. The 8 examined virtual forest stands mainly consist of Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) in equal shares, and a very low number of Scots pine (*Pinus sylvestris*) and sessile oak (*Quercus petraea* (Matt.) Liebl.). An age-class and an uneven-aged stand of each of the 4 types of species composition were set up: pure spruce (Figure 2 and Figure 3), pure beech (Figure 4 and Figure 5) a single-tree mixture of spruce and beech (Figure 6 and Figure 7), and a section-wise mixture of spruce and beech (Figure 8 and Figure 9). Each of the virtual stands measures 192 ha and contains 12 squares of different forest type patches (16 ha). The 8 virtually designed forest stands are comparable in their soil and growing conditions and mean tree size distribution (Table 6).

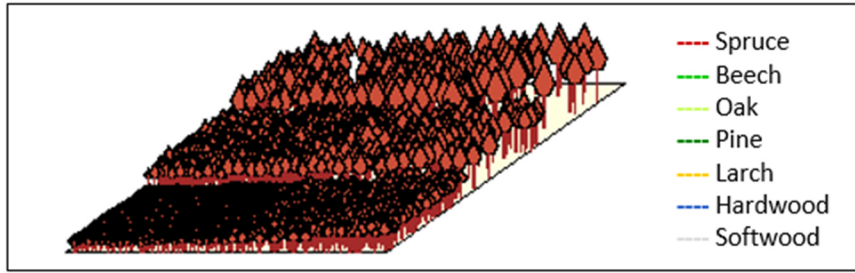


Figure 2: Age-class pure spruce stand (Zeller et al., 20xx)

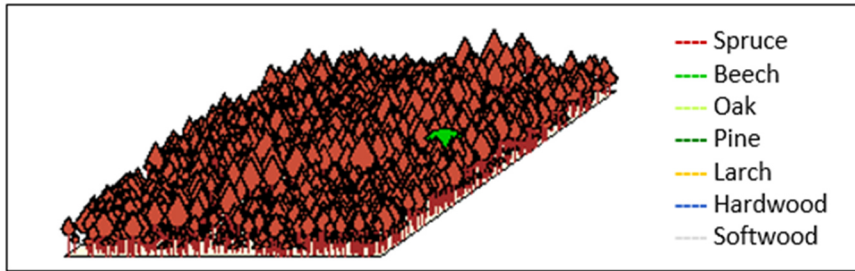


Figure 3: Uneven-aged pure spruce stand (Zeller et al., 20xx)

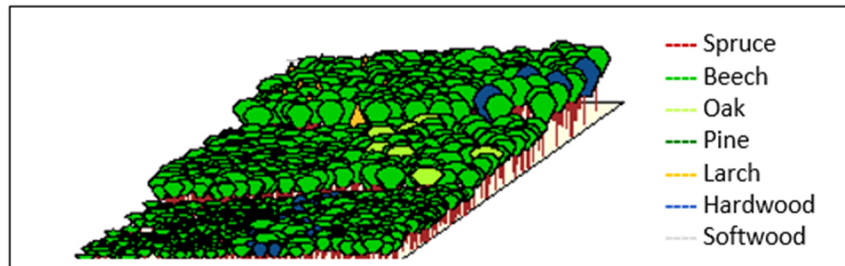


Figure 4: Age-class pure beech stand (Zeller et al., 20xx)

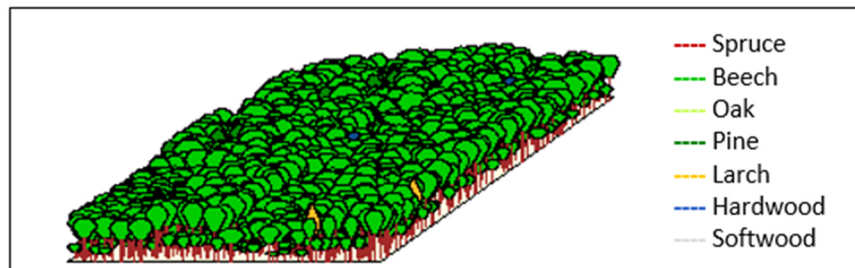


Figure 5: Uneven-aged pure beech stand (Zeller et al., 20xx)

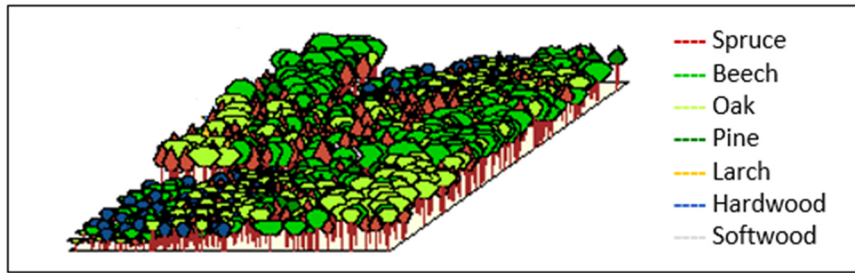


Figure 6: Age-class single-tree mixed stand (Zeller et al., 20xx)

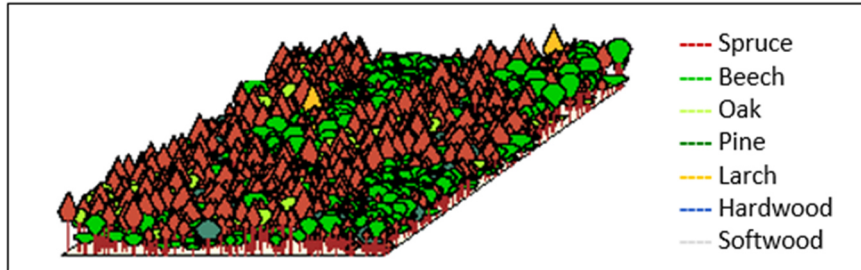


Figure 7: Uneven-aged single-tree mixed stand (Zeller et al., 20xx)

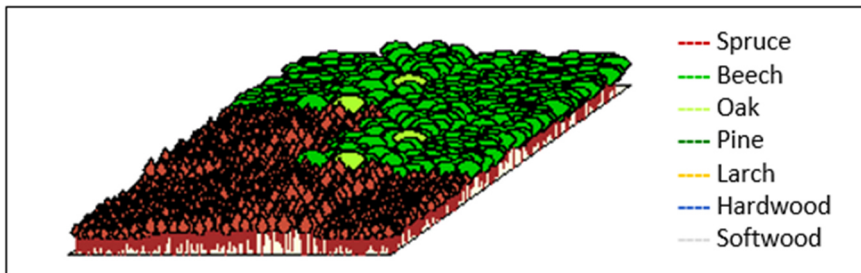


Figure 8: Age-class section-wise mixed stand (Zeller et al., 20xx)

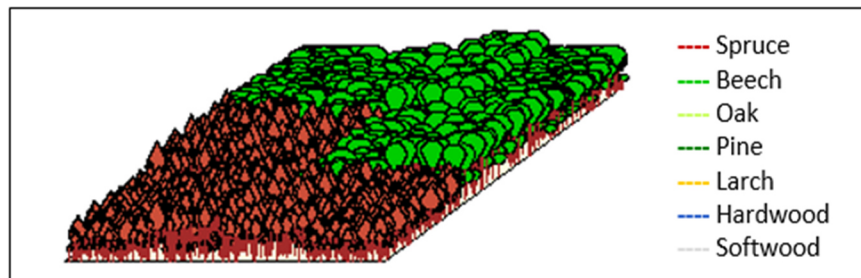


Figure 9: Uneven-aged section-wise mixed stand (Zeller et al., 20xx)

Table 6: Characteristics of the initial virtual forest stands (Zeller et al., 20xx)

mixgroup	Group	dbh (cm)			height (m)			tree volume (m ³)			trees (n ha ⁻¹) per forest type patch (16 ha)			volume (m ³ ha ⁻¹) per forest type patch (16 ha)							
		min	mean	max	sd	min	mean	max	sd	min	mean	max	sd	min	mean	max	sd				
pure spruce	age-class	7	16	62	11	6	14	41	8	0	0	5	0.71	94	1711	2538	748	14	218	914	207
pure spruce	uneven-aged	7	19	82	13	4	17	42	8	0	0	8	0.80	789	1086	1706	297	246	483	636	117
pure beech	age-class	7	22	68	13	7	19	42	8	0	1	8	0.77	96	610	848	246	9	250	681	205
pure beech	uneven-aged	7	19	58	11	6	20	36	8	0	1	5	1.07	714	1045	1475	281	209	537	690	150
single-tree mix	age-class	8	24	70	13	5	18	37	8	0	1	6	0.85	259	692	992	276	28	308	815	248
single-tree mix	uneven-aged	7	21	80	13	5	17	38	8	0	1	6	0.95	441	1082	1611	382	270	454	669	157
section-wise mix	age-class	14	23	61	7	14	19	28	4	0	0	5	0.44	232	1013	1588	460	243	352	470	91
section-wise mix	uneven-aged	7	17	57	11	6	17	36	8	0	0	4	0.61	714	1194	1706	350	209	470	594	145

2.2 Methods

2.2.1 Comparison of pure and mixed stands

Tree ring width and tree ring wood density of Scots pine and European beech were measured using a LIGNOSTATION™, thus by high-frequency densitometry and were calibrated through comparison with the water displacement method (Kemmerer, 2016). High-frequency densitometry is non-destructive and time-efficient (Schinker et al., 2003) compared to X-ray densitometry (Wassenberg et al., 2014). It works by measuring how much of a transmitted electromagnetic signal is received through the wood on the other side of a shield (Schinker et al., 2003). For the statistical analysis, linear mixed effects models were applied by using the lme function of nlme package in R (Pinheiro et al., 2018). The following model functions were set up to examine the difference in tree ring width and tree ring wood density between pure and mixed stands while considering stand density:

$$RW_{ij} = a_0 + a_1 * Mix_{ij} + a_4 * SDI_{ij} + a_6 * Mix_{ij} * SDI_{ij} + b_i + \varepsilon_{ij} \quad (\text{Eq. 1})$$

$$MD_{ij} = a_0 + a_1 * Mix_{ij} + a_2 * DBH_{ij} + a_4 * SDI_{ij} + a_5 * Mix_{ij} * DBH_{ij} + a_6 * Mix_{ij} * SDI_{ij} * b_i + \varepsilon_{ij} \quad (\text{Eq. 2})$$

In all equations, RW_{ij} is the mean ring width per tree j on triplet i and MD_{ij} is the mean tree ring wood density per tree j on triplet i . The effect of mixing on tree ring width or tree ring wood density for tree j on triplet i is described by Mix_{ij} . SDI_{ij} covers effects induced by stand density on tree j on triplet i . The random effect b_i for triplet i considers differences in site characteristics between the triplets and the error term ε_{ij} covers remaining unexplained variation. In stepwise reduction, non-significant variables and three-way or two-way interactions were eliminated. The obtained tree ring width and tree ring wood density values were then used to calculate and compare the biomass of Scots pine and European beech in pure and mixed stands.

2.2.2 Spatial analysis and interaction between species richness and tree size heterogeneity

Two Generalized additive models (GAMs) (Crawley, 2007; Zuur, 2009) were set up using the mgcv package (Wood, 2011) in R (R Development Core Team, 2008) to analyze the effects of tree species richness, stand structure, and climate on stand productivity.

$$P_i = a + f_1(Lon_i, Lat_i) + f_2(Temperature_i, Precipitation_i) +$$

$$f_3(SDI_i, dq_i) + f_4(R_i, CVd_i) + \varepsilon_i \quad (\text{Eq. 3})$$

In the model, productivity P on inventory plot i is explained by the geographical location Longitude Lon and Latitude Lat species richness R , stand structural heterogeneity CVd , stand density SDI , the quadratic mean diameter dq , mean annual temperature and annual precipitation. The model's intercept is a and f_1, \dots, f_4 are non-linear smoothers to be fitted. Remaining errors are contained in the random error term ε .

$$CVd_i = a + f_1(Lon_i, Lat_i) + f_2(Temperature_i, Precipitation_i) + f_3(SDI_i, dq_i) + f_4(R_i) + \varepsilon_i \quad (\text{Eq. 4})$$

CVd is the dependent variable and therefore eliminated from the interactive smoother f_4 . The lowest AIC values and highest R^2 , compared to reduced versions of the models, were achieved in the full model functions, which were therefore used as final model functions.

2.2.3 Effect of developmental stage

Indices

Stand productivity ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$), stand density index (SDI) (Reineke, 1933), coefficient of variation of dbh and Gini coefficient of dbh (Binkley et al., 2006), diameter differentiation index, and aggregation index (del Río et al., 2015) were used to analyze the effect of structural heterogeneity on stand productivity in the different developmental stages at tree level and plot level.

Model

Two linear mixed models were used to test the interactive effect of tree species diversity and structural heterogeneity on stand productivity at stand level (Eq. 5) and tree level (Eq. 6).

$$\log(ivoli) = a + \log(f_1(voli)) * (f_2(str_i) + f_3(SDI_i)) * f_4(shan_i) + \varepsilon_i \quad (\text{Eq. 5})$$

$$\log(ivoli) = a + \log(f_1(voli)) * (f_2(ddif_i) + f_3(SDI_i)) * f_4(shan_i) + \varepsilon_i \quad (\text{Eq. 6})$$

$Ivol_i$ represents the stand productivity ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$) on plot i . The developmental stage is represented by the standing volume ($\text{m}^3 \text{ha}^{-1}$), the structural coefficient str_i in Eq. 5 represents different structural parameters that led to similar results. The parameter $ddif_i$ (Eq. 6) is the diameter

differentiation at tree level. Stand density index (SDI) and Shannon index (shan) serve as additional explaining variables and ε is the random error term containing further unexplained information.

2.2.4 Effect of silvicultural management, time, and spatial scale

A multifunctional and a production-oriented scenario were applied to show the differences in management impact, depending on the different initial structures. As reference, a set-aside scenario was used where no management was conducted.

The management scenarios include silvicultural practices that are representative for the current challenges in forest management (Pretzsch et al., 2007). These contain details for every target tree species modelled in SILVA (Pretzsch et al., 2002). Depending on the dominant species of each stand, the silvicultural interventions were defined for each height phase, i.e. stand development stage. The simulations cover a range of 100 years.

Then, the coefficient of variation of dbh (dbh.cv) (del Río et al., 2015; Pretzsch, 2009) was selected to characterize the structural heterogeneity of the forest stands. Both dbh.cv and stand productivity were standardized (str and prod, both ranging from 0 to 1) for the setup of the trade-off:

$$t_{i,j,k} = \frac{\text{str}_{i,j,k}}{\text{prod}_{i,j,2000}} \quad (\text{Eq. 7})$$

The trade-off $t_{i,j,k}$ is the ratio between the standardized structural heterogeneity str on stand i in year j on the spatial scale k and the standardized productivity prod of stand i in year j . It ranges from 0 to 1. A higher t shows that a stand provides a higher structural heterogeneity per unit of productivity. The trade-off t was calculated for each stand i , point in time j , spatial scale k and for each of the 3 management scenarios.

For analyzing the trade-off t on different spatial scales, a growing window technique was used. Around each of 30 random point per stand, circles were drawn with increasing radius (5, 10, 25, 50, 75, 100, 150, 250, 500, 750, 1000, and 2000 m). The examined increasing area around each random point therefore ranged from 79 m² up to the maximum area of the virtual forest stand (192 ha). One mean value per virtual forest stand, point in time and radius was then calculated and used for further analysis.

Generalized additive mixed models (GAMM) (R Core Team, 2018) were then set up to examine how the standardized structural heterogeneity str per unit of productivity ($prod$) developed over time and spatial scale under different management scenarios (Eq. 8) and depending on the initial stand structure (age-class vs. uneven-aged) (Eq. 9):

$$t_{\text{group}} = \text{scen} * (f(\text{SDI}_i) + f(\text{year}_j) + f(\text{radius}_k)) + \varepsilon \quad (\text{Eq. 8})$$

t_{group} describes the trade-off $str/prod$ inside the group (age-class and uneven-aged) as dependent variable, influenced by time (year) j , and spatial scale (radius) k . The three different management scenarios applied to each stand i are contained in the factor variable $scen$. The random error term ε covers the remaining unexplained variation. The model function was applied separately to the spruce stand, beech stand, single-tree mixture and patch-wise mixture, comparing the three different management scenarios.

$$t_{\text{scen}} = \text{group} * (f(\text{SDI}_i) + f(\text{year}_j) + f(\text{radius}_k)) + \varepsilon \quad (\text{Eq. 9})$$

t_{scen} describes the trade-off $str/prod$ and tests the difference between the two groups of age-class vs. uneven-aged stands in each of the three scenarios $scen$. Further variables as described above.

3 Results

3.1 QI: Are stand productivity and wood quality in terms of tree ring width and tree ring wood density different in pure and mixed stands?

We found the tree ring width of Scots pine in mixed stands to be by 14% higher than in pure stands, whereas European beech in mixed stands had a by 5% lower tree ring width. The tree ring wood density of Scots pine and European beech was by 12% and 8% lower, respectively, in mixed stands compared to pure stands (Figure 10). When extending the model function and also considering the structural parameters tree size and stand density index (SDI), the tree ring width of European beech was still not significantly different in pure and mixed stands. The tree ring width of Scots pine was found to be by 16% higher in mixed stands compared to pure stands. Tree ring wood density of Scots pine was still found to be by 12% lower in mixed compared to pure stands after considering tree size and stand density. Also European beech showed a by 7% lower tree ring wood density in first and in the extended model function.

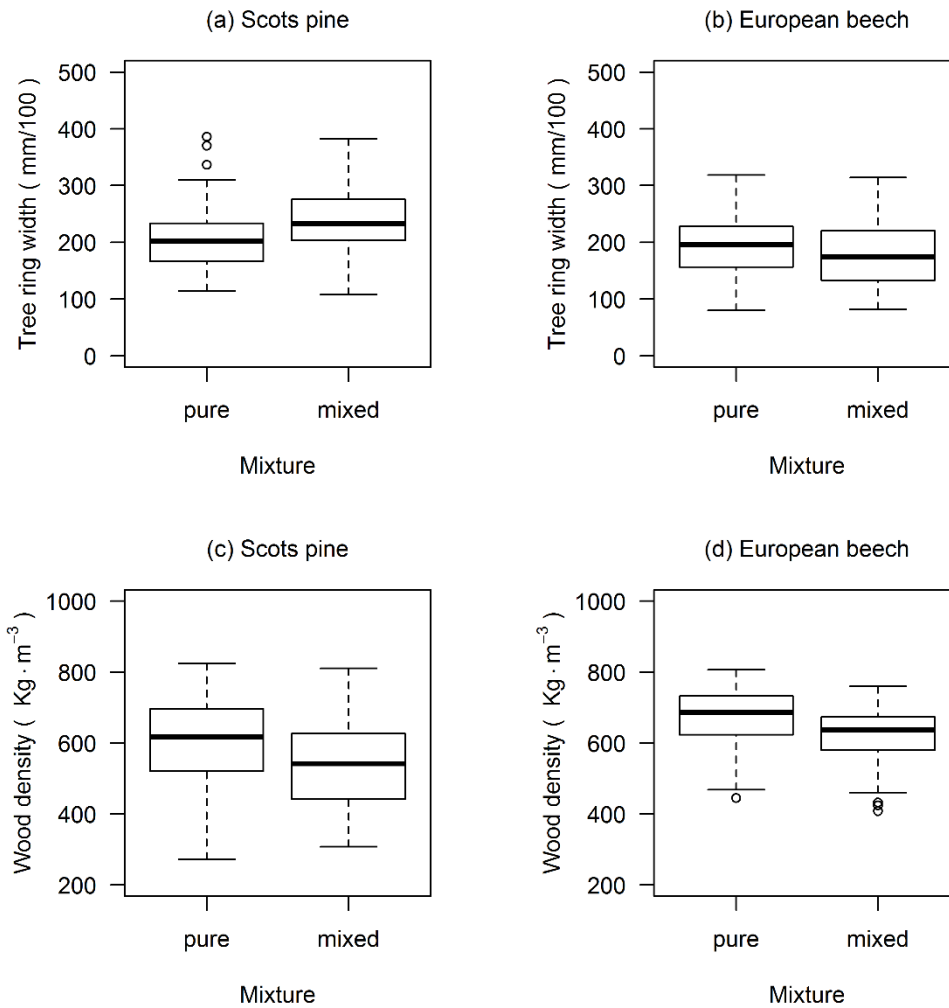


Figure 10: Differences between pure and mixed stands in mean tree ring width of Scots pine (a) $p < 0.05$, $R^2 = 0.07$ and European beech (b) n.s. and differences in mean tree ring wood density of Scots pine (c) $p < 0.001$, $R^2 = 0.39$ and European beech (d) $p < 0.001$, $R^2 = 0.09$ (Zeller et al., 2017).

Tree ring wood density values and volume measurements from previous studies on the same triplets (Pretzsch et al., 2015) were then used to calculate the biomass production of pure and mixed Scots pine and European beech stands. Scots pine was found to produce 11% more biomass, whereas European beech produced 8% less biomass in mixed stands compared to pure stands.

3.2 QII: How do tree species richness, tree size heterogeneity, mean annual temperature, and precipitation influence stand productivity?

When looking at forest growth on a larger geographical range, forest productivity was increasing towards the north of Germany, from $\sim 10 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ to $\sim 13 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ (Figure 11, a). SDI was positively influencing productivity (Figure 11, c) and tree size (dq) had only a small effect on productivity. Species richness and structural heterogeneity, however, had a significant influence on productivity (Figure 11, d). For stands of up to two tree species, a higher structural heterogeneity led to a drop in stand productivity from 14 to $12 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$. For forest stands with more than three tree species, stand productivity was positively influenced by structural heterogeneity, leading to a productivity of $\sim 16 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ for stands with eight tree species. A combination of a low tree species diversity and a high structural heterogeneity was therefore least productive, whereas additional tree species could lessen the negative effect of structural heterogeneity on stand productivity.

The highest productivity in the USA was found in the southeastern part (Figure 12, a). The location and climatic conditions (Figure 12, b) explained the largest part (up to $\sim 4 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) of the variation in productivity among the inventory plots. Tree size (dq) and SDI had only small positive effects on productivity (Figure 12, c). On plots of up to 10 different tree species, species richness had a positive effect on productivity. This trend reversed in case of more than 10 tree species. Structural heterogeneity CVd had only a small positive effect on productivity (Figure 12, d).

How is forest productivity influenced by precipitation and temperature?

In Germany, the amount of precipitation was positively influencing productivity and explained an increase in productivity from ~ 8 to $13 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ for an increase in annual precipitation of 400 to 1000 mm (Figure 11, b). Only for an annual precipitation larger than 1000 mm, productivity was negatively influenced. Mean annual temperature had a positive effect on productivity. The interaction between precipitation and temperature showed, that especially a low amount of precipitation in combination with high temperatures had a negative effect on stand productivity. Temperature could only positively influence productivity in case of the optimum amount of precipitation of around 1000 mm.

In the USA, productivity was mostly influenced by annual precipitation (Figure 12, b). Along the range of precipitation up to 2000 mm, stand productivity increased from 5 to $\sim 7 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$

¹. Along the range of the mean annual temperature from ~ 6.5 °C to 20 °C, stand productivity was decreasing from 6.5 to 5.5 $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$.

Does growth limitation due to water scarcity or low temperature enhance structural heterogeneity?

In Germany, precipitation and temperature and species richness were leading to a higher tree size heterogeneity (Figure 13, b). Only for more than eight tree species, tree size heterogeneity was negatively influenced (Figure 13, d). In the USA, the highest structural heterogeneity was found on plots with a low annual precipitation, whereas temperature did not have a clear effect on structural heterogeneity (Figure 14, b). Tree species richness was clearly positively correlated with structural heterogeneity (Figure 14, d).

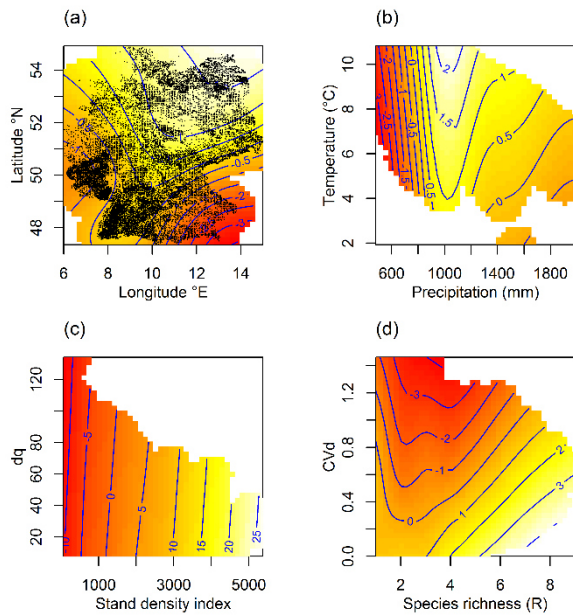


Figure 11: Effects of longitude (a), latitude (b), annual precipitation (c), mean annual temperature (d), tree species richness (e), and tree size heterogeneity (f) on stand productivity of German inventory plots. Each variable was tested on its own while other variables were set to the mean (Zeller et al., 2018).

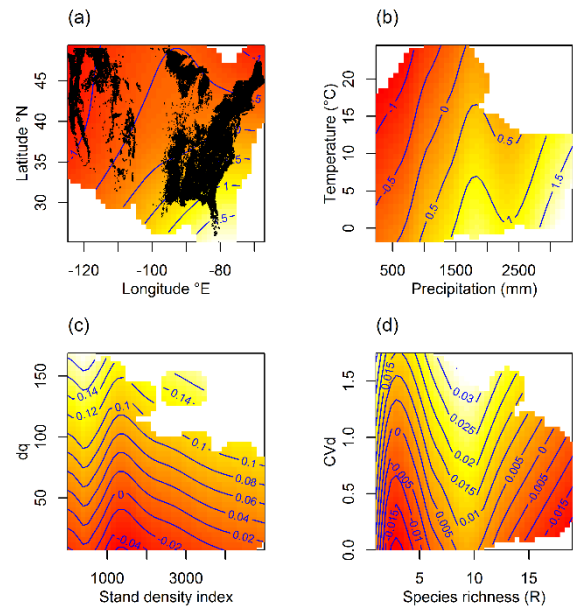


Figure 12: Effects of longitude (a), latitude (b), annual precipitation (c), mean annual temperature (d), tree species richness (e), and tree size heterogeneity (f) on stand productivity of US inventory plots. Each variable was tested on its own while other variables were set to the mean (Zeller et al., 2018).

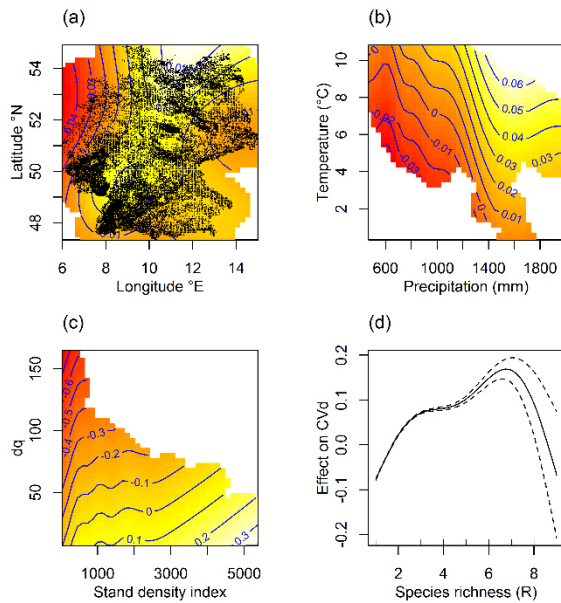


Figure 13: Effects of location (a), climate (b), and stand density and tree species richness (c) on tree size heterogeneity of German inventory plots. Yellow = positive effect on productivity, red = negative effect on productivity. Blue contour lines show where the function has a constant value (Zeller et al., 2018).

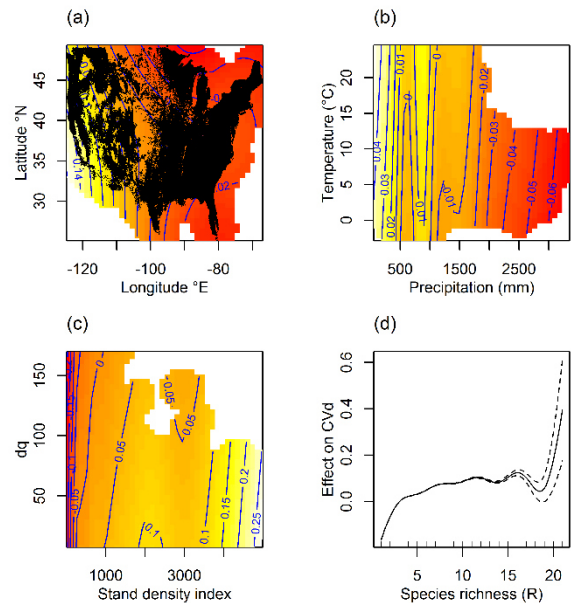


Figure 14: Effects of location (a), climate (b), and stand density and tree species richness (c) on tree size heterogeneity of US inventory plots. Yellow = positive effect on productivity, red = negative effect on productivity. Blue contour lines show where the function has a constant value (Zeller et al., 2018).

3.3 QIII: Does the effect of structural heterogeneity on stand productivity depend on tree species richness and the forest developmental stage?

Structural heterogeneity was found to influence stand productivity in different ways, depending on tree species diversity and the developmental status of a forest. In this case, climatic and other site-dependent effects could be excluded. The diameter differentiation index (tree level) showed that in early developmental stages of a forest (standing volume $< 200 \text{ m}^3 \text{ ha}^{-1}$), structural heterogeneity had a negative effect on stand productivity (Figure 15, a). This negative effect was strongest in species-diverse stands, which were also found to be more productive than monocultures. In older developmental stages (standing volume $600\text{-}800 \text{ m}^3 \text{ ha}^{-1}$ and $> 800 \text{ m}^3 \text{ ha}^{-1}$), stand structural heterogeneity was positively influencing productivity and this effect was strongest in mixed stands (Figure 15, d and e).

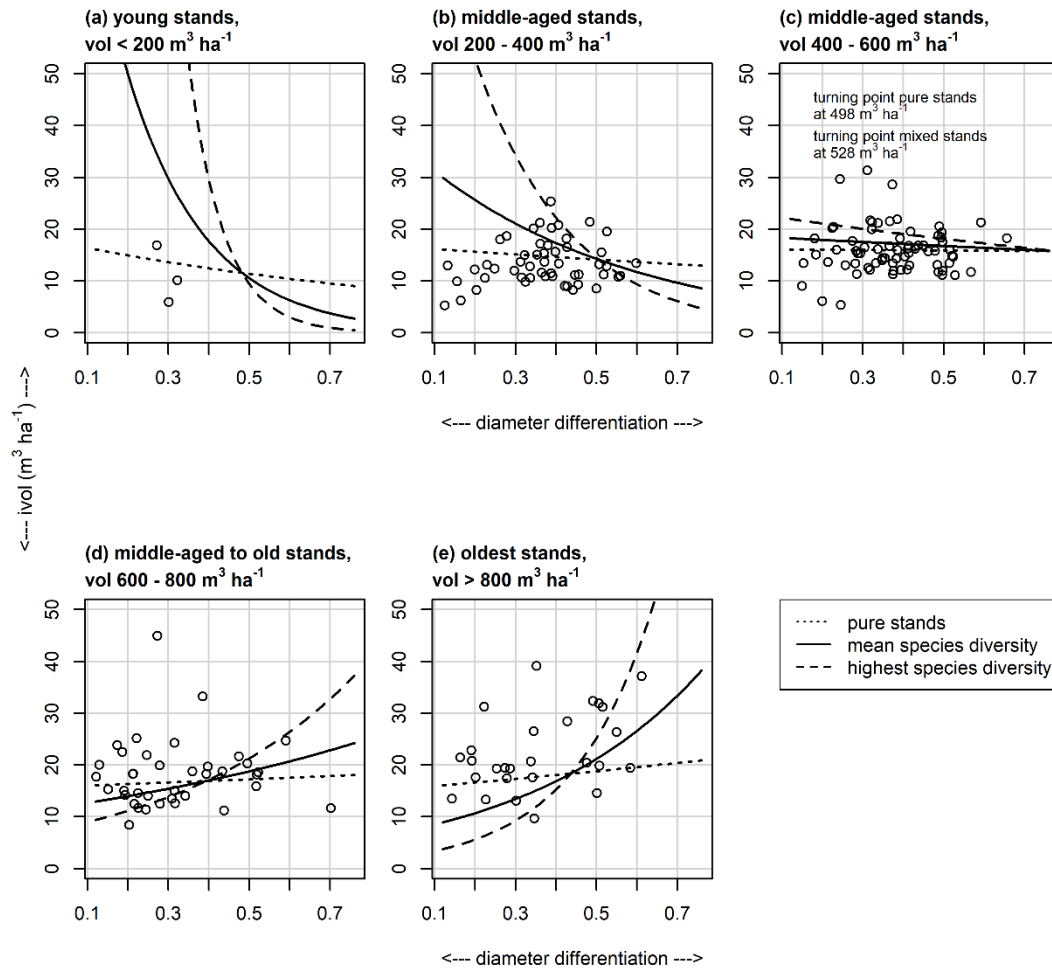


Figure 15: Effect of structural heterogeneity at tree level on stand productivity between developmental stages (a)–(e). Structural heterogeneity at tree level quantified by diameter differentiation. Developmental stages (a)–(e) were quantified by standing volume ($\text{m}^3 \text{ha}^{-1}$). Ivol stand volume increment ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$). 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 (Zeller and Pretzsch, 2019).

3.4 QIV: How does stand structural heterogeneity in age-class vs. uneven-aged stands develop over time and spatial scale in different management scenarios?

First, structural heterogeneity $dbh.cv$ and the relative productivity $rel.ivol$ in age-class and uneven-aged stands in the three different management scenarios were descriptively presented (Figure 16).

In the age-class stands (Figure 16, I) the $rel.ivol$ and $dbh.cv$ were mostly stable over time in all management scenarios. In the uneven-aged stands, however, the production-oriented scenario led to contradicting trends of $dbh.cv$ and $rel.ivol$ (Figure 16, II). The conflicting trade-off between a high structural heterogeneity and a high stand productivity in the uneven-aged stands is already visible in the descriptive part of the results. A further investigation of this opposite trend was conducted based on GAMMs.

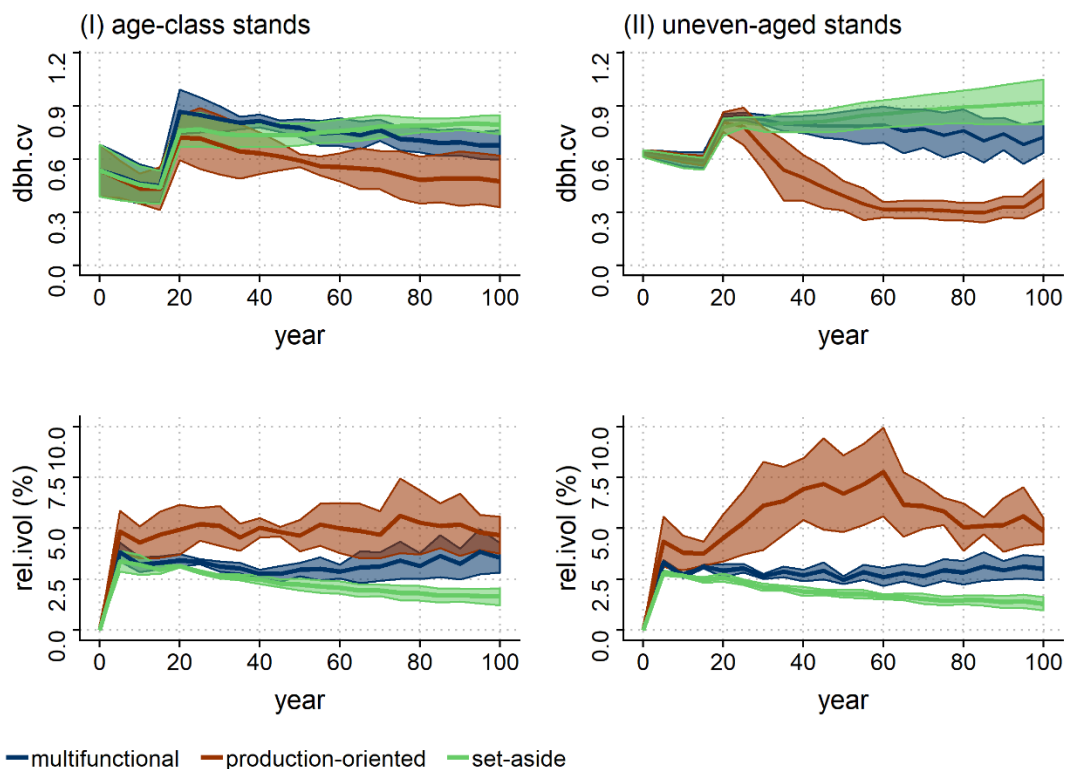


Figure 16: coefficient of variation of dbh ($dbh.cv$) and the relative ivol $rel.ivol$ (%) in (I) age-class stands and (II) uneven-aged stands over time in the multifunctional (blue), production-oriented (red), and set-aside scenario (green). Confidence intervals at 95% (Zeller et al., 20xx).

The applied GAMMs analyze the difference in the trade-off between the standardized structural heterogeneity *str* and the standardized productivity *prod* (*str/prod*) over time, spatial scale and between the three different management scenarios and between age-class and uneven-aged stands. SDI covered potential dependencies of stand productivity on stand density.

The most important finding was the difference between age-class stands and uneven-aged stands concerning the production-oriented scenario. In the uneven-aged stands did the production-oriented scenario lead to a decrease in structural heterogeneity per unit of productivity (*str/prod*) (Figure 17, II, row 2, b), whereas this was not the case in age-class stands (Figure 17, I, row 2, b). With increasing spatial scale did *str/prod* increase more strongly in the production-oriented scenario than in the multifunctional and the set-aside scenario in both age-class stands (Figure 17, I, row 3) and uneven-aged stands (Figure 17, II, row 3). With increasing spatial scale was the increase in *str/prod* found to be stronger in age-class stands compared to uneven-aged stands.

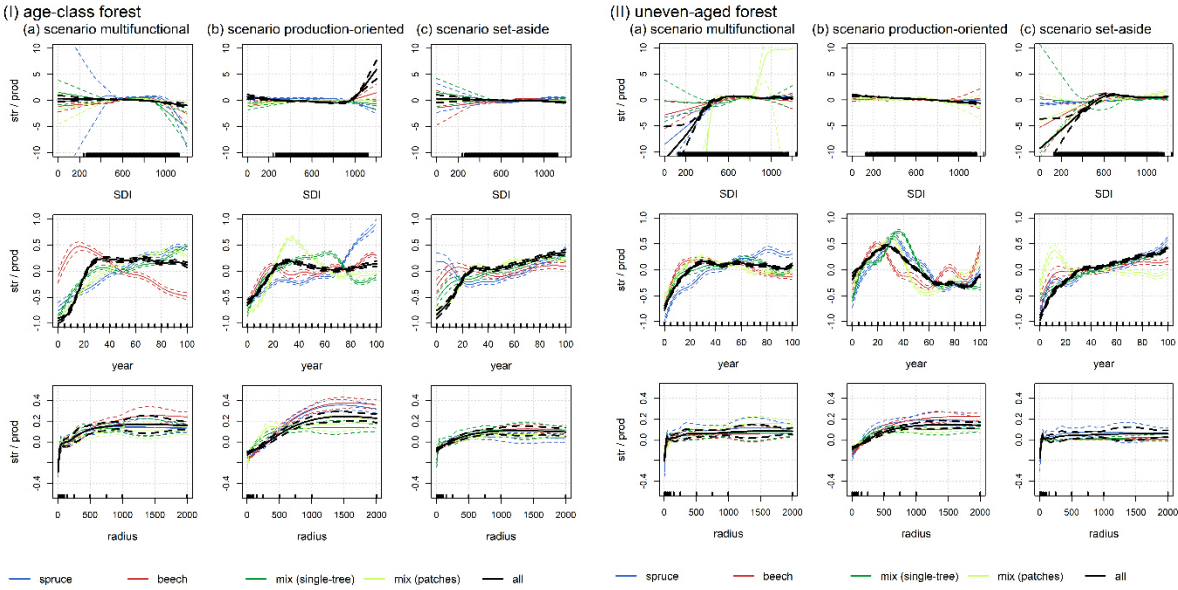


Figure 17: GAMM results showing development of the trade-off coefficient of variation/ivol in the examined area in (I) age-class stands and (II) uneven-aged stands depending on SDI (row 1), over time (row 2) and spatial scale (row 3) in a (a) multifunctional, (b) production-oriented, and (c) set-aside scenario. Confidence intervals at 95% (Zeller et al., 20xx).

4 Discussion

QI: Are stand productivity and wood quality in terms of tree ring width and tree ring wood density different in pure and mixed stands?

In mixed stands, the tree ring width of Scots pine was found to be higher than in pure stands, which is in line with findings of volume overyielding in volume in mixed stands (Pretzsch et al., 2015; Steckel et al., 2019). As soon as not only wood volume, but also its quality is of interest, tree ring wood density becomes an important factor. We found tree ring wood density of both Scots pine and European beech to be lower in mixed stands compared to pure stands. For Scots pine, that resulted in a by 7 % higher biomass in mixed stands whereas the biomass of European beech was by 10 % lower in mixed compared to pure stands. In total, a by 8% lower biomass in mixed stands compared to pure stands was found, despite the volume overyielding in mixed stands. The effect of mixing on wood quality, i.e. a lower tree ring wood density, therefore has to be considered in forest management as it can lower the overall biomass, the mechanical stability (Anten and Schieving, 2010), the hardness and abrasiveness of the produced wood (Bacher and Krzosek, 2014; Pretzsch and Rais, 2016), and the amount of stored carbon (Aryal et al., 2013). Apart from species mixing, stand structure has been found to influence tree ring wood density (Bues, 1985; Grammel, 1990; Hapla, 1985; Moore et al., 2015), and as a consequence also stand productivity. It is expected that tree species mixing and forest stand structure are strongly connected (Silva Pedro et al., 2017). Since the partial effects of mixing and stand structure are often difficult to detect, the interaction between tree species richness and tree size heterogeneity and their effect on stand productivity was analyzed in the second part of this thesis.

QII: How do tree species richness, tree size heterogeneity, mean annual temperature and precipitation influence forest productivity?

Both tree size heterogeneity and tree species richness influenced stand productivity in the national forest inventory plots of Germany and the USA. In Germany, tree size heterogeneity had a negative effect on stand productivity. In the USA, a slightly higher stand productivity was found in structurally more diverse stands.

For the German plots, the productivity was lower in two-species plots than in monocultures, as stated by others (Binkley, 1984; Chen and Klinka, 2003; Soares et al., 2016). A possible reason can be the generally high productivity of the previously established monocultures in Germany.

In times of changing growing conditions, this high productivity of monocultures is expected to decrease due to a higher risk of biotic and abiotic disturbance (Felton et al., 2016; Morin et al., 2014). Not only tree species richness, but also forest structure, and the interaction between the two, are influencing forest productivity (Silva Pedro et al., 2017). A negative influence of a high structural heterogeneity on productivity was found for the German plots. This negative relationship between tree species richness and productivity was less strong in stands of more than one tree species. This effect can result from the different shade-tolerance of some species (Bourdier et al., 2016), leading to a better niche exploitation and resource use in case of structured, multi-layered stands (Lei et al., 2009; Pretzsch, 2005; Zeide, 1987). In monocultures, a higher structural heterogeneity can rather lead to an increased competition load and a decrease in productivity, especially in young stands, where a vertical stratification might not be possible yet (Zeide, 1987; Zeller and Pretzsch, 2019).

The inventory plots in the USA showed a positive effect of tree species richness on productivity for up to 10 tree species. This positive diversity-productivity relationship has also been stated by others (Gamfeldt et al., 2013; Kelty, 2006; Liang et al., 2016). Structural heterogeneity had a slightly positive effect on productivity. In the US inventory plots, the effects of structural heterogeneity and species diversity on productivity were small as most of the variation in productivity was explained by the location and climate of the plots.

The differences in the diversity-structure-productivity relationship between the German and the US inventory plots might be explained by their location on different parts of a gradient concerning latitude, annual precipitation, temperature, stand structure, and productivity.

The results suggest that if a high structural heterogeneity is aimed for due to its beneficial reasons on different ecosystems functions and services (Danescu et al., 2016; Díaz-Yáñez et al., 2017), a potential negative effect on stand productivity (Bourdier et al., 2016) might be mitigated by a higher tree species richness. Still, conflicting results on the effect of stand structure on stand productivity, as one of the most important forest services, are found (Ali, 2019) which exhibited the need for further clarification. The developmental stage was therefore expected to have a strong influence on the effect of structural heterogeneity on stand productivity and was tested in the third study of this thesis, based on long-term experimental plot data.

QIII: Does the effect of structural heterogeneity on stand productivity depend on tree species richness and the forest developmental stage?

Our approach showed that an increase in structural heterogeneity led to a lower stand productivity in young stands, even more so in case of a high tree species diversity. In advanced developmental stages, however, structural heterogeneity had a positive effect on stand productivity in monocultures, and an even stronger positive effect in species-diverse stands. This finding provides an explanation for the conflicting results on the interdependencies among those variables in other studies (Bourdier et al., 2016; Danescu et al., 2016; Zeller et al., 2018) after excluding other context-related effects (Vanhellemont et al., 2018). Although structural heterogeneity can lead to niche complementarity resulting in a higher productivity (Lei et al., 2009), this might not be the case in all developmental stages (Pretzsch, 2013). In situations where trees compete mainly for light, as other resources are sufficiently provided (Pretzsch and Biber, 2010; Schwinning and Weiner, 1998), a complementary light use might only be possible in case of a larger vertical stratification. In young stands this stratification might not yet be possible due to the lower tree height. In later developmental stages, a strong stratification through multiple layers can result in a better light use efficiency, leading to a positive effect of structural heterogeneity on stand productivity (Silva Pedro et al., 2017). The effect can be even stronger in mixed stands, due to a complementary resources use of different tree species (Richards and Schmidt, 2010).

The finding of the developmental stage as an important factor for structure-productivity relationships is vital for forest management. In commercially used forests, as in most forests in Central Europe, there is the possibility of modifying forest structure through silvicultural interventions.

QIV: How do the trade-offs between different biodiversity-relevant structural indicators and productivity change over time and spatial scale depending on silvicultural management?

Based on a descriptive and statistical analyses, the differences between management scenarios, as well as between age-class and uneven-aged stands were shown. In uneven-aged stands, but not the age-class stands, the production-oriented scenario was leading to a decrease in the structural heterogeneity per unit productivity. In uneven-aged stands, the multifunctional scenario was more suitable to cover a high structural heterogeneity per unit of productivity. A possible explanation is that the applied thinnings homogenized the uneven-aged forest stands, whereas in the age-class stands each thinning was only applied to a certain age-class. A higher structural heterogeneity could thus be maintained in a mosaic of different age-classes (Schall et al., 2018), at least when measured at a larger spatial scale. Also in terms of the species composition, which

closely influences stand structure, a mosaic landscape mixture can have advantages compared to a single-tree mixture (Heinrichs et al., 2019). In uneven-aged stands, light-demanding species might not have enough habitat species due to the continuous crown cover. In age-class stands, the younger age-classes provide different growing conditions compared to the old age-classes and can therefore offer a broader range of different habitats, which is the basis for the benefits of a high structural heterogeneity and species diversity. Still, the old-growth phase of forests is missing in most commercial forests. An inclusion of set-aside patches could help as those are important for fauna (Gärtner and Reif, 2004; MacArthur and MacArthur, 1961), flora (Benítez et al., 2015) and other ecosystem functions and services (Fedrowitz et al., 2014; Mensah et al., 2018).

5 Conclusions and Outlook

In the challenging times for forest ecosystems in Europe and worldwide, a holistic view on the interactions between different factors that influence the performance of multifunctional forests is needed. A more detailed consideration of the interactions between forest stand structure and other factors analyzed in the present thesis therefore contributes to seeing and managing forests as complex systems (Filotas et al., 2014; Messier et al., 2013). By using different types of data and considering different aspects like wood density and biomass (Zeller et al., 2017) geographical location and climate (Zeller et al., 2018), stand development (Zeller and Pretzsch, 2019), as well as spatial scale and silvicultural management (Zeller et al., 20xx), this thesis contributes to that overarching understanding. It helps to clarify the role of forest structure by showing that the effect of a high structural heterogeneity on forest productivity can have different shapes, depending on the context. The utilized data and the holistic approach seem to be reasonable in order to understand and manage forest ecosystems in times of climatic and socio-economic challenges. Through the testing of silvicultural management scenarios, it adds a practical aspect to the knowledge on forest ecosystems and can support decision-makers to modify forest stand structure with the aim of fostering the multifunctionality of forest ecosystems in the long-term.

For a complete understanding of the role of forest structure, research can focus on examining the partial effects of each influencing factor. Apart from the geographical location, tree species composition, developmental stage and silvicultural management, also changing climatic conditions and altered growing conditions should be considered. Changing climatic conditions might be incorporated through climate-sensitive models (Härkönen et al., 2019; Trasobares et al., 2016) in combination with simulations by a growth simulator, e.g. SILVA. Through the design of virtual initial forest stands of different stand structure, the effect of a certain stand structure on various output variables supporting different ecosystem functions and services in the future can be tested. Also long-term experimental plot data from regions that correspond with the climatic conditions of Germany in the future can be further used for estimating the role of forest structure in the performance of forest ecosystem under future growing conditions.

In times of big data (Lokers et al., 2016), forest research can benefit from new technologies that enable the collection and analysis of different types and large amounts of data from around the world (Global Forest Biodiversity Initiative, 2016; Henry et al., 2015). Also forest structure might then be more easily captured and analyzed in the future. In this thesis mostly structural indices were used that are based on measured tree sizes that represents horizontal and vertical

stand structure. Further indices combining horizontal and vertical tree size distribution with further stand characteristics (Pastorella and Paletto, 2013; Storch et al., 2018) can be added. In the future, airborne laser scanning (Mura et al., 2015) and terrestrial laser scanning (Pascu et al., 2019; Seidel et al., 2019a) can be used more and more to quantify the 3-dimensional stand structure more efficiently. Still, an automatized recognition of single trees remains a challenge (Othmani et al., 2013) and often requires additional traditional inventory methods. As soon as an automatized recognition of single trees also in structurally complex and dense mixed stands is achieved, stand structure and tree species composition might be more easily captured in inventories and included in analyses of stand characteristics. A combination of terrestrial laser scanning and fractal analysis might then be the next step for a better quantification and understanding of forest structure in further detail (Dorji et al., 2019; Seidel et al., 2019b).

In the present thesis, stand productivity was quantified through the volume increment per ha and year. This is of course a general quantification ending at the border to a potential economic quantification. A higher productivity in terms of a higher volume growth might imply a higher carbon storage and production of fuel wood. In case of a lower wood density (Zeller et al., 2017) or lower wood quality (Pretzsch and Rais, 2016) this higher productivity can lead to lower economic yields. This effect might contradict an economic optimization were certain valuable assortments are needed. In future studies, not only overall volume growth, but also a more specific characterization of assortments and how those are influenced by a low or high structural heterogeneity could be included. Experimental plots that are treated with different types and intensities of silvicultural interventions can help to estimate the effect of silvicultural management on forest stand structure.

Thinning interventions are one way to modify stand structure. Thinning from below can homogenize a forest stand, while thinning from the top can enhance structural heterogeneity (Pretzsch, 1998). The aim of silvicultural management also shapes the performance of a forest in terms of the different ecosystem functions and services. Production-oriented management that implies a stronger thinning intensity than a multifunctional management, can lower structural heterogeneity and stability (Yücesan et al., 2015). In the present thesis, silvicultural management was tested depending on different initial stands, that can help to create comparable starting situations (Zeller et al., 20xx). Both on experimental plots where different management has been applied, as well as through the simulation of silvicultural interventions can the long-

term effects on stand structure and productivity be estimated. Even in managed forests, a conscious forest structure management, e.g. in terms of a close-to-nature silviculture (Schütz et al., 2016) can foster the provision of a broad range of forest ecosystem functions and services.

For the quantification of structural effects on specific ecosystem functions and services, a backwards approach of providing a list of attributes of structural characteristics that foster the habitats of trees and plants and that support further ecosystem functions and services might be a useful contribution. A broad literature review and the incorporation of experts could be a way to further quantify the needed stand structure for certain functions and services. Those key structures can then be set as a goal to reach through silvicultural management.

6 Original Publications

6.1 Contributions of the candidate to concept, data sampling, and analysis

The candidate and the supervisor Hans Pretzsch designed the concepts for the present publications. The candidate prepared and processed the German national forest inventory data for publication 2 with the help of Susanne Brandl. During a research stay in the USA, the candidate retrieved and prepared the national forest inventory data of the USA in cooperation with Jingjing Liang. The candidate prepared and processed the long-term experimental plot data for publication 1 and 3. Astor Toraño Caicoya and Hans Pretzsch supported the candidate in conceptualizing publication 4. The candidate set up the virtual forest stands, and the structural indicators for publication 4 and Astor Toraño Caicoya conducted the simulation runs for the strata in SILVA. The candidate calculated the structural indices and conducted the data analyses, interpretation of results and writing of the publications 1-4. Hans Pretzsch supervised all publications.

6.2 Lead authorships

6.2.1 Publication 1

Titel: Tree ring wood density of Scots pine and European beech lower in mixed-species stands compared with monocultures

Authors: Zeller, Laura; Ammer, Christian; Annighöfer, Peter; Biber, Peter; Marshall, John; Schütze, Gerhard; del Río Gaztelurrutia, Miren; Pretzsch, Hans

Year: 2017

Journal: Forest Ecology and Management

5-year Impact Factor: 3.601

DOI: 10.1016/j.foreco.2017.06.018

Authors' contributions: The candidate and the supervisor Hans Pretzsch designed the concept for the study. The candidate prepared and analysed the sample cores and conducted the statistical analyses with the support of Peter Biber. Christian Ammer, Peter Annighöfer, John Marshall, Gerhard Schütze, and Miren del Río Gaztelurrutia provided data and supported the writing of the manuscript.

Abstract: Mixed species stands are on the advance in Central Europe and many recently published studies have reported that they can overyield monocultures in terms of volume growth. However, as forest research has in the past been focused on monocultures, knowledge of how mixed-species stands and monocultures compare in terms of wood quality remains limited. Based on five triplets of fully stocked monocultures and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), we analyzed whether tree species mixing modifies wood quality and, more precisely, tree ring wood density.

From a total of 322 trees we sampled increment cores for the analyses of tree ring width and tree ring wood density using a lignostationTM. We found that tree ring width of Scots pine was, on average, 14% wider in mixed compared with pure stands. Tree ring width of European beech did not differ between pure and mixed stands. Tree ring wood density was lower in mixed stands compared to pure stands for both Scots pine (−12%) and European beech (−8%). Tree ring wood density and tree ring width were negatively correlated in the case of Scots pine and positively correlated for European beech.

When considering tree size and Stand density index, it was found that only tree ring width and mean tree ring wood density of European beech were influenced by stand density. Tree size had a significant effect only on tree ring wood density of European beech. The overall result of larger tree rings of Scots pine in mixed stands and a lower tree ring wood density of both species in mixed stands compared to pure stands was not influenced by stand density or tree size.

Based on the measured values of tree ring wood density we conducted estimates of how mixed stands performed in terms of biomass. We found stem biomass to be 8% lower in mixed stands compared to pure stands. Reasons for the revealed differences in tree ring wood density and consequences for, among others, overyielding, carbon storage, and wood quality are discussed.



Tree ring wood density of Scots pine and European beech lower in mixed-species stands compared with monocultures



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ABSTRACT

Mixed species stands are on the advance in Central Europe and many recently published studies have reported that they can overyield monocultures in terms of volume growth. However, as forest research has in the past been focused on monocultures, knowledge of how mixed-species stands and monocultures compare in terms of wood quality remains limited. Based on five triplets of fully stocked monocultures and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), we analysed whether tree species mixing modifies wood quality and, more precisely, tree ring wood density.

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1. Introduction

Many recent studies provide evidence that mixed-species stands can overyield monocultures by up to 30% (Bielak et al., 2014; Zhang et al., 2012). Such comparisons can be based on basal area growth (Hein and Dhôte, 2006), stem volume growth (Pretzsch et al., 2015), stem biomass growth (Thurm et al., 2016), or total above-ground biomass (Pretzsch et al., 2010). On a series

of 32 triplets in pure and mixed-species stands of Scots pine and European beech along a gradient through Europe, Pretzsch et al. (2015) and Pretzsch et al. (2016) found an average overyielding of 12% in basal area and 8% in volume growth on mixed stands. Concerning the five triplets examined in this study (Pretzsch et al., 2015), volume growth and basal area growth were found to be about equal in pure and mixed stands. Scots pine was more productive in mixed stands in terms of basal area growth (+18%) and volume growth (+18%) while European beech was negatively influenced by the mixing (basal area growth −21%, volume growth −12%) when compared to the neighbouring pure stands (Table A5).

The mean overyielding in volume growth of mixed stands found on the 32 triplets and possibly the higher productivity of Scots pine

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in mixed stands found on the selection of five triplets may result from a more complex structure in mixed stands – both above and below ground (Pretzsch, 2014) – leading to a complementary resource use by the associated species (Richards et al., 2010) and a resulting reduction in competition (Vandermeer, 1989). Positive effects of a more complex structure on productivity can additionally result from e.g., hydraulic lift, atmospheric nitrogen fixation or frost protection, potentially leading to a facilitation (Callaway and Walker, 1997) of one or more species in mixture and can result in an overyielding (Forrester et al., 2006; Vandermeer, 1989). Such an overyielding is often achieved through morphological acclimation to inter-specific environments (Metz et al., 2013; Pretzsch and Dieler, 2012) where mixing can modify e.g. crown morphology (Bayer et al., 2013; Pretzsch, 2014) and root-shoot relationship (Bolte et al., 2004; Robinson et al., 2010). However, not much is known about how wood properties may be influenced by inter-specific neighbourhoods.

When exploring structural differences between pure and mixed stands and the performance of species in a mixture, tree ring width and tree ring wood density can reveal more information on the processes behind mixing effects. In the case of drought, Metz et al. (2016) found wider tree rings for European beech in mixed stands compared to pure stands; this is explained by an enhanced water supply for Beech in mixed stands, which is consistent with their analysis of stable isotopes. Wider tree rings in coniferous trees are known to result in a lower tree ring wood density (DeBell et al., 1994; Franceschini et al., 2013). For European beech, tree ring wood density is not particularly influenced by tree ring width (Diaconu et al., 2016). The actual effect of tree ring width on tree ring wood density might furthermore depend on the timing of climatic events influencing growth throughout the growing season (Bouriaud et al., 2004; Franceschini et al., 2013) and the general fertility of sites (Diaconu et al., 2016). Dutilleul et al. (1998) found that the negatively correlated tree ring width and tree ring wood density in Spruce was no longer valid for very high growth rates induced by site fertility or climatically favourable conditions.

A reduction in tree ring wood density might be an appropriate indicator for reduced stress from drought events. Schuldt et al. (2016) recently showed that the vessel diameter of European beech increased and the vessel number decreased on sites with high precipitation, while the contrary was found on dry sites. As vessel density was negatively related to tree ring wood density (Schuldt et al., 2016) and Beech was found to be less water stressed in the neighbourhood of Pine (Metz et al., 2016), one may expect lower tree ring wood density in mixtures of Pine and Beech.

However, other than by Kennel (1965), the effect of mixing on tree ring wood density has hardly been explored. This is a significant lack of knowledge, as tree ring wood density has a strong effect on stem stability, wood quality, carbon content and storage, as well as on decomposition rates. If tree ring wood density differs between monocultures and mixed-species stands, it can also change how mixed stands perform in terms of dry mass productivity and C-fixation compared with monocultures.

In order to address this topic, we sampled tree ring wood density on five triplets of fully stocked monocultures and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) at different locations in Europe in order to analyse whether tree species mixing modifies wood quality. As it has the advantage of being non-destructive and time-saving, we applied high-frequency densitometry to measure tree ring width and tree ring wood density.

By further exploring the previously found overyielding in volume of mixed stands of Scots pine and European beech, we tried to find out: if tree ring width and tree ring wood density are, on average, different in pure and mixed stands (QI); if tree ring wood density is independent of tree ring width (QII); and if tree ring

width and tree ring wood density in pure and mixed stands are different for equal tree size and at equal stand density (QIII). Based on QI–QIII we developed the following hypotheses:

HI: Mean tree ring width and mean tree ring wood density in pure and mixed stands are equal.

HII: Tree ring width and tree ring wood density are independent.

HIII: For trees of equal size and at equal stand density, mean tree ring width and mean tree ring wood density in pure and mixed stands are equal.

2. Material and methods

2.1. Material

2.1.1. Study area

Each of the five locations examined in this study consists of a triplet containing one mixed stand of Scots pine and European beech and one pure stand of each species. Three of the triplets are located in the south of Germany (Alzenau, Bamberg and Steigerwald), one in eastern Germany (Teupitzer Forst) and one in northern Spain (Huerta de abajo) (Fig. 1). Their similarity in terms of stand characteristics (Pretzsch et al., 2015) provides the basis for comparisons between pure and mixed stands. Geographical data of the five triplets is presented in Table 1.

2.1.2. Data

In this study we measured the tree ring width and tree ring wood density of 163 tree cores of Scots pine and 159 tree cores of European beech, sampled in 2015. Only dominant trees were sampled. Among those, random sampling was applied. The stands are between 40 and 80 years old (Pretzsch et al., 2015), when relating to total tree age. All tree cores (one per tree) were taken either from the northern or the eastern side of the trees at breast height. The latest fully built tree ring valid for our analysis is from 2014. Due to a decreasing sample size when going back further in time, we included only tree rings from 1950 and later. Since only a few samples contained juvenile wood and did not change model outcomes significantly in test runs, all tree ring data from 1950 until 2014 was included. There has been no thinning on the plots in recent years, which is why stand density index (SDI) is close to maximum (Pretzsch et al., 2015).

SDI values of the mixed stands were calculated by adding up individual SDI values per species in the mixture in order to obtain one SDI value per mixed stand and triplet.

Table A1 shows the most important characteristics of the five locations and their pure and mixed stands of Scots pine and European beech examined in this study. For a more detailed overview of the trees examined in this study see Table A2.

2.2. Methods

2.2.1. High-frequency densitometry

For the measurements of ring width and tree ring wood density of Scots pine and European beech, we used a LIGNOSTATION™. The use of high-frequency densitometry allows for non-destructive and quick measurements (Schinker et al., 2003) compared to the commonly used X-ray densitometry (Wassenberg et al., 2014).

For the measurements using a LIGNOSTATION™, a probe moves along the wood surface with a pressure of 1 N, which is needed to prevent the measurement of air between the probe and wood sample material (Schinker et al., 2003). The tip of the probe contains a transmitting electrode as well as a receiving electrode; the two being separated from each other by a metal shield to avoid direct

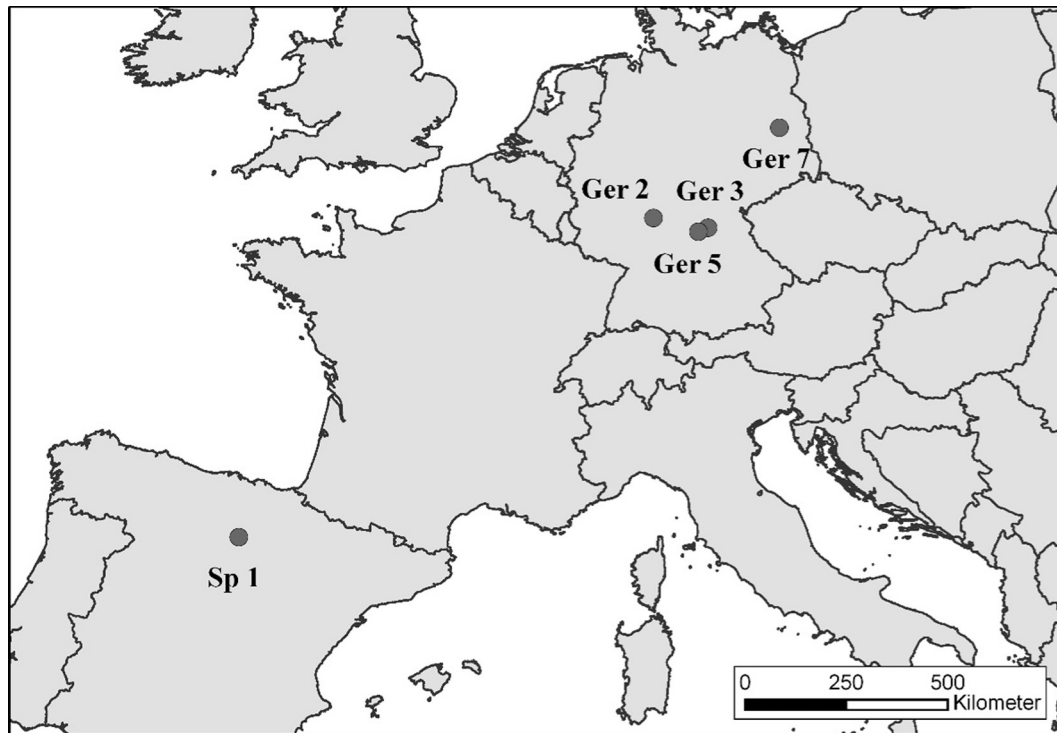


Fig. 1. The analysed triplets Alzenau (Ger 2), Bamberg (Ger 3), Steigerwald (Ger 5), Teupitzer Forst (Ger 7), Huerta de abajo (Sp 1).

Table 1
Geographical information about the triplets.

Name	Code	Latitude N	Longitude E	Altitude a.s.l. (m)	Precipitation (mm year ⁻¹)	Temperature (°C)	Geological substrate
Alzenau	Ger 2	50°06'48.74"	09°03'54.36"	250	720	9.0	Slightly loamy sand
Bamberg	Ger 3	49°53'11.64"	10°58'13.12"	250	650	8.0	Loamy sand
Steigerwald	Ger 5	10°38'10.10"	49°47'55.91"	125	713	9.5	Slightly loamy sand
Teupitzer Forst	Ger 7	52°04'45.55"	13°37'06.05"	60	520	8.6	Sandy
Huerta de abajo	Sp 1	42°05'57.00"	-03°-10'-19.00"	1290	860	8.9	Sandy loam

Reference period for climate data: 1994–2013.

'flow' of the electromagnetic field. The dielectric properties of wood are determined by the ratio of cell wall material and air. By measuring the amount of the transmitted signal received on the other side of the shield, the tree ring wood density of the sample material is calculated automatically (Schinker et al., 2003).

All tree cores were stored in the same room prior to the scanning process to avoid big differences in humidity and temperature. If no diamond fly cutter is available, Wassenberg et al. (2015) suggest sanding for sample preparation as the best solution. We sanded the sampled tree cores with 180-, 400- and 800-grid sanding paper using a belt sander and 1200-grid sanding paper in manually applied sanding in order to achieve an adequately smooth surface to ensure an accurate and uninterrupted scan (Wassenberg et al., 2015, p. 11). Even though the absolute values of tree ring wood density obtained in this way may differ from other measuring methods, relative comparisons are still possible because all samples were measured under the same conditions and adjustments. The only alteration we applied was to reduce the adjustments for height by 1 mm for European beech leading to a higher pressure of the probe on the wood surface for the samples of this species. We did so because using the same height adjustments for European beech as for Scots pine did not yield any reasonable measurement results. We assumed that the higher tree ring wood density of European beech created the need to apply a higher pressure on the sample surface.

When comparing values for tree ring wood density measured in this study to mean values per species generated by water displacement measurements in other studies, the differences between values produced by the two methods, especially for European beech, become visible. Further calibration of the LIGNOSTATION™ would be needed to generate absolute values in tree ring wood density. We assumed that our samples had a humidity of about 12% after they had been stored at room temperature. When comparing high-frequency densitometry and water displacement measurements from different untreated stands, Kemmerer (2016) and Räbel (2016) found values from high-frequency densitometry to be 4% higher for Scots pine and 20% lower for European beech compared to water displacement measurements. Correction factors of 0.92 for Scots pine and 1.19 for European beech (Table A6) deduced from this comparison were used in our study to convert measured values of the LIGNOSTATION™ into absolute tree ring wood density values. These were then used for biomass calculations (Table A5).

Since the focus of our study was to compare pure and mixed stands, measuring relative differences in tree ring wood density was the main objective. In order to estimate the difference between our results measured and real values of tree ring wood density (Table A6), we compared our results to 30 samples of Scots pine and 30 samples of European beech analysed in water in displacement measurements (Saranpää, 2003b). The samples come

from different sites and are aggregated into a mean value which serves as a reference.

2.2.2. Linear mixed effects model

Dealing with hierarchical or nested data means taking into consideration that samples are not independent from each other. Samples belonging to one group or repeated measures of a certain location or individual might have the same random effects (Crawley, 2009, p. 627). The sampling data does therefore not meet the assumption of independence which would be necessary in linear regression models (Zuur et al., 2009, p. 102). By including not only fixed effects but also random effects, linear mixed effects models are applied in order to avoid the so-called 'pseudoreplication' (Crawley, 2009, p. 629). The random effect included in our models addresses intercorrelation of the samples caused by being part of the same triplet as well as tree rings belonging to one tree.

In order to address hypotheses HI–HIII, we set up model functions to describe the effect of mixing, diameter at breast height (DBH) and stand density index (SDI) on ring width and tree ring wood density using linear mixed effects models. Non-significant factors in the initial model functions were then eliminated in stepwise reduction resulting in final model functions ([1.a], [1.b], [2], [3.a], [3.b]). Stepwise reduction is used in order to acquire a model function with correct p-values describing the effect of different factors on a variable (Crawley, 2009, p. 635). For HI, only the mixing effect and the nested design of the data are considered ([1.a], [1.b]) and predictions for operational decisions concerning mean ring width and mean tree ring wood density per tree over all examined triplets are made. For HII, using single tree ring data was necessary for analysing the influence of ring width on tree ring wood density ([2]). The model functions for HIII are supposed to analyse the effects of mixing on mean ring width and mean tree ring wood density in pure and mixed stands for equal tree size and stand density ([3.a], [3.b]). Here, as for HI, we used mean values per tree to enable values of stand density to be included in the model function.

For the application of linear mixed-effects models we used the lme function of the nlme package in R (Pinheiro et al., 2016).

We set up the following model functions in order to address questions QI–QIII:

QI: Are mean tree ring width and mean tree ring wood density equal in monocultures and mixed-species stands?

The following model functions describe the mixing effect on mean ring width and mean tree ring wood density, respectively, in order to examine if there are significant differences between pure and mixed stands.

$$RW_{ij} = a_0 + a_1 * Mix_{ij} + b_i + \varepsilon_{ij} \quad (1.a)$$

$$MD_{ij} = a_0 + a_1 * Mix_{ij} + b_i + \varepsilon_{ij} \quad (1.b)$$

RW_{ij} is the mean ring width per tree j on triplet i . MD_{ij} is the mean tree ring wood density per tree j on triplet i . Mix_{ij} is the effect of mixing on tree ring width or tree ring wood density for tree j on triplet i . Parameter a_0 is the intercept, thus tree ring width or tree ring wood density in pure stands, i.e. the mixing factor equals 0. Potential differences in site characteristics on the different triplets are addressed by a random effect b_i for triplet i . The error term ε_{ij} contains the remaining unexplained variation for tree j on triplet i .

QII: Is tree ring wood density independent from tree ring width?

The influence of tree ring width on tree ring wood density is defined by the following model function.

$$D_{ijk} = a_0 + a_1 * Mix_{ij} + a_3 * RW_{ijk} + b_{ij} + \varepsilon_{ijk} \quad (2)$$

D_{ijk} is the tree ring wood density of a tree ring k (according to the calendar year) of tree j on triplet i . RW_{ijk} is the width of a tree ring k of tree j on triplet i and is examined as the main effect. Differences between the triplets due to site characteristics and the nested design of tree rings belonging to one tree are addressed by random effect b_{ij} . All remaining variation that is not explained by the model is contained in ε_{ijk} .

QIII: Are tree ring width and tree ring wood density equal in pure and mixed stands for equal tree size and stand density?

In order to analyse if the effect of mixing on tree ring width depends on stand characteristics, we included stand density index in the model. As tree ring width and DBH in even-aged stands represent the same information, DBH was not included in this model function.

$$RW_{ij} = a_0 + a_1 * Mix_{ij} + a_4 * SDI_{ij} + a_6 * Mix_{ij} * SDI_{ij} + b_i + \varepsilon_{ij} \quad (3.a)$$

For analysing the mixing effect on tree ring wood density for equal tree size and at equal stand density we chose to include diameter at breast height (DBH) and stand density index (SDI). Even though values of individual tree rings were used for the analysis under HII, we used mean values per tree for tree ring width and tree ring wood density in this case in order to enable the expansion of the model by the static SDI values. Non-significant factors, such as three-way and most of the potential two-way interactions were eliminated in stepwise reduction. The interaction term of a main effect with the mixing factor Mix_{ij} addresses the influence of a main effect in the mixed stand. Model functions were only applied if a visual pre-check of the data was considered meaningful.

$$MD_{ij} = a_0 + a_1 * Mix_{ij} + a_2 * DBH_{ij} + a_4 * SDI_{ij} + a_5 * Mix_{ij} * DBH_{ij} + a_6 * Mix_{ij} * SDI_{ij} * b_i + \varepsilon_{ij} \quad (3.b)$$

We then applied a correction factor to the tree ring wood density values measured in this study (Table A6) and used volume measurements from previous studies on the same triplets (Pretzsch et al., 2015) for a rough calculation of biomass of both species in order to compare their performance in pure and mixed stands (Table A5).

3. Results

Tree ring width in Scots pine and European beech declined over time (Fig. 2). Tree ring wood density was more constant over time and was lower in mixture than in pure stands for both species.

3.1. QI: Are mean tree ring width and mean tree ring wood density equal in pure and mixed stands?

First, when only examining the effect of mixing, Scots pine appeared to have a 14% higher tree ring width in mixed stands compared to pure stands. Tree ring width of European beech showed an opposite trend in mixed stands (−5%) compared to pure stands but the difference was non-significant. Tree ring wood density of Scots pine was 12% lower in mixed stands compared to pure stands. For European beech, tree ring wood density was 8% lower in mixed stands compared to pure stands (Fig. 3 and Table 2).

3.2. QII: Is tree ring wood density independent from tree ring width?

When looking at all tree rings, tree ring wood density of Scots pine was negatively correlated with tree ring width and thus significantly decreased with increasing tree ring width (Fig. 4 and Table 2). Tree ring wood density in European beech was positively correlated with tree ring width and therefore significantly

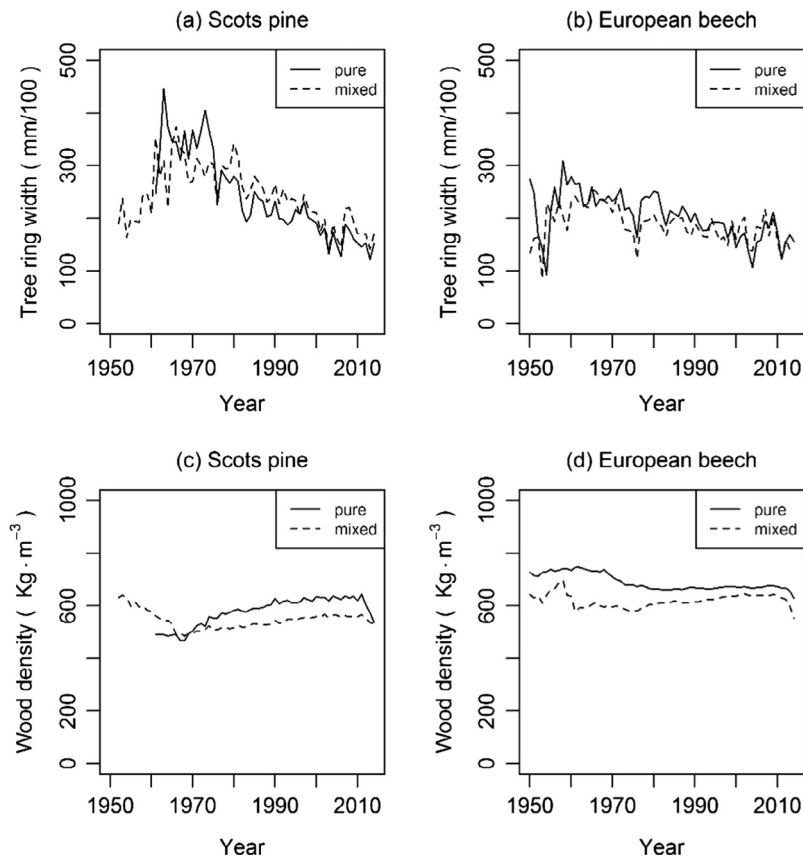


Fig. 2. Tree ring width of Scots pine (a) and European beech (b) and tree ring wood density of Scots pine (c) and European beech (d) in pure and mixed stands from 1950 to 2014.

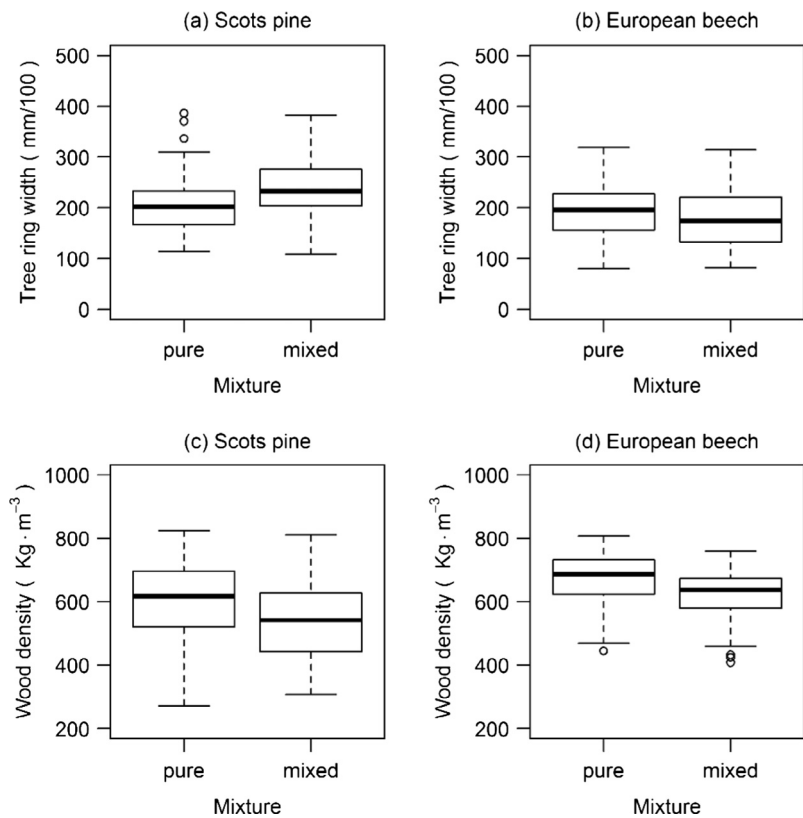


Fig. 3. Differences between pure and mixed stands in mean tree ring width of Scots pine (a) $p < 0.05$, $R^2 = 0.07$ and European beech (b) n.s. and differences in mean tree ring wood density of Scots pine (c) $p < 0.001$, $R^2 = 0.39$ and European beech (d) $p < 0.001$, $R^2 = 0.09$.

Table 2
Results of linear mixed-effects model functions QI–QIII.

Model function	Depend. var.	Species	Value	Intercept	Mix	DBH	RW	SDI	Mix * DBH	Mix * SDI	Mixing effect (%)	R ² (conditional)	
				a ₀	a ₁	a ₂	a ₃	a ₄	a ₅	a ₆			
QI	Mean ring width	Sc.p.	Mean			239.3	219.90	986.50					
		E.be.	Mean			227.00	186.96	815.70					
	Mean ring width	Sc. p.	Value	206.80	29.03							14.04	0.07
			SE	6.25	8.92								
			p-value	.000	.001								
	Mean ring width	E. be.	Value	191.38	−10.21							−5.33	0.07
			SE	10.33	8.81								
			p-value	.000	.248								
	Mean wood density	Sc. p.	Value	595.63	−72.87							−12.23	0.39
			SE	28.16	15.79								
			p-value	.000	.000								
	Mean wood density	E. be.	Value	665.43	−50.1							−7.53	0.09
SE			11.09	13.35									
p-value			.000	.000									
QII	Wood density	Sc. p.	Value	629.27	−95.85		−0.10					0.79	
			SE	38.98	3.13		0.01						
			p-value	.000	.000		.000						
	Wood density	E. be.	Value	637.93	−12.00		0.048					0.66	
			SE	8.05	2.95		0.008						
			p-value	.000	.000		.000						
QIII	Mean ring width	Sc. p.	Value	190.8	30.44				n.s.	n.s.	15.95	0.07	
			SE	22.88	9.11								
			p-value	.000	.001								
	Mean ring width	E. be.	Value	254.99	n.s.				−0.08	n.s.	0.00	0.12	
			SE	28.57					0.03				
			p-value	.000					.017				
	Mean wood density	Sc. p.	Value	not analysed ^a									
			SE										
			p-value										
	Mean wood density	E. be.	Value	490.17	−48.14	0.27			0.14	n.s.	n.s.	−7.23	0.18
			SE	46.61	12.98	0.09			0.04				
			p-value	.000	.000	.003			.001				

Scots pine, Sc. P.; European beech, E. be.; grey parts, not included in model; non-significant effects eliminated in stepwise reduction, n.s.

Values in bold significant at $p < 0.05$.

Calculation of mixing effect (%) by inserting mean values in linear mixed-effects model function.

^a Visual pre-check showed no meaningful dependency of data.

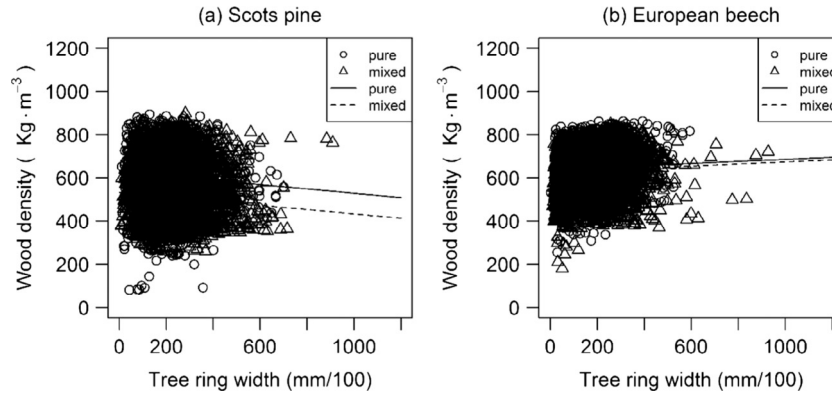


Fig. 4. Correlation of tree ring width and tree ring wood density in pure and mixed stands of Scots pine (a) $p < 0.001$, $R^2 = 0.79$ and European beech (b) $p < 0.001$, $R^2 = 0.66$. Total number of observations/tree rings: 13301.

increased with increasing tree ring width. Interaction effects with mixture were eliminated due to non-significance.

3.3. QIII: Are mean tree ring width and mean tree ring wood density equal in monocultures and mixed-species stands of equal tree size and equal stand density?

When examining not only mixing, but also stand density index (SDI) as potential effects on tree ring width, it was found that SDI did not have any effect on tree ring width of Scots pine. For European beech, tree ring width and stand density index were negatively correlated. After considering the effect of stand density

index, it was shown that mixing still did not have any effect on tree ring width in European beech (Fig. 5 and Table 2).

When calculating tree ring width using the expanded model function (Tables 2 and A3), it was found that tree ring width of Scots pine in mixed stands was 16% higher than in pure stands. For European beech no difference in tree ring width between pure and mixed stands was found. These values differ slightly from HI due to different model functions used for their calculation. Nevertheless, the results show that when considering tree size and stand density, the mixing effect found under HI for Scots pine remains valid.

The effects of mixture, DBH and SDI on tree ring wood density of Scots pine and European beech are presented in Fig. 7 and Table 2.

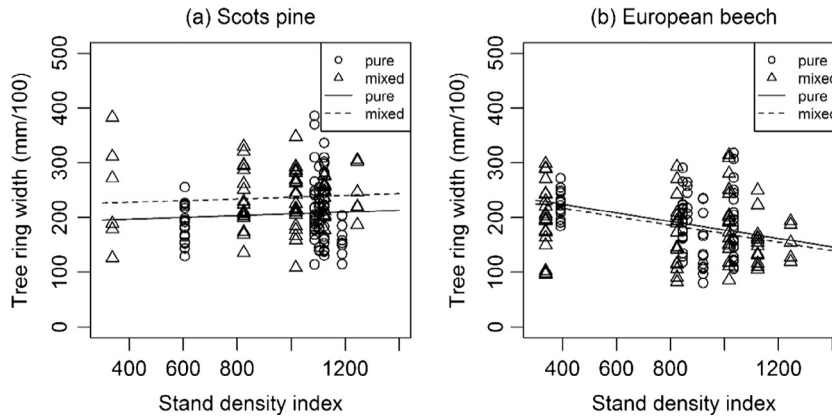


Fig. 5. Effect of stand density index on tree ring width of Scots pine and European beech. For Scots pine ($R^2 = 0.07$): SDI (a) n.s. For European beech ($R^2 = 0.12$): SDI (b) $p < 0.05$.

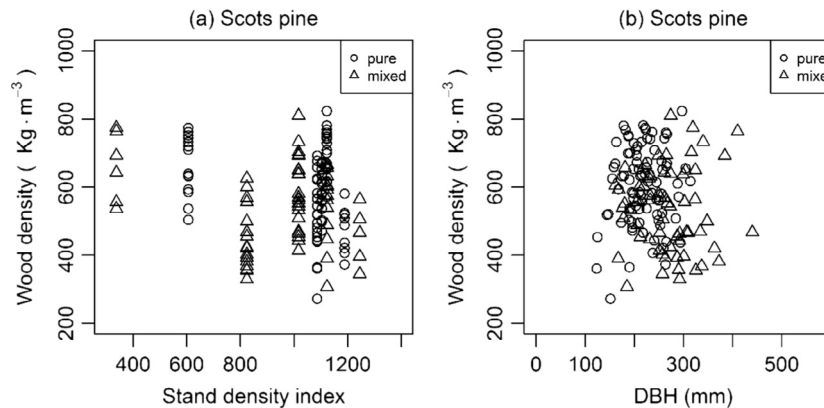


Fig. 6. Tree ring wood density, SDI and DBH in pure and mixed stands of Scots pine. No model was fitted to the data.

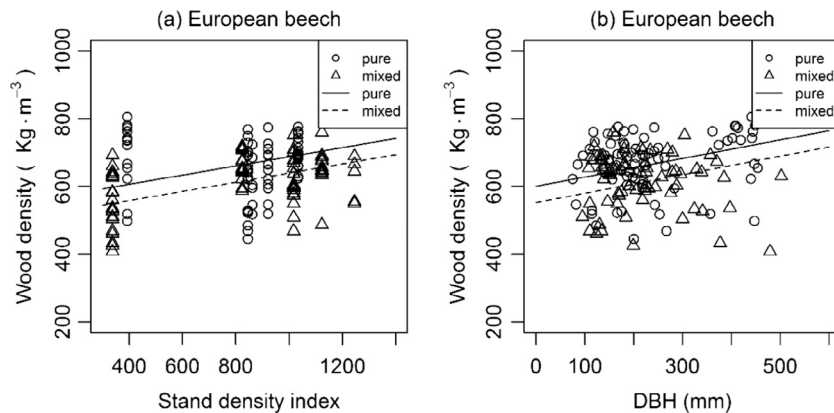


Fig. 7. Tree ring wood density, SDI and DBH in pure and mixed stands of European beech. (a) and (b) Mixing effect, SDI and DBH significant $p < 0.005$, $R^2 = 0.18$.

For Scots pine, testing of possible relationships between DBH, SDI and tree ring wood density were not considered after a visual pretest showed that in the given data no relationships can be found (Fig. 6). The 12% lower tree ring wood density of Scots pine in mixed stands found under HI therefore remains valuable and demonstrates that the mixing effect is reliable and does not change with stand density or tree size. The negative relationship between tree ring wood density and tree ring width is not visible in DBH since mean DBH values per tree are used.

For European beech, SDI and DBH significantly influenced tree ring wood density, but the size of the effect was equal in pure and mixed stands. In the mixture, tree ring wood density of European beech was found to be 7% lower than in pure stands. This shows that the mixing effect found under HI (−8%) is still present and significant after excluding the effects of tree size and stand density index (Tables 2 and A4).

After measuring mean tree ring wood density of pure and mixed stands, we used the generated values from HI to calculate how mixed stands were performing compared to pure stands in terms of biomass production (Table A5). Scots pine was producing 11% more biomass in mixed stands than in pure stands. European beech in mixed stands produced 10% less biomass. In total, biomass was 8% lower in mixed stands compared to pure stands. To calculate biomass we applied correction factors of 0.92 for Scots pine and 1.19 for European beech in order to enable comparisons of tree ring wood density values between the two species. Correction factors were derived from an internal study comparing high-frequency densitometry and water displacement measurements (Table A6) and help to overcome the issue of high-frequency measurements not providing absolute tree ring wood density values (see Methods).

4. Discussion

4.1. Interpretation of results

Tree ring width of Scots pine was found to be significantly higher in mixed stands versus pure stands, whereas tree ring width of European beech was not significantly influenced by the mixing with Scots pine. Tree ring wood density was lower in mixed stands for both species.

The results can contribute to understanding the differences between pure and mixed stands in terms of basal area growth and volume growth. When trying to explain mixing effects on volume growth, significant variations in allometric variables between species can play an important role and should therefore be considered (Monserud and Marshall, 1999).

Studies about tree ring wood density are still rare but Kennel (1965) found that tree ring wood density of European beech was not affected by the mixing with Norway spruce when examining

fully stocked mixed stands of Norway spruce and European beech. Norway spruce, however, had a significantly higher tree ring wood density in the mixed stands. Pretzsch and Rais (2016) found that in seven of the nine reported comparative studies concerning complex and homogeneous stands, tree ring wood density was not influenced by the mixing of species even though tree ring width variability seems to increase in complex stands.

We hypothesise that the differences in tree ring wood density between the pure and mixed stands of our study are a result of acclimatisation to an inter-specific neighbourhood. For that purpose, tree species may change their growth partitioning in mixed-species stands. The internal tree resource allocation may prioritise growth and expansion at the expense of stability and defence when coping with inter-specific competition. The size growth of a tree enhances its access to light and, consequently, both species will follow the strategy of growth rather than defence (Matussek et al., 2005, 2012).

Most of the comparisons of productivity in mixed and pure stands are based on stem volume production (Liang et al., 2016; Pretzsch et al., 2015). Comparisons based on total biomass production may produce different results, as tree species mixing can change stem-crown allometry (Bayer et al., 2013), root-shoot relationship (Thurm et al., 2017) and also tree ring width and tree ring wood density (Pretzsch and Rais, 2016). An increase in crown size in relation to stem size in mixed-species stands as reported by Dieler and Pretzsch (2013) and Pretzsch (2014) would mean that the overyielding is even higher when calculated for the total above-ground volume of mixed versus pure stands. However, the decrease in root in relation to shoot growth as reported by Thurm et al. (2017) and the lower tree ring wood density in mixed stands revealed in our study can consequently modify the overyielding of mixed stands as soon as total biomass is taken into account. In our study, biomass in mixed stands calculated from stem volume and tree ring wood density is lower than in pure stands despite the measured overyielding in volume on mixed stands.

When examining the relation between tree ring width and tree ring wood density, we found tree ring wood density of both Scots pine and European beech to be clearly dependent on tree ring width, negatively related in the case Scots pine and positively related in the case of European beech. Supporting our findings, Genet et al. (2012) state that the way in which tree ring width and tree ring wood density are related depends on whether the tree is a conifer, ring-porous hardwood or diffuse-porous hardwood. In ring-porous trees like oak or ash, growth rate and tree ring wood density were found to be positively correlated, whereas softwood species like Pine show a decreasing tree ring wood density with increasing growth rate. Tree ring wood density in diffuse-porous hardwood species, like beech, acer or birch is usually not influenced by tree ring width (Diaconu et al., 2016; Hakkila, 1989).

Finally, when also considering tree size and stand density for HIII in order to test if the differences between pure and mixed stands found for HI represent real mixing effects, the mixing effect on tree ring width were shown to still be significant for Scots pine.

Tree ring width of European beech remained unaffected by mixing for equal tree size and stand density as found under HI.

When looking at tree ring wood density, the non-existing influence of stand density and tree size on tree ring wood density of Scots pine show that the mixing effects found under HI are valid.

For European beech, we found a 7% lower tree ring wood density in mixed compared to pure stands. Differing values in the results found under HI come from an only approximate means of calculating tree ring wood density involving the insertion of mean values in the final model function. Nevertheless, the significantly lower tree ring wood density of European beech in mixed stands compared to pure stands is visible even though stand density is considered in HIII.

The fact that stand structure can influence tree ring wood density is also stated by Bues (1985), Grammel (1990), Hapla (1985), Todaro and Macchioni (2011), Brazier and Mobbs (1993), Larocque and Marshall (1995), Moore et al. (2015) and Zhang et al. (2006) who found a reduction in tree ring wood density of coniferous trees with increasing spacing and thinning which could not be shown in our study. Tree ring wood density of deciduous trees is rather known to remain unaffected in most cases (Metzger, 1998; Pérez and Kanninen, 2005). This differs from the results of our study which showed a significant effect of SDI on tree ring wood density for European beech. These findings still suggest that stand density should be taken into account when examining mixing effects in order to exclude potential dependencies of tree ring wood density on stand density. Apart from stand structure and species-specific traits, climatic conditions and site characteristics can have an impact on the correlation of tree ring width and tree ring wood density (Bernhart, 1964; Kreml, 1977).

4.2. Relevance for forest management

The consequences of a reduction in tree ring wood density could include e.g. a loss of mechanical stability (Anten and Schieving, 2010) against e.g. breakage by wind or snow since tree ring wood density is strongly correlated with timber strength (Saranpää, 2003b), hardness and abrasiveness (Bacher and Krosek, 2014; Pretzsch and Rais, 2016). It still remains to be proven whether or not the reduction in tree ring wood density in mixed stands found in this study negatively influences stability.

When it comes to carbon storage, a lower tree ring wood density results in lower carbon content in a given stock of standing volume. Our finding that tree ring wood density of both species in mixed stands is lower than in pure stands indicates a lower amount of carbon storage under *ceteris paribus* conditions; i.e. if other characteristics such as stem shape, root-shoot and stem-crown allometry are similar in pure and mixed stands. As the proportion of crown, branches and twigs in relation to stem is higher in mixed than in pure stands (Dieler and Pretzsch, 2013) part of the lower biomass associated with tree ring wood density reduction may be cancelled out or overcompensated by a higher branch fraction. Allometric functions made for pure stands will have to be adapted to mixed stands and include differences in allometric traits of individual trees in mixture and interaction effects (Pretzsch, 2014) in order to estimate and compare productivity of pure and mixed stands.

When the resource-use efficiency of a forest (Binkley, 2012), e.g. biomass per ha of forest, is calculated, an overyielding in volume of mixed forests can lead to the conclusion that resource-use efficiency is higher. When focussing on the production of quality timber only, an overyielding in stem volume found on mixed stands can be an advantage disregarding a lower tree ring wood density, given that stability is still sufficient despite reductions in tree ring

wood density. Ongoing studies on within-tree growth partitioning in mixed versus pure stands will clarify how mixed stands perform compared to pure stands. Here, results depend on whether stand productivity is defined by stem volume productivity, which is of primary interest for forestry, or by total biomass production, which is relevant for ecosystem understanding and carbon balance.

4.3. Methodological considerations

The analysis of tree ring wood density in this study is especially interesting as it is usually measured by weight and volume or X-ray scanning (Beall, 2007; Saranpää, 2003a). The new method used in our analysis, high-frequency densitometry, offers an alternative to these time-consuming and destructive methods. When comparing high-frequency densitometry and X-ray densitometry, Schinker et al. (2003, p. 235) found similar results for tree ring wood density of Norway spruce. Until now, high-frequency densitometry has mostly been used to calculate relative values and variations in tree ring wood density. To achieve absolute mass density values, a more accurate calibration for each tree species would be necessary (Wassenberg et al., 2014).

Concerning sample preparation, an extra device – when using a belt sander instead of a diamond fly cutter – can be useful for a more precise alignment of the sample on the belt sander. Manually induced contact of the sample on the belt sander can lead to a lower geometrical accuracy of the surface. Reducing the grain size of the sanding paper in order to reduce problems caused by sanding dust on the wood surface could also be considered to improve scanning results (Wassenberg et al., 2015, p. 14). More studies on the precision of high-frequency densitometry are currently being conducted.

Concerning the statistical method in our study, a larger sample size and stands with more homogenous stand densities could help to clarify the effect of SDI on tree ring width and tree ring wood density. Biomass calculated in this study also varied between locations. This suggests the need to verify correction factors through an expansion of this study to the whole set of 32 triplets and also to measure tree ring wood density of all examined triplets also in water displacement measurements. Since some of the tree rings included in this analysis were juvenile wood and thus not as representative as a normal tree ring, we also ran parts of the analysis for the last 30 years only and compared results. As results were not significantly different from the dataset containing all 65 years from 1950, the data was still included in the analysis thereby providing a larger sample pool.

4.4. Perspectives

This study is based on a limited dataset. In further studies, more triplets could be included in order to find out if the outcome of this study applies to other triplets, different site characteristics and climatic conditions. Also, inter-annual climatic conditions, which can influence tree ring width and tree ring wood density tested on pure and mixed stands (Bouriaud et al., 2004; Miina, 2000; Olivar et al., 2015; Ponton et al., 2001), might have to be considered. Additionally, different species compositions could be tested for inter-species reactions, potential competition or niche separation and resulting differences in tree ring width or tree ring wood density. In ongoing research, mixing effects on tree ring wood density are also being analysed in greater detail by taking tree cores not only from breast height, but also from different heights across the tree stem.

Another relevant topic is the effect of inter-annual climatic conditions on tree ring wood density. Since the triplets examined in this study have not undergone any silvicultural treatments in recent years, similar studies on more intensively managed and productively used sites could provide further results. In particular, the combination of initial stand structure and short-term and long-term silvicultural treatments that imply changes in stand structure seems to be an interesting topic in the investigation of mixing

effects and should be analysed more intensively in this context. In any case, tree ring wood density should be examined further in order to improve estimates of biomass production, carbon storage, stem stability and decomposition rates in mixed-species forests. These factors may be especially important when trying to gather a more complete estimate of forest resources and the question of how to manage them sustainably in the long term.

Acknowledgements

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Appendix A.

See Tables A1–A6.

Table A1
Stand characteristics of pure and mixed stands of Scots pine and European beech.

Triplet	Species	n	Stand age (years)	N (trees ha ⁻¹)	d _q (cm)	h _q (m)	SDI (ha ⁻¹)	V (m ³ ha ⁻¹)	IV (m ³ ha ⁻¹ year ⁻¹)
Ger 2	Sc p. mono	22	55	1461	21.21	25.28	1122	581	21.90
	Sc p. mixed	22	55	471	26.83	27.39	528	329	10.50
	E. be. mono	21	55	2022	16.46	22.39	1034	474	21.50
	E. be. mixed	20	55	604	21.94	25.98	490	300	13.73
Ger 3	Sc p. mono	21	47	2054	16.81	20.69	1086	407	19.99
	Sc p. mixed	13	47	1529	15.56	20.59	714	255	12.97
	E. be. mono	19	47	2090	14.22	20.95	845	334	16.87
	E. be. mixed	13	47	1099	13.49	19.29	408	144	7.19
Ger 5	Sc p. mono	19	57	1324	22.31	22.43	1103	517	17.69
	Sc p. mixed	19	57	346	29.55	26.15	452	256	7.27
	E. be. mono	14	57	1635	17.48	23.88	921	482	22.50
	E. be. mixed	16	57	489	21.07	24.99	372	219	8.76
Sp 1	Sc p. mono	9	40	1667	20.24	16.20	1188	399	12.40
	Sc p. mixed	6	40	1082	21.32	17.33	838	310	11.65
	E. be. mono	6	40	2542	12.75	16.38	862	248	15.34
	E. be. mixed	5	40	1477	11.20	15.22	407	99	5.23
Ger 7	Sc p. mono	16	80	1579	13.75	15.49	605	162	7.77
	Sc p. mixed	6	80	82	25.94	21.79	87	44	1.94
	E. be. mono	18	80	300	29.54	24.40	392	266	9.36
	E. be. mixed	20	80	327	21.17	17.31	250	105	5.04

Five triplets were included consisting of one mixed-species stand and two mono-specific stands each.

Scots pine, Sc. P.; European beech, E. be.; monocultures, mono; mixed-species stands, mixed.

Tree number (trees ha⁻¹), N; quadratic mean diameter (cm), d_q; height of the tree with quadratic mean diameter (m), h_q; stand density index (trees ha⁻¹), SDI; standing volume (m³ ha⁻¹), V; periodic annual volume increment (m³ ha⁻¹ year⁻¹), IV.

Table A2
Sample trees of Scots pine and European beech in pure and mixed stands.

Species	Unit	Mean	SD (±)
Sc. p. mono (n = 87)	Diameter at breast height	mm	218.06
	Crown radius ^a	m	1.49
	Crown ratio	m m ⁻¹	0.29
	Tree ring width	mm/100	207.24
Sc. p. mixed (n = 66)	Diameter at breast height	mm	267.27
	Crown radius ^a	m	1.44
	Crown ratio	m m ⁻¹	0.28
	Tree ring width	mm/100	236.51
E. be. mono (n = 78)	Diameter at breast height	mm	237.16
	Crown radius ^a	m	1.79
	Crown ratio	m m ⁻¹	0.52
	Tree ring width	mm/100	191.67
E. be. mixed (n = 74)	Diameter at breast height	mm	216.39
	Crown radius ^a	m	2.22
	Crown ratio	m m ⁻¹	0.61
	Tree ring width	mm/100	182.01

Five triplets were included consisting of one mixed-species stand and two mono-specific stands each.

Scots pine, Sc. P.; European beech, E. be.; monocultures, mono; mixed-species stands, mixed

^a No data available for triplet Ger 7.

Table A3

Calculations of overall tree ring width resulting from linear mixed effects model QIII.

	Intercept	Mix	DBH	SDI	Mix * DBH	Mix * SDI	Result	Diff. absolut	Diff. in%
	a ₀	a ₁	a ₂	a ₄	a ₅	a ₆			
Results lme Sc. P.	190.8	30.44							
Mean value									
Ring width Sc. p. pure							190.80		
Ring width Sc. p. mixed							221.24	30.44	15.95
Results lme E. be.	254.99			−0.08					
Mean value				815.70					
Ring width E. be. pure							189.73		
Ring width E. be. mixed							189.73	0.00	0.00

Scots pine, Sc. p.; European beech, E. be.; linear mixed-effects model, lme.

Table A4

Calculations of overall tree ring wood density resulting from linear mixed effects model QIII.

	Intercept	Mix	DBH	SDI	Mix * DBH	Mix * SDI	Result	Diff. absolut	Diff. in%
	a ₀	a ₁	a ₃	a ₄	a ₅	a ₆			
Results lme Sc. P.	Not analysed ^a								
Mean value									
Wood density Sc. p. pure									
Wood density Sc. p. mixed									
Results lme E. be.	490.17	−48.14	0.27	0.14					
Mean value			227	815.7					
Wood density E. be. pure							665.66		
Wood density E. be. mixed							617.52	−48.14	−7.23

Scots pine, Sc. p.; European beech, E. be.; linear mixed-effects model, lme.

^a Visual pre-check showed no meaningful dependency of data.**Table A5**

Calculation of basal area, volume and biomass on the five triplets examined in this study and the difference between pure and mixed stands.

Stand variable	Mixed _{obs} /Mixed _{exp}		Sc.p.m/Sc.p.p		E.be.m/E.be.p	
	Mean	SE	Mean	SE	Mean	SE
BA	1.03	0.10	1.13	0.20	0.92	0.05
V	1.07	0.10	1.22	0.18	0.91	0.08
PAIBA (m ² ha ^{−1} year ^{−1})	0.98	0.08	1.18	0.35	0.79	0.19
PAIV (m ³ ha ^{−1} year ^{−1})	1.02	0.09	1.18	0.25	0.88	0.10
Biomass (kg)	0.92	0.12	1.11	0.13	0.90	0.13

Variables listed include basal area (BA), volume (V), periodic annual basal area increment (PAIBA) and periodic annual volume increment (PAIV).

Table A6

Correction factors deduced from study on the comparison of water displacement measurements and high-frequency densitometry.

Species	Wood density (kg m ^{−3})		Correction factor
	Water displacement	High frequency	
Sc. p.	554.25	609.74	0.92
E. be.	701.85	592.70	1.19

Scots pine, Sc. P.; European beech, E. be., mean values from internal study on comparison of water displacement method and high-frequency densitometry.

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6.2.2 Publication 2

Titel: Tree species richness enhances stand productivity while stand structure can have opposite effects, based on forest inventory data from Germany and the United States of America

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Authors' contributions: The candidate and Jingjing Liang compiled the US inventory data sets and conducted the big data analysis. Hans Pretzsch established the direction and hypothesis of the study, and contributed to the interpretation of the results. The candidate drafted the manuscript, conducted data preparation and statistical analyses. All authors contributed to the writing of the manuscript.

Abstract: Background: In recent studies, mixed forests were found to be more productive than monocultures with everything else remaining the same. Methods: To find out if this productivity is caused by tree species richness, by a more heterogeneous stand structure or both, we analyzed the effects of forest structure and tree species richness on stand productivity, based on inventory data of temperate forests in the United States of America and Germany. Results: Having accounted for effects such as tree size and stand density, we found that: (I) tree species richness increased stand productivity in both countries while the effect of tree size heterogeneity on productivity was negative in Germany but positive in the USA; (II) productivity was highest at sites with an intermediate amount of precipitation; and (III) growth limitations due water scarcity or low temperature may enhance structural heterogeneity.

Conclusions: In the context of forest ecosystem goods and services, as well as future sustainable forest resource management, the associated implications would be:

- Tree species richness is vital for maintaining forest productivity.
- As an optimum amount of precipitation is accompanied by the highest productivity, changes in climatic conditions should be considered when planning.

- Resource limitations enhance structural heterogeneity, which in turn can have positive or negative effects on stand productivity.

Furthermore, we discuss the difficulties encountered when analyzing different national forest inventories and large data sets.

RESEARCH

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Tree species richness enhances stand productivity while stand structure can have opposite effects, based on forest inventory data from Germany and the United States of America

Laura Zeller^{1*} , Jingjing Liang² and Hans Pretzsch¹

Abstract

Background: In recent studies, mixed forests were found to be more productive than monocultures with everything else remaining the same.

Methods: To find out if this productivity is caused by tree species richness, by a more heterogeneous stand structure or both, we analyzed the effects of forest structure and tree species richness on stand productivity, based on inventory data of temperate forests in the United States of America and Germany.

Results: Having accounted for effects such as tree size and stand density, we found that: (I) tree species richness increased stand productivity in both countries while the effect of tree size heterogeneity on productivity was negative in Germany but positive in the USA; (II) productivity was highest at sites with an intermediate amount of precipitation; and (III) growth limitations due water scarcity or low temperature may enhance structural heterogeneity.

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- Resource limitations enhance structural heterogeneity, which in turn can have positive or negative effects on stand productivity.

Furthermore, we discuss the difficulties encountered when analyzing different national forest inventories and large data sets.

Keywords: Big data, Overyielding, Tree size heterogeneity, Tree species mixing, Climate, Biodiversity–productivity relationship

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Background

Economic and political relationships, environmental issues, and the network of supply and demand for wood products and ecosystem services have become more global. Meanwhile, the pressure on forest ecosystems is increasing due to climate change (Schröter et al. 2005; Wohlgemuth 2015) and a growing world population. Therefore, the need for globalizing and connecting forest research from different parts of the world to use synergy effects and combine knowledge is therefore becoming more and more important. Many countries are already advanced in forest research and are conducting national forest inventories to monitor the status, as well as to predict the future development, of forests. The Global Forest Biodiversity Initiative (GFBI) aims to connect the knowledge and data worldwide on forest biodiversity while spreading and using the available data more effectively for sustainable forest ecosystem management (Global Forest Biodiversity Initiative 2016).

The joint analysis of forest structure, tree species richness and stand productivity is becoming more relevant as recent studies have shown the different relationships among these attributes (Bohn and Huth 2017), which can now be analyzed on a global scale thanks to the so-called “big data era” (Lokers et al. 2016).

There are many current silvicultural programs that are restoring, stabilizing, and diversifying forests in terms of tree species and stand structure to render forests more productive, resilient, and sustainable in the long run (Ammer 2008; Knoke et al. 2008). In particular, a broader supply of forest ecosystem goods and services will be provided by more natural forest ecosystems. Not only would the provision of wood products be ensured, but the stabilizing function of water and nutrient cycles, the maintenance of different habitats, possibilities for hunting, the lowering of the risks of fire, wind throw, and land degradation, as well as the recreational and educational functions of forest areas, would also be secured (UN General Assembly 1987; MCPFE 1993; The Montréal Process 2015).

Forest management has been criticized for demolishing forest structure, diversity of habitats, and tree size heterogeneity by focusing only on timber production (Dieler et al. 2017). As counteracting strategy, mixing and structuring forests has become a common measure in the transition of mainly timber-oriented forestry toward more sustainable management. The goal is a multi-functional forestry that ideally covers all ecosystem goods and services while striving to reduce risk (Puettmann et al. 2009; Paquette and Messier 2011; Puettmann et al. 2015; Lindenmayer et al. 2016). Those tendencies, however, raise the question whether the achievement of a wider scope of functions and services would result in a reduction of forest productivity.

Not only is the paradigm of a multi-functional forest reinforcing the interest in the relationship among productivity, species richness, and structural diversity, but also the evidence that species mixing and structural diversity can increase productivity. Liang et al. (2016), for example, found positive relationships between tree species richness and forest productivity on a global scale. Pretzsch et al. (2015, 2017) made the same discovery with long-term mixed-species experimental plots of mixed species. Morin et al. (2014) showed that increasing tree species richness could also increase the continuity of forest productivity over time, as different species respond differently to disturbances, and so, can mitigate drops in productivity. Other researchers have also found positive relationships between forest structure and tree species diversity (Ishii et al. 2004; Hakkenberg et al. 2016) or between forest productivity and biodiversity in general (Paquette and Messier 2011). However, Wang et al. (2016) state that depending on the spatial scale of the analysis, both positive and negative diversity-productivity relationships can be found.

Many concepts of mixing and structuring forests are targeting a diversification at the stand level to provide multiple types of habitats (Dieler 2013). Under which conditions could the combination of tree species diversity and forest structure increase or decrease productivity, is still being debated. Answering this question would enable forest management to explore the advantages and disadvantages, as well as quantify the costs and benefits, of structural diversification. At the tree level, Danescu et al. (2016) showed that structural diversity had a significant influence on tree productivity while species diversity had no effect. At the stand level, however, both species diversity and structural heterogeneity were found to have a positive effect on productivity and ecosystem dynamics. Bourdier et al. (2016) discovered that a negative relationship between tree size heterogeneity and productivity could result from lower light interception and use efficiency in the case of an enhanced stand structure. Others have discovered negative relationships between structural diversity and productivity (Edgar and Burk 2001) in temperate forests or tropical Eucalyptus stands when structural diversity is present, but genetic and species diversity are absent (Soares et al. 2016). Chen and Klinka (2003) however, did not find any relationship between structure and productivity.

To differentiate among structural, diversity and climatic effects when analyzing forest productivity, the interaction between structural diversity and tree species richness, as well as the effects of climatic factors on structural traits, is important. Structural effects may occur only in certain types of mixtures, or within a certain range of temperature or precipitation. A potential overyielding in productivity by mixed forest stands could

be eliminated or even augmented by structural diversification.

This study collected big data selected from the national forest inventory data in the US national forest inventory FIA (O'Connell et al. 2014), which was provided and unified by GFBI, as well as in the German national forest inventory BWI (BMEL - Bundesministerium für Ernährung und Landwirtschaft 2014). The aim of this study was to discover how forest productivity is determined by tree species richness, climate and forest structure, i.e., tree size heterogeneity. Productivity was defined as the mean annual increment of the stem volume of a forest stand in $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Forest structure was quantified by indices based on diameter at breast height, which was available for all sample plots. The location of each plot and climatic characteristics were also included in the analysis. The effect of increasing temperature can have a mainly positive effect on forest productivity, as long as the water supply is not decreasing due to the higher temperature, as in the process of evapotranspiration (Yang 2005; Boivenu and Running 2006). Chertov (2010) suggests that productivity is increasing in times of global warming. Thus, climatic conditions should thus be considered when examining the effects of tree species mixing and structural diversification on productivity.

In regard to the above-mentioned background, we formulated the following questions that were to be answered by this study:

QI: How is forest productivity dependent on tree species richness and tree size heterogeneity when other effects, such as tree size and stand density, have been accounted for?

QII: How is forest productivity influenced by temperature and precipitation?

QIII: Do limitations to growth resulting from water scarcity or low temperatures enhance structural heterogeneity?

Material and methods

Material

Inventory data

The data set used in this study partly consists of nearly 56,000 inventory plots of the third national forest inventory data of Germany (BMEL - Bundesministerium für Ernährung und Landwirtschaft 2014). Additionally, ~ 576,000 plots belonging to the national forest inventory of the United States of America were used (O'Connell et al. 2014). All plots were located in the conterminous USA, because the Pacific islands and Alaska represent climatic zones quite different from the rest of the country. Different conditions along a climatic gradient for temperate forests on both the North American and the European continents were represented.

Both inventories were conducted using the angle count sampling method and only trees with a diameter

of 7 cm or more at breast height were included. For Germany, we used the third national forest inventory from 2012, which was the latest inventory conducted (BMEL - Bundesministerium für Ernährung und Landwirtschaft 2014). The latest USA national inventory data, taken between 2012 and 2016, was used (O'Connell et al. 2014).

Both inventories contain only approximate coordinates due to national legislation protecting the privacy of forest owners. The real locations of the inventory plots can differ by up to 1 km in Germany (Henning 2016) and by 0.8–11.6 km in the USA (O'Connell et al. 2014).

The German inventory is based on a 4 km × 4 km grid (base grid), but a smaller grid size (2.83 km × 2.83 km or 2 km × 2 km) was used in some regions. Each inventory plot is a square of 150 m × 150 m, of which each corner represents a subplot when an angle count sampling with a counting factor of 4 is applied. We treated the independent subplots as individual plots, as the subplots could be part of different forest types, and so, cannot be correlated.

The US inventory plots are 0.04 ha in size and are placed on a hexagonal grid so that one plot represents every 2428 ha of forested land (O'Connell et al. 2014). Each plot consists of a cluster of four circular subplots spaced out in a fixed pattern. As most tree measurements are taken at the level of the subplots, we also treated the US inventory subplots as individual plots. Spatial correlation, in general, was covered in the generalized additive model.

US inventory plots having large stand density index (*SDI*) values of more than 5000 were omitted from the analysis because the high numbers had obviously been created by the calculation method of *SDI*, which used small sample plots and deduced the number of stems per hectare. The maximum *SDI* of the German data set was just above 5000, so that we did not set an additional limit.

Productivity

For the German data, the tree and stand growths from the national inventories, BWI II and BWI III, collected in 2002 and 2012, respectively, were used. Stand volumes in $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ were calculated for the second and the third inventories, as well as for the group of trees present in the third inventory, but not in the second. The stand volume of the second inventory was subtracted from that of the third, then the volume of the removal stand was added. The resulting values in $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ divided by the length of time between the inventories represent the productivity of each stand.

Stand productivity for the US plots was derived from the periodic annual increment growth between the two inventories for the US inventory plots where more than one inventory was conducted (Liang et al. 2016). The original worldwide map of stand productivity was

downscaled from a 53 km × 53 km to a 3 km × 3 km resolution using geospatial interpolation (Liang et al. work-in-progress). For improved accuracy, we extracted productivity values from the downscaled map to the locations of the US inventory plots used in this analysis.

Climate data

The annual precipitation and mean annual temperature for 1970–2000 from the WorldClim data Version 2 were used with a resolution of 2.5 min (Fick and Hijmans 2017).

The mean annual temperatures of the inventory plots for 1970–2000 were 8.3 °C and 11.6 °C for the Germany and US data, respectively. The mean annual precipitation were 830 and 1054 mm for the German and US plots, respectively (Tables 1 and 2).

Tree and stand characteristics

The data sets of the tree and stand characteristics in Germany and the USA are presented in Tables 1 and 2, respectively.

Species richness *R* is lower in Germany than in the USA due to, firstly, the lower number of existing tree species, and secondly, the very common one- and two-species stands in Germany. The mean diameter *d* and quadratic mean diameter *dq* are higher in Germany, possibly due to a higher stand age or different silvicultural treatment as compared to the inventory plots in the USA. Tree size heterogeneity *CVd* is higher in the USA, whereas the *SDI* is higher in Germany. The overall climate is warmer and wetter in the USA, but productivity is higher in Germany.

Methods

Quantifying stand structure and tree species richness

To quantify forest structure, the quadratic mean diameter (*dq*), coefficient of variation of the tree diameter at breast height (*CVd*), and stand density index (*SDI*) were calculated for each inventory plot (Eq. (1)). Single tree positions that would allow for the calculation of the

Table 1 Descriptive data of inventory plots (Germany)

	<i>R</i>	<i>d</i>	<i>dq</i>	<i>CVd</i>	<i>SDI</i>	<i>Temp</i>	<i>Precip</i>	<i>P</i>
mean	2.02	27.14	28.59	0.32	1158.02	8.32	842.12	12.24
sd	1.06	12.2	12.18	0.19	603.3	0.93	250.52	8.96
se	0	0.05	0.05	0	2.54	0	1.05	0.04
min	1	7	7	0	38.67	0.31	467	0
max	9	165	165	1.46	5375.02	10.83	1984	103.59
<i>n</i>	56,449							

R number of species, *d* diameter at breast height (cm), *dq* quadratic mean diameter (cm), *CVd* coefficient of variation of diameter, *SDI* stand density index, *Temp* mean annual temperature, *Precip* annual precipitation, *P* stand productivity (m³·ha⁻¹·yr.⁻¹)

Table 2 Descriptive data of inventory plots (USA)

	<i>R</i>	<i>d</i>	<i>dq</i>	<i>CVd</i>	<i>SDI</i>	<i>Temp</i>	<i>Precip</i>	<i>P</i>
mean	4.67	19.91	21.97	0.44	522.63	11.56	1055.95	6.22
sd	2.82	8.17	8.81	0.19	464.31	5.6	357.02	0.64
se	0	0.01	0.01	0	0.61	0.01	0.47	0
min	1	7.11	7.11	0	0.16	-2.88	56	4.01
max	21	169.93	169.93	1.9	4998.34	24.57	3353	8.02
<i>n</i>	576,415							

R number of species, *d* diameter at breast height (cm), *dq* quadratic mean diameter (cm), *CVd* coefficient of variation of diameter, *SDI* stand density index, *Temp* mean annual temperature, *Precip* annual precipitation, *P* stand productivity (m³·ha⁻¹·yr.⁻¹)

spatial structure indicators were not available for the data sets used in this study.

Quadratic mean diameter (*dq*) As the inventory data were angle count samples, *dq* was calculated by:

$$dq = \sqrt{\frac{\sum_{i=1}^N d_i^2 \cdot n_i}{\sum_i n_i}} \tag{1}$$

Equation 1 includes the number of trees counted per inventory plot *N*, the diameter at breast height of the *i*th tree per plot, *d_i*, and the number of stems per ha represented by the *i*th tree, *n_i*.

Stand density index (*SDI*) The *SDI* by Reineke (1933) was calculated using a plot’s total stem number per ha, *N_p* = ∑_{*i*=1}^{*N*} *n_i*, and *dq*:

$$SDI = N_p \cdot \left(\frac{25}{dq}\right)^{-1.605} \tag{2}$$

SDI was used in this study because it produces stand density information that allows for the comparison of forest stands of any age or stage of development. We used the generalized allometric exponent by Reineke (1933), as species-specific exponents were not available for many of the included tree species.

Coefficient of variation of tree diameters (*CVd*) The coefficient *CVd*, of variation of tree diameters relates their standard deviation *sd* to their arithmetic mean \bar{d} :

$$CVd = \frac{sd}{\bar{d}} \tag{3}$$

This coefficient serves as a relative measure of tree size heterogeneity per inventory plot. However, due to angle count sampling, the representative stem number *n_i*, of each tree *i* per inventory plot had to be taken into account when calculating *sd* and \bar{d} :

$$\bar{d} = \frac{\sum_{i=1}^N d_i \cdot n_i}{\sum_{i=1}^N n_i} \quad (3a)$$

$$sd = \sqrt{\frac{\sum_{i=1}^N (d_i - \bar{d})^2 \cdot n_i}{\sum_{i=1}^N n_i - 1}} \quad (3b)$$

Equations (3), (3a) and (3b) use the same notation meanings as does Eq. (1).

Tree species richness Tree species richness as used in this study is the absolute number of different tree species on a plot (Pretzsch 2009, p. 279).

Generalized additive model (GAM)

To investigate the effect of climate on forest structure, we used parts of the same model but exchanged productivity as the dependent variable with the coefficient of variation of diameter at breast height.

Model function for QI + QII To answer the research questions, QI (the effects of tree species richness and stand structure on stand productivity) and QII (the effect of climate on stand productivity), we formulated a GAM function (4):

$$P_i = a + f_1(Lon_i, Lat_i) + f_2(Temperature_i, Precipitation_i) + f_3(SDI_i, dq_i) + f_4(R_i, CVd_i) + \varepsilon_i \quad (4)$$

This model seeks to explain stand productivity P as a function of species richness R , the stand structural heterogeneity expressed by the diameters' coefficient of variation, CVd , stand density, SDI , mean tree size, represented by mean tree diameter, dq , mean annual temperature and annual precipitation. The index i represents an inventory point, ε represents the remaining errors, a is the model's intercept, which is to be estimated, and f_1, \dots, f_4 are non-linear smoothers to be fitted. These smoothers are two-dimensional, i.e., they cover the possible interactions between two explanatory variables each. Here, smoother f_1 is based on geographical longitude Lon and latitude Lat , and is intended to cover the effects of unobservable influence variables connected with the geographical position of a plot. Smoother f_2 covers the climate effect, f_3 covers a stand density effect, which may be size-dependent. Such effects would bias the findings on the influence variables of interest if the smoothers were not used. The variables of interest, accounted for by the smoother f_4 , are the effects of tree species richness and structural diversity.

To check for the effect of climate on forest structure (QIII), we used a similar function but with the coefficient of variation of diameter as the dependent variable.

Finally, we set up the model function (5):

$$CVd_i = a + f_1(Lon_i, Lat_i) + f_2(Temperature_i, Precipitation_i) + f_3(SDI_i, dq_i) + f_4(R_i) + \varepsilon_i \quad (5)$$

Equation (5) uses the same meaning of notation as does Eq. (4). The smoothers, f_1 for geographical longitude and latitude, f_2 for climate effects, and f_3 for a potentially size-dependent stand density effect, were included in the model to cover those effects not explained by species richness R .

All variables tested in the GAMs of our study were significant. We compared the full model functions to their reduced versions by eliminating the smoothers. In our case, the full model functions yielded lower AIC values and higher R^2 as compared to the reduced versions, and so, were thus selected as the final model functions.

For our analysis we set up the generalized additive models (GAM) (Crawley 2007; Zuur 2009) using the mgcv package (Wood 2011) in R (R Development Core Team 2008).

Results

Statistical analysis

When applying our models, the full model versions always yielded the lowest AIC, and so, were chosen as the final models. To interpret the GAM results, two-dimensional heat maps were used and the effect of each variable was isolated while all other variables were set to their mean values. When testing each variable by varying its value from the minimum to the maximum, its isolated effects on the dependent variable were observed.

QI: How is forest productivity influenced by tree species richness and tree size heterogeneity?

Germany

Location The effect of location covered by the interaction term for longitude and latitude showed mostly a strong positive effect of latitude on stand productivity. Our model showed that stand productivity increased from $\sim 10 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ to $\sim 13 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ along the range of 47.33° N up to 54.92° N (Fig. 1b), indicating that productivity was increasing toward the northern part of Germany (Fig. 2a).

Stand density and tree size SDI clearly explains part of the variation in stand productivity. An increase in SDI up to $2000 \text{ stems} \cdot \text{ha}^{-1}$ (where most of the data was represented) made productivity rise from 7 to $17 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fig. 1e). Tree size (dq) had only a small negative effect (Fig. 2c). For an increase in dq from 0 to 100 cm ,

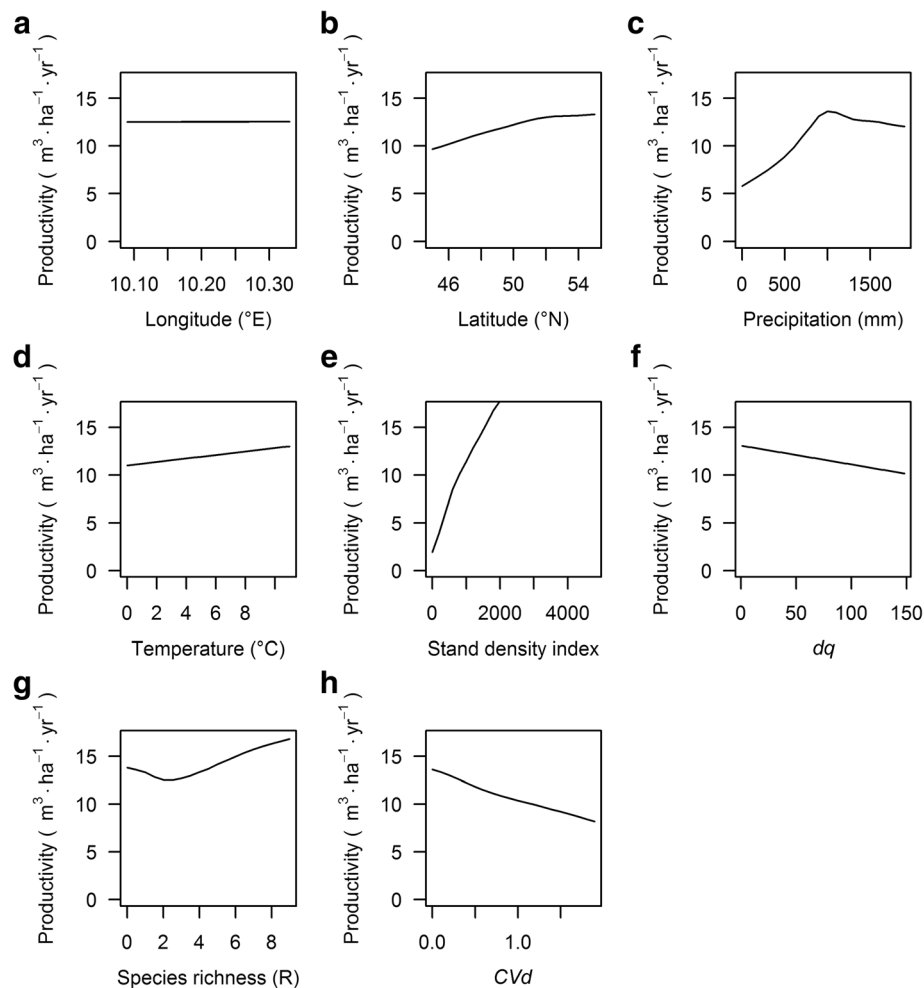


Fig. 1 Effects of longitude (a), latitude (b), annual precipitation (c), mean annual temperature (d), tree species richness (e), and tree size heterogeneity (f) on stand productivity of German inventory plots. Each variable was tested on its own while other variables were set to the mean

the effect on stand productivity explains a variation of $\sim 3 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in productivity (Fig. 1f).

Species richness and structure For up to two different species, stand productivity decreased with increasing tree species richness from about 14 to about 12 $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, which means that inventory plots with two species on average had a $\sim 2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ lower stand productivity than did monocultures. For more than three tree species the trend was the opposite and stand productivity increased again up to $\sim 16 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for stands with eight tree species (Figs. 1g and 2d).

Since the mean number of tree species in the German plots was two, stands with a high number of species were represented only by a small sample size. The effect of structural heterogeneity was negative. With a mean CVd of ~ 0.32 and most of the data occurring around this value, the valid part of the model still describes a

negative effect of structure on stand productivity by $\sim 2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ along the range of CVd from 0 to ~ 1.0 , covering most of the data (Figs. 1h and 2d).

The least productive combination was a low number of tree species with a high tree size heterogeneity. Additional tree species could partly mitigate the negative effect of tree size heterogeneity on stand productivity.

USA

Location Most of the productivity in our model was determined by location and climatic conditions, which together explained up to $\sim 4 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ of the variation among the plots. From the western part (-124.7°E) to the most eastern part of the conterminous USA (-67°E), productivity increased from ~ 5 to more than $6 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fig. 3a). Latitude explained a drop of more than $1.5 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in productivity from the most southern

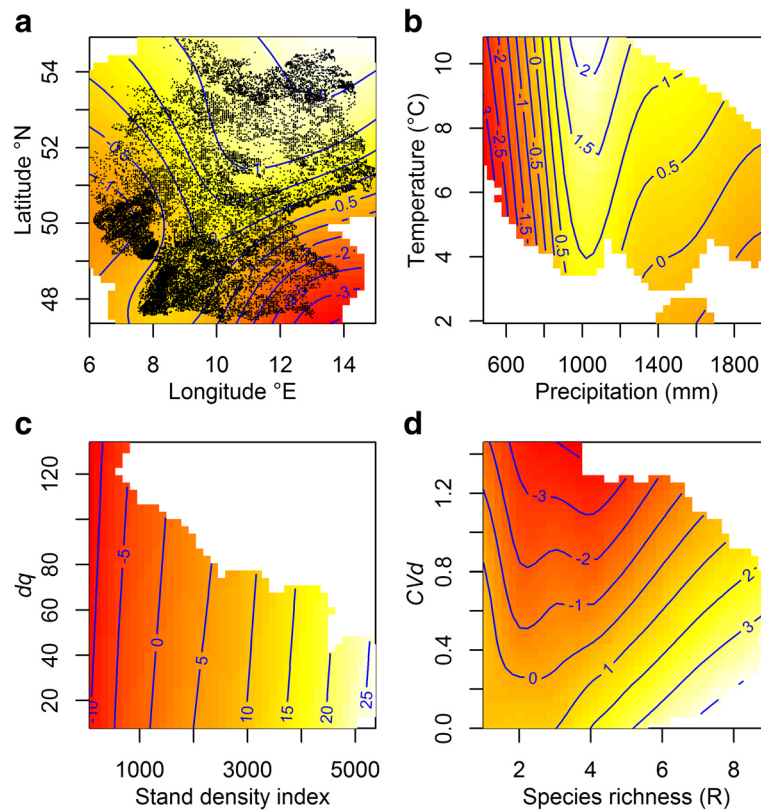


Fig. 2 Effects of location (a), climate (b), tree species richness and tree size heterogeneity (c), and stand density and tree size (d) on stand productivity of German inventory plots. Yellow = positive effect on productivity, red = negative effect on productivity. Blue contour lines show where the function has a constant value

part (25.07° N) to the most northern part (49.35° N) (Fig. 3b). Productivity was, therefore, highest in the southeastern part of the US (Fig. 4a).

Stand density and tree size Tree size had a small but positive effect and explained about $0.2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ of the variation in stand productivity (Fig. 3f). Stand density had a small positive influence on stand productivity up to an *SDI* of ~ 500 . For an *SDI* > 500 , the effect was contrary (Fig. 3e). Figure 4c shows the combination of both effects.

Species richness and structure The number of species showed a small but positive effect on stand productivity for up to 10 different tree species. For more than 10 species the relationship between species richness and stand productivity was found to be negative (Fig. 3g). Tree size heterogeneity dq had a slightly positive influence on stand productivity (Fig. 3h). As most of the variation was already by location and climatic influence, the effects of tree species richness and tree size heterogeneity were small but still evident. The combination of both effects is shown in Fig. 4c.

Q11: How is forest productivity influenced by precipitation and temperature?

Germany

Stand productivity was mainly enhanced by, and so, is positively correlated with the amount of precipitation. For up to 1000 mm, the effect of precipitation was clearly positive and explained productivity's increase from ~ 8 to $13 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ with annual precipitation's increase from ~ 400 to 1000 mm. For more than 1000 mm per year, the influence of precipitation on stand productivity was reverse, thus negative (Fig. 1c). Mean annual temperature had a positive effect on productivity. By increasing mean annual temperature from 0 °C to 10 °C, stand productivity increased from ~ 11 to $\sim 13 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, explaining up to $2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ of the variation in the productivity of the German plots (Fig. 1d). The main finding concerning climate was the negative effect of a dry climate especially in combination with high temperatures. Only in the case of an optimum amount of annual precipitation did temperature show positive effects (Fig. 2b).

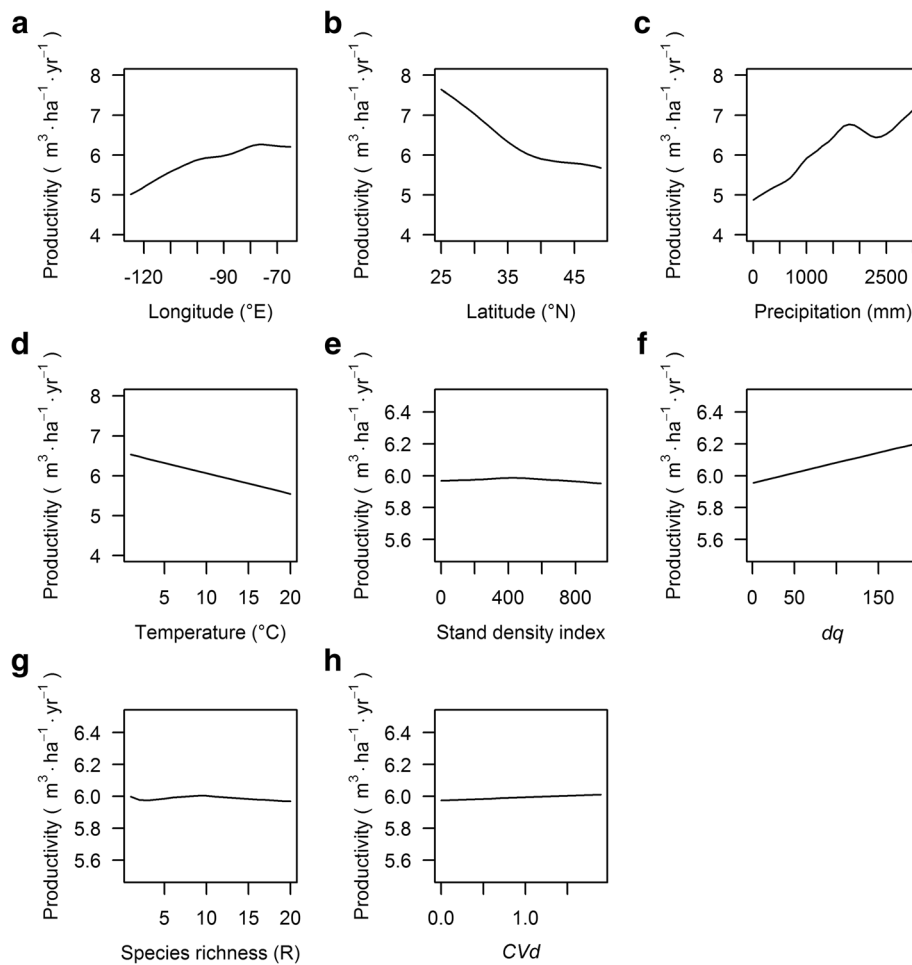


Fig. 3 Effects of longitude (a), latitude (b), annual precipitation (c), mean annual temperature (d), tree species richness (e), and tree size heterogeneity (f) on stand productivity of US inventory plots. Each variable was tested on its own while other variables were set to the mean

USA

Precipitation was the main climatic driver for stand productivity in the USA, leading to an increase in stand productivity from 5 to nearly 7 $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ along the range of precipitation up to 2000 mm (Fig. 3c). Temperature had a negative effect. Along the range from ~ 6.5 °C to 20 °C, stand productivity decreased from 6.5 to 5.5 $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fig. 3d). Our model showed that a warm and dry climate was negatively influencing stand productivity (Fig. 4b).

QIII: Do growth limitations due to water scarcity or low temperatures enhance structural heterogeneity?

Germany

Location Neither longitude nor latitude had any large effect on tree size heterogeneity, meaning that stand structure was rather homogeneous from south to north. Only toward the most northern part of Germany did

tree size heterogeneity show a slight increase (Figs. 5a, b and 6a).

Climate Annual precipitation and mean annual temperature had small positive effects on tree size heterogeneity *CVd*. Increasing precipitation from ~ 600 to 1400 $\text{mm} \cdot \text{yr}^{-1}$ showed an increase in *CVd* from ~ 0.35 to 0.4 (Fig. 5c). *CVd* was increasing from 0.26 to 0.3 along a range of a mean annual temperatures from 0 °C up to 10 °C (Fig. 5d). In Germany, the analyzed forest inventory plots were more heterogeneous in tree size at warm and wet sites (Fig. 6b).

Stand density and tree size *SDI* only showed a positive effect on tree size heterogeneity up to an *SDI* of ~ 500 (Fig. 5e). With increasing tree size *dq* from 10 to 80 cm, tree size heterogeneity decreased from ~ 0.45 to ~ 0.2 (Fig. 5f), indicating that stands with larger trees on average were less heterogeneous in tree size. Forest stands

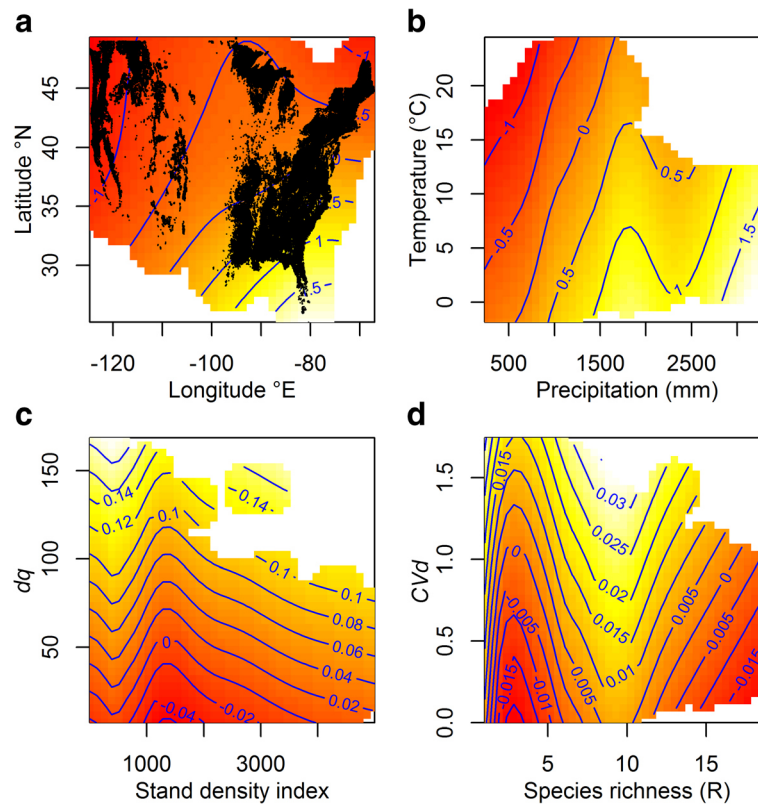


Fig. 4 Effects of location (a), climate (b), tree species richness and tree size heterogeneity (c), and stand density and tree size (d) on stand productivity of US inventory plots. Yellow = positive effect on productivity, red = negative effect on productivity. Blue contour lines show where the function has a constant value

with a combination of a high *SDI* and a lower *dq* showed the highest tree size heterogeneity (Fig. 6c).

Tree species richness The number of species was clearly positively related to stand heterogeneity *Cvd*, which increased from 0.3 up to 0.6 along a range of species richness of 2 to ~7 species per plot (Fig. 5g). For more than ~8 tree species, species richness had a negative effect on tree size heterogeneity. The graphical representation of species richness R as a single variable shows its effect on *Cvd* on the y -axis (Fig. 6d).

USA

Location Structural heterogeneity increased from the eastern part to the western parts of the USA with a coefficient of variation (*Cvd*) of 0.4 to about 0.6 (Fig. 7a). The effect of location on a north-south gradient had a lower effect on tree size heterogeneity, showing the highest tree size heterogeneity between 35° N and 40° N (Fig. 7b). On sample plots that were more northerly, stand structure was less heterogeneous. The overall variation explained by location is shown in Fig. 8a.

Climate The effect of climate was not very pronounced but a slightly lowering effect of annual precipitation on structure was found (Fig. 7c). Mean annual temperature did not show any clear effect on tree size heterogeneity *Cvd* (Fig. 7d). The combination of precipitation and temperature highlights the strong role of precipitation as a driver of tree size heterogeneity (Fig. 8b). Thus, structural heterogeneity was highest at sites with low precipitation.

Stand density and tree size Stand density and tree size heterogeneity *Cvd* were positively correlated. *Cvd* increased from ~0.30 to ~0.7 for an increase in *SDI* along a range from 0 up to 5000 (Figs. 7e and 8c). Tree size had a slightly negative effect on *Cvd* (Figs. 7f and 8c).

Species richness The number of tree species had a vital effect on tree size heterogeneity. An increase in tree species richness from 1 to 20 led to a more heterogeneous stand structure *Cvd*, increasing from ~0.4 to ~0.6 (Fig. 7g). The single effect of species richness R on *Cvd* is presented on the y -axis (Fig. 8d).

The results of using the GAMs are presented in Tables 3 and 4. They show the intercept a of the model function, its standard error, the significance of each

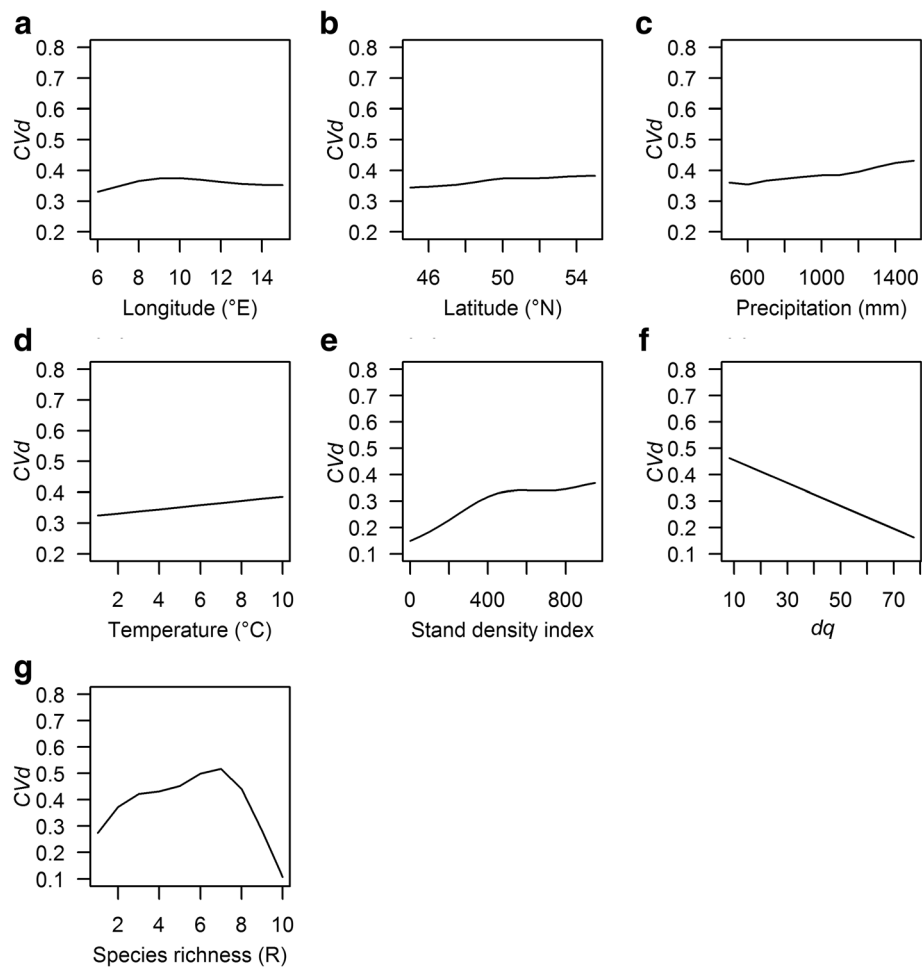


Fig. 5 Effects of longitude (a), latitude (b), annual precipitation (c), mean annual temperature (d), tree species richness (e), and stand density (f) on tree size heterogeneity of German inventory plots. Each variable was tested on its own while other variables were set to the mean

model, and the R-square (adjusted). Based on AIC, the full versions of the models were selected.

Discussion

Stand productivity

Tree size heterogeneity did not have a stronger positive effect on stand productivity than did tree species richness (QI), which was found to influence stand productivity, as well as tree size heterogeneity, in both the German and US inventory plots. In Germany, structure had a negative effect on stand productivity, whereas, in the USA, structurally more diverse stands were slightly more productive.

In the German inventory plots, we found the lowest stand productivity in the case of two tree species. Comparing monocultures to the two-species mixed stands showed lower productivity for the two-species plots, as explained by others (Binkley 1984; Chen and Klinka 2003), possibly due to the more efficient use of resources by the highly productive monocultures. For more than

two tree species, a positive biodiversity–productivity relationship appeared. For the US data set, there was a similar trend seen of increasing productivity with increasing tree species richness. Despite the findings of Binkley (1984) and Chen and Klinka (2003), the US inventory plots having up to 10 different tree species showed an increase in productivity. The positive relationship of tree species richness with stand productivity found in US and German inventory plots with more than two tree species matches the positive biodiversity–productivity relationships described by Kelty (2006), Gamfeldt et al. (2013), Vilà et al. (2013), Pretzsch et al. (2015), Liang et al. (2016) and Pretzsch et al. (2017).

We wanted to test the interaction of tree species richness and structure in particular. Silva Pedro et al. (2017) found that species composition and stand structure are strongly connected, and that their combination could quite influence forest productivity. In the case of a lower productivity due to a lower crown cover in mixed-species stands, a more heterogeneous stand structure

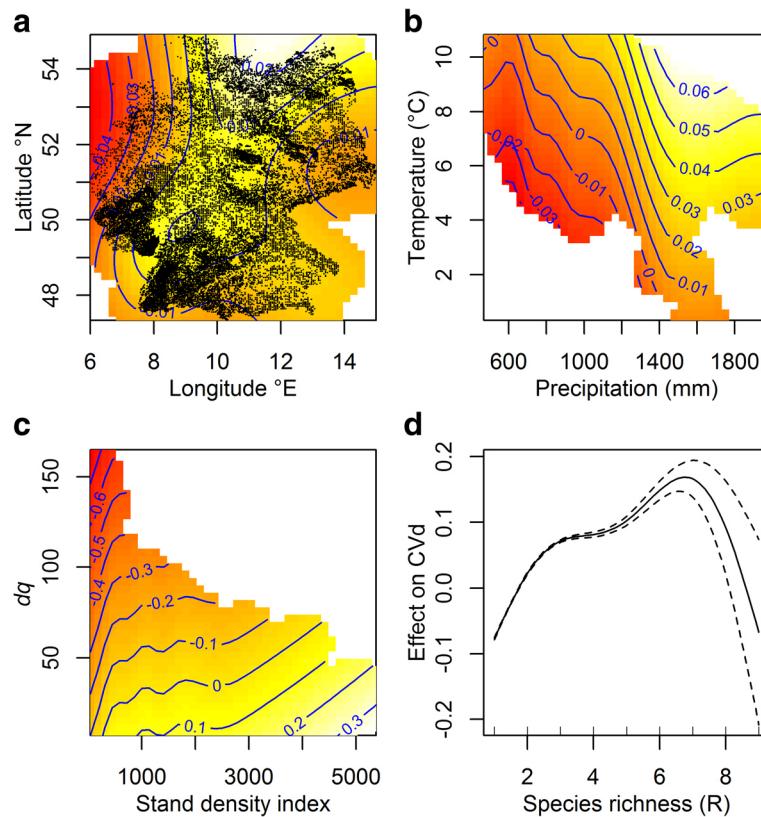


Fig. 6 Effects of location (a), climate (b), and stand density and tree species richness (c) on tree size heterogeneity of German inventory plots. Yellow = positive effect on productivity, red = negative effect on productivity. Blue contour lines show where the function has a constant value

could mitigate the potential loss. In our case, as most of the variation in productivity among the sample plots was already explained by location and climate, for the US inventory plots, effects of species and structure were very small but still present. This finding matched those by Bohn and Huth (2017), who had discovered a positive correlation between structure and productivity. Potential benefits of a higher structural heterogeneity, which leads to overyielding can result from more efficient use of resources through multiple forest layers and a better exploitation of niches. However, contrary results were found for the German inventory plots. The negative effect of structure on stand productivity was strongest on stands with about two to four tree species. Mitigated by tree species richness, mono-specific stands and stands with more than four tree species experienced weaker negative effects of structure. Similar trends were also found by Bourdier et al. (2016), who show that tree size heterogeneity would also decrease productivity, depending on the shade-tolerance of the tree species. Also, Luu et al. (2013) and Soares et al. (2016) reported a negative effect of tree size heterogeneity on stand productivity.

Stand productivity can also be negatively or positively correlated with stand density (Uhl et al. 2015). Stand

density and tree size were, therefore, considered in our model. In the German plots, productivity was positively correlated with stand density, whereas the effect of tree size was very small. In the US plots, the influence of stand density on productivity was less clear and tree size did not show any effect. A lower mean stand density and lower productivity in the US plots compared to a higher stand density and a higher stand productivity in the German plots is in line with findings of higher yields in mixed stands resulting from a higher stand density (Pretzsch and Biber 2016).

Explaining the opposite effects of structure on stand productivity in Germany and the USA, we hypothesize that the two countries are located along a gradient concerning latitude, annual precipitation, temperature, and also productivity, and structure. Possibly, the inventory plots from the two inventories are at different development stages with consequently different structure-productivity relationships. Tree size heterogeneity, here CVd , in the German inventory plots (0.32) was already lower than in the US plots (0.44), and stand productivity was higher in Germany (12.24) than in the USA (6.22). Precipitation and temperature were lower in Germany (842 mm, 8.3 °C) than in the USA (1056 mm, 11.6 °C).

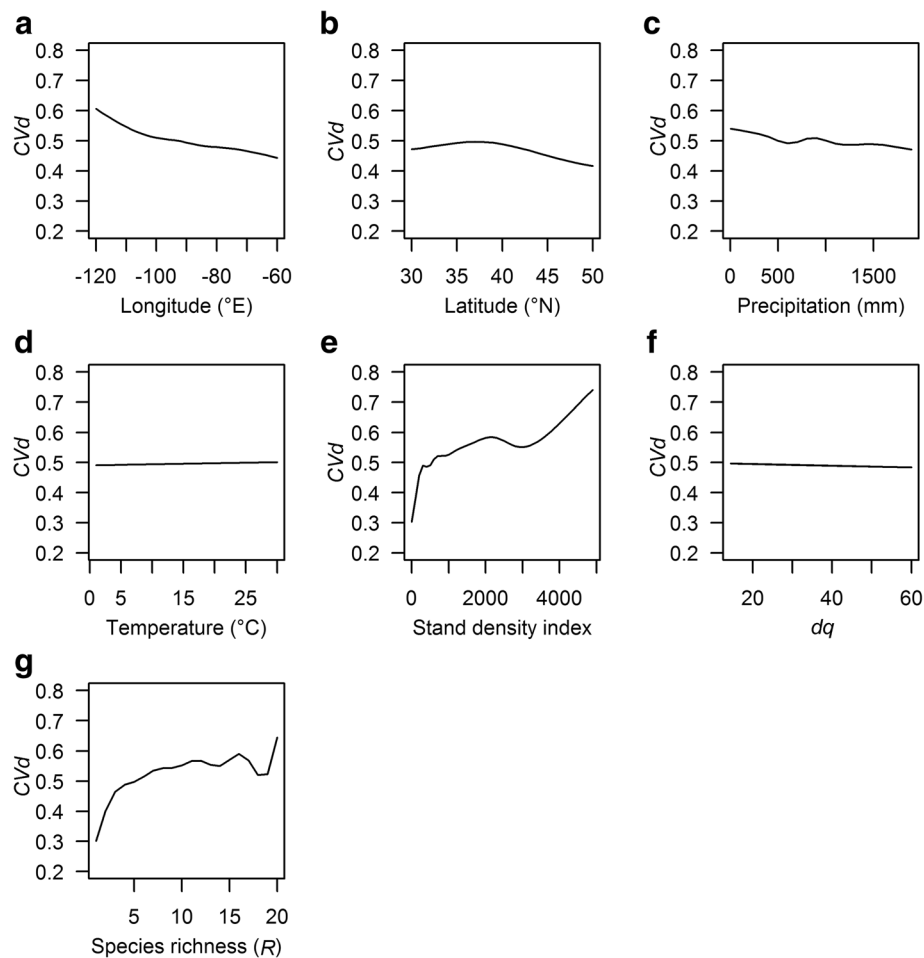


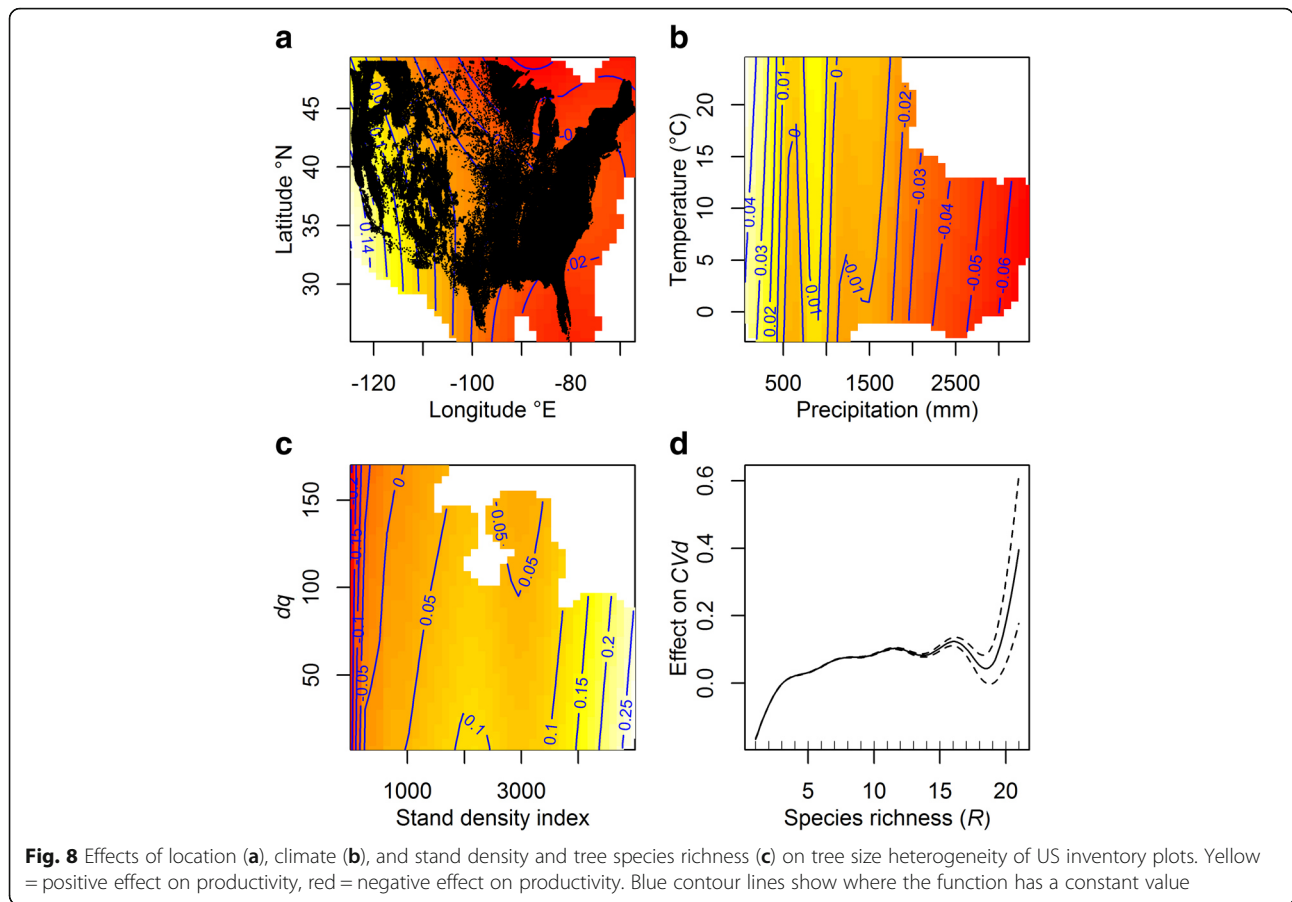
Fig. 7 Effects of longitude (a), latitude (b), annual precipitation (c), mean annual temperature (d), tree species richness (e), and stand density (f) on tree size heterogeneity of US inventory plots. Each variable was tested on its own while other variables were set to the mean

This would mean that Germany is located at the northern end of the gradient and adjacent to the USA. The lower number of tree species and temperatures in the German plots can lead to a lower structure while highly productive even-aged monoculture-type forest stands are still present with combined high productivity and low tree size heterogeneity. The forest stands in Germany are much longer and more intensively shaped by even-aged management (Paillet et al. 2010; Schall et al. 2017), while in the USA structural heterogeneity is still higher due to disturbances and climatic shifts (Oliver 1980; Dolanc et al. 2014; McIntyre et al. 2015).

Climate

Apart from the location which already explains a large part of the variation in stand productivity, climate played a major role. We found that a warm and dry climate can especially decrease stand productivity (QII) but only with regard to precipitation, which was a strong predictor of stand productivity, as the latter is restricted by

lower annual precipitation. This trend has also been described by others (Toledo et al. 2011; Żywiec et al. 2017). We found that for both countries, there is an optimum amount of annual precipitation beyond which additional units of precipitation were rather counterproductive. In Germany this effect could come from large quantities of precipitation, especially in the mountain areas and along the coastline, with counterproductive effects due to a shorter vegetation period in the mountainous areas and strong winds along the coast (Friend and Woodward 1990; Pretzsch et al. 2015). In the USA, we also saw a similar pattern where the Pacific Coast was generally lower in forest productivity than was the Atlantic Coast, despite the Pacific's greater annual precipitation. Regardless of the differences in biomes and other underlying silvicultural and environmental factors, our findings of an optimum beyond which additional annual precipitation could not lead to a higher stand productivity supported the saturation effect inherent in the biodiversity–productivity relationship (Liang et al. 2015).



Mean annual temperature’s effect on stand productivity in Germany was opposite to those in the USA. Trees in the German inventory plots were benefiting from the warmer climate, whereas in the US plots, higher temperatures in combination with a low amount of precipitation were leading to lower growth rates. We speculate that the effects of temperature in the US could come from a less flexible situation of inventory plots, which are situated in

regions where temperature cannot increase productivity anymore because trees, e.g., tropical trees, are already growing at their optimum temperature. Any additional temperature would be rather counter-productive (Way and Oren 2010). In Germany, trees are rather growing on sites below their temperature optimum, so a higher mean annual temperature consequently can lead to higher growth rates as compared to colder sites. Our speculation

Table 3 Results of GAMs applied to inventory data from the USA

		USA			
	Term	Intercept a	Std. error	Sig.	R-sq. (adj)
QI/QII	f_1 (Lon × Lat)	6.22	0.00	***	0.90
	f_2 (Precip × Temp)			***	
	f_3 (R × CVd)			***	
	f_4 (SDI × dq)			***	
QIII	f_1 (Lon × Lat)	0.44	0.00	***	0.37
	f_2 (Precip × Temp)			***	
	f_3 (SDI × R)			***	

Lon longitude, Lat latitude, Precip annual precipitation, Temp mean annual temperature, R species richness, CVd coefficient of variation of diameter, SDI stand density index, dq quadratic mean diameter (cm). Sig. Significance values: 0 ****, 0.001 ***, 0.01 **, 0.05 *

Table 4 Results of GAMs applied to inventory data from Germany

		Germany			
	Term	Intercept a	Std. error	Sig.	R-sq. (adj)
QI/QII	f_1 (Lon × Lat)	12.24	0.04	***	0.19
	f_2 (Precip × Temp)			***	
	f_3 (R × CVd)			***	
	f_4 (SDI × dq)			***	
QIII	f_1 (Lon × Lat)	0.32	0.00	***	0.29
	f_2 (Precip × Temp)			***	
	f_3 (SDI × R)			***	

Lon longitude, Lat latitude, Precip annual precipitation, Temp mean annual temperature, R species richness, CVd coefficient of variation of diameter, SDI stand density index, dq quadratic mean diameter (cm). Sig. Significance values: 0 ****, 0.001 ***, 0.01 **, 0.05 *

is supported by the acceleration of growth due to effects of the climate changes found in Europe (Pretzsch et al. 2014), as well as in boreal Canada (Wu et al. 2014), but not in the USA (Silva et al. 2010). Especially if higher temperatures occur in combination with higher amounts of precipitation, the effect on growth can be positive (Gustafson et al. 2017). Moreover, species traits, species composition, forest structure (Bohn and Huth 2017) and forest type (Vilà et al. 2013) determine how forest productivity is influenced by climate and could have shaped the relationships found in our study.

Stand structure

Finally, we also tested if water scarcity or low temperatures could enhance structural heterogeneity through the limitation of growth (QIII). Stand structure quantified by tree size heterogeneity was found to be highest in German plots with a high annual precipitation and high temperatures, and in US plots with low and intermediate amounts of annual precipitation.

Water limitation may foster the growth of small trees at the expense of their taller neighbors and reduce the size-asymmetry of competition. This phenomenon may be due to tall trees' being more exposed to the sun in sites with low water availability, especially during dry years. The tall trees close their stomata earlier and cannot make longer use of their preferential access to light. In contrast, under warm and dry conditions, the small trees in contrast may be less affected by or may even benefit from the reduced water consumption of their taller neighbors. So, the growth partitioning between the trees in stands on water-limited sites may favor the smaller members of the population, keeping them in the play, thereby fostering the diameter variation and structural heterogeneity (Pretzsch et al. 2012).

In both the German and the US plots, with more species, more structural heterogeneity was found. This effect could potentially result from the different allometry and functions of tree species, so that niches could be filled with a certain species, thereby creating more stand structure. Also, stand density was positively correlated with structure. These trends are well described in the European and Anglo-American literature (Zeide 2001; Pretzsch 2005).

Considering that species richness fosters structural heterogeneity and structure, which, in turn can increase stand productivity even more, the combination of tree species richness and structure would be recommended while keeping in mind that other ecosystem services also benefit from species richness and structure, e.g., stability and the distribution of risk. Furthermore, a characterization of forest stands by species can still result in different outputs (all ecosystem goods and services) depending on regional peculiarities or the genetic variation of each species (Boydén et al. 2008). Higher productivity in mixed stands

could be related to the species' traits more than to tree diversity in general (Jacob et al. 2010). Forming groups of species according to their functional traits rather than their taxonomy could, therefore, be useful. Analyzing the effect of species richness on stand productivity, as done in this study, could then potentially yield much clearer results, as the effects may not be hidden by intra-specific variation in traits.

Methods

Applying GAM models to large data sets, as performed in our study, will automatically lead to high significance values, which mean that the interpretation of p -values should be completed by analyzing the single effects of each variable. The size of the effect of each independent variable on the dependent variable must still be tested to estimate if the effect is only a slight trend. The major problem in our analysis was the use of different methods to obtain productivity values for each plot in Germany and the US. Conducting large inventories such as the one in the USA is an expensive endeavor and not all sample plots can be measured regularly. If productivity on inventory plots is calculated only for the ones measured more often and interpolated to all the other inventory plots, very different plots can become assigned to the similar productivity value. The variation in productivity as a dependent variable may then not be large enough to be explained by variables other than location or climate. Considering that the effects of species richness and structure on productivity in our model can only be very small, we can still take them seriously and interpret their trends. The US inventory data can be expected to comprise a comparable high degree of inexplicable variation due to the method of estimating and interpolating productivity.

Including successional stages through stand age would have been useful as well but no reliable data was available as the stand ages given in the inventories were roughly estimated without considering the different ages of the different layers. Therefore, we used *SDI* and tree size to cover the potential effects of development stages. Assuming that a higher stand density results from a higher number of smaller trees that yield higher relative growth rates and a lower stand density can be explained by fewer larger trees with a lower relative growth (Caspersen et al. 2011), our model promotes the choice of *SDI* as a substitute for the lack of information on stand age. Analyzing the relationship of structure, species mixing and productivity along the developmental stages in terms of stand age could be a worthwhile study for the future.

Conclusion

Our results do not include aspects such as the stability, resilience or biodiversity of other plant species other

than trees. Our study focused on productivity and tree species richness rather than overall ecosystem productivity and biodiversity. However, knowing how tree species richness, structure and productivity are correlated helps us understand the whole forest ecosystem. Apart from climate and site conditions, tree species richness can be the most important driver for productivity. Hence, biodiversity and productivity can complement each other and enable the provision of multiple forest ecosystem goods and services. In the case of a negative structure–productivity relationship, as found in the German inventory plots, in combination with the need for forest structure (e.g., as a stabilizing function or for the aim of conservation), species richness can mitigate the potentially negative effects of structure on stand productivity. In our case, favoring forest stands with more than four species over monocultures would be a solution for the trade-off of combining structural heterogeneity and high yields. In the case of a positive structure–productivity relationship, as found in the US inventory plots, an increase in structural heterogeneity implies a boost in productivity while enhancing other structure-related forest ecosystem functions. All in all, there is no need to disapprove of structural heterogeneity, because a combination of high productivity and the benefits of a structurally diverse stand can be achieved.

Knowing the climatic influence on productivity, e.g., an optimum range of precipitation where productivity peaks, can help to adjust forest management to the expected climatic conditions of the future. This knowledge could be especially valuable for estimating the consequences of shifting climatic conditions for a forest ecosystem that includes certain species and is already located in its optimum range of precipitation and temperature or is at the border of a climatic zone.

The collection and use of global inventory data will enable big data research to contribute to better management and use of forest ecosystems worldwide, as well as to find out more about the relationships between the different characteristics of a forest. The major problems faced by this study when using inventory data were the different ways of achieving productivity values, which led to partly vague model outcomes. The more often national inventories are conducted, the more precisely can volume increment, and consequently, stand productivity, be calculated. On the downside, conducting forest inventories is cost intensive, especially if much detailed information must be collected frequently. Therefore, the collection and combination of worldwide inventory data as done by GFBI is crucial and will help research conducted on forest ecosystems be easier, more universal, and more efficient.

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Authors’ contributions

LZ and JL compiled the US inventory data sets and conducted big data analysis. HP established the direction and hypothesis of the study, as well as contributed to the interpretation of the results. LZ drafted the manuscript, conducted data preparation and statistical analyses. All authors contributed to the writing of the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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6.2.3 Publication 3

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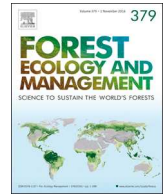
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Abstract: Recently, many studies have found positive biodiversity–productivity relationships in forests. In contrast, different types of correlations have been identified in the analyses of tree diversity–structure–productivity relationships. We suspect 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.



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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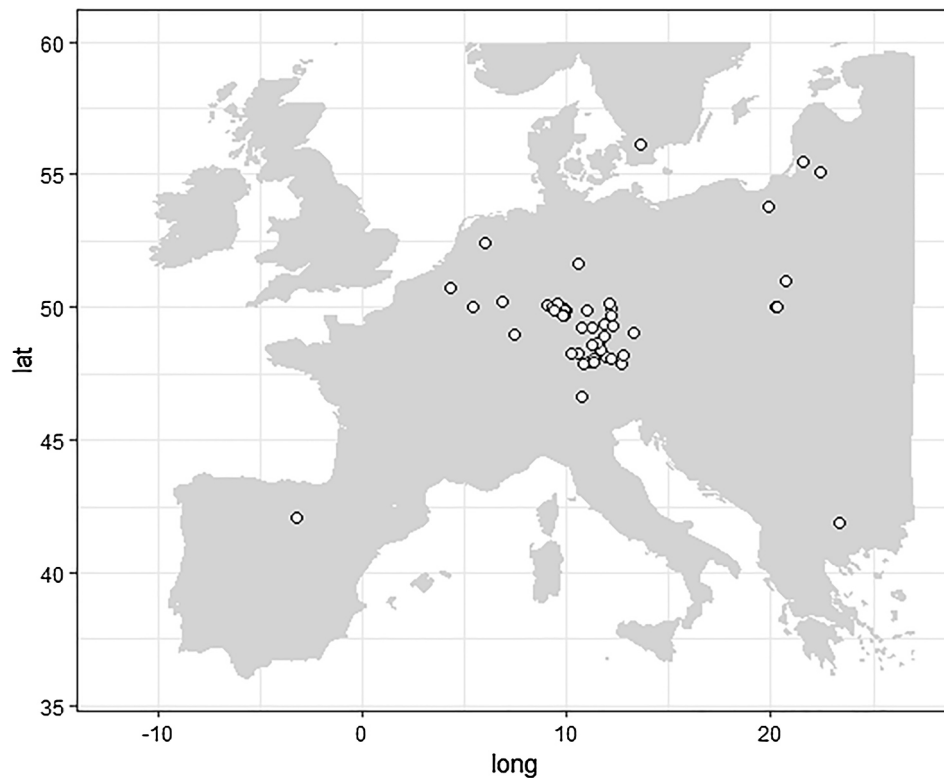


Fig. 1. Location of long-term experimental plots in Europe analyzed in this study. Long longitude, lat latitude.

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 Gadwo 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

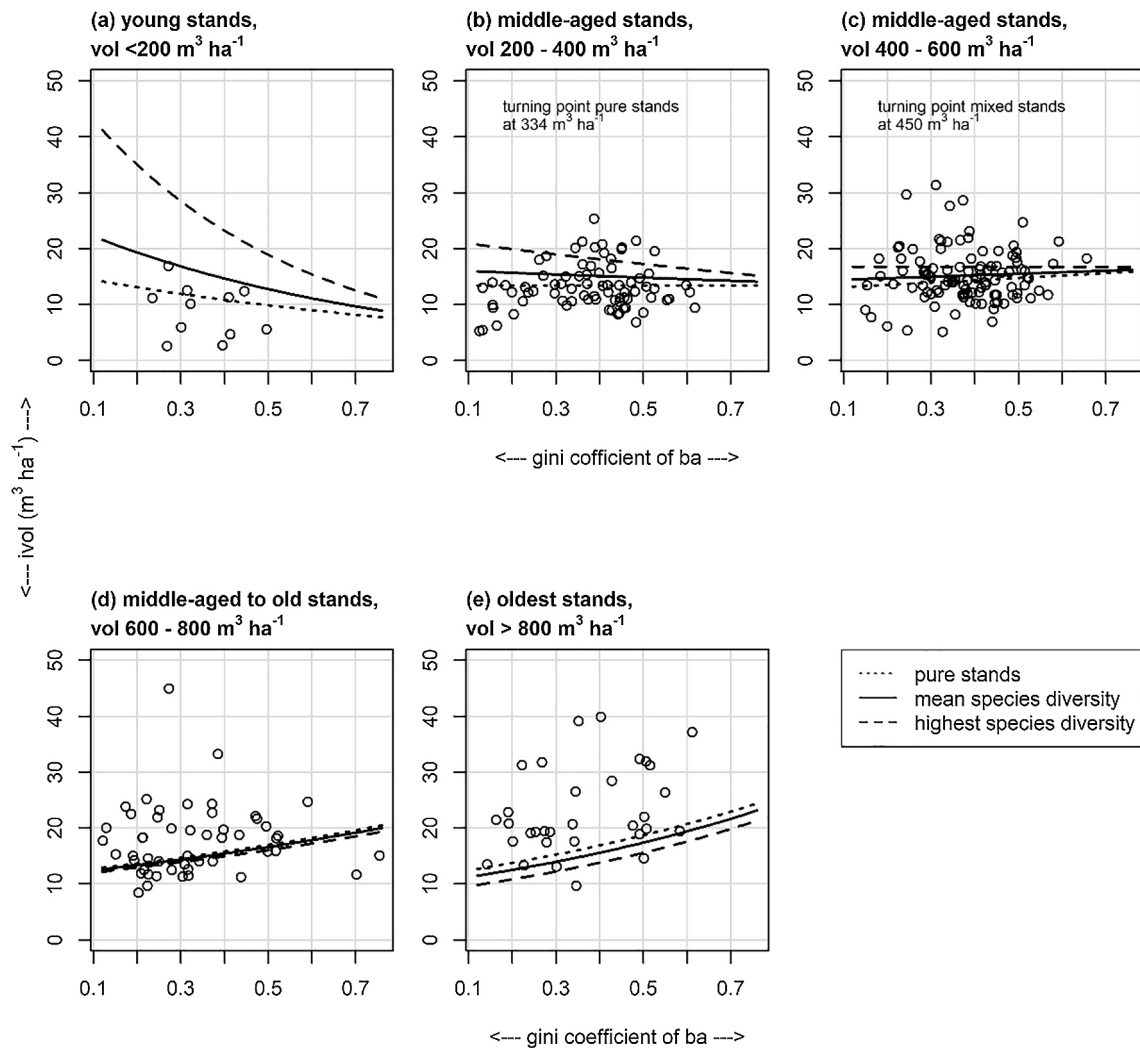


Fig. 2. Effect of structural heterogeneity at the stand level on stand productivity in various developmental stages (a)–(e). Structural heterogeneity at the tree level quantified by the Gini coefficient of basal area. Developmental stages (a)–(e) were quantified by standing volume (m³ ha⁻¹). Ivol stand 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.

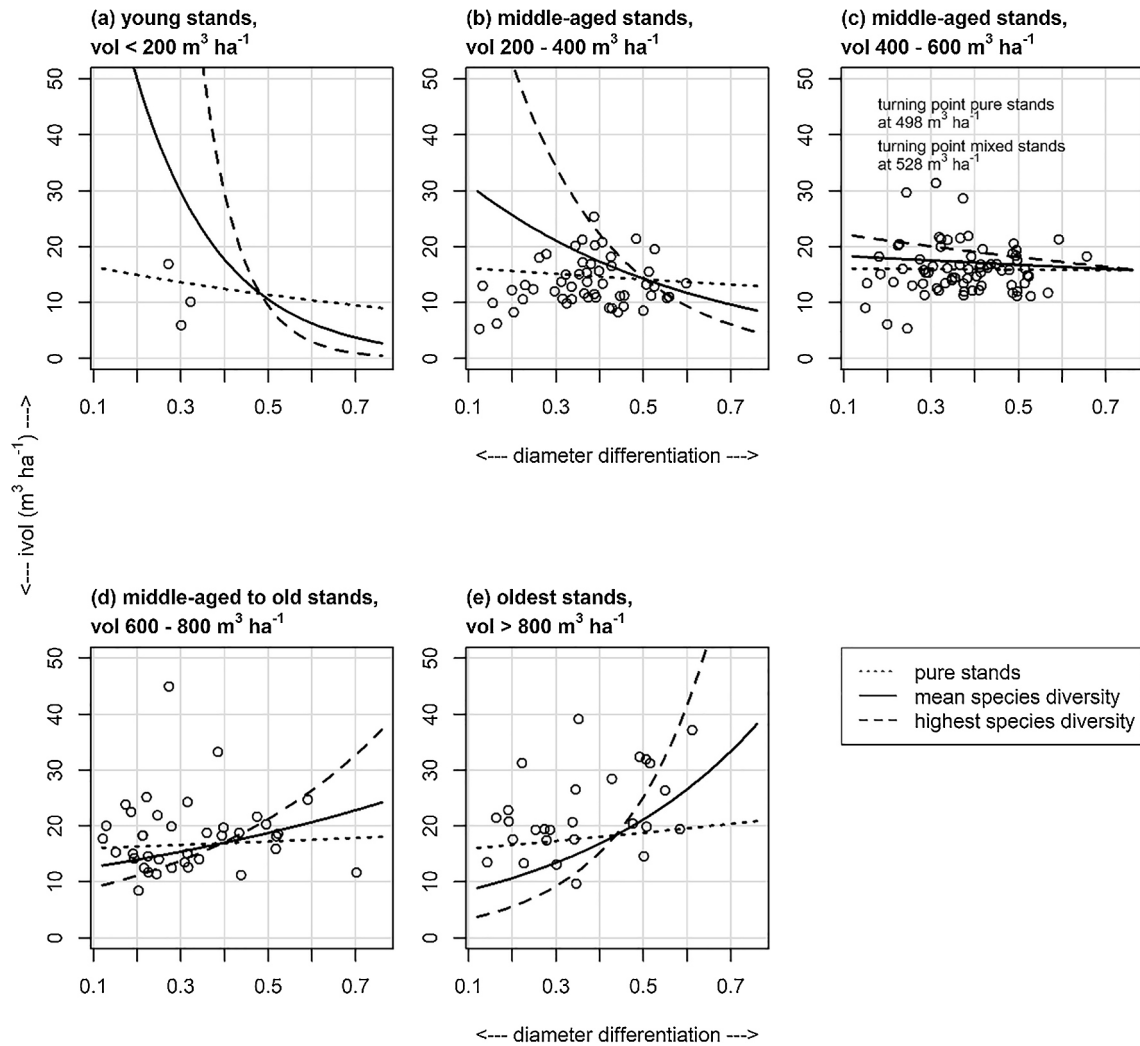


Fig. 3. Effect of structural heterogeneity at tree level on stand productivity between developmental stages (a)–(e). Structural heterogeneity at tree level quantified by diameter differentiation. Developmental stages (a)–(e) were quantified by standing volume (m³ ha⁻¹). Ivol stand volume increment (m³ 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.

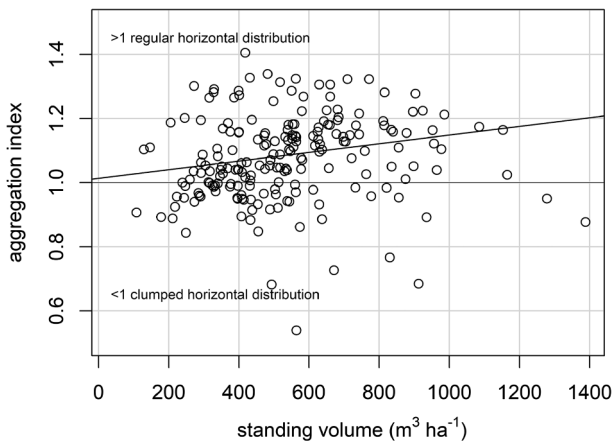


Fig. 4. Aggregation index over stand development. Horizontal distribution of trees quantified by mean aggregation index per measurement over stand development [standing volume (m³ ha⁻¹)]. Aggregation index > 1.0 regular distribution, 1.0 random distribution, < 1.0 clumped distribution.

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.

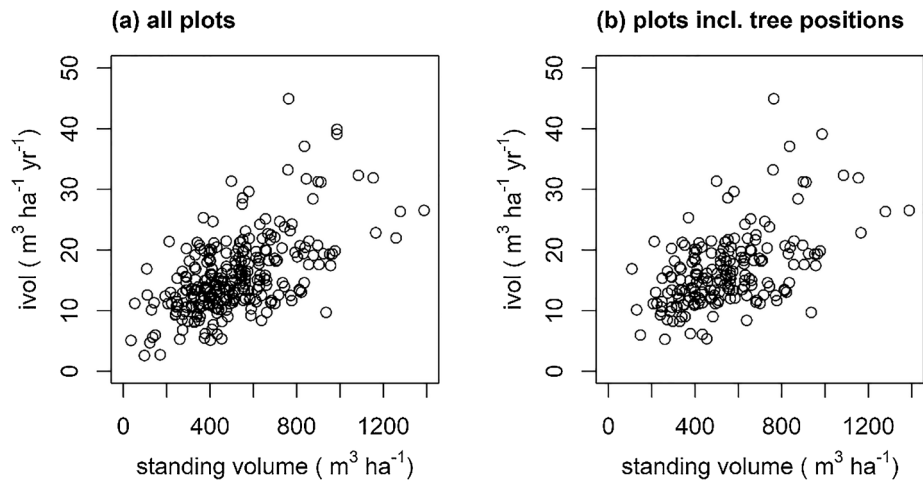


Fig. A.1. Data points (measurements) used in the first part [all plots (a)] and the second part [plots including tree positions (b)] of the study. *Ivol* volume increment.

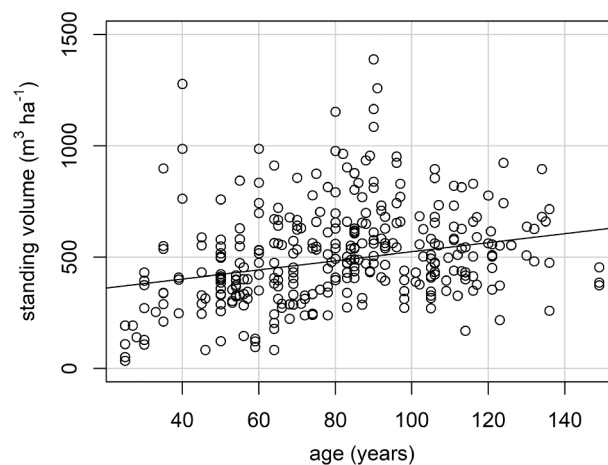


Fig. A.2. Standing volume over estimated stand age of all measurements in experimental plots.

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6.2.4 Publication 4

Titel: Analyzing the effect of silvicultural management on the trade-off between stand structural heterogeneity and productivity over time

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Abstract: Research Highlights: This study combines an empirically-based simulation with an analysis of biodiversity-relevant structural indicators depending on time, spatial scale and silvicultural management. It supports forest management in planning the multifunctionality of future forest ecosystems while prioritizing a high wood production. Background and Objectives: The planning of future forest ecosystems is often difficult due to various assumptions concerning climatic changes and the future demand of wood products and other ecosystem functions and services. Whereas volume growth and tree species diversity have been examined in detail, the role of forest structure and its interdependencies with stand productivity and biodiversity have just lately become a stronger research focus. Materials and Methods: We used the SILVA growth simulator to examine the development of different biodiversity-relevant structural indicators in pure and mixed spruce and beech stands at different spatial scales over a range of 100 years. Those stands are based on typical forest types in Bavaria and are representative for Central Europe. We examined how potential trade-offs between the diversity-relevant structural indicators and productivity are modified by a multifunctional, a production-oriented and a set-aside management scenario. Results: The production-oriented management scenario applied to uneven-aged stands led to a reduction in biodiversity-relevant structural indicators over time. In age-class stands, the production-oriented scenario was able to maintain

the initial structural heterogeneity. The multifunctional scenario led to a decrease in the structural parameters if applied to the pure beech age-class stands, which was not the case in uneven-aged stands. Beyond a radius between 300-1000 m, the structural indicators and trade-offs did not increase further with increasing spatial scale. Conclusions: Depending on the initial stand, the management scenario can favor or hinder the development of biodiversity-relevant structures over time. Spatial explicit scenario analyses support the management of forest ecosystems for multifunctionality.

1 Article

2 Analyzing the effect of silvicultural management on 3 the trade-off between stand structural heterogeneity 4 and productivity over time

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11 **Abstract:** *Research Highlights:* This study combines an empirically based simulation with an analysis
12 of the trade-off between structural heterogeneity and stand productivity depending on time, spatial
13 scale, and silvicultural management. It supports forest management by testing a modification of
14 forest structure and thus fostering the multifunctionality of forests while maintaining a high
15 productivity. *Background and Objectives:* The planning of future forest ecosystems is often difficult
16 because of various assumptions concerning climatic changes and the future demand for wood
17 products and other ecosystem functions and services. Whereas volume growth and tree species
18 diversity have been examined in detail, the role of forest structure and its interdependencies with
19 stand productivity have only lately become a stronger research focus. *Materials and Methods:* We
20 used the growth simulator SILVA to examine the development of stand structural heterogeneity
21 and its trade-off with stand productivity in age-class vs. uneven-aged pure and mixed spruce and
22 beech stands at different spatial scales over 100 years. Those stands are based on typical forest types
23 in Bavaria and are representative of forests in Central Europe. We examined how stand structure
24 and its trade-off with productivity is modified by a multifunctional, a production-oriented and a
25 set-aside management scenario. *Results:* The production-oriented management scenario applied to
26 uneven-aged stands led to a reduction in structural heterogeneity per unit of productivity over time.
27 In age-class stands, the production-oriented scenario was able to maintain the initial structural
28 heterogeneity. The structural heterogeneity per unit of productivity increased more strongly with
29 increasing spatial scale in age-class stands compared to uneven-aged stands. *Conclusions:*
30 Depending on the initial stand, the silvicultural management approach could favor or hinder the
31 development of structural heterogeneity per unit of productivity over time. Combining forest stand
32 simulation with scenario analyses is an exemplary method for testing the effect of silvicultural
33 management alternatives on forest structure before it is applied to real forests.

34 **Keywords:** forest ecosystem functions and services, forest stand growth, management scenarios,
35 multifunctionality, structural complexity, virtual forest

36

37 1. Introduction

38 Sustainably maintaining multifunctional forest ecosystems has become a widespread objective
39 of forest management [1,2], and this development increases the interest in analyzing the potentially
40 strong influence of tree species diversity [3,4] and forest structure on ecosystem functions and
41 services [5–7]. Previously established monospecific and even-aged forests had the aim of a high yield
42 and the homogeneous provision of one product [8]. Silvicultural management has shifted its focus to
43 multifunctional mixed forests [9]. Here, stand structural heterogeneity emerges as an important
44 factor when the aim of management is to provide a broad range of forest ecosystem functions and

45 services [5]. Different studies show positive [10], but often negative [11,12] effects of stand structural
46 heterogeneity on wood production. The potential negative effect of structural heterogeneity on wood
47 production is balanced by a broad range of beneficial effects on habitat heterogeneity [13],
48 biodiversity [14,15], carbon storage [16], mechanical stability [17,18], and resilience [19].

49 Stand structural heterogeneity is commonly quantified using indices based on tree size
50 distribution [20,7]. These indices are easily calculated also by forest practitioners and based on data
51 that is usually sampled in forest inventories [21,22]. We selected a coefficient of variation of dbh
52 (diameter at breast height (1.3 m)) for our study because it is a commonly used measurement [22–24]
53 and is suitable for describing stand structural heterogeneity in general.

54 High structural heterogeneity originates partly from tree species mixing due to the differences
55 in growth rates and requirements among tree species [24]. In Germany, Norway spruce and European
56 beech are the most common coniferous and deciduous tree species, respectively, and together
57 represent about 40% of the forest area in Germany [25]. A shift from Norway spruce and Scots pine
58 (*Pinus sylvestris* L.) monocultures to mixed continuous cover forests [8] is intended for many regions
59 in Germany for economic [26,27], ecological [28], and other reasons [28]. The advantages of a
60 transition to species-diverse forests is also being discussed in other parts of Europe [29,30] and
61 worldwide [4,31].

62 To test the effect of silvicultural management on the structure-productivity relationship in both
63 age-class and uneven-aged pure and mixed stands in the long-term, simulation can be a useful tool
64 [32–34]. We generated virtual forest stands consisting of mainly Norway spruce (*Picea abies* (L.) H.
65 Karst.) and European beech (*Fagus sylvatica* L.) with different initial stand structure (age-class vs.
66 uneven-aged) and spatial arrangements (pure stands, single tree mixture and section-wise mixture)
67 to test the effects of silvicultural management on the structural heterogeneity in those different types
68 of stands.

69 Age-class stands still exist in Germany but have been increasingly transformed into uneven-
70 aged stands [35,36], which is why we compared age-class and uneven-aged stands in our study. The
71 chosen initial stand structure and tree species composition therefore represent existing forest types
72 that are of practical concern and part of the current debate on the sustainable and multifunctional
73 management of forests in Europe [37–40].

74 Even though forest management intends to incorporate other ecosystem functions and services
75 into their portfolio, a high production of wood products is still often the first priority. Production-
76 oriented forestry is often associated with the above-mentioned even-aged stands that automatically
77 have a lower structural heterogeneity than uneven-aged stands. In German forestry, the most
78 common type of forest can be described as a so called “high forest”. Two common management
79 approaches in high forest management concerning regeneration, thinning, and harvesting are age-
80 class (even-aged) forest management and continuous cover forestry [41]. In the case of age-class forest
81 management, artificial or natural regeneration is applied after harvesting at the end of the rotation
82 period. There are usually only one or two layers present. The rotation period is an important
83 determinant of the amount and time of harvesting activities. The selection of tree species is rather
84 focused on fast-growing conifers. Pure forests with one or two layers managed by age-class
85 management are still present but have increasingly been transformed into continuous cover forests.

86 In continuous cover forestry, trees of different ages grow next to each other and selective cutting
87 is applied. The resulting stands can therefore be called uneven-aged stands [42]. Regeneration also
88 happens continuously below and in between older trees. Continuous cover forestry aims to provide
89 continuous crown cover, tree species mixing and regeneration with deciduous tree species.
90 Continuous cover forestry also results in increased tree size inequality and thus increased structural
91 heterogeneity. An increase in stand structural heterogeneity, however, has in many cases been found
92 to negatively influence stand productivity [12,43,44], particularly in pure stands [11,45]. Continuous
93 cover forestry attempts to integrate multifunctionality into production forests [46].

94 In national parks or other set-aside areas, no commercial management is applied. This hands-off
95 approach can reveal how forests develop without intervention, or after abandonment. Structural

96 heterogeneity can be higher than in production forests and includes an old-growth phase with very
97 old and large tree and parallel regeneration [47].

98 In our study we represent the three common management approaches age-class or even-aged
99 forestry, continuous cover forestry, and the conservation approach by the three scenarios
100 “production-oriented”, “multifunctional”, and “set-aside”. The management scenarios used in this
101 study therefore represent the common silvicultural management approaches applied in Germany
102 that have resulted in the existing age-class forests, continuous cover forests, and set-aside forests,
103 respectively [40]. By applying all three scenarios to both initial age-class and uneven-aged stands, we
104 test the effects of management on the most common existing types stand structures.

105 The negative effect of high structural heterogeneity on the wood production found in some cases
106 [45,11] can result in a trade-off between stand structure and productivity [5,30]. It is of great interest
107 how forest management can modify this trade-off since structural heterogeneity is known to enhance
108 the mechanical stability of a forest [18], as well as it is key to many other ecosystem functions and
109 services [7]. As the interest of this study is the relative dependency between the two, quantifying the
110 trade-off by a simple ratio was applicable. The aim of increasing either wood production or sacrificing
111 productivity for a higher structural heterogeneity was incorporated in the management scenarios
112 prioritizing different aims.

113 The extent of structural heterogeneity in forests moreover depends on the spatial scale at which
114 it is measured [48–50]. Depending on the purpose of a forest, a provision of certain stand
115 characteristics might be sufficient or particularly important at a larger spatial scale [51,52]. In some
116 cases, instead of a high structural heterogeneity at tree level, habitat heterogeneity was found to be
117 particularly important at larger spatial scales for overall biodiversity [53,15,54]. The selected virtual
118 forest stands enable the comparison between structural heterogeneity at tree level (uneven-aged
119 stands) or at stand level (age-class stands).

120 Based on German forestry practice, we analyzed the effect of silvicultural management on stand
121 structural heterogeneity and its trade-off with stand productivity in age-class vs. uneven-aged forest
122 stands over time and on different spatial scales. This study represents an overarching approach
123 complementing existing findings on the effects of forest management [55,56,30] and aims at linking
124 aspects, such as stand structure, productivity, silvicultural management, time, and spatial scale,
125 which are often examined individually [57]. It addresses the management of future forest ecosystems
126 by examining the following research question:

127
128 How does stand structural heterogeneity in age-class vs. uneven-aged stands develop over time
129 and spatial scale in different management scenarios?

130 2. Materials and Methods

131 2.1. Data and virtual stands

132 Virtual stands were formed based on forest types of 16 ha (strata) that resulted from a stratification
133 of the German National Forest Inventory. This process is part of the standard simulation process of the
134 forest simulator SILVA [58], which was then used to elaborate the scenarios. The individual inventory
135 points for the State of Bavaria were grouped according to structural characteristics (tree size
136 distribution, species composition) and to the ecological region that they represent. The strata were
137 defined by specific structures and average spatial distributions. All data points belonging to each
138 stratum were used to generate a representative stand of a defined surface (16 ha) using the STRUGEN
139 algorithm [23]. During this process, simulated individual trees were distributed by point process
140 algorithms over the area until they fulfilled the stated stand structures. This stratification process
141 ensures that each forest type represents real forests in Bavaria [25].

142 We generated 8 virtual forest stands that mainly consist of Norway spruce and European beech in
143 equal shares, and very low numbers of pine and sessile oak (*Quercus petraea* (Matt.) Liebl.). The
144 resulting 8 different virtual forest stands consist of 12 patches of different forest-type patches (16 ha),
145 leading to a total stand size of 192 ha each. One age-class stand and one uneven-aged stand of each of

146 the 4 types of species compositions were set up: pure spruce (Figure A 1 and Figure A 2), pure beech
 147 (Figure A 3 and Figure A 4), a single-tree mixture of spruce and beech (Figure A 5 and Figure A 6), and
 148 a section-wise mixture, that included 1 section (96 ha) of pure spruce and 1 section (96 ha) of pure beech
 149 next to each other (Figure A 7 and Figure A 8). For a comparable starting situation, the selected forest
 150 types cover a similar range of tree sizes (dbh and height distribution), number of trees per ha, and
 151 standing volume ($\text{m}^3 \text{ha}^{-1}$) (Table 1). Variation in the spatial allocation of the trees in the stand results
 152 from the age-class vs. uneven-aged stand structure. The number of trees per ha and volume per ha was
 153 first calculated per forest-type patch (16 ha) to show the variability between the forest type patches
 154 inside the forest stands (Table 1). All forest-type patches forming the virtual forest stands were based
 155 on the same soil and growing conditions. Apart from the intended differences in the management and
 156 initial structure (age-class vs. uneven-aged), the stands were thus similar.

157 Table 1: Characteristics of the initial virtual forest stands

mixgroup	group	dbh (cm)				height (m)				tree volume (m^3)				trees (n ha^{-1}) per forest type patch (16 ha)				volume ($\text{m}^3 \text{ha}^{-1}$) per forest type patch (16ha)			
		min	mea n	max	sd	min	mea n	max	sd	min	mea n	ma x	Sd	min	mean	max	sd	min	mea n	ma x	sd
pure spruce	age- class	7	16	62	11	6	14	41	8	0	0	5	0.71	94	1711	2538	74 8	14	218	914	207
pure spruce	uneven- aged	7	19	82	13	4	17	42	8	0	0	8	0.80	789	1086	1706	29 7	246	483	636	117
pure beech	age- class	7	22	68	13	7	19	42	8	0	1	8	0.77	96	610	848	24 6	9	250	681	205
pure beech	uneven- aged	7	19	58	11	6	20	36	8	0	1	5	1.07	714	1045	1475	28 1	209	537	690	150
single-tree mix	age- class	8	24	70	13	5	18	37	8	0	1	6	0.85	259	692	992	27 6	28	308	815	248
single-tree mix	uneven- aged	7	21	80	13	5	17	38	8	0	1	6	0.95	441	1082	1611	38 2	270	454	669	157
section- wise mix	age- class	14	23	61	7	14	19	28	4	0	0	5	0.44	232	1013	1588	46 0	243	352	470	91
section- wise mix	uneven- aged	7	17	57	11	6	17	36	8	0	0	4	0.61	714	1194	1706	35 0	209	470	594	145

158 2.2. Growth simulation by SILVA

159 The growth of the virtually designed forest stands was simulated over 100 years using the single-
 160 tree-based forest growth simulator SILVA. SILVA was developed, and evaluated, and has been
 161 successfully applied in forest practice since 1989 by the Chair of Forest Growth and Yield of the
 162 Technical University of Munich. This simulation program considers single-tree positions, competition
 163 with neighbor trees, as well as tree age in pure and mixed stands and is suitable for forests in Central
 164 Europe [59,60]. SILVA enables the testing of the effect of different types of silvicultural practices on
 165 forest growth [61] and other ecosystem functions and services [62,32,63].

166 2.3. Management scenarios

167 The management scenarios considered in this study comprise a large set of silvicultural practices
168 that represent the current challenges in forest management [64]. These provide species-specified details
169 for every target tree species modeled in SILVA (Norway spruce, Scots pine, silver fir, European larch,
170 European beech, sessile and common oak, Douglas-fir, hardwood deciduous, and softwood deciduous)
171 [65]. Each intervention is defined depending on the dominant species in the stand and is applied
172 specifically to the defined height phases, i.e., stand development stages. In our study we have not
173 included climate-related changes and have instead set climate as a stable assumption to focus purely
174 on the effect of management.

175 A multifunctional and a production-oriented scenario were applied to show the differences in
176 management impact, depending on the different initial structures (age-class vs. uneven-aged stands) in
177 different species compositions (pure spruce, pure beech, single tree mixture spruce-beech, section-wise
178 mixture spruce-beech). For reference, a set-aside scenario was used where no management was
179 conducted.

180 The multifunctional scenario (Table 2) is oriented towards a multifunctionality of forests [37] by
181 integrating ecosystem functions and services into the management of production forests [46,66]. This
182 includes the goal of a continuous crown cover, as well as a high structural heterogeneity and species
183 diversity, including a higher share of deciduous species. Depending on the dominant tree species of
184 each forest type (Table 2, column 1), silvicultural management was conducted. From stand
185 establishment to the stand stage with a dominant height of 12 m, a stem number reduction and a
186 removal of 15 m³ ha⁻¹ at maximum per intervention was carried out. Selective thinning was conducted
187 at a dominant height between 12 m and 32 m, which removed up to 55 m³ ha⁻¹ in deciduous-dominated
188 stands and up to 70 m³ ha⁻¹ in coniferous-dominated stands per intervention. The target diameter
189 harvest phase started at a dominant height of 32 m and removed between 80 and 144 m³ ha⁻¹ of conifers
190 and 70 m³ ha⁻¹ in deciduous-dominated stands. All the conducted treatments were applied in turns of
191 2 simulation periods (10 years) [67]. In this scenario, natural regeneration was the main contributor to
192 the ingrowth. To improve species diversity, Scots pine (500 trees ha⁻¹) was planted during the
193 regeneration phase in the conifer-dominated stands. In the deciduous-dominated stands, in addition to
194 the natural regeneration, Scots pine (250 trees ha⁻¹), European beech (6000 trees ha⁻¹), and Douglas-fir
195 (250 trees ha⁻¹) were planted during the regeneration phase to increase the multifunctionality.

196 The production-oriented scenario (Table 3) focused on the production of wood, following the
197 expected increase in the demand for wood products in Europe [68,69]. The amount of harvested wood
198 was set as the first priority by reducing the rotation period and promoting conifers and fast-growing
199 tree species. In the production-oriented scenario, stem reduction was applied on deciduous tree species,
200 removing up to 25 m³ ha⁻¹ per intervention, while no stem reduction was applied to conifer-dominated
201 stands. In the deciduous stands starting at a dominant height of 12 m up to 17 m, a selective thinning
202 and a thinning from below was then applied removing up to 25 m³ ha⁻¹. The final felling was conducted
203 by minor selective thinning and a target-diameter felling of trees with a dbh between 20 and 200 cm
204 and a removal of up to 500 m³ of the standing volume. In the conifer stands, strong selective thinning
205 and target-diameter felling was applied in two height phases. During the first phase from 12 to 19 m
206 dominant height up to 60 m³ ha⁻¹ were removed targeting conifers with a dbh between 40 and 200 cm
207 and deciduous trees with diameters > 5 cm. During the second phase up to 120 m³ ha⁻¹ were removed
208 for diameters between 50 and 200 cm for all species. The final felling phase was aimed at trees with a
209 height > 31 m, applying a light selective thinning and a target-diameter felling with a removed standing
210 volume of up to 500 m³ ha⁻¹ and a diameter between 5 and 200 cm for deciduous trees and a diameter
211 between 20 and 200 cm for conifers. In this scenario, in addition to natural regeneration [62], Norway
212 spruce (4000 trees ha⁻¹) and Douglas-fir (*Pseudotsuga menziesii*) (100 trees ha⁻¹) were planted during
213 the regeneration phase.

214 Table 2: Thinning and harvesting measures in the multifunctional scenario

Multifunctional

Domina nt tree species	Phase	Starts at dominant height (m)	Tree species	Treatment	Frequency	N future crop trees	N comp etitors	Target diamete r [cm]	% of targeted (trees ha ⁻¹) removed per treatment	Max. volume removed per treatment (m ³ ha ⁻¹)
Conifer ous	Precommerci al	0	coniferous	no treatment	2	0	0	0	0	15
			deciduous	stem number reduction	2	1000	0	0	0	15
	Commercial	12	coniferous	future tree concept	1	100	3	0	0	50
			deciduous	future tree concept	1	150	3	0	0	50
		26	coniferous	future tree concept	2	200	3	0	0	110
			deciduous	future tree concept (no treatment for beech)	2	300	3	0	0	110
	Harvest	35	coniferous	target diameter felling (gap opening and regeneration, plantation)	10	0	0	45-120	100	350
			deciduous	no treatment	10	0	0			
		37	coniferous	target diameter felling	2	0	0	45-120	100	80
			deciduous	no treatment	2	0	0			
Deciduo us	Precommerci al	0	coniferous	stem number reduction	2	1000	0	0	0	15
			deciduous	no treatment	2	0	0	0	0	15
	Commercial	12	coniferous	future tree concept	2	100	2	0	0	40
			deciduous	future tree concept	2	100	2	0	0	40
		18	coniferous	future tree concept	2	75	2	0	0	55

			deciduous	future tree concept	2	75	2	0	0	55
Harvest	32		coniferous	target diameter felling	2	0		45-80	95	80
			deciduous	target diameter felling	2	0		65-80	95	80

215

Table 3: Thinning and harvesting measures in the production-oriented scenario

Production-oriented										
Dominant tree species	Phase	Starts at dominant height (m)	Tree species	Treatment	Frequency	N future crop trees	N competitors	Target diameter (cm)	% of targeted trees removed per treatment	Max. volume removed per treatment (m ³ ha ⁻¹)
Coniferous	Precommercial	0	coniferous	0	2	0	0	0	0	0
			deciduous	0	2	0	0	0	0	0
	Commercial	12	coniferous	selective thinning and target diameter felling	2	0	0	40-200	50	60
			deciduous	selective thinning and target diameter felling	2	0	0	5-200	50	60
		19	coniferous	selective thinning and target diameter felling	2	0	0	50-200	50	120
			deciduous	selective thinning and target diameter felling	2	0	0	50-200	50	120
	Harvest	31	coniferous	selective thinning and target diameter felling	1	0	0	20-200	100	500
			deciduous	selective thinning and target diameter felling	1	0	0	5-200	100	500
Deciduous	Precommercial	0	coniferous	stem number reduction	1	0	0	0	0	25
			deciduous	stem number reduction	1	0	0	0	0	25

Commercial	12	coniferous	selective thinning	1	0	0	0	0	25
		deciduous	selective thinning	1	0	0	0	0	25
	17	coniferous	thinning from below	1	0	0	0	0	25
		deciduous	thinning from below	1	0	0	0	0	25
Harvest	30	coniferous	no treatment	1	0	0	20- 200	100	500
		deciduous	selective thinning and target diameter felling	1	0	0	20- 200	100	500

2.4. Characterizing the forest stands

The coefficient of variation of dbh (dbh.cv) was selected to characterize the forest stands. It is a commonly used and easy to replicate structural indicator [23]. The Stand Density Index (SDI) by Reineke [70] was included as an independent variable to cover the potential effects of stand density on stand structure. The standing volume ($\text{m}^3 \text{ha}^{-1}$) was estimated based on dbh, tree height, and form factors following the DESER standard [71] and represents the merchantable wood volume (log size > 7 cm diameter at smaller end) per hectare and year ($\text{m}^3 \text{ha}^{-1}$). The volume increment ivol was defined by the increment in the standing volume per ha and year ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$). The relative volume increment in % of the standing volume ($\text{m}^3 \text{ha}^{-1}$) rel.ivol was included in the descriptive part to visualize the development of stand productivity in the different management scenarios.

Table 4: Overview of structural indicators applied in this study

Code	Name	Equation	Description
dbh.cv	Coefficient of variation of dbh	$dbh.cv = \frac{sd}{\overline{dbh}}$	The dbh.cv [72] relates the standard deviation sd to the mean \overline{dbh} . It measures tree size heterogeneity within a defined area based on dbh.
SDI	Stand density index	$SDI = N \cdot \left(\frac{25}{dq}\right)^{-1.605}$	The SDI by Reineke [70] uses total stem number per ha, $N = \sum_{i=1}^N n_i$, and the quadratic mean diameter dq . SDI enables the comparison of forest stands of different ages.
vol	Standing volume	$Vol = \text{m}^3 \text{ha}^{-1}$	The standing volume vol is the quantity of merchantable timber per ha.
ivol	Volume increment	$ivol = \text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$	The ivol Quantifies the volume increment in merchantable timer per hectare and year.
rel.ivol	Relative volume increment	$rel.ivol = ivol / vol$	The rel.ivol is the volume increment ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$) per standing volume vol ($\text{m}^3 \text{ha}^{-1}$) in %.

2.5. Trade-off

228 For the calculation of the trade-off between structural heterogeneity dbh.cv and productivity ivol,
 229 dbh.cv and ivol were standardized for a comparable value range as applied by others [73,74]. The
 230 standardized dbh.cv and ivol called str and prod, respectively:

$$231 \quad str_{i,j,k} = \frac{dbh.cv_{i,j,k} - \min(dbh.cv_i)}{\max(dbh.cv_i) - \min(dbh.cv_i)} \quad (Eq. 1)$$

$$232 \quad prod_{i,j} = \frac{ivol_{i,j} - \min(ivol_i)}{\max(ivol_i) - \min(ivol_i)} \quad (Eq. 2)$$

233 str and prod are the standardized versions of dbh.cv and ivol on stand i in year j and at the spatial
 234 scale of radius k. One mean value of ivol ($m^3 \text{ ha}^{-1} \text{ year}^{-1}$) per stand was calculated, because productivity
 235 was of value only at the level of the whole stand. The stand was seen as a profit-making forest enterprise
 236 where the total value is of importance. The min and max are the minimum and maximum of dbh.cv of
 237 all stands, years and spatial scales. The standardized str and prod values ranged from 0 to 1.

238 The trade-off between the standardized structural heterogeneity str and the standardized
 239 productivity prod was then set up. The trade-off therefore describes the level of structural heterogeneity
 240 in relation to a certain level of productivity. In this way, the relative level of structural heterogeneity
 241 per unit of productivity can be measured, even if stands have a different absolute level of productivity:

$$242 \quad t_{i,j,k} = \frac{str_{i,j,k}}{prod_{i,j}} \quad (Eq. 3)$$

243 $t_{i,j,k}$ is the trade-off between the standardized structural heterogeneity str on stand i in year j on the
 244 spatial scale k and the standardized productivity prod of stand i in year j. A larger t value means that a
 245 stand provides more structural heterogeneity per unit of productivity. The trade-off t was calculated
 246 for each stand, point in time, radius, and each of the 3 management scenarios.

247 2.6. Growing window for different spatial scales

248 For the continuous analysis of structural heterogeneity at different spatial scales, we used a
 249 growing window technique [75]. A circle was drawn around each random point with increasing radius
 250 k for the radii 5, 10, 25, 50, 75, 100, 150, 250, 500, 750, 1000, and 2000 m, thus comprising an increasing
 251 area to be examined around each random point of 79 m^2 up to the maximum area of the virtual forest
 252 stand (192 ha). The method was conducted for 30 random points per stand. One mean value per stand,
 253 point in time, and radius were then calculated and used for further analysis.

254 2.7. Statistical analysis

255 After a descriptive presentation, we used generalized additive mixed models (GAMMs) [76] to
 256 examine how the trade-off between structural heterogeneity and productivity ivol developed over time
 257 and spatial scale under different management scenarios. For each of the two groups "age-class stands"
 258 and "uneven-aged stands", the model function was applied to test differences for significance. The
 259 model was also applied to the spruce stand, beech stand, single-tree mixture, and section-wise mixture
 260 but those results were only presented visually as they were not the main focus of this study.

$$261 \quad t_{group} = scen * (f(SDI_i) + f(year_j) + f(radius_k)) + \varepsilon \quad (Eq. 4)$$

262 t is the trade-off str/prod per group (age-class vs. uneven-aged) in each initial stand i depending
 263 on the SDI, time (year) j, and space (radius) k. SDI for each stand i was included in the model function
 264 to cover effects that were only based on stand density. Scen is the management scenario applied. The
 265 virtual forest stand i was also included as random effect to cover unknown dependencies between the
 266 forest stands. The model term ε covers the remaining unexplained variation.

267 For testing the differences between the two groups "age-class stands" vs "uneven-aged stands",
 268 another model (GAMM) was set up that was applied to each of the three scenarios separately:

$$269 \quad t_{scen} = group * (f(SDI_i) + f(year_j) + f(radius_k)) + \varepsilon \quad (Eq. 5)$$

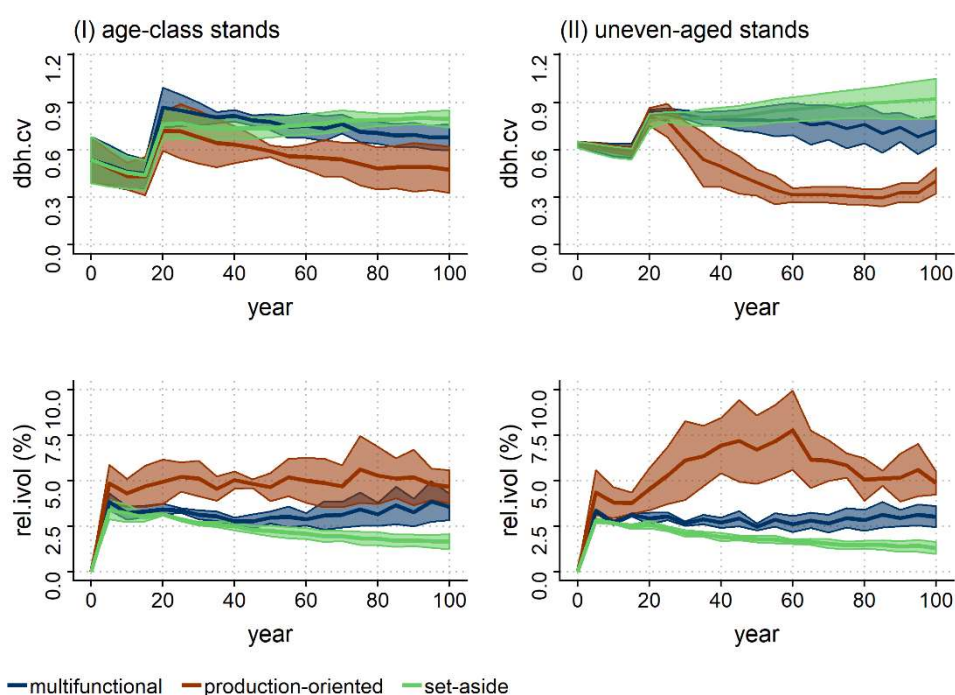
270 t_{scen} is the trade-off str/prod in scenario scen. The factor variable group contains the age-class vs.
 271 uneven-aged stands. The other variables are used as mentioned above.

272 3. Results

273 We answered the research question: “How does stand structural heterogeneity in age-class vs.
 274 uneven-aged stands develop over time and spatial scale in different management scenarios?” with a
 275 descriptive presentation (3.1. Structural heterogeneity and relative productivity over time) and by
 276 applying models for investigating the trade-off between structural heterogeneity and productivity
 277 (3.2. Trade-off between structural heterogeneity and productivity).

278 3.1. Structural heterogeneity and relative productivity over time

279 First, we give an overview of the structural heterogeneity dbh.cv and the relative productivity
 280 rel.ivol over time in the different scenarios (Figure 1).
 281



282 — multifunctional — production-oriented — set-aside
 283 Figure 1: Coefficient of variation of dbh (dbh.cv) and the relative ivol rel.ivol (%) in (I) age-class stands
 284 and (II) uneven-aged stands over time in the multifunctional (blue), production-oriented (red), and
 285 set-aside scenario (green). Confidence intervals at 95%.

286 In the age-class forest, a strong increase in the dbh.cv to > 0.70 was found for all scenarios in year
 287 20, due to the regeneration ingrowth (Figure 1, I, row 1). After that, the dbh.cv decreased in the
 288 multifunctional (blue line) and the production-oriented scenario (red line) resulting in a final value
 289 of ~ 0.7 and ~ 0.5 , respectively. In the set-aside scenario (green line), the dbh.cv remained higher over
 290 time and stabilized around 0.8. In the uneven-aged stands (Figure 1, II, row 1), the dbh.cv increased
 291 up to 0.8 in year 20 in all scenarios due to the ingrowing regeneration. After year 20, the dbh.cv
 292 decreased slightly in the multifunctional scenario (blue line), resulting in a value of ~ 0.70 after 100
 293 years and decreased strongly in the production-oriented scenario (red line) resulting in a value of \sim
 294 0.40. The set-aside scenario led to a slight increase in dbh.cv up to a value of ~ 0.90 .

295 The rel.ivol in age-class stands (Figure 1, I, row 2) was highest in the production-oriented
 296 scenario (red line) and stabilized around 5% over time. In the multifunctional scenario (blue line), the
 297 rel.ivol was around 3% and also mostly stable over time. In the set-aside (green line), the rel.ivol was
 298 lowest and resulted in a value of $\sim 2\%$ in the long-term. In the uneven-aged stands (Figure 1, II, row

299 2) the rel.ivol was highest in the production-oriented scenario (red line), compared to the other
 300 scenarios, with an increase from 4% up to 7.5% until year 60 and a decrease to 5% after that. In the
 301 multifunctional scenario (blue line), the rel.ivol remained at ~ 2.5 %. In the set-aside scenario (green
 302 line), a decrease from 2.5% to ~ 2% was found.

303 In sum, whereas in the age-class stands (Figure 1, I) the rel.ivol and dbh.cv were mostly stable
 304 over time, the production-oriented scenario led to contradicting trends of dbh.cv and rel.ivol in the
 305 uneven-aged stands (Figure 1, II). The descriptive part of the results already points at the conflicting
 306 relationship or trade-off between structural heterogeneity and productivity. For further investigation
 307 of this contrary trend, the trade-off between structural heterogeneity and productivity (str/prod) was
 308 set up and analyzed using the stated models.

309 3.2. Trade-off between structural heterogeneity and productivity

310 The models show changes in the trade-off between the standardized structural heterogeneity str
 311 and the standardized productivity prod (str/prod) over time and spatial scale depending on the
 312 silvicultural management applied while covering the potential effects of the SDI. The first model (Eq.
 313 4) tests the difference in the above-mentioned relationships between the management scenarios. The
 314 second model (Eq. 5) examines the differences between age-class and uneven-aged forest. The models
 315 mainly contain significant variables. Non-significant variables were automatically excluded during
 316 the model run. Yet, GAMMs are best interpreted by visual examination. The black line in the graphs
 317 represents all age-class and uneven-aged stands, respectively, each containing a pure spruce stand
 318 (blue line), a pure beech stands (red line), a single-tree mixed stand (dark green line), and a section-
 319 wise mixed stand (light green line). The separation into pure and mixed spruce and beech stands is
 320 presented only visually by the differently colored model curves, as the difference between species
 321 was not the main focus of this study. If the difference between the different mixtures was relevant, it
 322 was seen in confidence bands that did not overlap. The model curves are centered around 0, meaning
 323 that the intercept is the overall mean of the response variable. The curves do therefore not only vary
 324 inside the span of the dependent variable but show a negative (< 0) or positive (> 0) effect of the
 325 explaining variables on the mean of the response variable. We focussed on describing only effects
 326 that were both significant and relevant because of their extent; that is to say, the effects that were also
 327 visually present.
 328

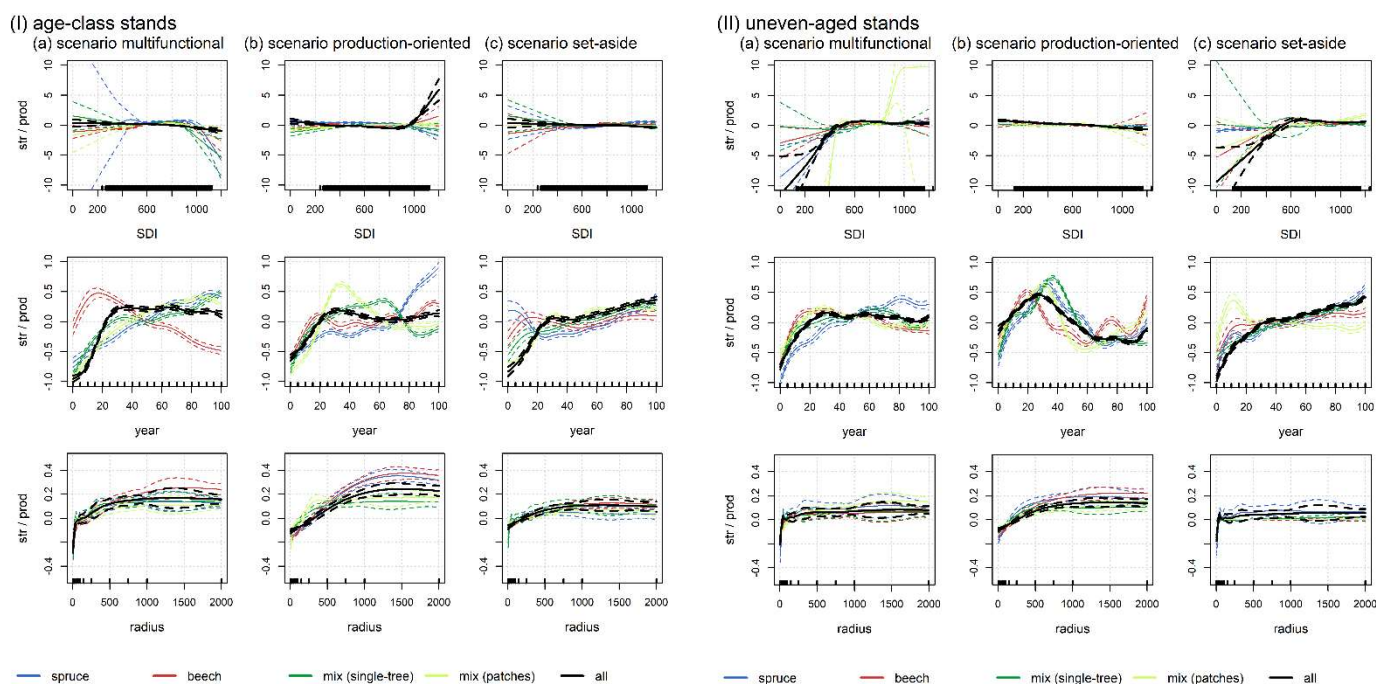


Figure 2: Model results showing development of the trade-off coefficient of variation/ivol in the examined area in (I) age-class stands and (II) uneven-aged stands depending on SDI (row 1), over time (row 2), and spatial scale (row 3) in a (a) multifunctional, (b) production-oriented, and (c) set-aside scenario. Confidence intervals at 95%.

SDI has been included in the model to cover the potential relationship between stand density and productivity (Table A 1). In the age-class stands, only in the production-oriented scenario, a very high SDI led to an increase in str/prod (Figure 2, I, row 1, b). In the multifunctional and the set-aside scenarios, the effect of SDI was around 0 for the model range covered with enough data (Figure 2, I, row 1, a and c). In the uneven-aged stands, SDI had a negative effect on str/prod when an SDI was below 400 and in the multifunctional and the set-aside scenarios (Figure 2, II, row 1, a and b). Yet, these effects only address the limits of the model range. In the valid model range covering most of the data ($200 < \text{SDI} < 1000$), the effect of SDI on str/prod was around 0. The effect of SDI on str/prod was also found to be significantly different between age-class and uneven-aged forest (Table A 2) mostly because of the differences at the limits of the model range for very low or high SDI.

Over time in the age-class stands, a significant difference in str/prod between the scenarios was found (Table A 1), especially between the multifunctional (Figure 2, I, row 2, a) and the production-oriented scenario (Figure 2, I, row 2, b). This difference was mostly seen in the pure beech stand (red line), where str/prod decreased over time only in the multifunctional scenario. In the set-aside scenario (Figure 2, I, row 3, c), str/prod increased towards year 100, whereas in the other scenarios the effect only a slight positive effect over time was found.

The most important finding in uneven-aged stands was the difference in the development of str/prod between the multifunctional (Figure 2, II, row 2, a) and the production-oriented scenario (Figure 2, II, row 2, b). Only in the production-oriented scenario did the str/prod increase strongly until year 20. After year 40, the effect of time on str/prod became negative, meaning a decrease in str/prod. Only in the set-aside scenario did the str/prod increase over time in both pure and mixed stands. The largest difference (by visual checks) between the species in uneven-aged stands was seen in an increase in str/prod after year 50 in pure age-class spruce stands (blue line), where str/prod decreased over time in the multifunctional but not in the production-oriented scenario (Figure 2, I, row 2, a, red line). The second model confirmed the significant difference between age-class and uneven-aged (Table A 2) concerning the development of str/prod over time. This is most clearly seen in the production-oriented scenario stands (Figure 2, I, row 2, b versus Figure 2, II, row 2, b).

In both age-class and uneven-aged stands, a stronger increase in str/prod with increasing spatial scale was found in the production-oriented scenario (Figure 2, I and II, row 3, b) compared to the multifunctional and the set-aside scenarios (Figure 2, I and II, row 3, a and c) (Table A 1). The increase in str/prod with increasing spatial scale in the multifunctional and the production-oriented scenarios was found to be significantly stronger in age-class stands than in the uneven-aged stands (Figure 2, I and II, row 3, a and b) (Table A 2).

3.3. Results summary

The production-oriented scenario led to a decrease over time in structural heterogeneity in the uneven-aged stands, but not in the age-class stands. In the case where high productivity is the first priority, age-class stands could be used without lowering the structural heterogeneity. With increasing spatial scale, str/prod increased more strongly in the age-class stands than in the uneven-aged stands and more strongly in the production-oriented scenario than in the multifunctional and set-aside scenarios.

4. Discussion

Since the demand for wood products in Europe is presumed to increase in the future [77], management is expected to remain production-oriented, even though other ecosystem functions and services need to be covered as well [78]. Most forests in Europe are managed, which enables decision

373 makers in forest management to shape the outcome of ecosystem functions and services. Usually,
374 tree size heterogeneity decreases as soon as a forest is economically managed [79]. We noted this
375 trend already in the descriptive part of the analysis (Figure 1). We then quantified the conflicting
376 interest between high wood production and high structural heterogeneity by using a trade-off value
377 (Figure 2). We used standardized measures to disentangle the trade-off from absolute values (which
378 depend also on the setup of the virtual stands) in order to develop a ratio of structural heterogeneity
379 per unit of productivity. An increase in the trade-off str/prod could therefore result from an increase
380 in structural heterogeneity str or in a decrease in productivity prod. We chose to use this kind of
381 trade-off to point out the competing relationships between stand structural heterogeneity and
382 productivity because the focus on high productivity was incorporated already in the management
383 scenarios (multifunctional, production-oriented, set-aside) and the initial stand structure (age-class
384 vs. uneven-aged) was the focus. If similar analyses are conducted on other plots with an overall lower
385 or higher level of productivity, the conflicting relationship between structure and productivity can
386 still be measured and compared.

387 Differences between the management scenarios and between age-class and uneven-aged stands
388 were visible in the descriptive part of the results (Figure 1) and statistically proven through the
389 application of the models (Eq. 4, Eq.5 and Figure 2).

390 The inclusion of SDI in the models used in this study enabled the specific testing of the effect of
391 silvicultural management on structural heterogeneity in relation to stand productivity as it covered
392 potential effects of higher stocking on stand structure and productivity [80]. Since the virtual forest
393 stands were already similar in stand density, effects of SDI were mostly found in the limits of the
394 model range, meaning for a very low or high SDI (Figure 2, I and II, row 1).

395 In the production-oriented scenario, the structural heterogeneity per unit of productivity
396 str/prod decreased significantly over time in the case of the uneven-aged stands, compared to the
397 age-class stands. The prescribed thinning in the production-oriented scenario incorporated a
398 commercial use of competitor trees through regular thinning from below. In uneven-aged stands, the
399 thinning operations were to the whole forest stand at the same time, which can lead to a more
400 homogeneous tree size distribution resulting in a lower structural heterogeneity, as stated by others
401 [81]. In the age-class stands, however, each age-class was thinned individually depending on tree
402 height. A higher number of different age-classes and tree heights was therefore possible, at least when
403 measured at the whole stand. In uneven-aged stands, the multifunctional scenario was therefore
404 more suitable for providing high structural heterogeneity in relation to stand productivity than the
405 production-oriented scenario.

406 Those results are only valid when assuming a provision of structural heterogeneity at stand level
407 instead of tree level. With increasing spatial scale, the structural heterogeneity per unit of
408 productivity increased more strongly in age-class stands compared to uneven-aged stands. The
409 maximum structural heterogeneity was therefore reached at a larger spatial scale in age-class stands.
410 Also, str/prod increased with increasing spatial scale more strongly in the production-oriented
411 scenario compared to the multifunctional and the set-aside scenario. In both cases, the thinning
412 operations rather homogenized the tree size distribution on a small spatial scale (through strong
413 thinning from below in the production-oriented scenario and through the same type of thinning
414 applied to a whole age-class in the age-class stands). In the multifunctional or set-aside scenarios,
415 especially in uneven-aged stands, the selective thinning maintained a higher structural heterogeneity
416 at tree level. With increasing spatial scale, the structural heterogeneity did therefore not increase so
417 strongly because it was already high at tree level. If the size of each age-class is rather small (16 ha in
418 this study), differently aged and sized trees can provide a heterogeneous forest even under the
419 production-oriented scenario. This finding is especially interesting as the consequences can be a
420 higher structural heterogeneity in age-class stands compared to uneven-aged stands [82,83], when
421 measured at a larger spatial scale, due to the provided mosaic of different habitat types [84]. The need
422 for open spaces, e.g., for light-demanding species, [85] can be embedded in a large heterogeneous
423 mosaic and influence biodiversity at the landscape scale [86,87]. Further can the stability at landscape
424 scale be increase through this higher structural heterogeneity [18]. Still, commercially used age-class

425 forests are often assumed to provide a lower number of large and old trees, as most trees are cut
426 before reaching the old growth phase. This could be addressed through a set-aside of parts of the
427 managed forests, as suggested by others [88]. The virtual forest stands were based on real forest types
428 in Bavaria. They are representative of forest ecosystems in Central Europe and enable an analysis of
429 the effect of silvicultural management. For testing the performance of forests under different
430 management in terms of trade-offs between ecosystem functions and services in advance of
431 application, simulation has proven to be a useful tool [89].

432 The simulation over a course of 100 years in our case aimed at testing silvicultural management
433 on already existing and partly mature stands. A negative or positive effect of structural heterogeneity
434 on productivity in young and old stands, respectively, found by others [90] could therefore not be
435 compared to the virtual stands in this study. Generally, the chosen approach of this study would also
436 be applicable for newly established stands to test the effect of silvicultural management on their
437 development in stand structure.

438 5. Conclusions and outlook

439 Our approach of combining stand simulation with an analysis of structural heterogeneity in relation
440 to stand productivity can be understood as an exemplary study to test the effect of silvicultural
441 management before its application in real forests and to identify and incorporate forest structure as
442 an important factor in multiple ecosystem functions and services [91]. The strong promotion of
443 continuous cover forestry seen in the last decades for the purpose of increasing uneven-aged stands
444 in temperate [26,92] and boreal regions [93,29,94] shows that the decision between the two
445 approaches is still an up-to-date topic. A critical comparison between stand types in terms of their
446 performance in structural heterogeneity and productivity can help to predict the outcome of
447 management before transforming all existing age-class stands to uneven-aged stands. Possibly, the
448 existing age-class stands can provide a high structural heterogeneity at a slightly larger spatial scale.
449 We found this to be the case in uneven-aged stands – where an appropriate management scenario is
450 applied, which in this case was the production-oriented scenario. Although some assumptions had
451 to be made for the simulation of stand growth in the future, rough trends can be helpful to support
452 forest management in their decisions. In further studies, additional variables like changes in growing
453 conditions and the connection to population models can be addressed.

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467 **Conflicts of Interest:** The authors declare no conflict of interest.

468

469

470

471

472 **Appendix A**

473 *A.1. Model result tables*

474

475 Table A 1: Model results for differences between management scenarios

str / prod	age-class						uneven-aged						
	edf	Ref.d	F	p-	sig.	R-sq.	edf	Ref.d	F	p-	sig.	R-sq.	
		f		value		(adj)		f		value		(adj)	
							7.1						
s(SDI):multi	4.05	9	16.00	0.000	***	0.726	s(SDI):scen1	8	9.00	96.86	0.000	***	0.658
							4.4						
s(SDI):prod	7.89	9	36.82	0.000	***		s(SDI):scen2	0	9.00	58.44	0.000	***	
							5.6						
s(SDI):setaside	3.88	9	11.76	0.000	***		s(SDI):scen6	7	9.00	72.47	0.000	***	
			249.7				8.2			209.1			
s(year):multi	8.44	9	0	0.000	***		s(year):scen1	3	9.00	2	0.000	***	
			113.5				8.4			292.2			
s(year):prod	7.53	9	4	0.000	***		s(year):scen2	6	9.00	7	0.000	***	
							8.1			184.7			
s(year):setaside	7.78	9	74.28	0.000	***		s(year):scen6	7	9.00	7	0.000	***	
							s(radius):scen	8.2					
s(radius):multi	7.87	9	48.03	0.000	***		1	8	9.00	26.59	0.000	***	
							s(radius):scen	3.0					
s(radius):prod	3.02	9	38.31	0.000	***		2	6	9.00	31.78	0.000	***	
							s(radius):scen	8.3					
s(radius):setaside	2.93	9	12.69	0.000	***		6	4	9.00	17.57	0.000	***	

476

477 Table A 2: Model results for differences between age-class and uneven-aged stands

Multifunctional						
	edf	Ref.df	F	p-value	sig.	R-sq.
s(SDI):age-class	4.58	9	21.94	0.000	***	0.653
s(SDI):uneven-aged	6.77	9	39.14	0.000	***	
s(year):age-class	8.65	9	339.98	0.000	***	
s(year):uneven-aged	7.84	9	172.03	0.000	***	
s(radius):age-class	8.20	9	64.11	0.000	***	
s(radius):uneven-aged	7.65	9	20.37	0.000	***	
Production-oriented						
	edf	Ref.df	F	p-value	sig.	R-sq.
s(SDI):age-class	6.84	9	23.81	0.000	***	0.553
s(SDI):uneven-aged	1.66	9	29.91	0.000	***	

s(year):age-class	7.48	9	94.53	0.000	***	
s(year):uneven-aged	7.95	9	151.33	0.000	***	
s(radius):age-class	2.83	9	28.25	0.000	***	
s(radius):uneven-aged	2.57	9	15.40	0.000	***	
	6.84	9	23.81	0.000	***	
Set-aside						
	edf	Ref.df	F	p-value	sig.	R-sq.
s(SDI):age-class	6.79	9	13.33	0.000	***	0.794
s(SDI):uneven-aged	6.54	9	29.19	0.000	***	
s(year):age-class	8.50	9	99.36	0.000	***	
s(year):uneven-aged	8.77	9	225.98	0.000	***	
s(radius):age-class	7.63	9	46.30	0.000	***	
s(radius):uneven-aged	8.63	9	37.49	0.000	***	

478

479 A.2. The virtual forest stands

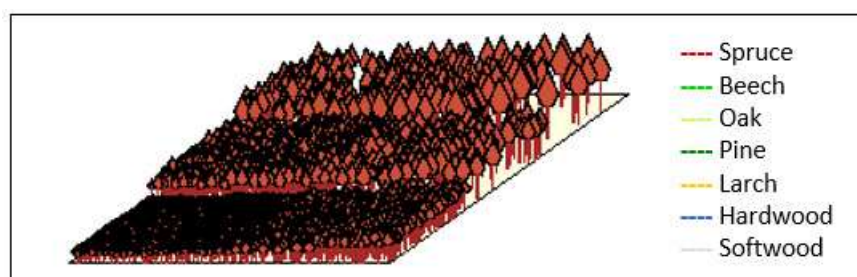


Figure A 1: age-class spruce stand

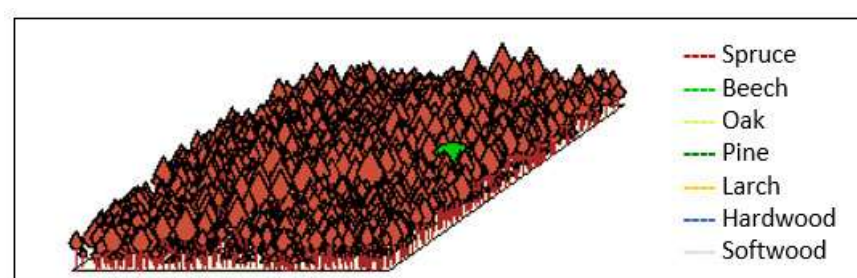


Figure A 2: uneven-aged spruce stand

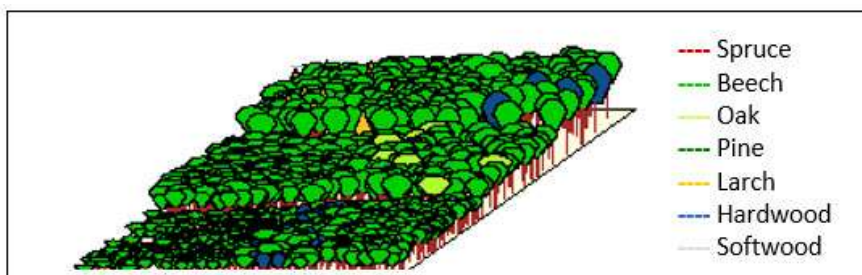


Figure A 3: age-class beech stand

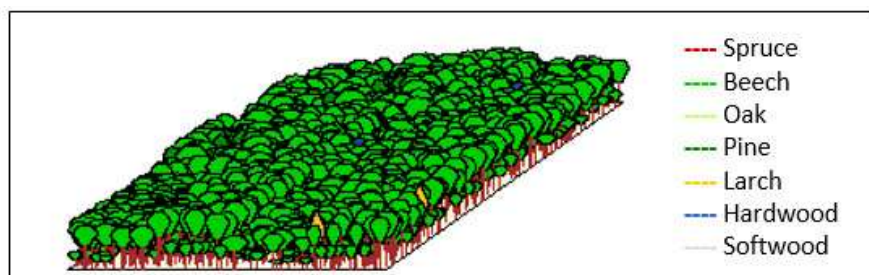


Figure A 4: uneven-aged beech stand

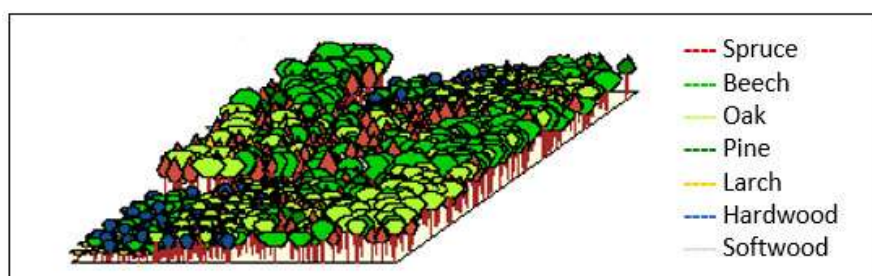


Figure A 5: age-class single-tree mixed stand

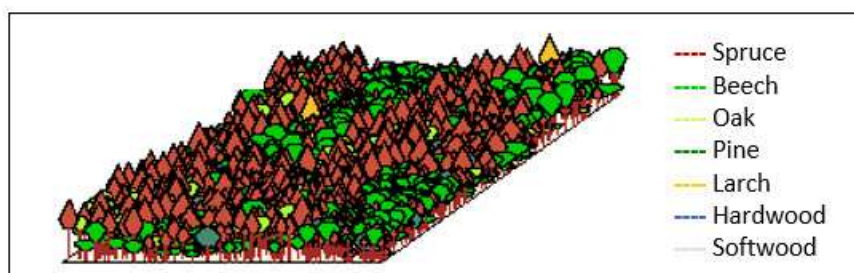


Figure A 6: uneven-aged single-tree mixed stand

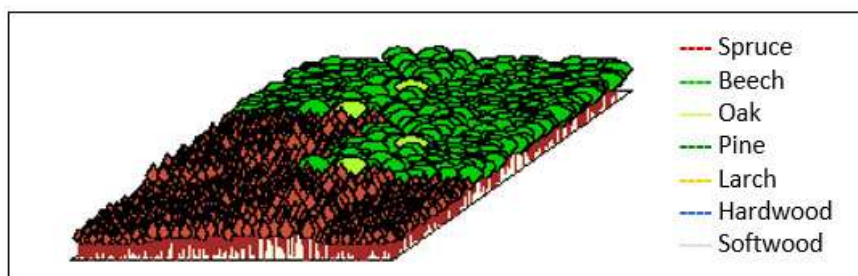


Figure A 7: age-class section-wise mixed stand

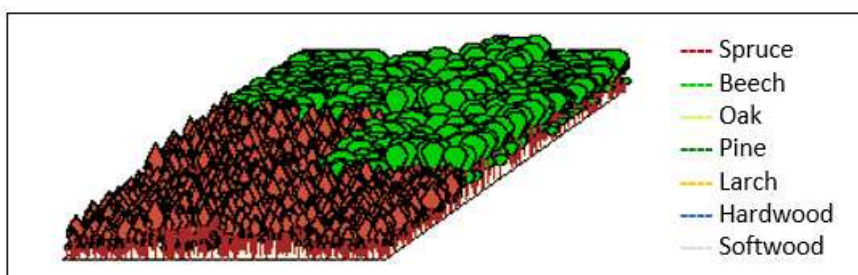


Figure A 8: uneven-aged section-wise mixed stand

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Eidesstattliche Erklärung

Ich erkläre an Eides statt, dass ich die bei der promotionsführenden Einrichtung
Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt

der TUM zur Promotionsprüfung vorgelegte Arbeit mit dem Titel:

Interactions between forest stand structure, tree species composition and stand productivity in spatial, temporal and silvicultural context

in der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt, Lehrstuhl für Waldwachstumskunde

Fakultät, Institut, Lehrstuhl, Klinik, Krankenhaus, Abteilung

unter der Anleitung und Betreuung durch: Prof. Dr. Dr. hc. Hans Pretzsch ohne sonstige Hilfe erstellt und bei der Abfassung nur die gemäß § 6 Ab. 6 und 7 Satz 2 angebotenen Hilfsmittel benutzt habe.

Ich habe keine Organisation eingeschaltet, die gegen Entgelt Betreuerinnen und Betreuer für die Anfertigung von Dissertationen sucht, oder die mir obliegenden Pflichten hinsichtlich der Prüfungsleistungen für mich ganz oder teilweise erledigt.

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Die öffentlich zugängliche Promotionsordnung der TUM ist mir bekannt, insbesondere habe ich die Bedeutung von § 28 (Nichtigkeit der Promotion) und § 29 (Entzug des Doktorgrades) zur Kenntnis genommen. Ich bin mir der Konsequenzen einer falschen Eidesstattlichen Erklärung bewusst.

Mit der Aufnahme meiner personenbezogenen Daten in die Alumni-Datei bei der TUM bin ich

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