Effects of local neighbourhood diversity on crown structure and productivity of individual trees in mature mixed-species forests

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RESEARCH

Effects of local neighbourhood diversity on crown structure and productivity of individual trees in mature mixed-species forests

Louis Georgi[1]* , Matthias Kunz[1], Andreas Fichtner[2], Karl Friedrich Reich[1], Anne Bienert[3], Hans-Gerd Maas[3] and Goddert von Oheimb[1]

Abstract

Background: Species-specific genotypic features, local neighbourhood interactions and resource supply strongly influence the tree stature and growth rate. In mixed-species forests, diversity-mediated biomass allocation has been suggested to be a fundamental mechanism underlying the positive biodiversity-productivity relationships. Empirical evidence, however, is rare about the impact of local neighbourhood diversity on tree characteristics analysed at a very high level of detail. To address this issue we analysed these effects on the individual-tree crown architecture and tree productivity in a mature mixed forest in northern Germany.

Methods: Our analysis considers multiple target tree species across a local neighbourhood species richness gradient ranging from 1 to 4. We applied terrestrial laser scanning to quantify a large number of individual mature trees ($N = 920$) at very high accuracy. We evaluated two different neighbour inclusion approaches by analysing both a fixed radius selection procedure and a selection based on overlapping crowns.

Results and conclusions: We show that local neighbourhood species diversity significantly increases crown dimension and wood volume of target trees. Moreover, we found a size-dependency of diversity effects on tree productivity (basal area and wood volume increment) with positive effects for large-sized trees (diameter at breast height (DBH) > 40 cm) and negative effects for small-sized (DBH < 40 cm) trees. In our analysis, the neighbour inclusion approach has a significant impact on the outcome. For scientific studies and the validation of growth models we recommend a neighbour selection by overlapping crowns, because this seems to be the relevant scale at which local neighbourhood interactions occur. Because local neighbourhood diversity promotes individual-tree productivity in mature European mixed-species forests, we conclude that a small-scale species mixture should be considered in management plans.

Keywords: Biodiversity, Tree growth, Crown architecture, Quantitative structure models, Terrestrial laser scanning, Neighbour classification

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Background

Forest canopies play a decisive role in shaping the local and global climatic conditions due to evaporation and carbon fixation (Li et al. 2015; Bastin et al. 2019), and constitute an important habitat for a multitude of species (Ozanne et al. 2003). Canopies are formed by crowns of individual trees, which strive for the optimisation of their own light access in order to maximize the photosynthesis potential. The crown architecture is of particular importance here, because of its direct link to a tree's light absorption (Ishii and Asano 2010; Sapijanskas et al. 2014; Forrester et al. 2018). While the fundamental architecture of the crown is embedded in the species-specific genotype (Costes and Gion 2015), the actual stature and allometry is strongly influenced by the local tree species composition and resource supply (De Kroon et al. 2005; Bayer et al. 2013; del Río et al. 2019). Besides abiotic factors, e.g. slope inclination (Lang et al. 2010), biotic interactions at the local level, e.g. crowding and species composition, are most crucial for the realized crown shape in closed-canopy stands (Pretzsch and Schütze 2009; Fichtner et al. 2013; Forrester et al. 2017). Photomorphogenetic responses of individual trees result in considerable crown plasticity, i.e. the environmentally driven intraspecific variability in crown architecture (Schröter et al. 2012; Pretzsch 2014). These light-related tree interactions for physical niche partitioning in canopy space have been found to be severely impacted by species mixing and are thought to be an important process in explaining the positive biodiversity – productivity relationships (BPRs) in forests (Morin et al. 2011; Huang et al. 2018; Kunz et al. 2019).

The diversity-driven modifications in the individual-tree crowns are based on variations in crown size and shape (Pretzsch 2014; Williams et al. 2017; Kunz et al. 2019). The underlying mechanisms operate at multiple hierarchical levels, ranging from shifts in branch morphology and ramification to modifications in the biomass allocation ratio between trunk and branches (Kunz et al. 2019; Guillemot et al. 2020). However, empirical evidence is rare about the impact of local neighbourhood species richness on tree crown architecture analysed at a very high level of detail.

Such analyses, with a very high spatial resolution, can be carried out effectively making use of terrestrial laser scanning (TLS) (Liang et al. 2016). The few studies cited below which have been conducted with high-resolution TLS in mature forests of Central Europe mainly compared the effects between intra- and interspecific tree interactions in pure and mixed stands and/or focused on only one tree species, namely European beech (*Fagus sylvatica* L.). In addition, the gradient in the number of neighbouring tree species was often short. In comparison to pure stands, Bayer et al. (2013) observed larger crown volumes (CV) for beech and Norway spruce (*Picea abies* (L.) H. Karst.) when growing in mixture. They also found species specific tree crown adaptions: in mixtures beech had flatter branch angles, whereas spruce showed longer branches. Metz et al. (2013) showed that neighbourhood diversity significantly influenced beech growth and that intraspecific competition from beech is stronger than interspecific competition from other, more translucent species. These patterns were more pronounced when crown dimensions and shapes were derived from TLS data compared to the use of conventional geometric crown shapes. Moreover, Juchheim et al. (2017) detected that beech trees in mixtures were associated with longer branches with flatter angles, a lower height-to-diameter ratio and a lower height of the maximal lateral crown extension. Correspondingly, Barbeito et al. (2017) showed that beech trees in mixed stands with Scots pine (*Pinus sylvestris* L.) had larger crowns, especially in the lower canopy. However, the site productivity had a strong impact on this mixing effect. In a biodiversity-ecosystem functioning (BEF) experiment with young subtropical trees in China, Kunz et al. (2019) observed significant diversity effects on the crown architecture along a broad gradient of local neighbourhood species richness.

To fill the knowledge gap for mature European forests we extended previous studies by analysing further deciduous tree species that might play an important role (besides beech we also included Common oak (*Quercus robur* L.), Common hornbeam (*Carpinus betulus* L.), sycamore (*Acer pseudoplatanus* L.), Common ash (*Fraxinus excelsior* L.) and European larch (*Larix decidua* Mill.) and considered a longer tree species richness gradient of up to four in the local neighbourhood. Furthermore, most of the previous studies incorporated a relatively low number of target trees (mainly because traditional crown measurements in mature forest are highly time-consuming and modern high-resolution inventory tools such as TLS are analytically demanding). In this study we extended substantially the number of trees analysed to obtain more valid results. For analysing effects occurring on the local tree-to-tree scale it is of great advantage when the spatial resolution of the analysis is very high. Airborne laser scanning (ALS) and TLS have been successfully applied to capture crown characteristics (for an overview see Vosselman and Maas 2010). The earlier generations of laser scanners, however, mostly lack a high-resolution acquisition of the complex tree crowns in dense mature forests. In this study we make use of state-of-the-art technology of full-waveform TLS with online waveform processing to measure a large number of individual trees in a highly accurate manner (Bienert et al. 2018; Georgi et al. 2018).

Of particular importance in examining a tree's local neighbourhood interactions is the identification of

potential competitors and facilitators and hence, the relevant scale the local neighbourhood interactions in situ. Different distance-dependent approaches exist for neighbour inclusion (Biging and Dobbertin 1992; Rivas et al. 2005). In contrast to tree plantations and experiments, the stem and size distribution in natural forests is much more heterogeneous, resulting in potentially large differences when using different neighbour inclusion approaches (Rivas et al. 2005). Hence, Metz et al. (2013) points out the importance of unstandardized approaches to consider the crown size variation among equally thick and tall trees.

Given the technical progress of surveying instruments, the options for more precise and accurate neighbour inclusion approaches are improving. In the past this progress led to a selection by overlapping tree crowns with the help of crown mirrors instead of being confined to the use of circular plots with fixed radii around a target tree. Using this approach, von Oheimb et al. (2011) found no significant impact of neighbourhood diversity on tree growth. However, they only used the average crown radius of the horizontal projection of each tree, disregarding the actual overlap. In this study, we proceed a step further by using full-waveform TLS to detect every single branch with full extend and with the precise location in three-dimensional space to identify potentially interacting neighbours.

The aim of this study is to address two questions:

(1) How does local neighbourhood tree species diversity influence the tree morphology in mature European forests?
(2) How does local neighbourhood tree species diversity impact individual-tree productivity?

Methods
Study area
This study was performed in the Lauerholz Forest, located in south-eastern Schleswig-Holstein, Northern Germany, at a mean altitude of 20 m above sea level (53°88′ N, 10°74′ E). The study area is dominated by mixed-species deciduous forest, with a large number of different tree species (in particular *F. sylvatica, Q. robur, C. betulus, F. excelsior, A. pseudoplatanus, Acer platanoides* L., *Prunus avium* L., *Betula pendula* Roth, *L. decidua*). With a mean annual temperature of 8.3 °C and an annual precipitation of about 800 mm, the study area is characterised by a suboceanic climate (Deutscher Wetterdienst 2017). The dominant soil texture is till with the associated soil types luvisols and pseudogleyic luvisols. The geological substrate originates from the last (Weichselian) glaciation.

TLS data acquisition and registration
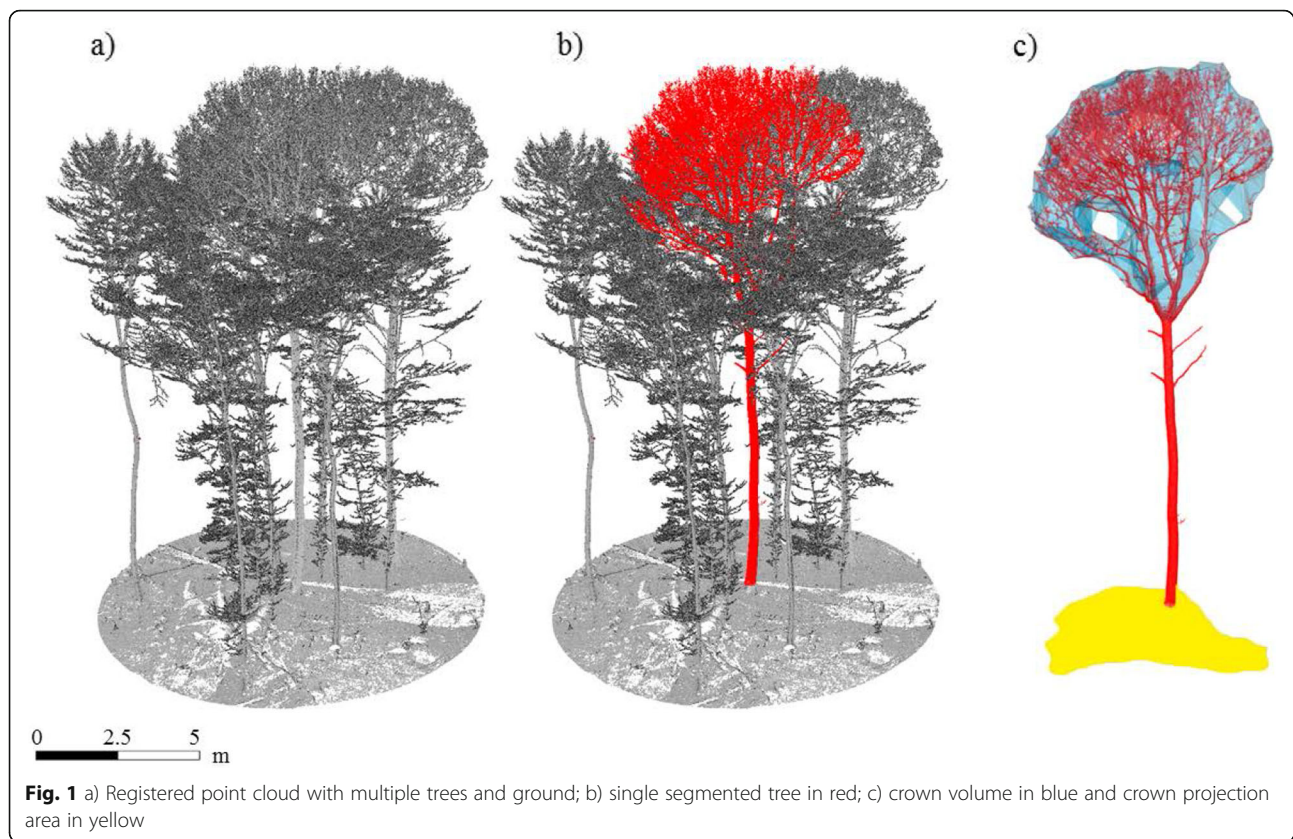For some of the analyses the growth data of the last decades were required (see below). Therefore, we investigated trees growing inside permanent circular inventory plots, each with a size of 500 m^2 (radius = 12.62 m). These plots were established in 1992, and inventory data were recorded in 1992, 2003 and 2013. Based on the inventory data of 2013, 11 plots with two or more tree species and a minimum age of 60 years were selected. In order to capture all possible neighbouring trees for the analysis, all trees in a circular plot area of 1600 m^2 (radius = 22.62 m) were sampled. Additionally, for exceptionally large individuals growing near the plot boundary, we manually selected also even more remote neighbours in order to meet the requirements of the neighbour inclusion approach based on realised crown overlap (see below).

TLS data were recorded in March 2017, using a RIEGL VZ-400i full-waveform terrestrial laser scanner (RIEGL Laser Measurement Systems GmbH, Horn, Austria). Each plot was scanned in a multiple scan mode from five scanner positions (Liang et al. 2016), with one scanning position in the centre of the plot and the other four distributed in the cardinal directions at a distance of 23 to 25 m from the centre (slightly variable distances were used to select positions that most effectively reduced occlusions). The angular resolution was 0.04 deg (corresponding to a resolution of 7 mm at 10 m). At the centre positions, the scanner was also tilted by 90° to overcome the limitation of the panoramic field of view. The instrument was mounted on a tripod and operated at a height of 1.30 m. All scans were performed under clear skies and nearly windless conditions.

TLS point clouds were co-registered using the registration tools "Automatic Registration 2" and "Multi Station Adjustment" of Riegl RiSCAN Pro 2.6.1, resultant in a registration accuracy between 2.2 and 2.7 mm (Fig. 1a). To achieve a higher quality point cloud, stray and noise points with a so-called surface reflectance less than − 25 dB or a pulse shape deviation greater than 15, both terms defined by the scanner manufacturer Riegl, were removed (Pfennigbauer and Ullrich 2010). The reflectance value in dB ranges from − 25 up to 5. The project coordinate system was defined by the plot centre point cloud and the other scanning positions were registered to this point cloud.

TLS data post-processing
All trees of the 11 plots with a diameter at breast height (DBH) ≥ 7 cm (*n* = 920) were segmented in a stepwise procedure. First, the TLS point clouds were automatically segmented in trees with the SimpleTree (4.33.06) software, a plugin of Computree (5.0.054b) (Hackenberg et al. 2015). Second, the automatically extracted trees were visually checked, and falsely classified tree segments were manually corrected using RiSCAN PRO

Fig. 1 a) Registered point cloud with multiple trees and ground; b) single segmented tree in red; c) crown volume in blue and crown projection area in yellow

Table 1 Morphologic traits measured for each sample tree

Measure	Abbreviation	Origin	Reference/Calculation
Basal area (cm^2)	BA	Point cloud/Inventory	DBH$^2 \times \pi/4$
Diameter at breast height (cm)	DBH	QSM	Raumonen et al. (2013)
Crown volume (m^3)	CV	Point cloud	See methods this publication
Tree height (m)	TH	Point cloud	$Z_{max} - Z_{min}$
Total wood volume (m^3)	V_{tot}	QSM	Raumonen et al. (2013)
Merchantable wood volume (m^3)	V_{mw}	QSM	See methods this publication
Volume of fine woody material (m^3)	V_{fwm}	QSM	See methods this publication
Crown base height (m)	CBH	Point cloud	See methods this publication
Crown projection area (m^2)	CPA	Point cloud	See methods this publication
Crown surface area (m^2)	CSA	Point cloud	See methods this publication
Basal area increment (cm$^2 \cdot$year^{-1})	BAI	Point cloud/Inventory	ΔBA/Δyears
Branch length sum (m)		QSM	Raumonen et al. (2013)
Mean branch angle 1st order (°)		QSM	See methods this publication
Mean branch angle 2nd order (°)		QSM	See methods this publication
Formula wood volume (m^3)	V_f	Inventory	Bergel (1973, 1974)
Formula wood volume increment (m$^3 \cdot$year^{-1})	V_fI	Inventory	ΔV_fI /Δyears

(Fig. 1b). The original point density was not reduced during the whole procedure to get the most accurate results.

Several tree characteristics (Table 1) and the aboveground wood volumes were derived for each segmented tree individual using quantitative structure models (QSMs). QSMs are a state-of-the-art approach (Raumonen et al. 2013) to quantify the 3D structure of a tree and its branching topology. QSMs deliver estimates of the aboveground wood volume with a high accuracy (Calders et al. 2015; Bienert et al. 2018). These models are a description of the tree as a hierarchical collection of geometric primitives (here: cylinders). They are embedded into the point cloud from which geometric and topological tree characteristics can be derived. To create the QSMs, we applied the TREEQSM (2.30) software developed by Raumonen et al. (2013), which runs within Matlab® (MathWorks, Natick, MA, USA) version R2018b on the Taurus high-performance cluster (HPC) of the TU Dresden. The method categorizes the point cloud in the stem and single branches and captures the tree's topology. Afterwards a volume model is compiled by fitting cylinders in the point cloud segments (Raumonen et al. 2015; Kunz et al. 2017). Due to the parameter sensitivity of the modelling process, we conducted a parameter optimisation test with a subset of trees. This led to the following parameter values: first minimum patch size: 5 cm; second minimum patch size: 1 cm; second maximum patch size: 2 cm; relative cylinder length: 4 cm; relative radius for outlier removal: 5 cm.

We extracted the basal area (BA), tree height (TH), total wood volume (V_{tot}) and branch length of the TREE QSM output. We also computed the merchantable wood volume (V_{mw}), defined as all aboveground woody structures with a diameter > 7 cm (i.e. the trunk and the larger branches). The volume of fine woody material (V_{fwm}; diameter < 7 cm) was calculated as the difference of V_{tot} and V_{mw}.

The trees mean branch angle was derived from all single branches and was calculated with the same method for the first- and second-order branches, respectively. To measure the branch's vertical orientation in space, we focused on the branch's exit angle by considering the first ten cylinders after the branch base, derived from the QSM. From those, the angle between the Z-axes of the coordinate system and the mean branch axes was computed.

Moreover, we extracted numerous crown morphological traits. The crown base height (CBH), defined as the height of the lowest living branch, was measured in RiSCAN Pro. The crown projection area (CPA), CV and crown surface area (CSA) for each tree were calculated

with a concave hull (alpha-shape with α-value = 0.3) using the Point Cloud Library (Rusu and Cousins 2011) and the Computational Geometry Algorithms Library (Kai et al. 2019) (Fig. 1c).

Target and neighbour tree selection

The primary aim of this study was to analyse the neighbourhood diversity effect on an individual-tree level. In addition to the selection of the affected trees (in the following "target tree"), the determination of influencing neighbours is of central importance.

To focus on vigorous trees as target trees, we included only trees taller than two-thirds of the highest tree growing in the plot for all analyses. Tree species with rare occurrence ($N \leq 2$) were excluded as target trees and one tree which was the only one having five neighbour tree species. A total of 920 trees was extracted from the TLS point clouds of which 148 were dedicated as target trees (61% *F. sylvatica*, 20% *Q. robur*, 12% *C. betulus*, 3% *F. excelsior*, 2% *A. pseudoplatanus* and 2% *L. decidua*). For 47 target trees a full set of DBH measurements from the past three inventories was available.

Two approaches to identify the local neighbours were used. The first approach was a fixed radial distance of 10 m from the target tree. Parameters which have been calculated with these trees are subscripted with "$_{radius}$". In the second approach, we used the highly accurate point cloud to classify all trees as neighbours which crowns were overlapping with that of the target tree (with alpha-shape; α-value = 1). Examples for the different outcomes resulting from the two neighbour selection approaches are shown in Fig. 2.

A total of 238 trees were determined as neighbour-only trees (63% *F. sylvatica*, 17% *Q. robur*, 15% *C. betulus*, 3% *F. excelsior*, 1% *P. avium* and 1% *L. decidua*).

Data analysis

We applied two different approaches to quantify tree diversity in the local neighbourhood of a target tree (Table 2). The number of tree species (neighbourhood species richness, NSR) and the exponential Shannon index (eH_S) based on the abundance of neighbouring trees (Shannon 1948; Jost 2006). B_i is the sum of BA of all neighbouring trees of a given species i and B is the BA of all neighbours. Based on BA, this index has been used in former studies to describe forest diversity (Liang et al. 2007; Ratcliffe et al. 2015).

$$eH_s = \exp\left(-\sum_{i=1}^{n_S} \frac{B_i}{B} \ln\left(\frac{B_i}{B}\right)\right)$$

The partitioning of canopy space was analysed using the crown complementarity index (CCI) according to
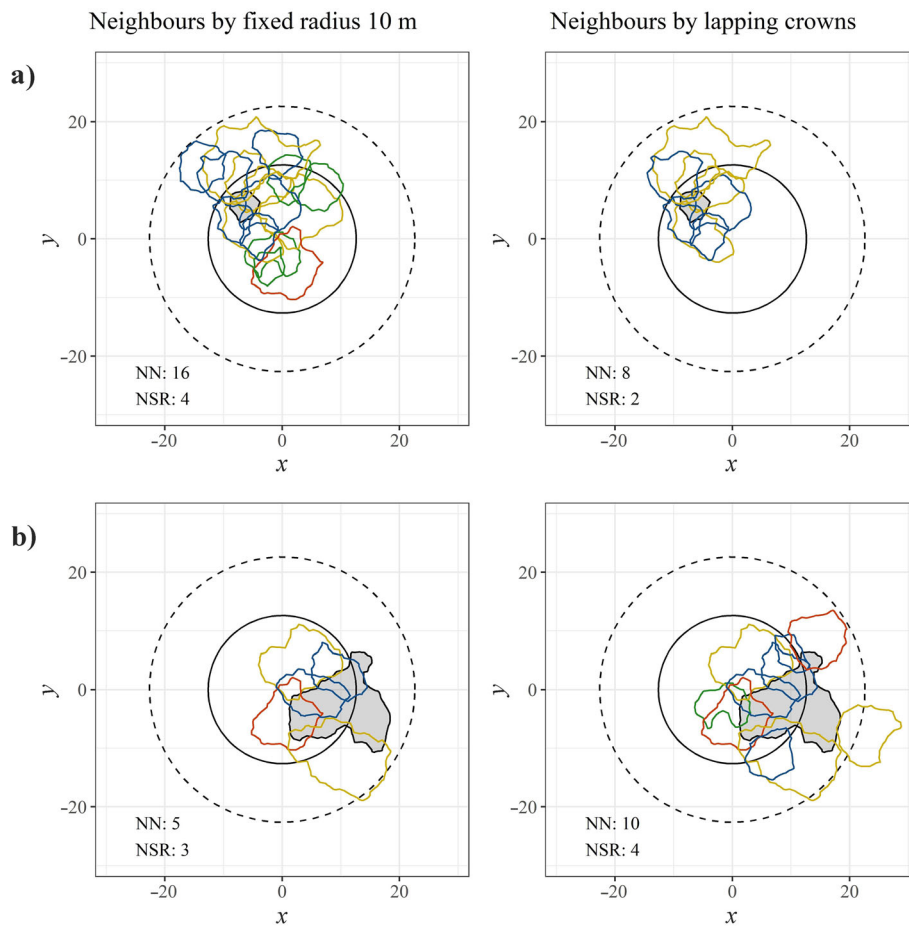
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Fig. 2 Examples for the variable outcomes resulting from different tree neighbour selection approaches: left: overlapping tree crowns; right: fixed radius of 10 m. A: *C. betulus*, DBH = 19.4 cm, height = 23.6 m; B: *Q. robur*, DBH = 81.0 cm, height = 31.0 m. Solid circle radius = 12.62 m; dashed circle radius = 22.62 m. NN = Number of neighbours; NSR = Neighbourhood species richness

(Williams et al. 2017). Crown complementarity (CC) was calculated for two trees as the difference in crown volume (V) between the two individuals (i and j) in each stratum (k) summed across all strata. The CCI of a tree is the mean of all its neighbour CCs. We calculated the CCI with a strata height of 0.5 m.

$$CC_{ij} = \frac{\sum |V_{ik} - V_{jk}|}{V_i - V_j}$$

$$CCI = \frac{\sum CC_{ij}}{n}$$

Basal area increment (BAI, cm^2·year^{-1}) and the merchantable formula wood volume increment (V$_f$I, m^3·year^{-1}) was calculated using DBH (by caliper) and height measurements (with vertex) from inventories in 1992 and 2013. Calculations for merchantable wood volume were based on volume functions by Bergel (1973; *F.*

sylvatica, C. betulus, L. decidua) and Bergel (1974; *Q. robur, F. excelsior, A. platanoides*).

We applied linear mixed-effects models to assess the effects of tree diversity and space occupation on growth of target trees at the local neighbourhood scale. Explanatory variables were NSR, eH$_S$ or CCI (either based on the fixed radius or crown overlap neighbour selection approach) and the current BA or, for the increment models, the BA$_{init}$. Target tree species identity and study plot were used as crossed random effects. The following response variables were used: CV, CPA, CSA, branch length sum, mean first order branch angel, mean second order branch angel, V_{tot}, V_{mw}, V_{fwm}, BAI and V$_f$I. To improve the linear model fit and reduce the residual variance, we log-transformed the response variables and the BA. The model assumptions were tested and validated according to Zuur et al. (2009). Due to co-linearity of the competition (according to Hegyi 1974; Martin and Ak 1984; Biging and Dobbertin 1992) with the BA, we excluded these from the models.

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Table 2 Biodiversity and space partitioning indices measured for each target tree

Measure	Abbreviation	Origin	Reference/Calculation
Neighbour species richness	NSR	Inventory	See methods this publication
Exponential Shannon-Index	eH$_S$	Point cloud/Inventory	Shannon (1948)
Crown complementarity index	CCI	Point cloud	Williams et al. (2017)

All statistical data analysis was performed with R (3.6.1; R Core Team 2019) using the packages nlme (Pinheiro et al. 2019), lmerTest (Kuznetsova et al. 2019), MuMIn (Bartoń 2019) and effects (Fox et al. 2019).

Results

Neighbourhood definition effect
The two neighbour selection approaches yielded highly variable results regarding the number of neighbours (NN) and NSR: the median ΔNN was 3, spanning a range from min = 0 to max = 18 and the median ΔNSR was 0, with a range of min = 0 and max = 2. An important factor to explain the differences between the two approaches is the tree dimension, especially the CPA. For trees with relatively small crowns, the NN is considerably higher using the fixed radius compared to the crown overlap approach. In contrast, an opposite pattern

was found for the NN of large-crowned trees (see example in Fig. 2).

Neighbourhood diversity effects on crown architecture and wood volume
Besides the strong positive effect of the BA, NSR and eH$_S$ significantly positively influenced the tree crown dimensions (CV, CPA, CSA), branch length sum and the wood volumes based on the neighbour selection approach "crown overlap" (Table 3 and Fig. 3). In contrast, no significant influence of NSR and eH$_S$ on the response variables was found when using the fixed radius selection approach (with the only exception of a positive NSR effect on CV, Table 2). With both selection approaches, no impact of the diversity measures on the mean first or second order branch angel was observed. Moreover, the
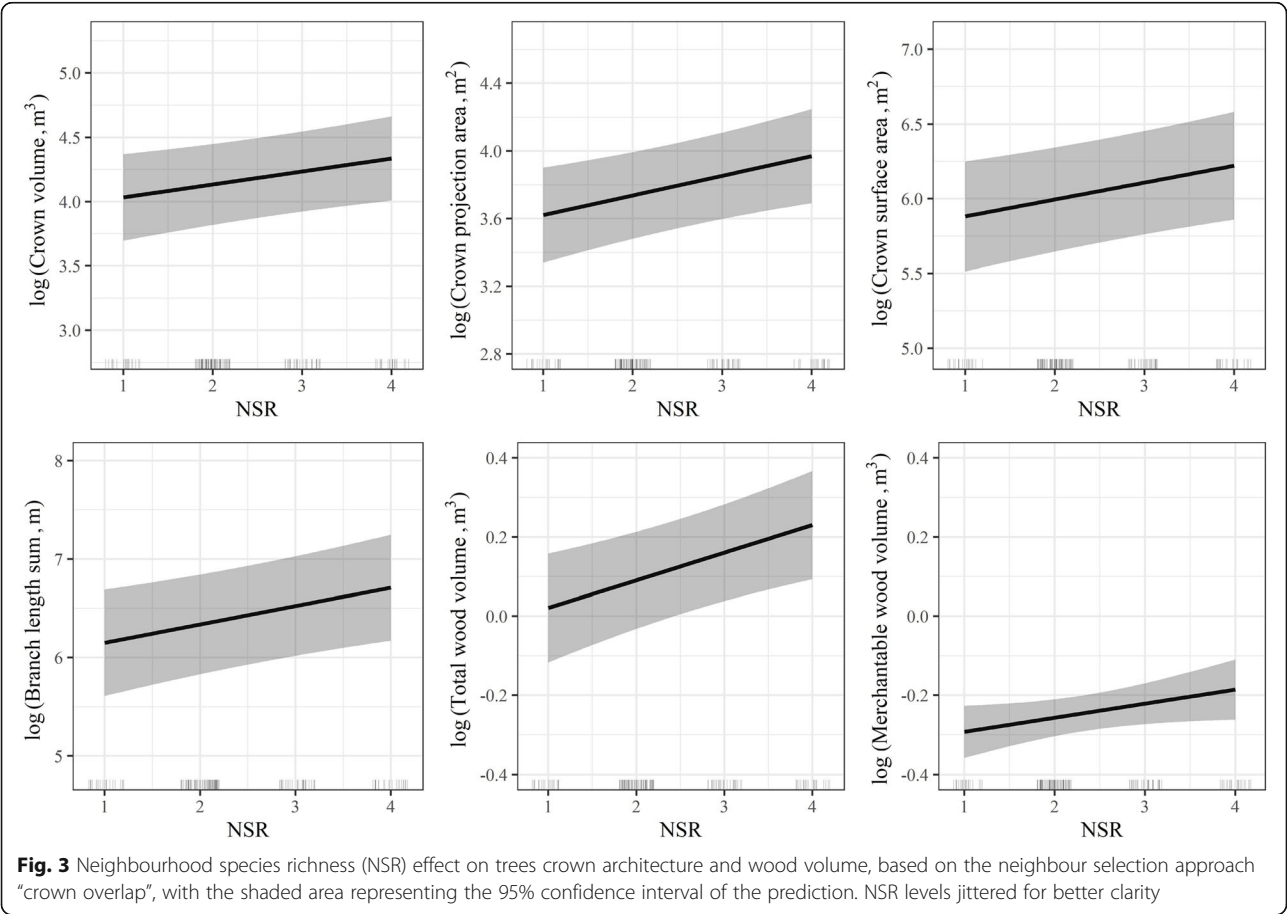

Fig. 3 Neighbourhood species richness (NSR) effect on trees crown architecture and wood volume, based on the neighbour selection approach "crown overlap", with the shaded area representing the 95% confidence interval of the prediction. NSR levels jittered for better clarity

Table 3 Results of mixed-effects models for the effects of neighbourhood tree species richness (NSR), exponential Shannon index (eH$_S$), crown complementarity index (CCI) and target tree basal area (BA$_{log}$) on crown dimensions, branch length and wood volume based on the two tree neighbour selection approaches fixed radius and "overlapping crowns" (n target trees = 148). In all models BA$_{log}$ p = .; $p < 0.1$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; n.s. = not significant

Response variable	Fixed effects	Fixed radius			Overlapping crowns		
		Estimates	p	R^2_c	Estimates	p	R^2_c
Crown volume (log)	NSR + BA$_{log}$	0.08 + 0.98	*	0.89	0.09 + 0.95	*	0.89
	eH$_S$ + BA$_{log}$	0.01 + 0.95	n.s.	0.89	0.08 + 0.96	*	0.89
	CCI + BA$_{log}$	0.04 + 0.95	n.s.	0.89	−0.10 + 0.93	**	0.89
Crown projection area (log)	NSR + BA$_{log}$	0.04 + 0.70	n.s.	0.85	0.10 + 0.70	**	0.86
	eH$_S$ + BA$_{log}$	−0.01 + 0.69	n.s.	0.85	0.08 + 0.71	*	0.86
	CCI + BA$_{log}$	0.04 + 0.69	n.s.	0.85	−0.02 + 0.69	n.s.	0.84
Crown surface area (log)	NSR + BA$_{log}$	0.06 + 0.93	n.s.	0.89	0.10 + 0.92	**	0.90
	eH$_S$ + BA$_{log}$	0.00 + 0.91	n.s.	0.89	0.08 + 0.93	*	0.90
	CCI + BA$_{log}$	0.01 + 0.91	n.s.	0.89	−0.05 + 0.89	n.s.	0.89
Branch length sum (log)	NSR + BA$_{log}$	0.09 + 0.70	n.s.	0.76	0.17 + 0.68	**	0.77
	eH$_S$ + BA$_{log}$	0.00 + 0.68	n.s.	0.75	0.13 + 0.69	*	0.77
	CCI + BA$_{log}$	0.01 + 0.68	n.s.	0.76	−0.07 + 0.67	n.s.	0.74
Total wood volume (log)	NSR + BA$_{log}$	0.02 + 0.96	n.s.	0.97	0.06 + 0.96	**	0.97
	eH$_S$ + BA$_{log}$	0.00 + 0.96	n.s.	0.97	0.05 + 0.96	**	0.97
	CCI + BA$_{log}$	−0.03 + 0.96	n.s.	0.97	−0.05 + 0.95	***	0.97
Fine woody material volume (log)	NSR + BA$_{log}$	0.06 + 0.70	n.s.	0.81	0.14 + 0.69	**	0.82
	eH$_S$ + BA$_{log}$	−0.01 + 0.69	n.s.	0.81	0.12 + 0.70	**	0.82
	CCI + BA$_{log}$	−0.01 + 0.70	n.s.	0.81	−0.07 + 0.67	**	0.80
Merchantable wood volume (log)	NSR + BA$_{log}$	0.01 + 1.07	n.s.	0.98	0.03 + 1.06	.	0.98
	eH$_S$ + BA$_{log}$	0.02 + 1.07	n.s.	0.98	0.03 + 1.06	.	0.98
	CCI + BA$_{log}$	−0.04 + 1.08	**	0.98	−0.04 + 1.07	**	0.98

CV and the wood volumes significantly increased with lower CCI.

Neighbourhood diversity effects on individual-tree productivity

The effects of NSR on tree productivity (BAI and V$_f$I) strongly depended on the initial size (i.e. BA) of a target tree. For small-sized trees, BAI was higher in conspecific than in heterospecific neighbourhoods, while large-sized trees benefitted from increasing NSR (Table 4 and Fig. 4). Interacting with the BA$_{init.log}$, NSR and eH$_S$ had significant positive impacts on both, BAI and V$_f$I, over the past 21 years. The local CCI interacting with the BA$_{init.log}$ also showed a tendency towards a positive influence on tree growth. Again, there is a high sensitivity of the results towards the neighbour selection approach, because most the investigated effects solely occurred or were stronger with the neighbour selection approach "crown overlap" than with "fixed radius" definition (data not shown).

Discussion

In the mature mixed-species forests examined in this study we observed significant impact of the local neighbourhood tree diversity on crown architecture as well as on wood volume and growth. These findings were, however, very sensitive to the approach used to select neighbouring trees. Whereas the fixed radial distance approach barely yielded significant results, this was always the case using the neighbour selection based on overlapping crowns. Mature forests composed of late successional tree species display a wide range of tree sizes at small spatial scales. The large differences in the performance of the two approaches points to an important role of aboveground interactions, i.e. competition for physical space and light. Previous studies used various different approaches to calculate a tree's zone of influence or its competitors (Bachmann 1998). Earlier methods to determine the exact crown dimensions and neighbours of a tree using a compass, hypsometer and crown mirror are error-prone and time-consuming. Hence, an often-used simple neighbour selection is

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Table 4 Results of mixed-effects models for effects of target tree initial basal area (BA$_{init}$), neighbourhood tree species richness (NSR), exponential Shannon index (eH$_S$) and crown complementarity index (CCI) on basal area increment and wood volume increment with the neighbour selection approach "crown overlap" ($n = 47$)..: $p < 0.1$; *: $p < 0.05$; **: $p < 0.01$

Fixed effects	Basal area increment (log)			Volume formula increment (log)		
	Estimate	p	R^2_C	Estimate	p	R^2_C
NSR × BA$_{init.log}$	0.161	.	0.79	0.186	*	0.82
eH$_S$ × BA$_{init.log}$	0.177	*	0.80	0.205	**	0.83
CCI × BA$_{init.log}$	0.116	.	0.76	0.110	.	0.78

the use of fixed radii, a worldwide uniform approach which is also cost effective without the use of TLS. This method, however, has two disadvantages. First, it only considers the fixed stem base location. This is the position where the seed sprouted and the tree individual has been able to prevail until today. However, the competition for light, water and nutrients at this spot changes in the course of decades. In our study area, water and nutrient supply are generally not limiting tree growth. Rather, trees compete for light (Schwinning and Weiner 1998) and competition effects occur on the crown distribution (Longuetaud et al. 2013). Therefore, it is reasonable to select neighbours based on the photosynthetically active part of a tree, the crown. The actual shape of a crown represents the accumulated competitive circumstances of the past. A second disadvantage of a fixed-radius approach is the neglect of tree size differences by using the same radius for a range of different sizes. It has often been found that the optimal radial distances strongly depended on tree size

dimensions (D'Amato and Puettmann 2004). In heterogeneous forests the choice of one specific radius will always remain a compromise. In our study, the minimum and maximum crown diameters were 3.48 and 17.00 m or 4.59 and 23.45 m, derived from the CPA and from the maximal chord, respectively. As an alternative to a single fixed radius, several studies used either a variety of radii (Lin and Augspurger 2006; Antos et al. 2010; Ratcliffe et al. 2015) or tree size dependent radii (von Oheimb et al. 2011). However, the strong advantage of the crown overlap approach is to focus on every individual tree and its actual surrounding structure in three dimensions (Zambrano et al. 2019). At this level of resolution, the procedure is only possible due to the application of highly precise TLS for forest science and ecology. Deploying this state-of-the-art technology enables enhanced insights in the outcome of tree-tree interactions at the local scale, even in temperate mature forests with canopy heights of up to 45 m.
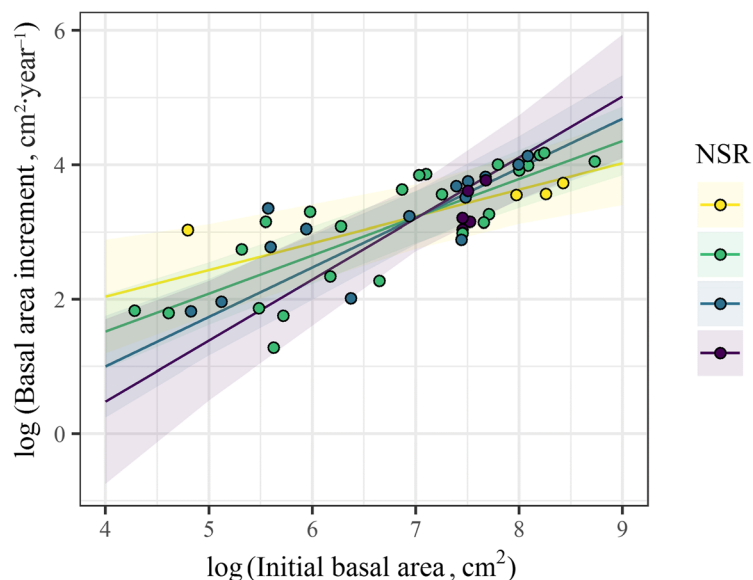

Fig. 4 Size-dependency of neighbourhood species richness (NSR) effects on the annual basal area increment with the neighbour selection approach "crown overlap", with the shaded area representing the 95% confidence interval of the prediction

Our results confirm previous findings that an increase in neighbourhood tree species richness allows trees to enhance their crowns in size and shape (Bayer et al. 2013; Kunz et al. 2019). The diversity-driven plasticity is gained by enhanced branch lengths and an increased biomass allocation to fine woody material (V_{fwm}), leading to larger CPA and greater CSA and thus to larger crown volume. Pretzsch (2014) stated, the more species, the larger the sum of the crown area. A tree's individual crown growth is a modular reaction to micro-environmental light heterogeneity (Kawamura 2010) and thus elementary in the compensatory feedback loop between structure, environment and growth (Bayer et al. 2013; Pretzsch 2014). Through the combination of species with different light ecology and crown morphology, the canopy is more diverse and the individual trees can respond and therefore utilize the canopy space in a more complementary way (Pretzsch 2014). Our results support the niche complementarity hypothesis, postulating the more efficient use of resources, here the physical partitioning in canopy space, by coexisting species (Tilman 1999; Forrester and Bauhus 2016). Along with higher architectural plasticity of individual trees the whole canopy might be packed denser (Cianciaruso et al. 2009).

With the enlargement of the crown and an increase in leaf-bearing branches of higher orders, there is an increase in photosynthetically active area. Under the significant impact of local neighbourhood diversity, the 47 observed trees in this study show an ambivalent growth pattern over 21 years. Smaller trees with a DBH smaller than 40 cm are impeded in their radial growth whereas larger trees benefitted from increasing NSR. These results are similar to those of Lasky et al. (2015) and Fichtner et al. (2017) who observed that taller tree individuals benefiting more from a diverse neighbourhood. This might be due to size-asymmetric competition (Schwinning and Weiner 1998) of larger trees receiving disproportionally more light in comparison to smaller individuals and thus the ability to occupy free niches earlier. Divers tree species mixtures could further enhance this effect.

In contrast to Williams et al. (2017) who studied young and comparatively small trees, we observed a negative effect of the CCI on CV and wood volume. However, a reverse reasoning is also plausible. The bigger the crowns, the more equal they are. Since we have studied mature trees, close to their maximum height, we suspect an upper growth limit and rather the CBH as a decisive influence on this parameter. Moreover, the averaging effect of the CCI is notable, neglecting a trees

opportunity to shift crown growth to a less competing direction (Ali 2019).

Since different structural characteristics induce various reactions among species with different resource-use strategies, the mixing effect is species-specific (Fichtner et al. 2017; Forrester 2019). To analyse the species-specific neighbour effects in temperate European mixed forests with precise laser scanning technology might be the next step, requiring even more trees to achieve statistically solid results.

Conclusions

With our study, we provide evidence that neighbourhood species mixing has a significant influence on individual tree morphology and productivity in mature European mixed-species forest. Moreover, we showed the importance of a precise neighbourhood definition and selection procedure to reveal diversity effects in mature natural and near-natural stands.

For future studies in heterogeneous mixed forests, it would be advantageous to include an even larger number of trees to facilitate analyses across extensive areas. A possible approach to advance in this direction is the application of mobile laser scanning (Bienert et al. 2018) in combination with largely automated individual-tree segmentation procedures. This can be used to clarify two important questions. On the one hand, it enables the mixture effects to be examined for species-specific mixing effects. On the other hand, the diversity effect can be studied on several spatial scales with the help of a much larger dataset.

productivity in forests: advancing the mechanistic understanding of spatio-temporal dynamics in canopy space filling using mobile laser scanning".

Availability of data and materials
Data are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
The subject has no ethic risk.

Consent for publication
Not applicable.

Competing interests
The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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