RESEARCH ARTICLE

Tree species richness promotes an early increase of stand structural complexity in young subtropical plantations

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Abstract

1. Forest structural complexity has been identified as an important driver for promoting simultaneously biodiversity across trophic levels and multiple ecosystem services. However, we still have a limited understanding of the processes that lead to structural complex stands and how they evolve over time.

2. Using terrestrial laser scanning (TLS), we quantified a three-dimensional (3D) stand structural complexity index (SSCI) in an experimental plantation with a long gradient of tree species richness (1–24 species). The plantation was established in 2009, and we made use of a multi-temporal TLS dataset recorded during 2012–2019.

3. We found a positive relationship between tree species richness and structural complexity. This relationship became stronger over time. Ten years after planting, SSCI was on average two-fold higher in 16- and 24-species mixtures than in monocultures. Furthermore, we demonstrate that tree species richness promotes 3D stand structural complexity indirectly by fostering a high vertical heterogeneity and thus greater spatial complementarity in canopy space.

4. *Synthesis and applications*. Our findings indicate that tree species richness plays a crucial role in promoting stand structural complexity in young plantations, and this role becomes more important already during early stand development. Thus, afforestation measures would benefit from planting multiple native tree species to initiate structurally complex stands.

KEYWORDS
BEF-China, biodiversity ecosystem functioning, restoration, stand structural complexity, terrestrial laser scanning, tree diversity, tree species mixtures

1 | INTRODUCTION

Forest plantations are established globally to provide multiple ecosystem services such as the production of timber, fuel and pulpwood (FAO, 2010). Specifically, global afforestation and reforestation efforts are among the major nature-based solutions employed to combat the adverse impacts of climate change. Currently, 168 Mha of degraded and deforested land, mainly located in the tropics and subtropics, has been pledged as restoration areas under the 'Bonn Challenge' (IUCN, 2020). A large part of this area is intended for

plantations of commercial trees, mostly as monocultures (Lewis et al., 2019). In recent years, however, there has been increasing criticism of monospecific stands due to their great susceptibility to adverse environmental conditions (e.g. storm, fire), pests, diseases and invasive species, and their negative effects on soil productivity and fertility (Liu et al., 2018; Piotto, 2008). Moreover, there is robust evidence of a strong positive relationship between tree species diversity and ecosystem services (e.g. primary productivity, carbon sequestration, nitrogen retention; Chen et al., 2020; Felipe-Lucia et al., 2018; Huang et al., 2018; Lang et al., 2014; Zemp, Gérard, et al., 2019). Diverse tree mixtures are also expected to promote species-rich communities across trophic levels (Schuldt et al., 2018) and have been found to show higher resistance to environmental stressors such as climate change (Fichtner et al., 2020). Importantly, Forrester and Bauhus (2016) and Schuldt et al. (2019) found that not only species richness and functional diversity but also the structural diversity of tree stands is a highly relevant mediator of these beneficial diversity effects. This is because growth characteristics, branching architecture and space occupation of trees affect the spatial complexity of the canopy space, microclimates and species interactions. Furthermore, the idea of 'resilience' or 'adaptive' complexity has been introduced into forest and plantation management in recent years in order to promote the resilience or adaptive capacity of managed stands to current and future environmental changes and stressors (Fahey et al., 2018). Management recommendations should therefore include measures to preserve and enhance structural complexity. From a scientific perspective, it is essential that we obtain a deeper understanding of the role of tree species richness in the restoration of stand structural complexity.

Species mixing has the potential to influence the canopy structure of tree communities because tree crown complementarity (i.e. the physical niche partitioning in canopy space) increases with tree species richness (Kunz et al., 2019; Williams et al., 2017). Crown complementarity can be explained by the functional diversity of tree mixtures and by the diversity-driven plasticity of tree crowns. Recent work has shown that changes in crown morphological plasticity may be the result of shifts in tree biomass allocation induced by neighbourhood interactions in mixed-species tree communities (Guillemot et al., 2020; Kunz et al., 2019). Notably, species mixing also leads to differences in the inner crown properties (Pretzsch, 2014). Trees growing in mixtures may have significantly more branches of the first orders and a higher sum of branch lengths than those in monocultures (Bayer et al., 2013; Guillemot et al., 2020; Kunz et al., 2019). As a result, these differences in the crown structure of individual trees enhance canopy space-use efficiency and, thus, above-ground resource utilisation in mixed-species stands. At the same time, the canopy space is more heterogeneously structured and more complex (Hess et al., 2018).

Stand structural complexity can be defined as the degree of heterogeneity of the three-dimensional (3D) distribution of biomass (Ehbrecht et al., 2021 and the conceptual framework therein). It has been described in various ways, covering both indices that include only single stand structural attributes (e.g. horizontal tree distribution, stand density, tree size differentiation) and indices that combine several attributes (so-called 'structural complexity indices'; Juchheim et al., 2019; McElhinny et al., 2005). Previous studies found varying relationships between tree diversity and stand structural complexity, ranging from positive to neutral responses (Hakkenberg et al., 2016; Neumann & Starlinger, 2001). All these measures of structural complexity using conventional approaches, however, are based on one- or two-dimensional attributes but do not consider the 3D nature of forest (stand) structures in detail. This lack might be a particular shortcoming when considering mixed-species stands, given the importance of diversity-induced tree crown architectural changes and plasticity-driven canopy space exploitation. Furthermore, complex 3D stand structures emerge through time. Trees store carbon in long-lived structural elements, such as trunks and branches, and therefore can be considered 'long-term records' of the effects of tree–tree interactions and growth responses of the past. In addition to patterns of species richness and composition, such tree–tree interactions might be shaped by the extent of tree age-disparity within a stand (i.e. even- vs. uneven-aged stands alongside with demographic variation and development). Analyses of stand structural complexity thus need to consider the temporal dynamics.

Terrestrial laser scanning (TLS) technology has proved to be an appropriate tool to quantify both the spatial and temporal dynamics of forest structural complexity (Liang et al., 2016). TLS is a time-efficient and non-destructive surveying technique for the measurement of the 3D structural elements of trees and delivers a fully 3D representation of tree stands. As such, it is a state-of-the-art technique that allows the study of forest structure in great detail and at high spatio-temporal resolution.

Ehbrecht et al. (2017) developed a stand structural complexity index (SSCI) that is based on TLS data and measures forest structural complexity according to the 3D spatial arrangement of all visible vegetation objects within a single laser scan. The index is comprised of two elements, the mean fractal dimension (MeanFrac, Figure S1) scaled by the effective number of layers (ENL, Figure S2). MeanFrac depends on the density of structural elements (e.g. branches, twigs), whereas ENL describes the vertical stratification. Applying the SSCI to mature temperate forests of Germany, Ehbrecht et al. (2017) and Juchheim et al. (2019) observed a positive, but saturating relationship between the SSCI and tree diversity. These forests are species-poor with one dominant tree species per plot and a few admixed species, with a maximum value of the exponential Shannon Index of about four. In a very young experiment (three years after planting) with six tree species planted in a tropical oil palm plantation, Zemp, Ehbrecht, et al. (2019) found the same relationship. At this very early stage of the experiment, MeanFrac showed the same pattern as SSCI, whereas no significant relation between ENL and tree diversity was observed. In all three studies, however, the diversity gradient was rather short (exponential Shannon-Index mainly lower than three and max. tree species richness of six), and the question remains as to whether these findings hold in a highly diverse system spanning a long tree diversity gradient under experimentally controlled conditions. Furthermore, as only one-time measurements were made and no time series analyses were conducted, the dynamics of tree interactions remained unexplored.

Here, we made use of TLS technology to analyse 3D stand structural complexity at a high resolution over multiple years in a large-scale forest biodiversity ecosystem functioning (BEF) experiment established in 2009 in the Jiangxi Province in subtropical China (BEF-China; Bruelheide et al., 2014). We quantified the SSCI based on six annual TLS data recordings conducted during 2012–2019 in plots covering a diversity gradient of tree species richness (TSR) ranging from monocultures to 24-species mixtures. We hypothesised that (a) TSR positively affects stand structural complexity, (b) TSR effects on stand structural complexity increase over time and (c) TSR effects on stand structural complexity are mainly mediated by changes of one of its elements, MeanFrac or ENL. We thus strive to determine to what extent and over what time-scale TSR can foster 3D structural complexity in forest plantations.

2 | MATERIALS AND METHODS

2.1 | Study site

The BEF-China tree diversity experiment is located in Jiangxi province in southeast subtropical China (29.08°–29.11°N, 117.90°–117.93°E, 100–300 m a.s.l.; Bruelheide et al., 2014). The natural forest around the study site consists of subtropical mixed broad-leaved species, both deciduous and evergreens. The mean annual temperature is 16.7°C and mean precipitation is 1,821 mm/year (averaged from 1971 to 2000; Yang et al., 2013).

The experiment consists of two sites (A and B), established in 2009 and 2010, respectively, with a total of 566 plots comprising tree species richness levels from 1 to 24 and different species compositions (with a random allocation of richness levels and composition to plots; see Bruelheide et al., 2014 for more details). On each plot, covering 25.8 × 25.8 m, 400 trees were planted in a regular grid with a planting distance of 1.29 m, with species randomly assigned to planting positions. Here, we analyse data from 49 plots of site A (for details on sample plot selection, see Methods S1). Plots have an experimentally established tree species richness gradient of 1, 2, 4, 8, 16 and 24 species, on 20, 15, 6, 3, 3 and 2 plots respectively. Each plot in our study was scanned at least twice using TLS within the period between 2012 and 2019 (see Table S1). Due to faster and lighter TLS systems, more plots have been scanned within the recent years 2015–2019 compared to 2012–2014. Because of that, we also tested our hypotheses in a subsample of 30 plots that were repeatedly scanned in 2013, 2015 and 2019. The plots included in our analyses showed tree mortality rates less than 80% (based on the inventory from 2016, see below). Further plot information is provided in Table S1.

2.2 | Terrestrial laser scanning data

Terrestrial laser scanning data were collected using a FARO Focus S120 and a FARO Focus X130 laser scanner in 2019, a FARO Focus S120 in 2016, 2015 and 2014 and a FARO Photon Scanner in 2013 and 2012 (FARO Europe, Korntal-Münchingen, Germany; for a detailed description of scan campaigns, see Kunz et al., 2019). All scan campaigns were conducted in February–March under leaf-off conditions of the deciduous tree species. A single scan was captured at the centre of each plot. We used a spatial resolution of 10,240 points per 360°, corresponding to a resolution of around 6 mm at a distance of 10 m. The laser scanner was set up on a tripod at 1.3 m height. All scans were performed under clear skies and almost windless conditions. For a test on the dependency of SSCI values on scanner position and leaf conditions, see Methods S2.

2.3 | Stand structural complexity index

For each single scan from the plot centre, we computed the SSCI according to Ehbrecht et al. (2017) (for detailed explanations of how the index works, see Ehbrecht et al., 2021). Prior to the SSCI computation, all scans were filtered for possible noise and stray points using a statistical outlier removal filter (SOR, $N = 10$, $SD = 3$) in CloudCompare 2.9.1 software. To ensure that the index only included points representing the plot structure, we restricted the point cloud to a radius of 10 m around the scan position (~315 m²).

The SSCI is defined as:

$$SSCI = MeanFrac^{ln(ENL)},$$

where 'MeanFrac' is the mean fractal dimension index and 'ENL' is the effective number of layers.

To calculate the MeanFrac (Ehbrecht et al., 2017), each point cloud was divided into 2,560 cross sections. The points of each cross section were sorted by angle and combined in a polygon. The MeanFrac was calculated as the mean value of the fractal dimension of the 2,560 cross sections (cf. Figure S1). For the calculation of ENL (Ehbrecht et al., 2016), we converted the 10 m radius point cloud to a voxel grid. We applied a slope correction to align the layers parallel to the ground surface. Then, we quantified the proportion of filled voxels in relation to the total voxels of each slice, and the ENL was computed using the inverse Simpson Index (for details on the calculation of ENL and slope correction, see Methods S3 and Figure S2).

SSCI, MeanFrac and ENL were computed using R 4.0.2 (R Core Team, 2018) with the packages VoxR (Lecigne et al., 2014) and sp (Pebesma & Bivand, 2005).

2.4 | Inventory-based structural indices

The trees in the core area of each plot have been measured since 2010 using traditional inventory methods (Li et al., 2014). Information on survival, species identity, stem diameter 5 cm above ground (ground diameter GD) and tree height were collected for each year between 2010 and 2016. We calculated inventory-based indices of structural complexity (in the vertical and horizontal domain) using the standard deviation (SD), coefficient of variation and Gini-coefficient

(Cowell, 2011) of GD and tree height for each plot and tested the relationship between these indices and TSR. We also calculated the mortality per plot using the last complete inventory data available from the year 2016.

2.5 | Statistical analyses

We fitted linear mixed-effects models (Zuur et al., 2009) to evaluate the effects of TSR and study year on stand structural complexity. To test for temporal dependency of TSR effects, we also considered the interaction TSR × year. Tree species composition and its interaction with year (correlated random slope), as well as study plot, were used as crossed random effects (Figure S3). Year 0 was considered as the year of plantation, 2009. The models were fitted separately to SSCI, MeanFrac, ENL and inventory-based structural complexity indices. To test whether our results depended on the consistency of temporal measurements, we additionally fitted the models to a subsample containing those 30 plots that were consistently scanned in 2013, 2015 and 2019. Fixed factors were standardised around their mean value with a standard deviation of one before fitting the models. Prior to analyses, the dependent variables and TSR were $\log_2$ transformed to meet model assumptions (i.e. homogeneity, independence and normality; Zuur et al., 2009). Residuals plots showed no violation of these assumptions. To test the relationship between all the structural complexity indices applied, we calculated Pearson's correlation coefficients.

To test how the SSCI–TSR relationship varies with species identity, we separately fitted linear regression models for 16 species measured in 2019. We analysed those tree species that were present in at least four of the analysed plots from 2019 (Table S2).

Furthermore, we conducted a path analysis to explore drivers for SSCI using a piecewise approach that allows for the implementation of random effects (using the same random structure as described above; Lefcheck, 2016). We tested the hypothesis that TSR effects on SSCI were mediated by changes in MeanFrac and/or ENL. We further hypothesised that changes in MeanFrac, ENL and SSCI are driven by stand development (study year). All variables were standardised and transformed as described above and the model fit was evaluated based on Fisher's C statistics (Lefcheck, 2016).

All statistical analyses were performed in R 4.0.2 (R Core Team, 2018) using the packages LMERTEST (Kuznetsova et al., 2017), PIECEWISESEM (Lefcheck, 2016) and MUMIN (Barton, 2019).

3 | RESULTS

In general, we observed a positive relationship between TSR and structural complexity (Figure 1, Table 1, Figures S4 and S5, Tables S3 and S4). Importantly, these effects became stronger over time for the TLS-based indices, as indicated by the significant two-way interactions (Figure 1, Table 1). Ten years after planting, we found a twofold increase of the SSCI in 16- and 24-species mixtures compared to monocultures. MeanFrac decreased slightly with TSR during the first years, while these effects became neutral to positive over time (Figure 1b, Table 1). These relationships were qualitatively the same when fitting the models to those plots that were repeatedly measured in 2013, 2015 and 2019 (Table S3, Figure S4).

The temporal development of TSR effects, however, differed among the inventory-based indices (Table S4, Figure S5). The positive relationship between the *SD* of GD and TSR was present from the first study year and remained constant over time (i.e. no significant interaction with year), whereas the positive relationship between the *SD* of tree height and TSR became stronger with time (i.e. positive interaction with year). In contrast, TSR effects varied with year for the coefficient of variation and the Gini coefficient of GD, but not for those of tree height (Table S4). All inventory-based indices were closely positively correlated to each other, whereas the correlations between SSCI and the inventory-based indices were mostly nonsignificant (Figure S6).
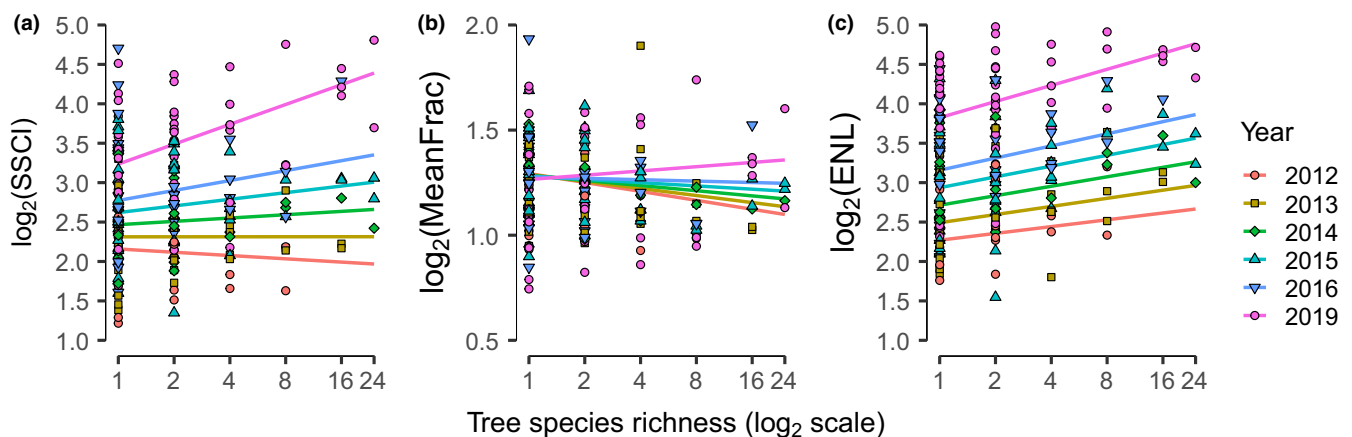

FIGURE 1 Temporal changes in the relationship between tree species richness and different components of stand structural complexity (a: stand structural complexity index (SSCI); b: mean fractal dimension (MeanFrac); c: effective number of layers (ENL)). Lines show the predictions of linear mixed-effects models, and symbols indicate observed values

TABLE 1 Results of mixed-effects models for the effects of tree species richness (TSR; log_2-transformed), year and their interaction on different components of stand structural complexity (SSCI, MeanFrac and ENL; all log_2-transformed). n = 315

Fixed effect	SSCI				MeanFrac				ENL			
	df_{num}	df_{den}	F	p	df_{num}	df_{den}	F	p	df_{num}	df_{den}	F	p
Intercept	—	—	—	<0.001	—	—	—	<0.001	—	—	—	<0.001
TSR	1	92.76	6.36	<0.05	1	103.42	12.16	<0.001	1	66.08	0.29	0.593
Year	1	54.35	76.64	<0.001	1	58.78	0.39	0.533	1	26.85	299.52	<0.001
TSR × Year	1	38.74	18.63	<0.001	1	44.57	6.09	<0.05	1	19.16	5.75	<0.05

Abbreviations: 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.

The positive relationship between TSR and SSCI was consistent across species: In 2019, all species showed a positive relationship between SSCI and TSR, meaning that monocultures display lower stand structural complexity than the mixtures where they were present (Figure 2). The relationship between TSR and SSCI was significant at $p < 0.01$ for six species (Table S2). Tree mortality did not affect SSCI ($p = 0.29$).

The path model resulted in a good fit to the data (Fisher $C = 1.25$, $df = 2$, $p = 0.536$) and TSR, ENL, MeanFrac and Year accounted for 97% of the variation in SSCI. ENL ($p < 0.001$) and MeanFrac ($p < 0.001$) had a positive direct effect on SSCI with ENL being the strongest driver for changes in SSCI (Figure 3). We found no significant direct pathway between TSR and SSCI ($p = 0.375$). Instead, TSR enhanced SSCI indirectly via increasing ENL ($p = 0.020$) and not via increasing MeanFrac ($p = 0.431$), indicating that TSR effects on SSCI are mediated by changes in ENL. ENL, in turn, was positively related to stand development ($p < 0.001$), while SSCI and MeanFrac were not directly affected by changes over time (SSCI: $p = 0.849$; MeanFrac: $p = 0.486$).

4 | DISCUSSION

Ten years after establishment, we found a significant positive relationship between 3D stand structural complexity (expressed as TLS-data-based SSCI) and TSR across a broad diversity gradient in a subtropical experimental tree plantation, thus confirming our first hypothesis that TSR positively affects stand structural complexity. This is an important finding because it demonstrates that, already in young plantations, management decisions can considerably contribute to the improvement of stand structural complexity. Stand structural complexity, in turn, is considered a key component of biodiversity in tree communities and an important driver of various ecosystem functions. For example, there is evidence that stand structural complexity positively affects the abundance and species richness of consumers (Schuldt et al., 2019), the robustness of multitrophic interactions (Fornoff et al., 2019), as well as the resilience to current and future environmental changes and stressors (Fahey et al., 2018).

Our findings are in part consistent with those from other studies using TLS-based SSCI assessments (Ehbrecht et al., 2017; Juchheim et al., 2019; Zemp, Ehbrecht, et al., 2019), but differ with regard to an important element: While those studies observed a nonlinear positive relation with saturation at relatively low tree diversity, we found that log-SSCI consistently increased with log-TSR across a long gradient of TSR (up to 24-species mixtures). This discrepancy might be partially explained by differences in the aboveground biomass of forests of different biomes, since subtropical tree species (as analysed in the present study) have the potential to accumulate significantly higher amounts of biomass in their canopy as compared to temperate tree species (Keeling & Phillips, 2007), but potentially also by the length of the diversity gradient itself and by the limited representation of plots with very high diversity levels in the studies by Ehbrecht
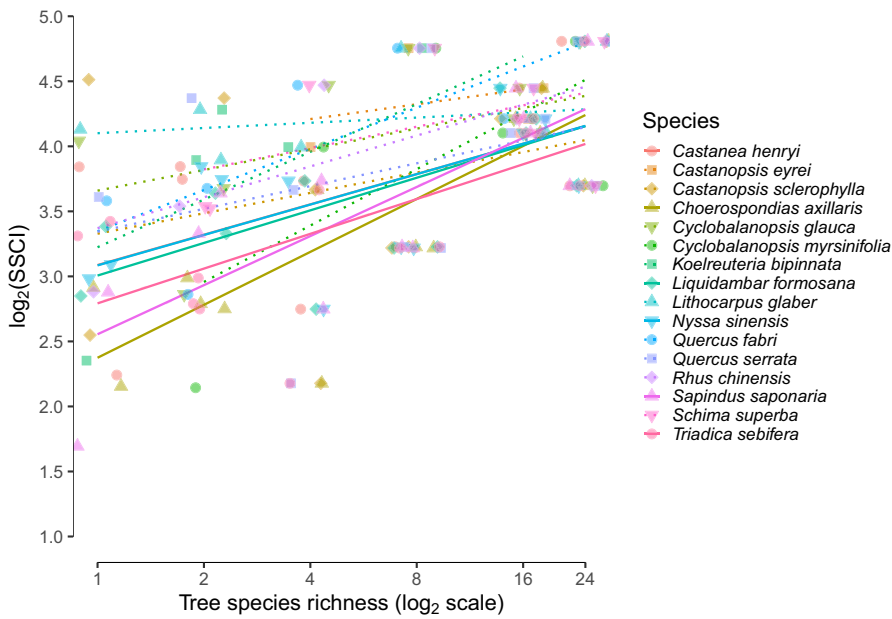
FIGURE 2 Relationship between tree species richness (TSR) and stand structural complexity index (SSCI) for 16 tree species measured in 2019. TSR = 1 means that the plot was planted as a monoculture. Dotted lines show non-significant ($p > 0.1$), solid lines indicate significant ($p < 0.1$) relationships. Symbols indicate observed values jittered to facilitate visibility
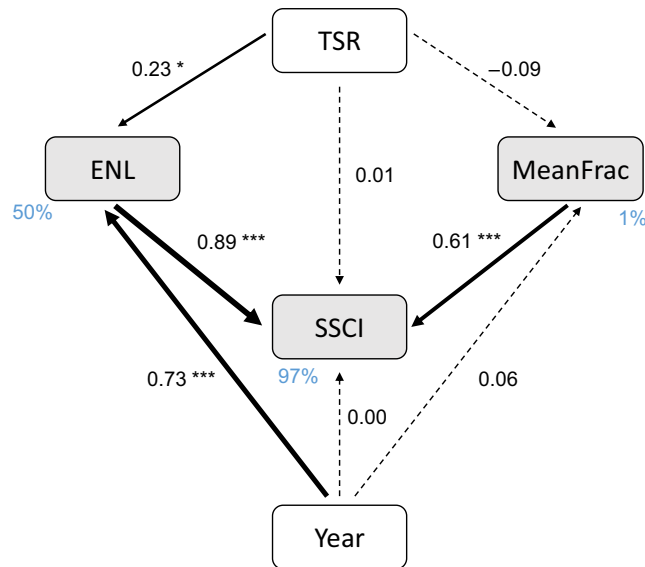

FIGURE 3 Path model linking the effects of tree species richness (TSR), effective number of layers (ENL), mean fractal dimension (MeanFrac), stand development (year) and stand structural complexity (SSCI). Solid arrows denote significant causal relationships (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$), while non-significant ($p > 0.05$) relationships are indicated by dotted arrows. Numbers beside arrows (standardised path coefficients) and arrow width denote the effect size of the pathways. Percentage values (blue) are explained variances of fixed-effects only (marginal R^2 values)

et al. (2017), Juchheim et al. (2019) and Zemp, Ehbrecht, et al. (2019). The temperate forests of Central Europe are generally poor in tree species, and accordingly, the tree diversity gradient in the studies by Ehbrecht et al. (2017) and Juchheim et al. (2019) was narrow. A cessation of the increase of the SSCI with increasing tree diversity already occurred at exponential Shannon index values of about 2.

In an experimental enrichment plantation of six native broadleaved tree species in commercial oil palm monocultures in tropical Sumatra, Indonesia, the tree species richness gradient ranged, in the majority of cases from 0 to 3, with only two five-species and one six-species plots (Zemp, Ehbrecht, et al., 2019). It thus remains open whether considerably longer tree diversity gradients in the temperate and the tropical biome would yield a similar linear increase in 3D stand structural complexity with increasing tree species richness, as observed in our subtropical plantation.

4.1 | Temporal changes in TSR–stand structural complexity relationships

Another important factor that might influence the mode of the relationships between tree diversity and SSCI is the age of the trees. This is of particular relevance in communities with long-living individuals such as trees, as they record the history of past growth and interactions with the environment in long-lasting woody structures. In accordance with our second hypothesis, stand development proved to be an important predictor for structural complexity: Whereas relationships between TSR and SSCI were slightly negative at the beginning of the measurement period in 2012–2013 (i.e. in the third and fourth year after planting), they proved to be strongly positive after 10 years. This is a clear indication that the importance of positive species interactions (e.g. resource partitioning and facilitation) strengthened over time. This in turn might be a key mechanism underlying positive TSR–SSCI relationships. Due to the high planting density in BEF-China, early onset of tree–tree interactions was observed already in the first years after planting (Li et al., 2014). However, diversity-mediated patterns in biomass allocation resulting in morphological adjustments in the 3D tree architecture and hence

positive diversity–productivity relationships need to develop (Kunz et al., 2019). Zemp, Ehbrecht, et al., (2019) conducted a single measurement 3 years after planting and found that the variability of SSCI was mainly explained by species identity effects rather than tree species interactions. However, the authors expected this pattern to change over time as trees develop larger, more complex and plastic crowns. In line with Zemp, Ehbrecht, et al. (2019), we observed a high variation of SSCI values in monocultures within the individual study years. This might be attributed largely to major trait differences among the planted tree species in BEF-China, which in turn result in substantial differences in growth rates (Li et al., 2014, 2017). In our study, however, we can exclude strong species identity effects on the overall TSR–SSCI relationship, since the positive relationship between TSR and SSCI in 2019 was consistent across the 16 tree species most abundant in our study, meaning that all the species, independently of their traits, showed lower stand structural complexity in monocultures than in mixtures 10 years after planting. This also suggests that differences in mortality rates are of minor importance. Based on the findings of Bruelheide et al. (2011), we do not expect a reduction of structural complexity in species mixtures in the long term, because, in a natural forest nearby the experimental site, young and old stands did not differ with respect to species composition or richness.

4.2 | Relationship between TSR and inventory-based stand structural complexity indices

Although all inventory-based indices displayed the same overall positive relation with TSR as SSCI, the development over time was different. Importantly, all TSR–inventory-based index relationships were positive from the beginning (i.e. year 2012). The indices based on the ground diameter (GD) either showed no significant (*SD* of GD) or a decreasing impact of TSR over time (coefficient of variation and Gini-coefficient of GD). By contrast, we found a slightly or non-significant increasing effect of TSR on all indices based on tree height over time. These observations suggest that, unlike the SSCI, the inventory-based indices showed strong species identity effects with high variability in GD and tree height due to species-specific differences in growth rates. Over time, GD appeared to be more evenly distributed across TSR levels, whereas a less even distribution in height developed. In addition, tree mixtures showed higher productivity, mainly driven by a neighbourhood-mediated enhancement of individual-tree growth (Fichtner et al., 2018; Kunz et al., 2019). We hypothesise that a tree's height growth is of higher priority than diameter growth when light is the main growth-limiting factor (Falster & Westoby, 2003; Pretzsch, 2009). In dense young plantations, like those in our study, preferential biomass investments in height growth are, therefore, to be expected (Li et al., 2017). For the tree species mixtures, competitive reduction has been found to be the main driving mechanism of positive diversity effects for fast-growing species (Fichtner et al., 2017).

4.3 | Role of density (MeanFrac) versus vertical stratification (ENL) in the relationship between TSR and SSCI

Our finding that the positive effects of TSR on SSCI are mediated by ENL rather than MeanFrac suggests that TSR promotes stand structural complexity indirectly by allowing for greater complementarity in canopy space (i.e. vertical stratification). The lack of a strong impact of TSR on MeanFrac may be partly explained by the regular (rasterised) pattern in which the trees were planted in the BEF-China experiment. Nevertheless, there is a temporal trend that might lead towards a positive relation between TSR and MeanFrac in the future, probably due to differences in mortality rates (i.e. self-thinning with a loss of the suppressed individuals). In contrast, ENL was a strong mediator of the TSR effects on SSCI and was also significantly positively related to stand development. This coincides with our finding of a highly variable height growth of the trees analysed, which then fosters a strong vertical differentiation of crown elements (i.e. branches) in higher mixtures. Species mixtures often show a higher crown complementarity than monocultures (Williams et al., 2017), in particular as a result of neighbourhood-driven changes in crown architecture (Guillemot et al., 2020; Kunz et al., 2019). Specifically, diversity-mediated changes may lead to a higher biomass allocation to branches, increased crown size, more sinuous crowns, higher branch ramification and more even vertical distribution of crown volume (Bayer et al., 2013; Guillemot et al., 2020; Kunz et al., 2019; Lang et al., 2012; Olivier et al., 2016). As a result, canopy space is more complex (and partly more heterogeneously structured), which in turn may cause increased canopy packing (Ehbrecht et al., 2016; Morin et al., 2011; Pretzsch, 2014; Williams et al., 2017).

4.4 | Management implications and conclusions

Given the huge area of afforestation projects currently in progress worldwide, particularly in Asia (Yang et al., 2010), the selection of appropriate tree species is key to achieving the intended ecosystem functions and services (IUCN, 2020; Tang & Li, 2013). However, many afforestation projects still utilise a limited range of the potentially available tree species typical of a respective site, and possibly miss opportunities related to such afforestation programmes (Gong et al., 2020). Taking subtropical forest plantations as an example, our study provides evidence that increasing the tree species richness of plantations has a positive influence on stand structural complexity, which in turn may foster the stands' resistance or resilience to environmental stressors or natural disturbances (Seidl et al., 2016). In the absence of sufficient knowledge about which species should be planted in mixtures for afforestations, the best current approach is to plant a large number of species. Our study demonstrates that species richness per se generally supports a high stand structural complexity with all its beneficial consequences. Tree species richness mainly promotes vertical heterogeneity, which supports ecosystem functions and services such as timber production or carbon

sequestration (Guillemot et al., 2020; Williams et al., 2017; Zemp, Ehbrecht, et al., 2019), but also positively affects the species diversity or abundance of higher trophic levels (Knuff et al., 2020; Schuldt et al., 2019) as well as the robustness of multitrophic interactions (Fornoff et al., 2019). Afforestation projects should therefore use a broad range of the tree species native to a respective site in order to promote both the functioning of the newly established forests (including related services) and the biodiversity they potentially host.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

The study was conceived by M.D.P.-G., G.v.O., W.H. and M.K.; M.D.P.-G. and M.K. performed the fieldwork; M.D.P.-G., M.K. and A.F. analysed the data; M.D.P.-G. wrote the first draft of the manuscript and all the authors contributed substantially to the submitted version.

DATA AVAILABILITY STATEMENT

Data available via the BEF-China project database: https://data.botanik.uni-halle.de/bef-china/datasets/637 (Perles-Garcia et al., 2020).

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