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LETTER

Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees

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Abstract

Local neighbourhood interactions are considered a main driver for biodiversity–productivity relationships in forests. Yet, the structural responses of individual trees in species mixtures and their relation to crown complementarity remain poorly understood. Using a large-scale forest experiment, we studied the impact of local tree species richness and structural variability on above-ground wood volume allocation patterns and crown morphology. We applied terrestrial laser scanning to capture the three-dimensional structure of trees and their temporal dynamics. We found that crown complementarity and crown plasticity increased with species richness. Trees growing in species-rich neighbourhoods showed enhanced aboveground wood volume both in trunks and branches. Over time, neighbourhood diversity induced shifts in wood volume allocation in favour of branches, in particular for morphologically flexible species. Our results demonstrate that diversity-mediated shifts in allocation pattern and crown morphology are a fundamental mechanism for crown complementarity and may be an important driver of overyielding.

Keywords

BEF-China, biodiversity, crown complementarity, ecosystem functioning, forests, productivity, terrestrial laser scanning.

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INTRODUCTION

Forests play a central role in hosting global terrestrial biodiversity and providing important ecosystem services, such as carbon sequestration or timber production (FAO 2010; Watson *et al.* 2018). This role, however, can be critically altered by ongoing dramatic global declines in biodiversity (IPBES 2019), as biodiversity has been demonstrated to enhance forest multifunctionality (Gamfeldt *et al.* 2013; van der Plas *et al.* 2016; Schuldt *et al.* 2018). During the last decade, numerous studies provided evidence for a positive net biodiversity effect on primary productivity (overyielding) in forests (Morin *et al.* 2011; Paquette & Messier 2011; Zhang *et al.* 2012; Liang *et al.* 2016; Tobner *et al.* 2016; Grossman *et al.* 2017; Fichtner *et al.* 2018; Huang *et al.* 2018). Although local tree–tree interactions are considered an important driver for such biodiversity–productivity relationships at the scale of tree communities (Stoll & Weiner 2000; Uriarte *et al.* 2004), empirical evidence of diversity-mediated processes at the local neighbourhood scale is sparse. For example, a recent study showed that interactions among local neighbours accounted for more than 50% of the variation in above-ground wood production of highly diverse subtropical tree communities (Fichtner *et al.*

2018), indicating the need to focus on individual trees and their local neighbourhood to elucidate the mechanisms that bring about overyielding in mixed-species forests.

The arrangement of the crown is decisive for light-related tree interactions and, thus, for the carbon balance of an individual tree (Ishii & Asano 2010). Spatial complementarity in tree crowns, which is physical niche partitioning in canopy space (hereafter ‘crown complementarity’), is thought to be an important biological mechanism underlying the positive mixture effects in forests (Pretzsch 2014; Sapijanskas *et al.* 2014; Niklaus *et al.* 2017; Williams *et al.* 2017; Barry *et al.* 2019). Crown complementarity can also arise in monocultures, but it is usually greater in mixtures (Pretzsch 2014; Jucker *et al.* 2015; Williams *et al.* 2017). Hence, for several reasons a thorough understanding of spatial aboveground complementarity in tree species mixtures is still lacking. Previous studies supposed inherent species-specific differences in crown architecture and neighbourhood-driven crown plasticity to be the main drivers for crown complementarity (Jucker *et al.* 2015; Niklaus *et al.* 2017; Williams *et al.* 2017). This view, however, considered inadequately the nature of crown plasticity: it is an important response in the feedback system between current tree structure, the local environment and tree growth

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(Schröter *et al.* 2012; Pretzsch 2014). Crown plasticity, i.e. the dynamic morphological adjustments of tree individuals to diversity-induced environmental variability (here: variability in canopy space), may therefore strongly enhance the intraspecific variation of crown architecture in species mixtures compared to monocultures. As a result, it is difficult to properly separate the effects of inherent species-specific differences and crown plasticity. A better mechanistic understanding of how tree species mixing impacts crown complementarity may be achieved by directly analysing what is the ultimate foundation of crown complementarity (both in monocultures and mixtures): the variation in crown size and crown shape among tree individuals (Pretzsch 2009; Williams *et al.* 2017).

Another important element of tree–tree interactions related to canopy space use is the spatial constellation of neighbouring trees. Generally, neighbourhood conditions experienced by an individual tree are expressed in size- and distance-related abundance measures (also known as competition indices). However, a high value of a local neighbourhood abundance measure *per se* may not restrict canopy space filling of a respective target tree if the spatial distribution is uneven or heterogeneous, allowing to make use of gaps and spaces in the canopy. It is therefore crucial to use a spatially explicit measure for both the size and the structural variability of the local neighbourhood to better understand crown complementarity. Furthermore, trees may exhibit an exceptional plasticity in crown size and shape, because they record their recent growth and interaction history in woody biomass allocation and tree architecture, which is an important prerequisite for further adjustments in growth and carbon allocation (Liu *et al.* 2018). Initial differences in size and shape are modified over time through structural crown adjustments, in response to light-related tree interactions. Thus, the three-dimensional (3D) appearance of tree crowns emerges through time, and spatial complementarity analyses need to consider the temporal dynamics of crown development. Finally, the complex 3D nature of tree crowns makes detailed investigations inherently demanding. So far quantifying crown characteristics of individual trees up with a very high resolution over a prolonged period of time has been logistically unfeasible, but such knowledge may be key to understand the biological mechanisms underlying crown complementarity.

In this study, we made use of terrestrial laser scanning (TLS) technology to analyse non-destructively the two basic elements of crown complementarity, size and shape variation, at a very high spatial resolution over five years in a large-scale forest biodiversity – ecosystem functioning (BEF) experiment. Crown size and shape ultimately depend on the differential aboveground biomass allocation within a tree, in particular the trunk-to-branch ratio. Thus, current crown characteristics are the result of complex mechanisms operating at different levels of organization, including the differential investments among branches of different orders, the mode of ramification and branch morphology (Niinemets 2010; Lang *et al.* 2012; Van de Peer *et al.* 2017a). While first order branches largely define the crown contour, second and higher order branches characterise the inner crown structure. Typical morphological adjustments in response to locally favourable light conditions are an increase in branching rate or the formation of longer and thicker branches (Stoll & Schmid 1998). By such morphological

changes at the branch level, trees modularly respond to micro-environmental light heterogeneity (Kawamura 2010), resulting in plasticity in crown characteristics among tree individuals within species and within tree individuals.

Previous studies varied in their support for the assumption that greater crown complementarity promotes productivity. Whereas Jucker *et al.* (2015) did not find a relationship between canopy packing and growth, Niklaus *et al.* (2017) and Williams *et al.* (2017) reported that crown complementarity was positively associated with biomass overyielding. In this study, we tested the impact of neighbourhood tree species richness on crown complementarity and its relationship to individual-tree growth. Specifically, we hypothesised that (1) crown complementarity increases with increasing neighbourhood tree species richness; (2) both crown size and crown shape variation contribute to crown complementarity, but the latter being more important in mixtures than in monocultures; (3) spatiotemporal tree diversity effects occur at different hierarchical levels, i.e. in trunk to branch allocation pattern, in branch morphology, and in crown architecture; and (4) higher crown complementarity promotes individual-tree growth.

MATERIAL AND METHODS

Study site and experimental design

The study was conducted in the BEF-China tree experiment, which is located near Xingangshan, Jiangxi Province in south-east subtropical China (29.08°–29.11°N, 117.90°–117.93°E, 100–300 m above sea level; Bruelheide *et al.* 2014). The experimental design is thoroughly described in the Supplementary Methods. Briefly, the experiment consists of two sites (A and B) established in 2009 and 2010, respectively. A total of 566 study plots of each 666.7 m² were randomly assigned to monocultures and two-, four-, eight-, 16-, and 24-species mixtures (derived from a pool of 40 tree species; Table S1). Each plot was planted with 400 (20 × 20) saplings in a raster pattern at equal projected distances of 1.29 m (Figure S1). Thus, each tree has potentially eight direct neighbours, which we here refer to as ‘the local neighbourhood’. Species were randomly assigned to planting positions within a plot, by which a large number of intra- and interspecific interactions were implemented. Local neighbourhood tree species richness (NSR) therefore ranged from zero (monoculture) to eight (all neighbours consists of different species).

Terrestrial laser scanning data and tree inventory data

Using TLS we sampled 30 plots on site A including eight tree species (Table S2). The richness levels of these plots ranged from monocultures to two-, four-, and eight-species mixtures. TLS data was collected annually in the years 2012 to 2016. We used a standardized sampling scheme that captured each tree in the central area of the plots from multiple positions to ensure sufficient coverage (Figure S1). For each tree individual we manually extracted a high-resolution 3D point cloud (with a resolution of at least the 3 mm level, Figure S2). In total we extracted point clouds for 1554 tree individuals, resulting in 5861 tree point clouds across all years (Table S2).

For technical information, scan registration and tree extraction procedure see Supplementary Methods.

To test whether the results from the selected 30 plots agree well with those from all plots of site A and B, we used inventory data from direct measurements of tree height and ground diameter which were taken annually between September and October from 2010 to 2016 in site A and from 2011 to 2016 in site B. The aboveground wood volume was estimated for a total of 37184 trees (site A: 17856, site B: 19328, further details in Supplementary Methods).

Characterisation of crown size and shape

To quantify and compare the sizes and shapes of tree crowns we derived a range of simple to more complex structural characteristics from the individual-tree point clouds (Figure S2). These included: crown length, crown projection area (CPA), crown width, crown displacement, crown volume, crown surface area, crown sinuosity (Martin-Ducup *et al.* 2016), crown compactness, the Gini coefficient (Cowell 2011) of crown volumes per strata, as well as ratios of crown-width-to-crown-length, crown-length-to-tree-height, crown-width-to-tree-height, crown-surface-area-to-crown-volume and crown-displacement-to-tree-height. CPA, crown volume and crown surface area were computed using 2D and 3D alpha-shapes. For further details on crown structure metrics see Supplementary Methods.

Quantitative structure models from TLS data

From the point clouds quantitative structure models (QSMs) were used to quantify tree compartments (i.e. trunk and branches) and their respective wood volumes. QSMs are hierarchical geometric primitive models that accurately approximate the tree branching structure, geometry, and volume from a point cloud (Raumonen *et al.* 2013; Calders *et al.* 2015). The method first segments the tree into stem and individual branches and simultaneously defines its topological branching structure (e.g. branching order). In the second step the method creates a surface and volume model of the segments by fitting cylinders. Finally, the tree characteristics of interest (i.e. wood volumes of the trunk and branches of the different orders, branch diameters and lengths, etc.) are available from the cylinder model (Figure S2a). We used *TreeQSM* software (Åkerblom 2017) to derive the QSMs. For the specific QSM modelling parameters see Supplementary Methods.

Crown complementarity analysis

We computed the crown complementarity of a target tree with its neighbours according to Williams *et al.* (2017). Crown complementarity (CC) between two trees (i and j) was defined as “the difference among trees in crown volume within strata from the ground to the top of the canopy.” It is computed as follows:

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

where V_i and V_j are the crown volume in each strata k and of the whole tree i and j . In our study, we compute a local crown

complementarity index (CCI_i) as the mean crown complementarity of a target tree i with all its direct neighbours (n):

$$CCI_i = \frac{\sum_j CC_{ij}}{n}$$

CCI_i can range between 0 (no complementarity) and 1 (complete complementarity). At the local neighbourhood scale elevation differences between planted trees did not affect CCI_i results.

To separate the effects of size and shape variation on the CCI_i we computed two neighbourhood measures that express each component. Local variation in crown size was computed as Rao's Q (Rao 1982, see Supplementary Methods) of all trees within the local neighbourhood. Local variation in crown shapes was computed as functional dispersion (Laliberté & Legendre 2010) using six crown characteristics (crown compactness, Gini coefficient of crown volume per strata, and the ratios crown-width-to-crown-length, crown-length-to-tree-height, crown-displacement-to-tree-height, crown-sinuosity-to-tree-height) of all trees in the local neighbourhood. These characteristics were selected because they were independent of tree size.

Species grouping based on tree (crown) morphology

To analyse groups of species in more detail we classified the eight tree species in our TLS study with regard to their ability for morphological flexibility (MF), i.e. the overall potential of a tree to respond with crown plasticity to changing environmental or competitive conditions. We considered a species as morphologically rigid when there is only little variation in morphological traits. In contrast, morphologically flexible species are characterised by a large variation in (crown) size and shape. To capture the complex nature of crown sizes and shapes, MF was quantified by a wide range of crown traits: crown sinuosity, crown compactness, Gini coefficient of crown strata volume, and the ratios of crown-width-to-crown-length, crown-length-to-tree-height, crown-surface-area-to-crown-volume, crown-displacement-to-tree-height, and crown-sinuosity-to-tree-height (Figure S3). To avoid possible effects of neighbourhood species richness on crown attributes, we only used trees from monoculture plots to compute species specific MF values (further details are provided in Supplementary Methods). Based on the morphological crown traits we derived a MF score for each tree species, which allowed to unequivocally assign each species to one of two groups: (1) morphologically flexible species (*Castanea henryi* (Skan) Rehder & E. H. Wilson, *Choerospondias axillaris* (Roxburgh) B. L. Burt & A. W. Hill, *Quercus serrata* Murray and *Sapindus saponaria* L.), and (2) morphologically rigid species (*Liquidambar formosana* Hance, *Castanopsis sclerophylla* (Lindley & Paxton) Schottky, *Triadica sebifera* (L.) Small and *Nyssa sinensis* Oliver).

Neighbourhood competition index

To account for the local neighbourhood conditions experienced by a target tree, size and spatial patterns of neighbouring trees have to be considered (Radtke *et al.* 2003). Therefore, neighbourhood conditions cannot be expressed as a simple quantity, e.g. neighbour basal area, but also

directional aspects of neighbourhood pressure have to be taken into account.

We regard a neighbourhood as highly competitive when: (1) neighbourhood basal area is high, (2) all neighbours are larger or equal in size compared relatively to the target tree, (3) competitive pressure on the target tree is formed from all directions, and (4) little variation in crown structural attributes exists. Largest competition intensity is then assumed to exist within a structurally homogeneous neighbourhood with a large number of strong competitors. Contrary, low levels of neighbourhood competition are expressed by fewer (and less strong) competitors and a structurally heterogeneous neighbourhood that enables better conditions for growth, e.g. through niche complementarity (Chen *et al.* 2016; Van de Peer *et al.* 2017b). We developed a neighbourhood competition index (NCI) which takes all these elements into account (for a detailed NCI description see Supplementary Methods).

Statistical analyses

To disentangle the effects of variation in crown size and shape of a local neighbourhood as drivers of local crown complementarity (CCI_i) in monocultures and species mixtures we used linear mixed-effects models with TLS data from 2015. For time-series analyses (2012 to 2016) we also applied linear mixed-effects models to test whether tree size and shape variables depended on NSR and NCI, and how these effects changed through time (i.e. years). In the models including time, we considered all possible two-way and three-way interactions. Moreover, we used the initial wood volume (inventory data from 2010) of a target tree as additional fixed effect. The target tree and study plot were used as nested random effects (tree nested in plot). Target trees' species identity and neighbourhood species composition were used as crossed random effects. The following response variables were used: aboveground wood volume, trunk wood volume, branch wood volume, ratio of trunk to branch wood volume, branch length, number of first and second order branches, diameter of first order branches, relative branch length (length/volume), crown volume, CPA, crown sinuosity and crown displacement.

For each model conditional and marginal r-squared values were computed to assess the amount of variance explained by both fixed (marginal) and random (conditional) effects. Response variables were log-transformed (except for CCI_i) as this resulted in an improved linear model fit and reduced residual variance. All predictors were standardised (divided by their standard deviation) before analysis. Parameter estimates of the models were based on restricted maximum likelihood (REML) estimation and are presented in Tables S3–S19. Variance inflation factors indicated no critical correlation (all VIFs < 1.5) between covariates. Model assumptions, including spatial independence, of our models were tested and confirmed according to Zuur *et al.* (2009). Residuals showed no significant sign of heteroscedasticity and were normally distributed around a zero mean. Effect size was computed as Cohen's *d* (Cohen 1988).

To explore how crown complementarity effects scale up from the local neighbourhood level to the plot level, we first calculated the net diversity effect (NE) at the stand level according to Loreau & Hector (2001) and distinguished

statistical selection effects (SE) from statistical complementarity effects (CE). We further weighted NE by the mean CCI_i of a given plot: $NE_{CCI} = NE * \overline{CCI_i}$, where NE_{CCI} is the crown complementarity-weighted net diversity effect at the plot level and CCI_i the local crown complementarity index of a target tree.

Statistical analyses were performed with R 3.3.0 (R Core Team 2016) using the R packages lme4 (Bates *et al.* 2014), lmerTest (Kuznetsova *et al.* 2016), MuMIn (Barton 2016) and variancePartition (Hoffman & Schadt 2016).

RESULTS

We found a positive relationship between neighbourhood tree species richness (NSR) and local crown complementarity (CCI_i) (Fig. 1). The lower boundary of CCI_i increased with increasing NSR, whereas the upper boundary was near to or equal to the maximum value of 1.0 along the NSR gradient. Thus, CCI_i displayed a larger variation of values in less diverse neighbourhoods (between 0.25 and 0.99 in monocultures). Both crown size and shape variation significantly contributed to the variation in CCI_i , but the explanatory power of shape variation was higher than that of size (Fig. 1, Table S3). The importance of crown shape variation as a predictor of CCI_i increased in mixtures, whereas the opposite was observed for size.

On the individual-tree level, we found a significant three-way interaction between NSR, neighbourhood competition (NCI) and time in 11 of the 12 response variables (Table 1).

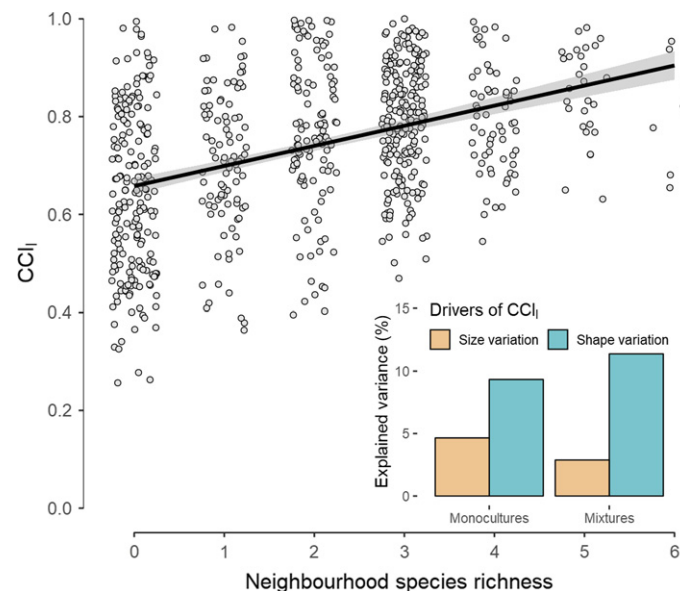


Figure 1 Neighbourhood species richness and crown complementarity. Gray dots represent crown complementarity (CCI_i) of a target tree with its local neighbours. Higher CCI_i values indicate higher complementarity. CCI_i computation was based on tree measurements in 2015 derived from point clouds (site A). The black line is a linear model fit ($R^2 = 0.17$, $P < 0.001$). Inset panel shows variance partitioning (based on a linear mixed model, see Methods) for the effects of crown size (size variation) and crown shape (shape variation) on CCI_i in monocultures and mixtures. Points are jittered for better clarity.

The effect of NSR on total wood volume and wood volume increment of individual trees strengthened through time with effects being modulated by NCI and focal trees' size, i.e. initial wood volume. The results were qualitatively the same based on inventory data from all plots at the two sites and for the subset of plots (site A) that were measured using TLS (Fig. 2a, Tables S4–S8, Figures S4–S5). The increase in wood volume was found for trunks and for branches, showing that both tree compartments benefitted from increased NSR

(Tables S9–S10). The trunk-to-branch volume ratio increased with time and shifted in favour of branches at increased NSR, more so at low NCI, while promoting the trunk at high NCI (Fig. 2b, Table S11). At the branch level, we found a higher number of first and second order branches, greater lengths and diameters as well as lower relative branch lengths in more species-rich and less competitive neighbourhoods (Tables S12–S15). At the whole crown level, we observed a significant increase in crown volume and crown projection area as well

Table 1 Mixed-effects models (ANOVA, type III sum of squares) for effects of initial tree wood volume (initial size), neighbourhood tree species richness (NSR), neighbourhood competition (NCI), year, and interactions on individual tree wood volumes and crown architecture ($n = 2773$)

Fixed effect	Above-ground wood volume (log)				Trunk wood volume (log)				Branch wood volume (log)			
	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>
Initial size	1	724.1	756.04	< 0.001	1	723.9	767.41	< 0.001	1	721.6	623.68	< 0.001
NCI	1	2581.4	49.35	< 0.001	1	2595.3	70.88	< 0.001	1	2526.1	28.07	< 0.001
NSR	1	1812.5	10.16	< 0.01	1	1842.2	5.15	< 0.05	1	1839.8	7.16	< 0.01
Year	1	2106.1	135.28	< 0.001	1	2107.3	238.76	< 0.001	1	2117.2	42.59	< 0.001
NCI*NSR	1	2676.8	13.75	< 0.001	1	2697.6	7.33	< 0.01	1	2673.2	10.03	< 0.01
NCI*Year	1	2058.2	9.78	< 0.01	1	2059.6	33.35	< 0.001	1	2069.0	0.81	0.370
NSR*Year	1	2135.6	15.60	< 0.001	1	2154.7	1.68	0.196	1	2166.2	24.41	< 0.001
NCI*NSR*Year	1	2129.4	20.28	< 0.001	1	2144.5	3.99	< 0.05	1	2153.4	26.58	< 0.001

Fixed effect	Trunk volume/ branch volume (log)				Branch length (log)				Number of branches (1st and 2nd order) (log)			
	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>
Initial size	1	695.283	66.19	< 0.001	1	728.8	682.97	< 0.001	1	721.9	578.13	< 0.001
NCI	1	2137.4	0.84	0.361	1	2522.9	43.58	< 0.001	1	2337.5	40.55	< 0.001
NSR	1	1745.3	5.65	< 0.05	1	1845.5	1.83	0.176	1	1743.8	2.41	0.121
Year	1	2218.1	25.58	< 0.001	1	2119.2	109.72	< 0.001	1	2149.8	80.56	< 0.001
NCI*NSR	1	2337.2	6.91	< 0.01	1	2663.4	4.43	< 0.05	1	2533.7	7.39	< 0.01
NCI*Year	1	2173.7	13.54	< 0.001	1	2069.8	14.70	< 0.001	1	2097.3	5.66	< 0.05
NSR*Year	1	2262.0	24.99	< 0.001	1	2165.7	3.41	0.065	1	2186.1	9.00	< 0.01
NCI*NSR*Year	1	2253.3	21.37	< 0.001	1	2154.8	3.89	< 0.05	1	2178.5	12.46	< 0.001

Fixed effect	Diameter 1st order branches (log)				Relative branch length (log)				Crown volume (log)			
	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>
Initial size	1	636.1	194.66	< 0.001	1	632.6	170.37	< 0.001	1	700.7	552.49	< 0.001
NCI	1	1888.1	0.78	0.378	1	1979.6	0.06	0.802	1	2367.8	41.52	< 0.001
NSR	1	1748.2	7.95	< 0.01	1	1672.4	13.97	< 0.001	1	1842.4	2.09	0.148
Year	1	2240.1	3.44	0.064	1	2213.2	6.45	< 0.05	1	2107.9	59.56	< 0.001
NCI*NSR	1	2157.6	8.27	< 0.01	1	2222.5	12.89	< 0.001	1	2564.7	4.15	< 0.05
NCI*Year	1	2209.3	6.24	< 0.05	1	2178.5	11.36	< 0.001	1	2062.0	7.06	< 0.01
NSR*Year	1	2223.5	20.85	< 0.01	1	2266.3	32.83	< 0.001	1	2143.0	4.55	< 0.05
NCI*NSR*Year	1	2231.2	21.32	< 0.01	1	2260.0	34.29	< 0.001	1	2134.3	4.58	< 0.05

Fixed effect	Crown projection area (log)				Crown sinuosity (log)				Crown displacement (log)			
	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>	df _{num}	df _{den}	<i>F</i>	<i>P</i>
Initial size	1	703.6	590.36	< 0.001	1	727.1	127.37	< 0.001	-	-	-	-
NCI	1	2528.1	90.60	< 0.001	1	2408.3	5.11	< 0.05	1	2356.2	88.96	< 0.001
NSR	1	150.9	0.53	0.464	1	1874.5	2.27	0.132	1	2525.1	19.32	< 0.001
Year	1	2182.9	99.68	< 0.001	1	2114.5	7.45	< 0.01	1	2232.9	28.78	< 0.001
NCI*NSR	-	-	-	-	1	2535.2	1.10	0.296	1	2598.8	15.14	< 0.001
NCI*Year	1	2150.6	5.86	< 0.05	1	2071.6	1.76	0.185	1	2203.2	42.22	< 0.001
NSR*Year	1	2082.5	14.61	< 0.001	1	2173.1	10.26	< 0.01	1	2266.7	20.29	< 0.001
NCI*NSR*Year	-	-	-	-	1	2158.6	4.67	< 0.05	1	2248.6	11.24	< 0.001

All tree parameters were derived using TLS based analyses. df_{num}, numerator degrees of freedom; df_{den}, denominator degrees of freedom. *F* and *P* indicate *F* ratios and the *P* value of the significance test, respectively. “-” indicates that terms were not included in the model.

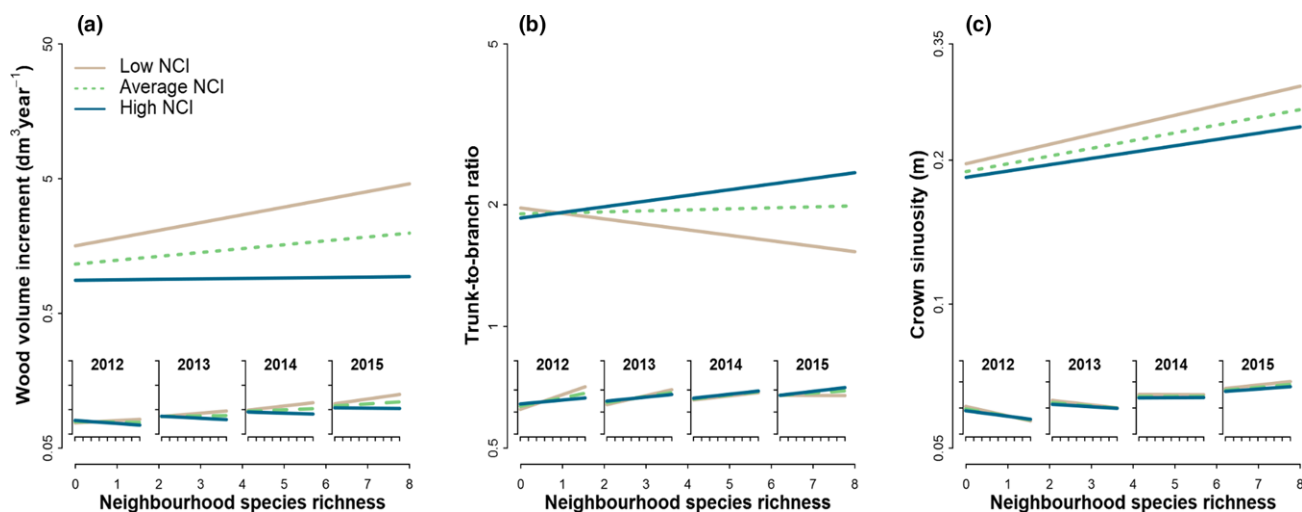


Figure 2 Interplay between neighbourhood species richness and competition over time. (a) Diversity-productivity relationship in relation to various intensities of neighbourhood competition (NCI). Lines correspond to the predicted response based on linear mixed-effects models for field observations ($n = 36556$ over 6 years) at experimental site A. Average NCI corresponds to mean NCI value, low and high NCI correspond to the lower (25%) and upper (75%) quartiles. Inset panel displays the temporal development during 2012 and 2015, while main panels display the growth response in 2016. Species richness corresponds to the number of heterospecific neighbours. Y-axis is logarithmic. Initial wood volume was kept at its mean. (b) Change of wood volume allocation pattern between trunk and branch (trunk-to-branch ratio) in relation to species richness under three different scenarios of competition (NCI) at the local neighbourhood scale. Lines correspond to the predicted response based on linear mixed-effects models for TLS-based observations ($n = 5861$ over 5 years) at experiment site A. Average NCI corresponds to mean NCI value, low and high NCI correspond to the lower (25%) and upper (75%) quartiles. Inset panel displays the temporal development during 2012 and 2015, while main panels display the growth response in 2016. Species richness corresponds to the number of heterospecific neighbours. Y-axis is logarithmic. Initial wood volume was kept at its mean. (c) Change of crown sinuosity, as a measure of crown plasticity, in relation to species richness under three different scenarios of competition (NCI) at the local neighbourhood scale. Lines correspond to the predicted response based on linear mixed-effects models for TLS-based observations ($n = 5861$ over 5 years) at experiment site A. Average NCI corresponds to mean NCI value, low and high NCI correspond to the lower (25%) and upper (75%) quartiles. Inset panel displays the temporal development during 2012 and 2015, while main panels display the growth response in 2016. Species richness corresponds to the number of heterospecific neighbours. Y-axis is logarithmic. Initial wood volume was kept at its mean.

as a greater crown displacement and sinuosity in more diverse neighbourhoods (Fig. 2c, Tables S16–S19). The latter two increased on average by 10% and 8%, respectively, compared to monocultures, indicating that crown plasticity of individual trees was higher in mixtures. This is in alignment with a greater importance of crown shape variation for CCI_i .

The power of the NSR effect for the 12 response variables was trait-dependent, with morphologically flexible species showing a stronger and morphologically rigid species a weaker effect (Fig. 3). These plasticity-driven differences translated into differences in crown complementarity, with higher CCI_i values for morphologically flexible species compared to rigid species (Figure S6).

Individual trees experiencing a low crown complementarity in the local neighbourhood showed an intermediate growth rate whereas a high crown complementarity was associated with both, very high and very low growth rates (data not shown). In our study with eight species, the four species in each of the two morphological trait groups showed different height growth rates (Figure S7). Therefore, to avoid simple size related effects on CCI_i and growth, we compared this relation only for two species each with similar high growth rates (morphologically flexible: *Choerospondias axillaris*, *Castanea henryi*; morphologically rigid: *Nyssa sinensis*, *Liquidambar formosana*). Trees in neighbourhoods of high CCI_i growing at low NCI showed higher growth rates compared to those growing at high NCI, and the relation changed from

negative to slightly positive/ neutral in morphologically flexible species in mixtures (Fig. 4).

At the stand level we observed a significant overyielding - mainly driven via statistical complementarity effects - with increasing species richness (Fig. 5, Figure S8). Therefore, the positive NSR and CCI effects at the local neighbourhood scale translated into stand-level effects over time.

DISCUSSION

Our study shows that crown complementarity increases with neighbourhood tree species richness, as diverse neighbourhoods allowed trees to optimize their crown morphology (crown size and shape) with effects being stronger for crown shape. This neighbourhood-driven plasticity was mainly brought about by enhanced biomass allocation to branches and changes in branch morphology, suggesting that diversity-mediated biomass allocation may be a fundamental mechanism of positive biodiversity-productivity relationships in forest ecosystems. These processes developed over time in the young experimental plantation, and differed between morphologically flexible and rigid species.

Our finding of higher crown complementarity in species mixtures coincides with our first hypothesis and was previously shown in observational and experimental studies (Jucker *et al.* 2015; Niklaus *et al.* 2017; Williams *et al.* 2017). In addition, our results denote the high importance of the level of

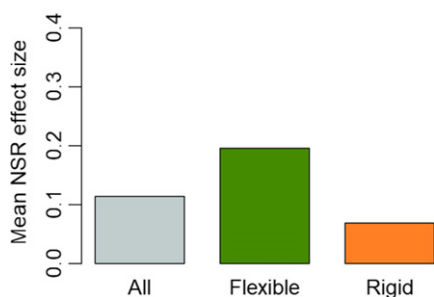


Figure 3 NSR effect size for species groups (based on morphological traits). Mean absolute effect size (Cohen's d) of neighbourhood species richness (NSR) for all trees and species groups was computed as the mean of the individual NSR effect size in each model across the 12 studied TLS-based tree parameters. Species are classified according to their variability in morphological traits: flexible (*Castanea henryi*, *Choerospondias axillaris*, *Quercus serrata*, *Sapindus saponaria*) and rigid (*Liquidambar formosana*, *Castanopsis sclerophylla*, *Triadica sebifera*, *Nyssa sinensis*). Samples size of target trees with full information on all neighbours: all = 2773, flexible = 1534, rigid = 1239.

species richness at the local neighbourhood, which had a strong impact on the minimum CCI_i values. The large range of CCI_i values in monocultures is only due to architectural differences within species. In conspecific neighbourhoods, size variation can solely stem from differences among tree individuals within a species, whereas shape variation can occur both among individuals within a species and within individuals. Even in monocultures a large variability in crown shapes is an important prerequisite for attaining a high crown complementarity. The considerable increase of lowest CCI_i values in mixtures shows that differences among species add an important amount of crown size and shape variation. The increased

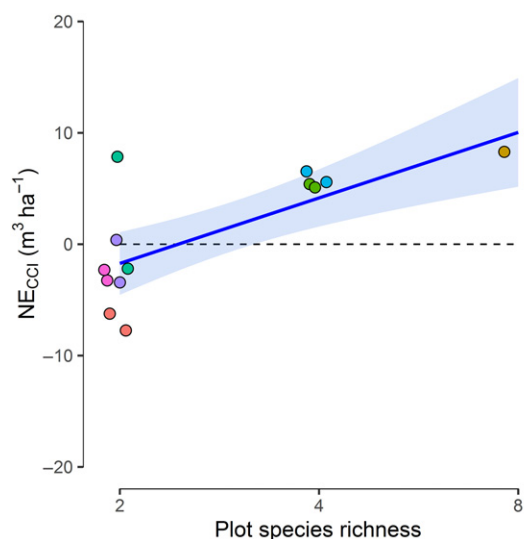


Figure 5 Relationship between the crown-complementarity-weighted net diversity effect (NE_{CCI}) and tree species richness at the plot level. Data points show crown-complementarity-weighted net diversity effect in the year 2015 for species mixtures in relation to their respective monocultures ($R^2 = 0.56$, $F = 15.17$, $P < 0.01$). The analysis is based on 30 plots that were surveyed using TLS. Colours indicate equal species combinations of the plots. The y-axis is square root-transformed. Points are slightly jittered for better visibility.

proportion of variance explained by crown shape compared to size, confirming our second hypothesis, suggests that diversity-driven shape plasticity of tree crowns is of great importance in mixtures, and that the relevance of crown plasticity might have been underestimated by the approaches used in previous studies (Jucker *et al.* 2015; Niklaus *et al.* 2017; Williams *et al.* 2017). Our analysis thus suggests that species diversity induces trait variability, here a high variability of crown architectural traits of individual trees in mixed-species stands.

The biological foundation for the diversity-mediated modifications in individual-tree crown architecture are mechanisms operating at different hierarchical levels of organisation, including differential aboveground biomass allocation within trees as well as the ramification mode and morphology of branches. At all levels we observed significant neighbourhood diversity effects, which supported our third hypothesis. For the BEF-China experiment it has been found that tree species richness increased productivity both at the individual-tree (Fichtner *et al.* 2017, 2018) and at the stand-level (Huang *et al.* 2018). Our analysis indicates that both main aboveground woody compartments, i.e. trunks and branches, benefitted from increased local neighbourhood species richness. Carbon investments in the trunk drive height primary growth with apical meristems and radial secondary growth. Because competition for light is typically size-asymmetric, height increment has the highest priority for biomass allocation when light is limiting growth (Falster & Westoby 2003; Pretzsch 2009). Preferential carbon investments in primary growth are, therefore, to be expected in the young tree communities at the study site, which is confirmed by the rapid height increments observed by Li *et al.* (2017) in this experiment. Crown dimensions and crown shape plasticity, however, critically depend

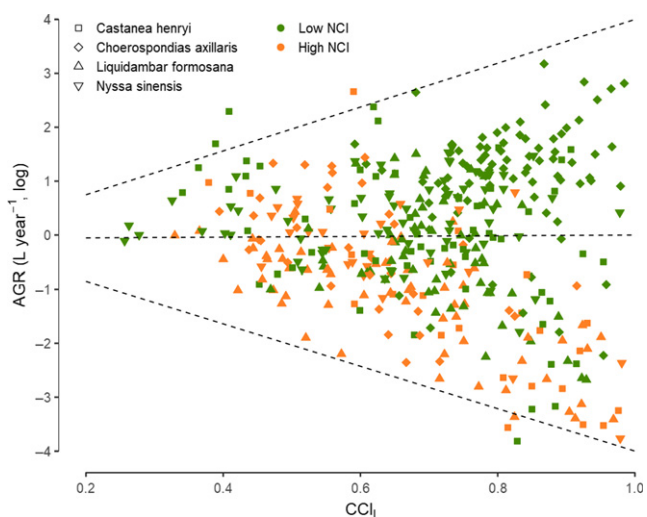


Figure 4 Crown complementarity and absolute growth rate. Data shows observed absolute growth rate per year (AGR, 2010 to 2015) of total wood volume in relation to local crown complementarity (CCI_i) for four species (indicated by different shapes) with similar height growth. Colours indicate low and high local neighbourhood competition (NCI). Horizontal dashed line displays median AGR. Sloped dashed lines indicate that, both, positive and negative crown complementarity–growth relationship can occur with increasing CCI_i .

on the proportion of biomass allocated to the branches. The trunk-to-branch volume ratio undergoes ontogenetic changes, leading to increased values over time because of higher growth rates in trunks than in branches (Niklas 1995; Silveira *et al.* 2012). In our study, however, we found that tree species richness modifies this trend in favour of branches, indicating that neighbourhood effects can compensate for age-related shifts in aboveground biomass partitioning patterns. These shifts in allocation might form an important mechanistic basis underlying enhanced crown plasticity in mixtures.

The observed diversity-driven responses at the branch level do not only facilitate an increased crown size (e.g. higher crown projection area and crown volume due to higher numbers and greater length of first order branches), but in particular lead to differences in the crown shape, including the inner crown properties. Our results confirm findings from Bayer *et al.* (2013) who reported that mature European beech (*Fagus sylvatica* L.) trees growing in mixture with Norway spruce (*Picea abies* (L.) H. Karst) had significantly more branches of the first three orders and a higher sum of branch lengths compared with those in monocultures. Finally, at the whole crown level, we found that crowns were more displaced and more sinuous in mixtures than in monocultures, demonstrating the ability of these young trees for lateral crown expansion away from the stem base position. The development of asymmetric crowns may be caused by branch expansion towards high light conditions (phototrophic growth) and by inhibition of branch growth and survival under unfavourable light conditions (correlative inhibition; Stoll & Schmid 1998). These results support the assumption that both vertical and lateral expansion of the crowns contribute significantly to physical niche partitioning in canopy space (Longue-taud *et al.* 2013; Forrester & Bauhus 2016; Martin-Ducup *et al.* 2016; Barbeito *et al.* 2017).

The response of all architectural variables to species richness was affected by neighbourhood competition (NCI) and varied over time. Our NCI can be interpreted as a spatially explicit standardised competition index of the local neighbourhood. The spatial arrangement of neighbouring trees is an important dimension in the competition for canopy space. For a target tree it might make a great difference whether neighbours are equally distributed around the tree or only occur in particular directions. Structural heterogeneity can modulate competition and biodiversity (McElhinny *et al.* 2005; Sabatini *et al.* 2015) and vice versa. Furthermore, the temporal impact is likely a consequence of the compensatory feedback loop “Structure → Environment → Growth → Structure” operating in the forest ecosystems (Pretzsch 2014; Martin-Ducup *et al.* 2016). A tree's stature and structure captures the effects of local neighbourhood interactions and growth responses of the past, and morphological adjustments in the 3D tree architecture need time to emerge. This might explain the differences between our findings and those of other studies using only a single measurement (Lang *et al.* 2012; Van de Peer *et al.* 2017a), according to which tree diversity appeared to be a poor predictor for aboveground biomass allocation and tree architecture. And it also provides an explanation for the finding that, in contrast to observations in grassland BEF-experiments, the positive biodiversity effects in tree communities emerge with time (Reich *et al.* 2012; Huang *et al.* 2018).

Functional traits largely regulate the local neighbourhood interactions (Butterfield & Callaway 2013). Fichtner *et al.* (2017) demonstrated that the driving mechanisms of diversity effects at the local neighbourhood scale depend on the target tree's resource-use strategy: these effects were brought about by competitive reduction for species with acquisitive traits, and by facilitation for species with a conservative resource-use strategy. In our study we used a subset of the species included by Fichtner *et al.* (2017), but seven of the eight species were acquisitive, and only one species conservative (namely *Castanopsis sclerophylla*). We therefore assume that competitive neighbour interactions prevailed in the present study, and target tree's ability for morphological flexibility largely determine its response to local neighbourhood tree species richness.

Moreover, we hypothesized that higher crown complementarity promotes individual-tree growth, which was only partly supported due to the large variation in growth rates at higher levels of crown complementarity. In part, these findings contrast those of Williams *et al.* (2017) who reported that crown complementarity at the plot level was positively related to stem biomass overyielding. This might be explained by the fact that in their study of very young tree communities crown complementarity was largely driven by species identity (selection effects) rather than statistical complementarity effects or by differences in the biomes (temperate vs. subtropical). Our findings, however, are in line with the conceptual model on the influence of stand structural attributes on forest functioning, which ranges from positive over neutral to negative (Ali 2019). A positive effect would be attributable to the enhancement of the resource use partitioning, whereas negative effects would result from asymmetric competition. Note that crown complementarity, measured as *CCI*, does not inevitably provide information on the competitiveness of a tree. Small or growth-inhibited trees can exhibit very high levels of *CCI*. Given that in our study species are mainly associated with an acquisitive resource-use strategy, smaller individuals and/or those experiencing a high NCI suffered from a high *CCI*. In these communities, high crown complementarity may result in competitive reduction in some cases and in increased competition in other cases. Nonetheless, altogether, species mixtures more frequently provide higher crown complementarity and structural variability leading to reduced competitive pressure that allowed trees to increase their productivity. This translated into overyielding at the stand level and is consistent with findings of Fichtner *et al.* (2018).

We are aware that we could not account for physiological responses, diversity-mediated effects of herbivory and pathogens, or belowground interactions which have been shown to be additional important factors for tree growth (Ishii & Asano 2010; Bu *et al.* 2017; Schuldt *et al.* 2017). Variation in topography and soil conditions may also effect tree growth but those factors were found to be of weak explanatory power in the BEF-China experiment (Kröber *et al.* 2015; Fichtner *et al.* 2018). We also note the limitation to generalize results from juvenile tree field-experiments to adult tree communities. However, overall, our results provide evidence that the temporal variation in tree productivity strongly depends on species richness and structural variability of the local neighbourhood of a target tree. Promoting high taxonomic and structural diversity at the local neighbourhood scale is therefore an important

goal for enhancing forest productivity. Moreover, we showed that trees are highly flexible in their morphology due to increased investment into trunk and branch wood under favourable neighbourhood conditions (i.e. species-rich and structurally less competitive neighbourhoods). Given the temporal importance of crown complementarity development, our study suggests that exploring neighbourhood diversity-mediated responses of carbon allocation and partitioning is a critical next step to deepen our understanding of the functional role of tree diversity in providing forest-based ecosystem services in future.

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AUTHORSHIP

MK and GvO conceived the idea of this study. HB, WH and GvO designed the research. GvO, WH and MK compiled the data and performed the literature search. MK, AF, HB and PR analysed the data. MK wrote the first draft of the manuscript and all the authors contributed substantially to the submitted version.

DATA AVAILABILITY STATEMENT

Inventory data sets are deposited in the BEF-China data portal under dataset numbers 593/594 (<http://china.befdata.biow.uni-leipzig.de/>) and under Dryad Digital Repository (<https://doi.org/10.5061/dryad.0gb5mkkwk>). Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

DATA DEPOSIT STATEMENT

Inventory data sets are deposited in the BEF-China data portal under dataset number 593/594 (<http://china.befdata.biow.uni-leipzig.de/>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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