



## Mixed-species tree plantings enhance structural complexity in oil palm plantations



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### ARTICLE INFO

#### Keywords:

Agroforestry  
Restoration  
Terrestrial laser scanning  
Complexity  
Structure  
Biodiversity

### ABSTRACT

Conversion of structurally complex rainforests into simplified oil palm monocultures leads to dramatic losses of biodiversity and ecosystem functioning. To alleviate negative ecological impacts, enrichment with native tree species may rapidly restore structural complexity in existing oil palm plantations. However, the mechanisms underlying the recovery of structural complexity in mixed-species tree plantings remain poorly understood. We measured structural complexity from terrestrial laser scanning in a biodiversity enrichment experiment with multiple tree species planted in an oil palm monoculture, forming agroforestry plots of varying tree species diversity and plot size. We find that three years after tree planting, structural complexity in oil palm increased by one third, representing 25% of the increase needed to restore the structural complexity of tropical forests. Changes in structural complexity were associated with denser and more complex filling of three-dimensional space, whereas vertical stratification was mainly influenced by oil palm. Furthermore, structural complexity increased with tree species diversity in the agroforestry plots. This relationship was mainly due the presence of well-performing species that contributed to higher levels of structural complexity. However, interactions among multiple species independently from the species identity were also detected. Finally, increasing plot size had a positive effect on a scale-independent measure of structural complexity. Our results provide evidence that planting multiple tree species in large agroforestry plots is a suitable strategy to rapidly enhance structural complexity in oil palm plantations.

### 1. Introduction

Conversion of structurally complex tropical rainforests into simplified tree cash crop plantations such as rubber or oil palm leads to dramatic losses of biodiversity and ecosystem functioning (Foster et al., 2011; Straaten et al., 2015; Drescher et al., 2016). Plant, invertebrate and microbial communities are directly impacted by land-use change (Drescher et al., 2016; Barnes et al., 2017; Rembold et al., 2017), leading to cascading effects at higher trophic levels (Barnes et al., 2017) and an overall change in food web structure and functioning (Barnes et al., 2014). Oil palm plantations are structurally much simpler compared with forests, with an even-aged canopy, an understorey vegetation dominated by a dense and low layer of grasses and shrubs (Rembold et al., 2017) and lower diversity of trees, epiphytes and litter

(Foster et al., 2011; Luskin and Potts, 2011; Rembold et al., 2017). As a consequence of simplify vegetation structure, the micro-climate in oil palm plantations is significantly warmer and hotter than forests (Hardwick et al., 2015), leading to reduced buffering capacity to extreme drought events (Meijide et al., 2018). Together, the ecological changes associated with conversion to oil palm plantations leads to reductions in the provisioning of vital ecosystem services, including water regulation and supply, non-harvested net primary productivity and carbon storage, and soil processes and fertility (Clough et al., 2016; Dislich et al., 2016).

The complexity of forest structure has been described with a variety of terms, e.g. structural heterogeneity or structural diversity, and quantified with numerous measures, ranging from the coefficient of variation in plant height to a summarizing index of basal area, density

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<https://doi.org/10.1016/j.agee.2019.06.003>

Received 10 December 2018; Received in revised form 30 April 2019; Accepted 2 June 2019

Available online 20 June 2019

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and percentage cover of plants (Tews et al., 2004; McElhinny et al., 2005; Stein et al., 2014; Schall et al., 2018). Following Pretzsch (2009), who argued that the three-dimensional (3D) nature of forest structure is probably its most important feature, we define stand structural complexity (hereafter simply ‘structural complexity’) as an integrative measure of the architectural and distributional pattern of tree individuals and their components in three-dimensional space at a given point in time (Ehbrecht et al., 2017).

Increasing structural complexity at local and landscape scales might alleviate the ecological impacts of conversion to oil palm plantations (Foster et al., 2011; Azhar et al., 2013, 2015; Nakagawa et al., 2013). Management practices to increase structural complexity at local scales include variable retention (i.e. thinning and replanting a new cohort of oil palms to create multiple vertical layers) (Luskin and Potts, 2011) or cultivating oil palm with multi-purpose tree species in agroforestry systems (Bhagwat and Willis, 2008; Koh et al., 2009). By structurally resembling forests, agroforestry systems that combine trees and agricultural crops have a positive effect on biodiversity (Bhagwat et al., 2008) and ecosystem services (Jose, 2009; Ribeiro de Carvalho et al., 2014; Ramos et al., 2018) without necessarily decreasing crop yields (Steffan-Dewenter et al., 2007; Clough et al., 2011; Rica et al., 2012; Gérard et al., 2017). In particular, multi-strata agroforestry systems incorporating multiple tree species provide habitats for diverse bee, bird and bat communities (Clough et al., 2009; Ashraf et al., 2018; Azhar et al., 2014; Ghazali et al., 2016; Yahya et al., 2017; Syafiq et al., 2016), with implications for pest control (Maas et al., 2015), seed dispersal and pollination services (Jose, 2009). Increasing structural complexity leads to a more stable and moist micro-climate (Luskin and Potts, 2011; Hardwick et al., 2015; Ehbrecht et al., 2019), thereby increasing litter decomposition rates (Crockatt and Bebbler, 2015) and buffering plant responses to global warming (Frenne et al., 2013). In human-modified landscapes, structurally complex agroforestry patches, or “woodland islets” (Rey Benayas et al., 2008), may act as “keystone structures” (Tews et al., 2004) supporting biodiversity and providing ecosystem services and a source of food and income for local population (Azhar et al., 2017; Bhagwat and Willis, 2008).

It has been suggested that increasing tree species diversity leads to higher structural complexity, due to complementarity in crown architectural and physiological traits (e.g., shade tolerance) among tree species and interactions involving crown plasticity in mixed-species neighborhoods (Pretzsch, 2014; Jucker et al., 2015; Castro-Izaguirre et al., 2016). In turn, structural complexity allows a better capture of available light (Hardiman et al., 2011; Forrester et al., 2018), potentially triggering a positive feedback loop between structural complexity and tree growth in mixtures (Pretzsch, 2014; Ammer, 2019). This hypothesis has been tested in forests, where both positive (Jucker et al., 2015; Pretzsch, 2016; Castro-Izaguirre et al., 2016; Ehbrecht et al., 2017) and no (Hardiman et al., 2011; Ehbrecht et al., 2017) structural complexity–diversity relationships have been found. Species identity effects are frequently confounded with species diversity and environmental factors in observational studies. Tree diversity experiments – which control species diversity and composition of tree communities experimentally (Paquette et al., 2018) can identify and quantify ecological mechanisms underlying species diversity effects on ecosystem functioning.

We measured different aspects of structural complexity using terrestrial laser scanning (Ehbrecht et al., 2016, 2017; Seidel, 2017) in a tree diversity experiment established in an oil palm plantation (Teuscher et al., 2016). In the EForTS-BEE experiment (BEE, biodiversity enrichment experiment), multiple tree species were planted between existing and partially thinned oil palms, thus forming agroforestry plots of varying size and tree diversity (Teuscher et al., 2016). First, we investigated how tree planting affects structural complexity compared to tropical forests and conventional oil palm plantations. Second, we tested the mechanisms underlying the structural complexity–diversity relationship by partitioning the variance in independent

effects of species identity (including complementarity) and interaction (Bell et al., 2009). We finally evaluated the effect of plot size on structural complexity.

We hypothesized that thinning oil palms and planting trees rapidly enhanced structural complexity, by creating a denser and more complex stand structure and increasing vertical stratification. We expected that tree species diversity would have a positive effect on structural complexity. We anticipated that this relationship would largely be driven by species identity effects reflecting interspecific differences in ecological and architectural characteristics. Lastly, we expected that larger plot sizes would have higher structural complexity, possibly due to reduced edge effects.

## 2. Method

### 2.1. Study sites

The primary study site of this study is the biodiversity enrichment experiment EForTS-BEE (Teuscher et al., 2016) located in Jambi province, Sumatra, Indonesia (Fig. A.1). The dominant soil type is loamy Acrisol, with a higher fraction of silt ( $40.5 \pm 8.3\%$ ) compared to sand ( $29.9 \pm 12.6\%$ ) and clay ( $29.5 \pm 8.3\%$ ), and a soil bulk density of  $1.09 \pm 0.1 \text{ kg cm}^{-3}$  prior to tree planting (Teuscher et al., 2016). The experiment was established within the EForTS [Ecological and socio-economic functions of tropical lowland rainforest transformation systems (Sumatra, Indonesia)] collaborative research center (Drescher et al., 2016) ([www.uni-goettingen.de/crc990](http://www.uni-goettingen.de/crc990)). In December 2013, six native tree species were planted in 48 plots in a conventional oil palm plantation. In addition to the 48 agroforestry plots, four plots were assigned to natural regeneration of the vegetation in oil palm (no tree planting). The experiment follows a random partitions design (Bell et al., 2009), with four partitions that differ in plot size ( $5 \text{ m} \times 5 \text{ m}$ ,  $10 \text{ m} \times 10 \text{ m}$ ,  $20 \text{ m} \times 20 \text{ m}$ ,  $40 \text{ m} \times 40 \text{ m}$ ). Each partition is divided into five blocks, one per tree diversity level (0, 1, 2, 3, and 6 species). Within each block, each species was randomly drawn from the species pool without replacement, and was therefore represented exactly once.

We selected tree species that occur in the study region and are valued by local farmers for producing fruit, timber, or latex, which are appropriate criteria given the applied context of our study (Teuscher et al., 2016). More specifically, three species producing fruits (*Parkia speciosa* Fabaceae; *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus*, Malvaceae) are common in agroforestry systems in the region (Götz et al., 2004; Hariyadi and Ticktin, 2012; Michon et al., 1986; Vincent et al., 2002; Clough et al., 2009). Two species are used for construction timber (*Peronema canescens*, Lamiaceae; *Shorea leprosula*, Dipterocarpaceae) and are commonly found in Dipterocarp forests (Newman et al., 1996) and agroforestry systems (Götz et al., 2004), respectively. One species is mainly used for latex and timber (*Dyera polyphylla*, Apocynaceae) and is used in agroforestry for peatland restoration in the region (Tata et al., 2016). The age of the planted seedlings varied between 7 and 9 months (*D. polyphylla*, *S. leprosula*, *D. zibethinus*) to 19 months (*A. pauciflorum*, *P. speciosa*, *P. canescens*).

Oil palm trees were planted 6–12 years prior to establishment of the experiment, following a 9.8 m triangular grid. In order to enhance light availability for tree establishment, some oil palms were felled prior to tree planting. The number of felled oil palms depended on the size of the plots, with an average of seven palms cut in the  $40 \text{ m} \times 40 \text{ m}$  plots, three palms cut in the  $20 \text{ m} \times 20 \text{ m}$  plots, one palm cut in the  $10 \text{ m} \times 10 \text{ m}$  plots and no palm cut in the  $5 \text{ m} \times 5 \text{ m}$  plots (Gérard et al., 2017). This oil palm thinning increased the gap fraction from  $14 \pm 10.0\%$  to  $27.5 \pm 14.9\%$  (Teuscher et al., 2016), and created heterogeneous oil canopy cover between and within plots (Khokthong et al., 2019). All experimental plots were fenced to prevent grazing from cattle and disturbances from wild boars and humans. Following the concept of woodland islets (Rey Benayas et al., 2008), the experimental plots were densely planted (2 m triangular grid) and sparsely

distributed in the landscape (at least 85 m from each other). More information on the experimental design is available in [Teuscher et al. \(2016\)](#).

In addition, we also used EForTS core plots in oil palm monocultures and ‘primary degraded forests’ (50 m × 50 m; eight plots per land-use type) in the study region ([Drescher et al., 2016](#)). The forests showed signs of selective logging ([Drescher et al., 2016](#)), and three forest plots were partly damaged by fire during a drought event approximately one year before laser scanning.

## 2.2. Structural complexity measured from laser scanning

In September and October 2016, multiple terrestrial laser scans were made in each plot to capture the 3D distribution of foliage and woody components using a FARO Focus terrestrial laser scanner (Faro Technologies Inc., Lake Mary, USA). The laser scanner was placed on a tripod in 1.3 m height, raised by up to 20 cm to position the instrument above the understorey vegetation. The instrument was set to scan with a field of view 360° horizontally and 300° vertically with a step width of 0.035°. Technically, the laser scanner can capture elements in a radius of up to 120 m. In practice, however, the area covered by the laser scan is limited and typically depends on the density of the vegetation.

The laser scans made at the center of each plot were then processed using Mathematica Software (Wolfram Research, Champaign, USA) to compute the stand structural complexity index (SSCI) following the procedure described by [Ehbrecht et al. \(2017\)](#). SSCI is composed of two components. (1) Mean fractal dimension index (MeanFRAC) is a scale-independent measure of structural complexity and depends on the density of vegetation elements ([Ehbrecht et al., 2017](#)). As such, a dense thicket with low canopy height can show similar MeanFRAC values as a dense, but tall forest with large trees. MeanFRAC is based on the mean fractal dimension of 1280 cross-sectional polygons, which were derived from the 3D point clouds. (2) The effective number of layers (ENL) describes vertical stratification based on the Simpson Index applied to the vertical layers that are effectively occupied by plants ([Ehbrecht et al., 2016](#)). Hence, ENL values increase with increasing stand height and a more even space filling along the vertical axis. SSCI is obtained by scaling MeanFRAC with ENL, and therefore is an integrative measure of structural complexity that takes vertical structure into account. All measures (i.e. SSCI, MeanFRAC and ENL) account for vegetation components above the terrestrial laser scanner, and therefore the understorey vegetation is not included. In a study by [Ehbrecht et al. \(2017\)](#), SSCI was correlated with other conventional indices describing forest structure (e.g. structural complexity index from [Zenner and Hibbs \(2000\)](#) and index of aggregation from [Clark and Evans \(1954\)](#)) and could better explain micro-climate fluctuation than those indices. In the same study, SSCI was positively correlated to tree species diversity and successfully differentiated forest types characterized by different management systems and main tree species. The highest SSCI recorded to date is  $7.3 \pm 1.7$  in European primary forests ([Stiers et al., 2018](#)).

We also quantified the box dimension ( $D_b$ ) based on fractal analysis as a scale-independent measure of structural complexity at the level of individual trees ([Seidel, 2017](#)). Differences in box dimension between species depend on their tree architectural characteristics ([Seidel, 2017](#)) but also on their development stage. Multiple scans assembled with the help of referenced objects installed in the scene (‘targets’) were used to extract individual trees from the 3D point clouds. A high  $D_b$  value (maximum of  $D_b$  is three by design) means that the species has a high space-filling character, while a value close to one would be found for a branch-free pole. The box dimension is species-specific, but also affected by growing conditions and levels of inter- and intra-specific competition. We therefore quantified for each species the box dimension for 8 randomly selected individuals in 6 different mixed-species plots.

## 2.3. Individual-based measurements

At the establishment of the experiment, the plots contained 6354 planted trees. We measured individual-based sizes and determined survival in January–February 2017. Tree height was measured using a Vertex (Haglöf) for tree exceeding 8 m height, a telescopic measuring rod for trees between 2 m and 8 m height, and a regular tape for trees smaller than 2 m. Accuracy assessment indicated that the vertex and the telescopic measuring rod led to an overall error of 0.6 m, i.e. 3.5% (see Table B.1). When a tree stem was tilted, the maximum height in the vertical was used instead of the total height, as the former variable is assumed to be more relevant for the present study. The relative height of a tree was calculated as a fraction of the maximum stand height. The maximum stand height was calculated as the maximum of the total number of layers using multiple terrestrial laser scans from various positions in each plot. Finally, stem diameter was measured at 10 cm above ground, because some trees still did not reach the height needed to measure diameter at breast height.

We measured the height and crown area of all oil palms inside the experimental plots, as well as one palm directly adjacent to each plot, resulting in a total of 267 measured oil palms. The oil palm height was measured as the vertical distance from the ground to the apical meristem (i.e. crown base) using a Vertex. The crown area of an oil palm was calculated as the average of horizontal distances between vital oil palm fronds in two directions (east–west and north–south).

## 2.4. Hemispherical photography

We took hemispherical photographs with a Nikon D5100 camera and a fisheye lens (SIGMA 4.5 mm F2.8 EX DC) at the same time as laser scanning. Photographs were taken at the center of each plot on a tripod at a height of 1.3 m, although the position of the camera might slightly vary with that of the laser scanner. Different exposure settings were performed and the best photograph for each plot was selected following [Beckschäfer et al. \(2013\)](#). The photographs were processed using the macro ‘Hemispherical<sub>2,0</sub>’ in ImageJ ([Beckschäfer, 2015](#)).

## 2.5. Linear model for random partition design

The relative importance of tree species identity and interaction effects for SSC was quantified using a linear model for random partition designs ([Bell et al., 2009](#)):

$$y = \beta_0 + \beta_{LR}x_{LR} + \sum_{i=1}^6 (\beta_i x_i) + \beta_{NLR}x_{NLR} + \beta_P x_P + \beta_M x_M + e \quad (1)$$

where  $x_{LR}$  is the number of planted tree species (1, 2, 3 or 6) as a continuous variable (‘linear species richness’),  $x_i$  indicates the presence/absence of the species  $i$  (‘species identity’),  $x_{NLR}$  the number of planted tree species treated as a discrete variable (‘nonlinear species richness’),  $x_P$  is the partition (i.e., plot size) as a discrete variable,  $x_M$  is the species composition (i.e., plot identification number) and  $e$  the residual term. The importance of species identity and non-linear species richness for explaining the variability in structural complexity (i.e., MeanFRAC, ENL and SSCI) was quantified using the mean square of the corresponding coefficients in an analysis of variance (ANOVA). The coefficients  $\beta_0$ ,  $\beta_{LR}$ ,  $\beta_i$  (for each species  $i$ ),  $\beta_{NLR}$ ,  $\beta_P$  and  $\beta_M$  were calculated in this order in sequential models, using the residuals of the previous model as dependent variable.

Mortality was considered as a response variable of the tree diversity experiment. Therefore, the model did not account for mortality in the number and composition of tree species in the experimental plots. Plots of natural regeneration (diversity level 0) were not included in the model.

The model has several advantages. First, the sum of the coefficients associated with each species equals zero ( $\sum_{i=1}^6 \beta_i = 0$ ). Hence, the

individual coefficient associated with each species  $i$  ( $\beta_i$ ) indicates its contribution to structural complexity relative to the ‘average species’. This is a key methodological advancement, as widely used frameworks (e.g. Loreau and Hector, 2001, but see Loreau, 1998) require the contribution of each species to the ecosystem function to be measurable, which is not the case for properties of the entire vegetation community such as structural complexity. Second, the effect of species identity and non-linear species richness are orthogonal. The order in which they are listed in the model hence does not matter. The non-linear species richness term is an indicator of the strength of interactions among species that is independent from the species identity effects. All statistical analyses were performed using R software version 3.3.1, using the packages *multcomp* (Hothorn et al., 2008), *sandwich* (Zeileis, 2004) and *lme* (Pinheiro et al., 2013).

### 3. Results

#### 3.1. Effect of restoration strategies on structural complexity

SSCI in the agroforestry plots (1–6 tree species planted) ( $4.36 \pm 0.83$ ) was significantly higher than in oil palm monocultures ( $3.27 \pm 0.56$ ) and significantly lower than in forests ( $6.68 \pm 1.73$ , or  $7.61 \pm 1.37$  without fire) (Fig. 2A). SSCI in experimental plots with natural regeneration (no trees planted) was intermediate ( $3.87 \pm 0.86$ ), although variability between plots was too high to detect any statistical difference.

Agroforestry plots compared with oil palm monoculture differed only in terms of MeanFRAC and not ENL, while both systems differed from rainforests in terms of ENL and not MeanFRAC (Fig. 2B, see also Fig. A.2).

SSCI was not significantly different between thinned and non-thinned experimental plots, although both had higher SSCI values than oil palm monocultures. Neither ENL nor MeanFRAC was significantly different in the thinned and non-thinned experimental plots (Fig. A.2).

#### 3.2. Other structural variables

The oil palms reached  $5.34 \text{ m} \pm 0.9$  at meristem. Maximum stand height was determined by the oil palm canopy and all planted trees grew underneath (Table 1). Approximately 50% of the planted trees died, and survival rates and height varied widely among species. On the one hand, *D. polyphylla* and *D. zibethinus* only started to overgrow the understorey (tree height of  $1.6 \pm 1 \text{ m}$ , representing 11% of stand top height) and had survival rates < 16%. On the other hand, *P. canescens* reached the height of the oil palm crown base (representing 36% of stand top height) and had a survival rate > 95%.

Principal component analysis (Fig. A.3) reveals that SSCI was negatively related to gap fraction. ENL was mainly associated with the

**Table 1**

Ecological and architectural characteristics of each species. Left: Survival rate (%), relative height ( $H_r$ , in % of stand top height) and box dimension ( $D_b$ , dimensionless). Mean values for each species are shown (standard deviations in brackets). And letters indicate significant differences ( $p$ -value < 0.05) based on a one-way ANOVA model followed by a single-step Tukey test. Height of oil palm is measured at crown base. Right: The coefficients  $\beta$  associated with the effect of each species in the linear model for random partition design for mean fractal dimension (MeanFRAC), effective number of layers (ENL) and stand structural complexity index (SSCI). Positive (negative) coefficients indicate that the species has an above-average (below-average) contribution. Estimates are shown (standard errors in brackets). Note: Statistical significances ( $p$ -value < 0.001 ‘\*\*\*’, < 0.01 ‘\*\*’, < 0.05 ‘\*’, < 0.1 ‘.’) of the coefficients are based on a  $T$ -test. Species: A, *Parkia speciosa*; B, *Archidendron pauciflorum*; C, *Durio zibethinus*; D, *Dyera polyphylla*; E, *Peronema canescens*; F, *Shorea leprosula*; O, *Elaeis guineensis* (oil palm).

	Survival	$H_r$	$D_b$	$\beta_{\text{MeanFRAC}}$	$\beta_{\text{ENL}}$	$\beta_{\text{SSCI}}$
A	84.7	28 (16) <sup>b</sup>	1.58 (0.10) <sup>ab</sup>	0.13 (0.06)*	-0.43 (0.39)	0.29 (0.21)
B	86.4	31 (17) <sup>c</sup>	1.79 (0.11) <sup>ac</sup>	0.04 (0.06)	0.19 (0.40)	0.31 (0.22)
C	16.0	11 (07) <sup>c</sup>	1.67 (0.15) <sup>a</sup>	-0.17 (0.06)**	0.26 (0.39)	-0.57 (0.22)*
D	13.3	11 (08) <sup>c</sup>	1.41 (0.15) <sup>b</sup>	-0.15 (0.06)*	0.52 (0.40)	-0.39 (0.22)
E	95.3	36 (16) <sup>a</sup>	1.73 (0.28) <sup>ac</sup>	0.28 (0.06)**	-0.85 (0.39)*	0.66 (0.21)**
F	21.8	23 (13) <sup>d</sup>	1.60 (0.05) <sup>ab</sup>	-0.12 (0.06)*	0.31 (0.39)	-0.31 (0.22)
O	-	36 (06)	1.97 (0.05) <sup>c</sup>			

**Table 2**

ANOVA of the mean fractal dimensions (MeanFRAC), effective number of layers (ENL) and stand structural complexity index (SSCI). Note: Df: degree of freedom, Sq: square. Statistical significances are indicated:  $p$ -value < 0.001 ‘\*\*\*’, < 0.01 ‘\*\*’, < 0.1 ‘.’. Non-linear richness is a proxy for interactions among species, which is independent from the species identity effect.

	Df	Sum Sq	Mean Sq	F-value	p-value
<i>MeanFRAC</i>					
Linear richness	1	0.11411	0.114107	3.6647	0.06355
Species identity	5	1.54804	0.309608	9.9433	4.908e-06***
Non-linear richness	2	0.07678	0.038392	1.2330	0.30343
Plot size	3	0.25319	0.084397	2.7105	0.05937
<i>ENL</i>					
Linear richness	1	3.539	3.5390	1.9831	0.1676
Species identity	5	12.804	2.5609	1.4349	0.2354
Non-linear richness	2	0.467	0.2336	0.1309	0.8777
Plot size	3	3.622	1.2073	0.6765	0.5721
<i>SSCI</i>					
Linear richness	1	0.2578	0.25782	0.5619	0.45838
Species identity	5	11.8835	2.37670	5.1795	0.00111**
Non-linear richness	2	2.9751	1.48757	3.2418	0.05075
Plot size	3	1.2795	0.42649	0.9294	0.43646

size of the oil palms (mean height and mean crown area), while MeanFRAC was mainly associated with the size of the trees (mean height and basal area). Linear correlation between variables confirms this finding. ENL was negatively correlated with mean tree size (height and diameter), tree diameter variability, and tree density, but positively correlated with mean oil palm size (crown area and height) (Fig. A.4). MeanFRAC, in contrast, was positively correlated with tree size (height and diameter) mean values and variability and tree density, but negatively correlated with oil palm crown area (Fig. A.5).

#### 3.3. Structural complexity and tree diversity

SSCI increased non-linearly with tree diversity (Fig. 3). A similar pattern was found for MeanFRAC, but no significant relationship was found for ENL (Fig. 3). SSCI in plots containing two particular tree species (*A. pauciflorum* + *P. canescens* and *P. speciosa* + *A. pauciflorum*) was higher than SSCI in plots where only one tree species was planted (Fig. A.6).

Explained variability in SSCI was dominated by species identity, whereas the effect of non-linear richness was smaller (Table 2). Most coefficient estimates associated with non-linear richness terms (NLR = 1, 2, 3, and 6) were not statistically significant for all response variables (ENL, MeanFRAC and SSCI), with one notable exception. The coefficient associated with non-linear richness in plots where three species were planted (NLR = 3) was positive for SSCI (estimate =  $0.48 \pm 0.22$ ,  $T$ -value = 2.14,  $p$ -value = 0.048). At this

intermediate level of diversity, SSCI positively deviated from the linear expectation, and this deviation could not be attributed to species identity.

### 3.4. Unequal contribution of species

Tree species contributed unequally to structural complexity (Table 1). *D. zibethinus* had a significant below-average contribution to SSCI, while *P. canescens* had a significant above-average contribution. More concretely, an agroforestry plot with *P. canescens* had a SSCI gain of  $0.66 \pm 0.21$  compared with a plot with 'average' species, and an agroforestry plot that contained *D. zibethinus* had a SSCI loss of  $0.57 \pm 0.22$ .

A similar but stronger pattern was found for the contribution of tree species to MeanFRAC. *P. canescens* had the highest contribution to MeanFRAC, followed by *P. speciosa*. Below-average contributions to MeanFRAC were found for *D. zibethinus*, followed by *D. polyphylla* and *S. leprosula*. A contrasting pattern was found for the contribution of tree species to ENL, with *P. canescens* having a below-average contribution.

### 3.5. Effect of plot size

Plot size did not explain significant amounts of variation in SSCI and ENL, but significantly explained variation in MeanFRAC (Table 2). Coefficient estimates associated with larger plots ( $40 \text{ m} \times 40 \text{ m}$ ) were significantly positive (estimate  $\pm$  standard error:  $0.10761 \pm 0.04608$ ,  $T$ -value: 2.335,  $p$ -value: 0.0241) for MeanFRAC. Hence, larger agroforestry plots exhibited higher MeanFRAC, compared with the smallest plot size ( $5 \text{ m} \times 5 \text{ m}$ ).

### 3.6. Space-filling characteristics of species

At the time of the laser scanning, *D. polyphylla* was still mainly found in its juvenile form, exhibiting a relatively simple geometry (Seidel et al., 2019). It had a significantly lower box dimension than *A. pauciflorum* ( $p$ -value  $< 0.001$ ), *P. canescens* ( $p$ -value = 0.007), and *D. zibethinus* ( $p$ -value = 0.04) (Table 1). In contrast, oil palm had fully developed crowns that occupied space almost evenly in all directions (Fig. 1). It had a significantly higher box dimension than *P. speciosa* ( $p$ -value  $< 0.001$ ), *S. leprosula* ( $p$ -value  $< 0.001$ ), *D. polyphylla* ( $p$ -value  $< 0.001$ ), *D. zibethinus* ( $p$ -value = 0.01), and *P. canescens* ( $p$ -value = 0.06).

## 4. Discussion

### 4.1. Restoration of structural complexity

Our results suggest that tree planting increases rapidly structural complexity in oil palm: 1/3 increase in SSCI after three years. Extrapolating this rate over time, we estimate that it would take 12 years to recover the structural complexity of tropical (degraded) primary forests. The recovery of forest structure by mixed-species tree planting and natural regeneration is, however, non linear (Grau et al., 2003; Martin et al., 2013; Shoo et al., 2015) and depends on numerous local, landscape and regional factors (Chazdon and Guariguata, 2016).

The structural complexity of oil palm agroforestry plots was lower than forests because they had lower ENL values, indicating lower maximum heights and an uneven occupation of vertical layers. Unlike in forests or other agroforestry systems, where a vertical stratification is created by various life forms (e.g. vines, epiphytes, trees, shrubs) (Vieira et al., 2009; Kanowski et al., 2003; Foster et al., 2011; Ehbrecht et al., 2016), here it was largely driven by oil palms (Fig. A.3). The tallest tree species, *P. canescens*, reached the vertical layers already occupied by the oil palm canopy after three years, thereby contributed below-average to ENL (Table 1). When well-performing tree species overgrow the oil palm canopy, they might contribute positively to vertical stratification in the future but will compete more directly with the oil palms, potentially leading to economic losses (Teuscher et al., 2016; Gérard et al., 2017).

Due to the large size and high space-filling characteristics of mature oil palms (relative to the planted trees, see Table 1), oil palm thinning might be necessary to accelerate restoration of structural complexity in agroforestry systems. Here, oil palm thinning did not affect SSCI (compared with the non-thinned plots, see Fig. A.2). At the establishment of our experiment, oil palm thinning increased gap fraction in the canopy (Gérard et al., 2017), probably reducing MeanFRAC (Fig. A.5). At the same time, oil palm thinning positively affected tree growth, possibly increasing MeanFRAC (Fig. A.5). At the time of our study, the net effect of thinning on structural complexity was neutral, but is expected to become positive as trees continue to grow and contribute positively to structural complexity.

### 4.2. Effect of species diversity and identity

Tree diversity was associated with increasing structural complexity in the oil palm agroforestry system (Fig. 3A), which coincides with

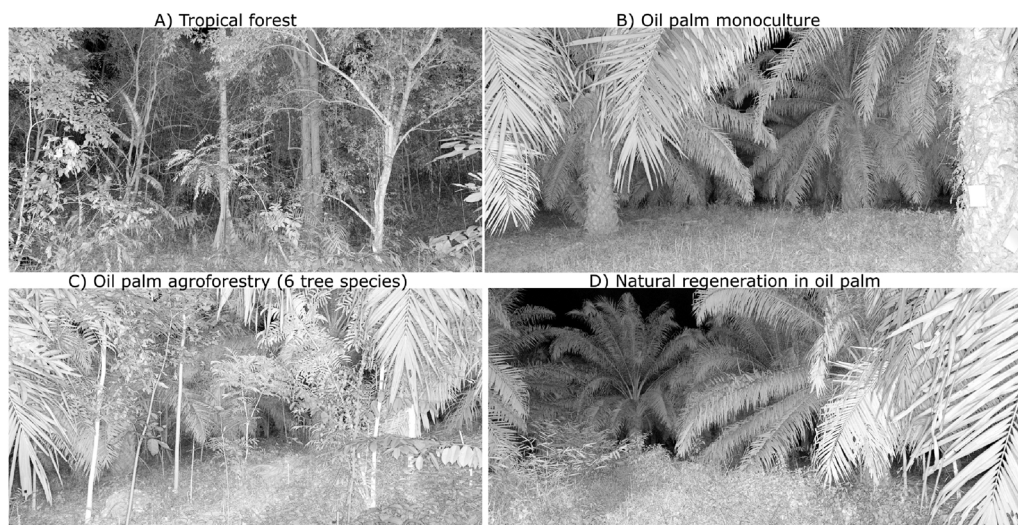
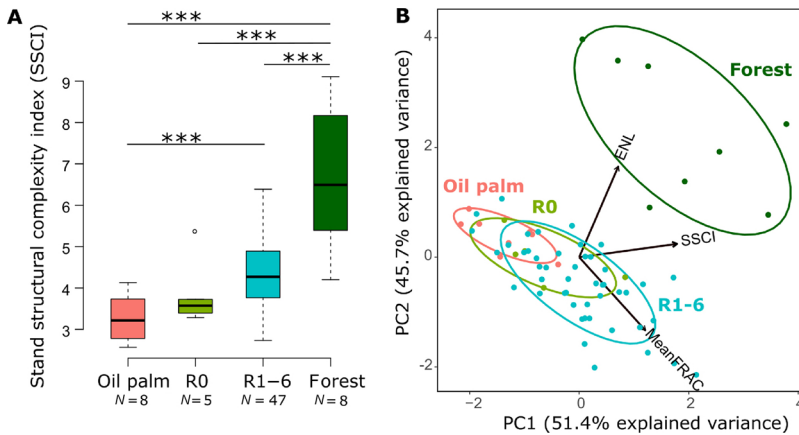


Fig. 1. Terrestrial laser scans. Views of the 3D point clouds obtained from terrestrial laser scanning in (A) forest, (B) oil palm monoculture, (C) agroforestry plot (6 planted tree species,  $40 \text{ m} \times 40 \text{ m}$ ) and (D) natural regenerating plot (no trees planted,  $40 \text{ m} \times 40 \text{ m}$ ).



**Fig. 2.** Restoration of structural complexity. (A) Stand structural complexity index (SSCI) of oil palm monoculture, experimental plots with natural regeneration (0 planted trees, ‘R0’), experimental plots with planted trees (species richness between 1 and 6, ‘R1–6’) and forest. Here species richness accounts for the mortality of the planted trees. The number of plots for each land-use type (N) is indicated. Statistical significances ( $p$ -value < 0.001 ‘\*\*\*\*’) are based on a one-way ANOVA model followed by a single-step Tukey test after correction for heteroscedasticity (using the ‘sandwich’ package). (B) Output of principal component analysis of the different components of structural complexity: mean fractal dimensions (MeanFRAC), effective number of layers (ENL) and SSCI. All variables were scaled to unit variance and centered around zero. The proportion of variance explained by the two principal components (PC1 and PC2) are indicated in the axes.

results from temperate forests (Jucker et al., 2015; Pretzsch, 2016; Ehbrecht et al., 2017). We found that the SSCI–diversity relationship was mainly driven by species identity effects, rather than interactions among co-occurring species. This finding is in line with most previous studies investigating growth–diversity relationships in early phases of tree diversity experiments (Tobner et al., 2016; Niklaus et al., 2017; Grossman, 2018) and seems to be a general finding (Ammer, 2019).

In our experimental design, each tree species was planted in equal proportions at each level of diversity (Teuscher et al., 2016) and hence was given the same chance to dominate the available space. Three years after planting, tree species varied in their establishment success, size, and space-filling characteristics, which seem to be tightly associated with their unequal contribution to structural complexity (Table 1). Species with higher survival rates, height, and box dimensions generally made above-average contributions to MeanFRAC and SSCI. This pattern is not surprising, because these measures are (by design) dependent on tree density (Fig. A.5 and Ehbrecht et al., 2017). At this early stage of the experiment, species’ survival rates and size were more strongly associated with their unequal contribution to SSCI, whereas the link between box dimension and SSCI was less pronounced. Dominance and competitive pressure of well-performing species hindering the establishment and growth of other species play a major role in young tree communities (Potvin and Dutilleul, 2009; Tobner et al., 2016). This pattern will likely change over time, as trees develop more complex architecture (Seidel, 2017), asymmetric crown shape (Seidel et al., 2011) and larger crowns (Jucker et al., 2015; Williams et al., 2017) when growing.

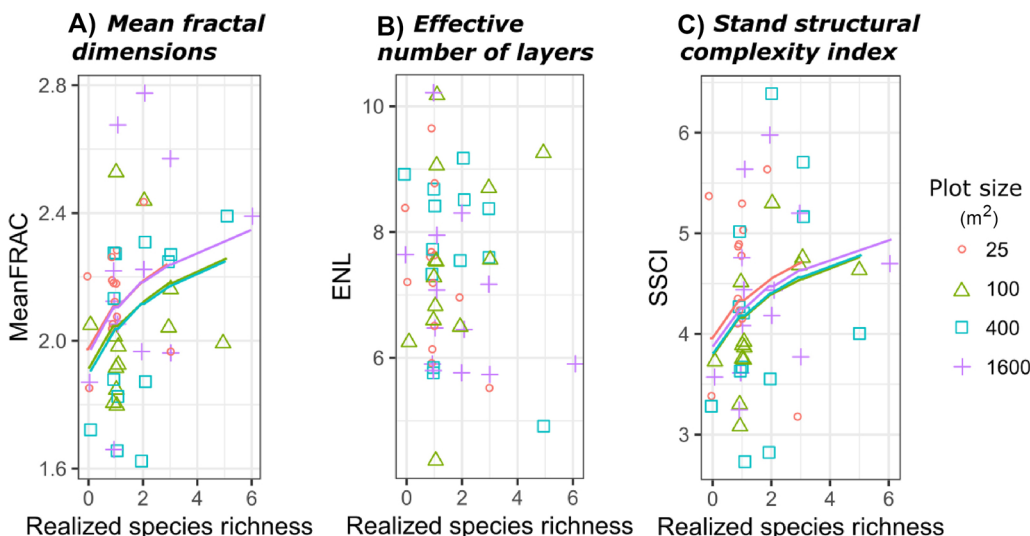
Although complementarity among selected species cannot be

directly inferred from our statistical framework, several observations support the idea that it plays an important role in the structural complexity–diversity relationship. Firstly, SSCI was highest when two of the well-performing species (i.e. *A. pauciflorum* + *P. canescens* and *P. speciosa* + *A. pauciflorum*) were combined. This is in agreement with recent findings from a subtropical tree diversity experiment, where functional diversity explained positive species diversity effects at low but not high diversity level (Huang et al., 2018). Secondly, a positive correlation between MeanFRAC and variation in tree size (Fig. A.5) suggests that differentiation in tree species’ sizes contributed to increasing structural complexity. Further efforts are needed to evaluate the importance of complementarity over time (Ewel and Mazzarino, 2008; Sapjanskas et al., 2014) and space (Morin et al., 2011; Williams et al., 2017) in mixed-species tropical (agro-)forests.

Planting density in our study site (2 m between trees) is comparable to other (sub)tropical tree diversity experiments (e.g. 2 m in BEF-China (Huang et al., 2018) and 3 m in Sardinilla experiment (Potvin and Dutilleul, 2009)) and therefore interactions among co-occurring species were expected to take longer to occur, e.g. > 5 years in Sapjanskas et al. (2014) and Huang et al. (2018). Despite the low planting density, we found that interactions among species enhanced SSCI three years after planting. Our results hence provide evidence of positive interactions among species leading to higher structural complexity in mixed-species agroforestry systems.

4.3. Effect of plot size

Our results indicate that MeanFRAC increased with plot size. Unlike



**Fig. 3.** Relationship between tree diversity and different components of structural complexity. The x-axis indicates the number of tree species accounting for tree mortality at the time of the study (realized species richness). Each point represents one agroforestry plot and the color indicates the plot size. To better visualize the relationship, a linear mixed-effect model has been fitted to the log-transformed realized species richness with plot size as random effect. Statistical significant models ( $F$ -test in ANOVA,  $p$ -value < 0.05) are shown as lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

other measures of vegetation structural complexity (Tews et al., 2004; Stein and Kreft, 2015), MeanFRAC by design does not co-vary with plot size. Hence, our results provide evidence of denser and more complex vegetation structure when trees are planted in larger areas, at least at the scale of the study (i.e. agroforestry plots and their immediate surroundings). The effect of tree planting on small-scale attributes of stand structure were not included in our analysis, such as leaf litter (Apijanskas et al., 2013), woody debris and understorey vegetation (Both et al., 2011; Bertacchi et al., 2016), which are important components of structural complexity (Kanowski et al., 2003; McElhinny et al., 2005; Luskin and Potts, 2011). Eventually, the area and scale at which structural complexity matters for biodiversity will likely depend on the species group (e.g. birds, insects) (Tews et al., 2004; Stein and Kreft, 2015; Schall et al., 2018), and therefore relying on scale-independent indices of structural complexity is relevant for biodiversity conservation.

## 5. Conclusions and outlook

Three years after tree planting, structural complexity in oil palm was significantly enhanced. The effect of the planted trees was mainly associated with a more complex and dense occupation of 3D space, whereas vertical stratification was mainly driven by oil palms. While the number of thinned oil palms increased with plot size by design, larger plots still had denser and more complex stand structure.

Structural complexity increased with tree species diversity in the agroforestry plots. This relationship was mainly due to well-performing tree species (in terms of their establishment success, size, and space-filling characteristics), which contributed to increasing structural complexity. Moreover, we detected significant interactions between species – independent from the species' identity effects – that are expected to become stronger as the trees continue to grow.

Our results suggest that planting well-performing species rapidly enhances structural complexity and directly associated ecosystem functions such as micro-climate stabilization (Ehbrecht et al., 2017). Effective ecological restoration in the tropics should, however, consider ecosystem multi-functionality over the long term (Lamb et al., 2005), which may be enhanced by a higher diversity of species mixtures (see e.g. Ramos et al., 2018; Azhar et al., 2014; Götz et al., 2004). Furthermore, oil palm farmers may be reluctant to increase structural complexity in their plantations as it can reduce oil palm yield (Teuscher et al., 2015; Gérard et al., 2017). Further research is needed to evaluate the ecological and socio-economic impacts of multi-species tree planting to provide recommendations for sustainable oil palm landscapes (Azhar et al., 2017). It may, for example, be that structural more complex oil palm plantations mixed with native tree species provide more ecosystem services than oil palm monocultures which offers options for compensating payments.

## Data accessibility

All data and R code files needed to reproduce the analyses and results are available at <https://doi.org/10.17632/ytjch4p7x3.1> (Zemp Delphine Clara et al., 2019).

## Acknowledgments

We thank Peter Puetz for his support on statistical analyses, Watit Khokthong, Juliandi, Eduard J. Sahaan, Toni Rohaditomo and Yohanes Bayu for their help in the field. We are grateful for the logistical support by the EForTS staff and coordination, as well as for research permit for D.C.Z by the Indonesia Ministry of Research and Technology (337/SIP/FRP/E5/Dit.KI/IX/2016). This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – project number 192626868 – SFB 990 in the framework of the collaborative German – Indonesian research project CRC990.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.agee.2019.06.003>.

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