Combining planting trees and natural regeneration promotes long-term structural complexity in oil palm landscapes

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ABSTRACT

Vegetation structural complexity has been identified as a vital factor for forest ecosystem function, stability, and resilience. However, agricultural land with much reduced structural complexity has largely replaced natural forests in the tropics. Therefore, restoring structural complexity in large-scale plantation monocultures by introducing agroforestry systems may counteract the loss of biodiversity and ecosystem functions. However, we still have limited knowledge of how the structural complexity of agroforests develops under different restoration treatments. We established a large-scale biodiversity enrichment experiment in a conventional monoculture oil palm plantation in Sumatra, Indonesia. In this experiment, agroforests were implemented by planting clusters of native trees ("tree islands") within the oil palm plantation, systematically varying initially planted tree richness ranging from 0–6 (0 corresponding to natural regeneration only) and plot area (25–1600 m^2). We tested the effect of the experimental treatments on nine years of the development of local structural complexity using a stand structural complexity index (SSCI) derived from terrestrial laser scanning. We found that tree planting and natural regeneration treatments promoted structural complexity by creating denser and more complex vegetation structures. Plots with a tree planting treatment tended to show greater structural complexity than plots with natural regeneration only. However, during the study period, oil palms still dominated heights, and the temporal change in structural complexity among plots with or without a tree planting treatment did not differ. As for plot area, our results indicate that structural complexity looking from the center of plots did not necessarily depend on the area during the study period, and even small tree islands can increase local structural complexity in a monoculture oil palm plantation. Initially planted tree richness did not significantly affect the development of structural complexity. Nine years after establishment, not planted trees but regenerated woody plants strongly positively affected vegetation density and structural complexity. Our findings highlight that sustaining vegetation density below oil palm canopies is a key strategy to increase the structural complexity of oil palm landscapes.

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1. Introduction

The expansion of agricultural lands is a main driver of deforestation in the tropics (Pendrill et al., 2022). In Southeast Asia, especially in Indonesia and Malaysia, agriculture-related deforestation is primarily ascribed to the expansion of oil palm lands (*Elaeis guineensis* Jacq.) (Pendrill et al., 2022). In 2019, the area of oil palm plantations in Southeast Asia was estimated at 19 million hectares, equivalent to 89 % of the total global area (Descals et al., 2021). The transformation of structurally complex tropical forests to structurally simple monoculture oil palm plantations (Zemp et al., 2019) has dramatically decreased biodiversity and ecosystem functions (Barnes et al., 2017; Clough et al., 2016; Grass et al., 2020; Rembold et al., 2017; Zemp et al., 2023) at the expense of economic growth and improved livelihoods of smallholder farmers (Grass et al., 2020). Protecting primary and selectively logged forests and increasing the area of secondary forests remains the top priority to prevent the further loss of high tropical biodiversity and ecosystem functions (Gibson et al., 2011; Koh and Wilcove, 2008; Meijaard et al., 2020). At the same time, we also urgently need restoration strategies that strike a balance between ecological and socio-economic benefits in oil palm landscapes since vast areas have already been converted for palm oil, and the demand is expected to increase (Iddris et al., 2023; Luke et al., 2020; Meijaard et al., 2020).

One promising restoration strategy is to increase the vegetation structural complexity of oil palm landscapes. This is because structurally complex ecosystems may optimize the distribution of energy and matter in three-dimensional (3D) space within the ecosystem, thereby improving ecosystem function and stability and increasing biodiversity through niche partitioning (LaRue et al., 2023; Seidel and Ammer, 2023). In forests, structural complexity is often positively associated with important ecosystem functions (e.g., above-ground productivity, microclimate regulation, habitat provisioning) (Coverdale and Davies, 2023), resistance (e.g., Mathes et al., 2024), plant diversity (Coverdale and Davies, 2023), and animal diversity with varying responses among taxonomic groups (e.g., Davies and Asner, 2014; Knuff et al., 2020; Wildermuth et al., 2023). Moreover, recent empirical results support the greater temporal stability of productivity in structurally complex forests with diverse tree species (Dolezal et al., 2020; Wales et al., 2020).

To increase structural complexity in oil palm landscapes, one can mix different ages of oil palms (Luskin and Potts, 2011) or diversify co-existing plant species (i.e., the implementation of agroforestry). Here, we define agroforestry as mixed cropping systems with at least one crop and one perennial woody plant species (Malézieux et al., 2009). Oil palms are considered both a crop and a woody plant. Oil palm agroforestry may incorporate herbaceous crops (e.g., banana, pineapple) (Ahirwal et al., 2022; Yahya et al., 2017), green manure crops (de Carvalho et al., 2014; Gomes et al., 2021), or fruit and timber trees (Gomes et al., 2021; Teuscher et al., 2016). Additionally, one may encourage understory vegetation in an oil palm plantation (Hood et al., 2020) or the natural regeneration of woody plants by thinning oil palms (Teuscher et al., 2016). To minimize oil palm yield loss, agroforestry can be partly applied within a monoculture oil palm plantation by planting clusters of native trees ("tree islands") (Teuscher et al., 2016). Tree islands can be implemented in different planting richness and sizes (Holl et al., 2020; Teuscher et al., 2016). The tree island approach has been shown to enhance structural complexity (Zemp et al., 2019), biodiversity, and ecosystem functioning (Zemp et al., 2023) locally and the heterogeneity of structural complexity and biodiversity at the landscape scale (Montoya-Sánchez et al., 2023) while maintaining oil palm yield at the plantation scale (Zemp et al., 2023). However, we still have limited knowledge of the optimal tree island design (i.e., planting richness and island size) needed to increase structural complexity in oil palm plantations (e.g., Zemp et al., 2019).

The structural complexity of forests can be efficiently quantified using indices derived from single terrestrial laser scans (e.g., Stand Structural Complexity Index (SSCI), Ehbrecht et al., 2017; Understory

Complexity Index (UCI), Willim et al., 2019). These indices quantify structural complexity in 3D space without targeting a single object. Thus, the indices are comparable across land use systems. However, studies quantifying the structural complexity of agroforestry systems are still rare (e.g., Seidel et al., 2021b; Steinfeld et al., 2024; Zemp et al., 2019). Besides, we are unaware of any study that quantitatively analyzed the development of structural complexity of agroforests over time. Structural complexity emerges from long-term woody plant-plant interactions (e.g., Perles-Garcia et al., 2021). Thus, quantifying the structural complexity of agroforests over time will help predict the long-term trajectories of vegetation structure and evaluate strategies for restoring structural complexity.

In this study, we utilized data from EFForTS-BEE, a large-scale, long-term biodiversity enrichment experiment established in a conventional monoculture oil palm plantation in Sumatra, Indonesia (Teuscher et al., 2016). In EFForTS-BEE, we implemented 52 tree islands, systematically varying in initially planted tree richness level (0–6, 0 corresponding to no planting or natural regeneration only) and plot area (25–1600 m^2). Here, we tested the effect of experimental treatments (tree richness and plot area) on nine years of the development of local structural complexity. We used the SSCI developed by Ehbrecht et al. (2017) as a holistic measure of 3D structural complexity (Ehbrecht et al., 2017; Reich et al., 2022), which was derived from a single terrestrial laser scan at the center of plots. Furthermore, alternative structural characteristics based on the terrestrial laser scans (e.g., canopy openness) and manual inventory data (e.g., basal area of planted trees) were incorporated to aid the interpretation of the SSCI.

We addressed two major questions. First, what is the experimental effect of tree planting on the development of structural complexity over time compared to no planting? We hypothesize that tree planting, compared to no planting, (H1) promotes the development of higher structural complexity, farther away from the conventional oil palm plantation and towards reference forests, and (H2) changes structural complexity more rapidly. This is because planted trees would add more structure through growth (Seidel et al., 2019) and also promote natural regeneration by attracting seed dispersers, such as birds, and shading competitive grasses and ferns (Holl et al., 2020, 2017; Zahawi and Augspurger, 2006). Second, how do the experimental effects of initially planted tree richness (planted tree richness (1–6) at the start of the experiment) and plot area on structural complexity vary over time? We hypothesize that (H3) initially planted tree richness positively affects structural complexity and that (H4) the effect strengthens over time due to the complementary growth of tree crowns (Perles-Garcia et al., 2021). Lastly, we hypothesize that (H5) plot area positively affects structural complexity and that (H6) the effect strengthens over time because a previous study from the experiment showed that larger plots harbored a higher taxonomic diversity and abundance of natural recruitments (Paterno et al., 2023).

2. Methods

2.1. Study site and experimental design

Our study was conducted in EFForTS-BEE, a biodiversity enrichment experiment located in Jambi province, Sumatra, Indonesia (Teuscher et al., 2016) (Fig. 1). The experiment is part of the EFForTS project (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems) (Drescher et al., 2016) and the largest global network of tree diversity experiments, TreeDivNet (Tree Diversity Network, https://treedivnet.ugent.be/). The climate of Jambi province is tropical humid, characterized by two peak rainy seasons in March and December and one dry period in July–August (Drescher et al., 2016). The mean annual temperature was 26.7 ˚C, and the mean annual precipitation was 2235 mm from 1991 to 2011 (Drescher et al., 2016). Loam Acrisol soils are prevalent in the region (Allen et al., 2015).

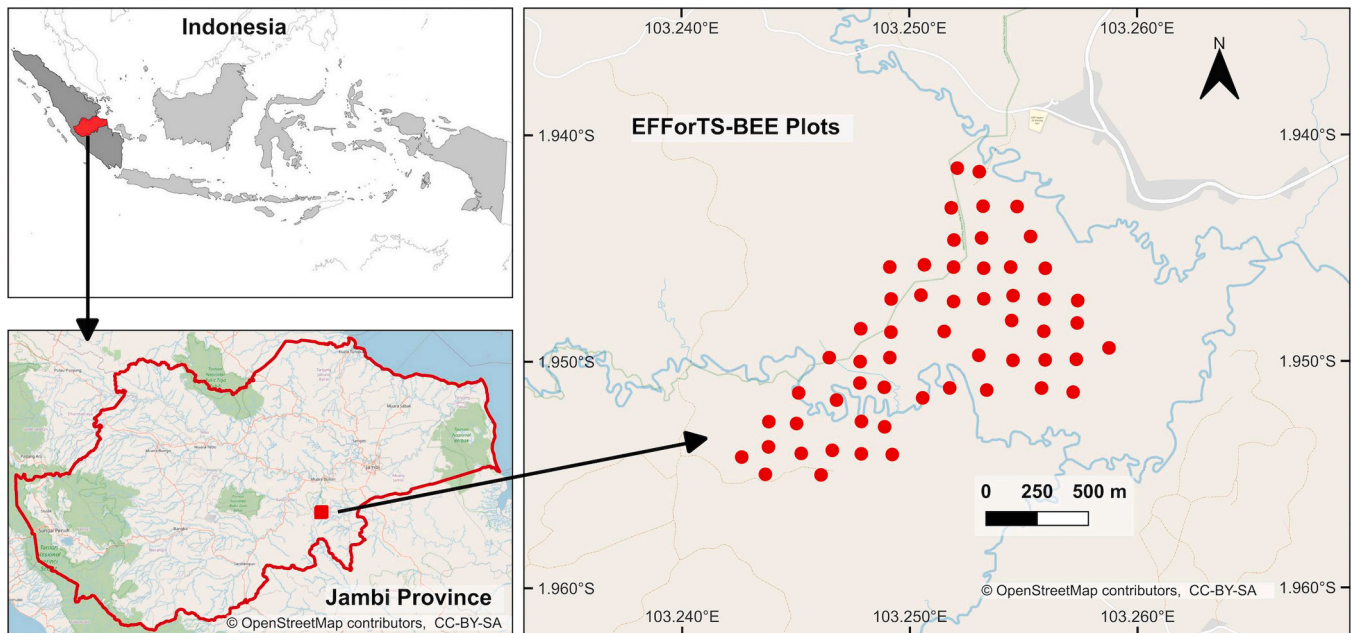The experiment was established in a conventional oil palm

Fig. 1. Study area map. The top left image represents Indonesia (gray), Sumatra (dark gray), and Jambi Province (red). The bottom left image represents Jambi Province (within the red frame) and the location of the experiment (EFForTS-BEE) (red rectangle). The red points in the right image show the distribution of the experimental plots. Please refer to Figure S1 for the experimental design.

plantation with a size of 140 ha (Teuscher et al., 2016; Zemp et al., 2023). At the establishment of the experiment, the plantation was young, with approximately six- to twelve-year-old oil palms planted between 2001 and 2006 in a 9 m × 9 m triangular grid (Teuscher et al., 2016). In December 2013, native trees were planted, systematically varying tree richness (0, 1, 2, 3, and 6 species) and plot (i.e., tree island) area (5 m × 5 m, 10 m × 10 m, 20 m × 20 m, and 40 m × 40 m), following a random partition design (Teuscher et al., 2016) (Figure S1). Six species were selected based on local availability and usage: fruits (*Archidendron jiringa* (Jack) I.C.Nielsen, Fabaceae; *Durio zibethinus* L., Malvaceae; *Parkia speciosa* Hassk., Fabaceae), timber (*Peronema canescens* Jack, Lamiaceae; *Rubroshorea leprosula* (Miq.) P.S.Ashton & J. Heck., Dipterocarpaceae (formerly classified as *Shorea leprosula* Miq.)) and latex (*Dyera polyphylla* (Miq.) Steenis, Apocynaceae).

Each tree species was represented once at each plot area so that 48 experimental plots were established, plus four plots with a species richness level of 0 (i.e., no planting). Additionally, there are four control plots (i.e., the conventional oil palm plantation) with a size of 100 m². Different numbers of trees were planted with the same density according to the plot areas ($N = 6$ (25 m²), 25 (100 m²), 100 (400 m²), 400 (1600 m²)), resulting in 6354 trees in total (Teuscher et al., 2016). The distance between planted trees was 2 m. On mixed-species plots, each species was represented equally in number, and the intraspecific neighborhood was minimized. Before planting, approximately 40 % of oil palms were removed to improve light conditions on the plots, except for the 25 m² plots, which are located between pre-existing oil palms, and the control plots (Teuscher et al., 2016). Conventional practices, including weeding and the use of herbicide, pesticide, and fertilizer, were maintained on the control plots. All other plots were manually weeded for the first two years to prevent weeds from competing with trees, allowing natural succession afterward. More detailed information is found in Teuscher et al. (2016).

We used forest ("degraded primary forest") plots in the study region (50 m × 50 m, eight plots located in Harapan Rainforest) as remnant reference forests (see Drescher et al., 2016 for details). The plots show signs of past selective logging, and three plots experienced damage due to fire during a drought event about one year before the terrestrial laser scanning (TLS) campaign (Drescher et al., 2016; Zemp et al., 2019).

2.2. Terrestrial laser scanning

TLS was conducted on all the experimental plots with a FARO Focus M70 (Faro Technologies Inc., Lake Mary, USA) in 2016 (September–October), 2020 (January), and 2022–2023 (December–January). TLS was not conducted on the control plots in 2016, and two tree-planting plots were not scanned in 2020. For the reference forest plots, TLS was conducted only in 2016 (November–December) with the same scanner. The laser scanner was placed on a tripod at the height of 130 cm and raised up to 20 cm in cases where understory vegetation was blocking the area required for operation. The field of view was set to 360° horizontally and 300° vertically with a step width of 0.035° (Zemp et al., 2019). The maximum scan distance is 70 m, which is, however, usually more limited by the vegetation (i.e., occlusion) (Ehbrecht et al., 2016). Consequently, neighboring plots did not affect scans, considering that the minimum distance between the plots was 85 m (Teuscher et al., 2016).

2.3. Structural indices based on terrestrial laser scanning

For all the experimental plots, we used a single scan taken at the center of the plots, considering the relatively small plot areas (5–40 m edge length) (Ehbrecht et al., 2016). This also ensured that the calculated indices mainly characterized the vegetation around the plot center. Each scan was filtered to remove noise by applying a standard algorithm with the default parameters in FARO SCENE (Faro Technologies Inc., Lake Mary, USA). Then, each scan was converted into the XYZ format using FARO SCENE and imported to Mathematica software (Wolfram Research, Champaign, USA) to compute the indices described below (Equivalent R code for the stand structural complexity index (SSCI) is publicly available at: https://github.com/ehbrechtetal/Stand-structural-complexity-index—SSCI.).

The SSCI was calculated following Ehbrecht et al. (2017). The SSCI integrates two different indices: the mean fractal dimension (MeanFrac) and the effective number of layers (ENL). The MeanFrac is the mean of the fractal dimension index of 1280 cross-sectional polygons derived from a single-scan point cloud (see Ehbrecht et al., 2017 for details). It quantifies structural complexity based on above-ground vegetation

density and distribution (e.g., branches, stems, leaves). Due to its scale invariance, a young stand with dense, short trees can yield equal or higher MeanFrac than a mature, vertically stratified stand with sparse trees. While this is mathematically correct, it would defy the purpose of such an index. For the computation of the ENL, a single scan point cloud was sliced into vertical layers of 1 m thickness. Then, the ENL was calculated as the inverse Simpson index from the proportion of the number of filled voxel grids (20 cm side-length) in each layer to the total number of filled voxel grids of all the layers (see Ehbrecht et al., 2016 for details). Therefore, the ENL quantifies the vertical stratification of vegetation components accounting for evenness and height of vegetation. This ENL is then used for scaling MeanFrac to create a holistic measure of stand structural complexity (i.e., SSCI). Numerous studies have applied the SSCI to understand the association of structural complexity with, for example, tree diversity (e.g., Ehbrecht et al., 2017; Juchheim et al., 2019; Perles-Garcia et al., 2021) and ecosystem functioning (e.g., Donfack et al., 2021; Ray et al., 2023; Steinfeld et al., 2024).

It is worth mentioning here that the concept of the SSCI rests on the use of all data points (laser hits) detected from the scanner's perspective (sampling approach). The approach is not sensitive to occlusion because it only utilizes the first hit in any direction of travel of a laser beam. Therefore, the index value would not change if a complete, occlusion-free point cloud were used for calculation. In fact, the complexity of the pattern of laser hits in the scanner's surroundings constitutes the MeanFrac. Please refer to Ehbrecht et al. (2021), (2017) for details and illustrations.

The SSCI, MeanFrac, and ENL do not consider vegetation below the scanner height (1.3 m). We, therefore, also calculated the understory complexity index (UCI) following Willim et al. (2019) and Seidel et al. (2021a). Briefly, the UCI is the fractal dimension of a polygon derived from the point cloud between 0.8 m and 1.8 m that was projected onto a horizontal plane. The index accounts for point clouds within 15 m of the scanner (see Willim et al., 2019 for details). As common ecological indicators, maximum canopy height and canopy openness were also estimated. Approximate maximum canopy height was calculated as the number of total vertical layers of 1 m thickness, derived from the computation process of the ENL. Percentage canopy openness was calculated with an aperture angle of 60° from the scanner's perspective, as described by Ehbrecht et al. (2021), following the ideas of Zheng et al. (2013). For the reference forest plots, all single scans ($N = 73$; 8–11 scans per plot) were averaged by plot.

2.4. Inventory-based measurements

Total vertical height from the ground and basal diameter at 10 cm above the ground (BD) of alive and standing dead planted trees were measured annually from 2015 to 2022 in January–April. For diameter measurements, only the largest stem was measured when an individual had multiple stems. In tree-planting and no-planting plots, all naturally regenerated woody plants with a height $\geq$ 1.3 m, including trees, shrubs, lianas, and bamboos, were recorded, and the sizes were measured with the same method as for planted trees in 2022 (June–October). In the case of bamboo (*Gigantochloa scortechinii* Gamble), which grows in clusters, the three culms with the largest, average, and smallest diameters were visually selected and measured. Then, the total number of culms was counted. We took the average of the sizes of measured stems to represent each culm.

For the final sampling year (2022), separately for planted trees and naturally regenerated woody plants, we calculated plot-level mean BD, mean height from the scanner (i.e., vertical height from the ground minus 1.3 m), basal area per hectare based on BD, and density per hectare. For the calculation, we considered all individuals with a vertical height >1.3 m. To describe the inequality of a distribution, we also calculated the standard deviation, the coefficient of variation, and the Gini coefficient of BD and height from the scanner. The *Gini* function

from the R package *DescTools* (Signorell, 2023) was used to compute the Gini coefficient. In the case of bamboo, the basal area of an individual was obtained by multiplying the average BD by the stem number. For the other indices using BDs, we estimated the BD of a bamboo individual as the diameter of a circle with an equal area to its basal area, assuming that a bamboo forms a hypothetical large stem as a bundle of many culms. For the indices using heights, the average height of the bamboo culms was used as the height for the individual.

For oil palms, the vertical height from the ground to the meristem (the base of the youngest frond) and the crown diameters were measured in 2016–2017 (December–May), 2019 (October), and 2022 (December) (Zemp et al., 2019). For the final sampling year, the mean meristem height from the scanner and the mean crown area at the plot level were computed. For the calculation, we also included two oil palms adjacent to each plot, except for the largest plots (1600 m²) because the SSCI depends on the vegetation visible from the scanner within the maximum scan distance, and visible oil palms outside the plots were also considered a part of the structural components. Two oil palms adjacent to each plot were located at different levels of distance from a plot (mean distances: 3.5 m and 12.2 m) (see Fig. 1 in Gérard et al., 2017). This ensured that oil palms within approximately 20 m from the scanner were considered in the above indices, irrespective of the plot area.

2.5. Statistical analyses

To test if the experimental treatments (control, no planting, and tree planting) and the reference forests differed in the SSCI after nine years of tree planting, we conducted a one-way Analysis of Variance (ANOVA), followed by a Tukey test using the function *glht* from the R package *multcomp* (Hothorn et al., 2008). For the Tukey test, we corrected unequal variance between the treatments and the reference forests using the *sandwich* function from the R package *sandwich* (Zeileis, 2006; Zeileis et al., 2020).

To test for the experimental effects of tree planting and its temporal effects on structural complexity, we used a linear mixed model (LMM) and a subsequent Wald Chi-square test. We used the SSCI as a response variable. For the predictors, we used the year as a categorical variable (2016, 2019, 2022). We also included treatment (tree planting vs no planting) and its interaction term with the year. We did not include control due to the absence of scans in 2016. Plot ID was included as a random term to account for repeated measurements. We fitted the LMM using the *glmmTMB* function from the R package *glmmTMB* (Brooks et al., 2017). Due to the sampling imbalance between tree planting ($N = 44$–48) and no planting ($N = 4$), we used the sum-to-zero contrasts for treatment. We used the *Anova* function from the R package *car* (Fox and Weisberg, 2019) to perform a Wald Chi-square test with the type III sum of squares. To visualize the LMM, we plotted predicted values conditioned on the fixed effects using the *ggemmeans* function from the R package *ggeffects* (Lüdecke, 2018). To fit the LMM, we used maximum likelihood estimation for the Wald Chi-square test and restricted maximum likelihood estimation for visualization and presenting the model summary (Zuur, 2009).

For the LMM, we conducted data exploration and graphical model assessments, according to Santon et al. (2023), using their supplementary R codes. In the data exploration, we found three extreme SSCI values (> 9 equivalent to structurally complex primary tropical forests (Ehbrecht et al., 2021)) from tree-planting plots (two scans in 2019 and one scan in 2022) using a dotplot (Cleveland, 1993) and checked the point cloud images from the corresponding scans using CloudCompare (ver. 2.13.alpha) (https://www.danielgm.net/cc/). We concluded that the scans were invalid due to ill-scanning conditions (the scanner directly under leaves of the understory vegetation, the scanner right next to a plant stem, and the presence of litter traps), and they were removed from all the analyses. In the model assessments, we found no concerning issues with respect to model fit and spatial autocorrelation using the model residuals.

To link different structural characteristics to the SSCI, we conducted a principal component analysis (PCA) using the SSCI and other TLS-based indices from the experimental plots (2016–2022) and the reference forest plots. First, we created a PCA biplot. Then, in the PCA space, we visualized the trajectory of each experimental treatment's mean scores from 2016 to 2022 (De Cáceres et al., 2019). Before the PCA, we scaled all the variables to zero mean and unit variance.

To test the significance of the effects of initially planted tree richness and plot area and their temporal dependency on structural complexity in tree-planting plots, we used a LMM and a subsequent Wald Chi-square test. We used the SSCI as a response variable. For the predictors, we used the year as a categorical variable and planted tree richness and plot area as continuous variables. We also included an interaction term between planted tree richness and year and an interaction term between plot area and year. Plot ID was again included as a random effect. To improve model fit, we log-transformed planted tree richness and plot area.

To explore which vegetation components (oil palms, planted trees, regenerated woody plants) in tree-planting plots are related to which structural characteristics nine years after tree planting, we conducted a PCA using TLS- and inventory-based structural indices. To visualize the result, we created a PCA biplot using the function *fviz_pca_biplot* from the R package *factoextra* (Kassambara and Mundt, 2020). To confirm the potential monotonic relationships observed in the PCA, we computed Spearman's rank correlation coefficient (Puth et al., 2015) among each pair of TLS- and inventory-based structural indices.

All data analyses, except for the computation of TLS-based indices, were conducted in R version 4.3.0 (R Core Team, 2023). We used a significance level of p-value < 0.05 for all the statistical tests.

3. Results

3.1. Effects of tree planting on the development of structural complexity

Tree planting promoted the recovery of structural complexity towards the values observed for the reference forests compared to the conventional oil palm plantation and no planting (i.e., natural regeneration only) (Figs. 2, 3, 4).

Nine years after planting (2022), SSCI values of tree-planting plots (4.91 ± 1.27 SD; t-value = 6.32, p-value < 0.001) and no-planting plots (4.20 ± 0.53 SD; t-value = 2.64, p-value = 0.050) were significantly higher than the conventional oil palm plantation (3.51 ± 0.29 SD) but lower than the reference forests (7.32 ± 0.68 SD) (Fig. 3 A). Tree-planting plots tended to show higher SSCI than no-planting plots, while SSCI values of tree-planting plots varied largely from 3.25 to 7.35. The difference in the SSCI between tree-planting and no-planting plots was not statistically significant (t-value = 2.45, p-value = 0.077).

The model that included treatment (tree planting vs no planting), year, and their interaction term showed that SSCI and its development did not significantly differ between the two treatments, although tree-planting plots tended to have higher SSCI values (treatment: Chi^2 = 1.067, degrees of freedom (df) = 1, p-value = 0.302; treatment × year: Chi^2 = 0.059, df = 2, p-value = 0.971) (Fig. 3B, Table S1). Tree-planting plots exhibited high variation in the SSCI across the years. Overall, SSCI significantly increased from 2016 to 2019 (Estimate = 0.894, Z-value = 2.432, p-value = 0.015). However, SSCI seemed to decrease slightly from 2019 to 2022, resulting in insignificant differences in the SSCI between 2016 and 2022 (Estimate = 0.491, Z-value = 1.337, p-value = 0.181) (Table S2).

According to the PCA of different structural characteristics based on TLS, different treatments (oil palm plantation, no planting, and tree planting) showed changes in similar directions, but overall, tree planting was more related to high SSCI, MeanFrac, and UCI than oil palm plantation and no planting in the vegetation structure space (Fig. 4). The first
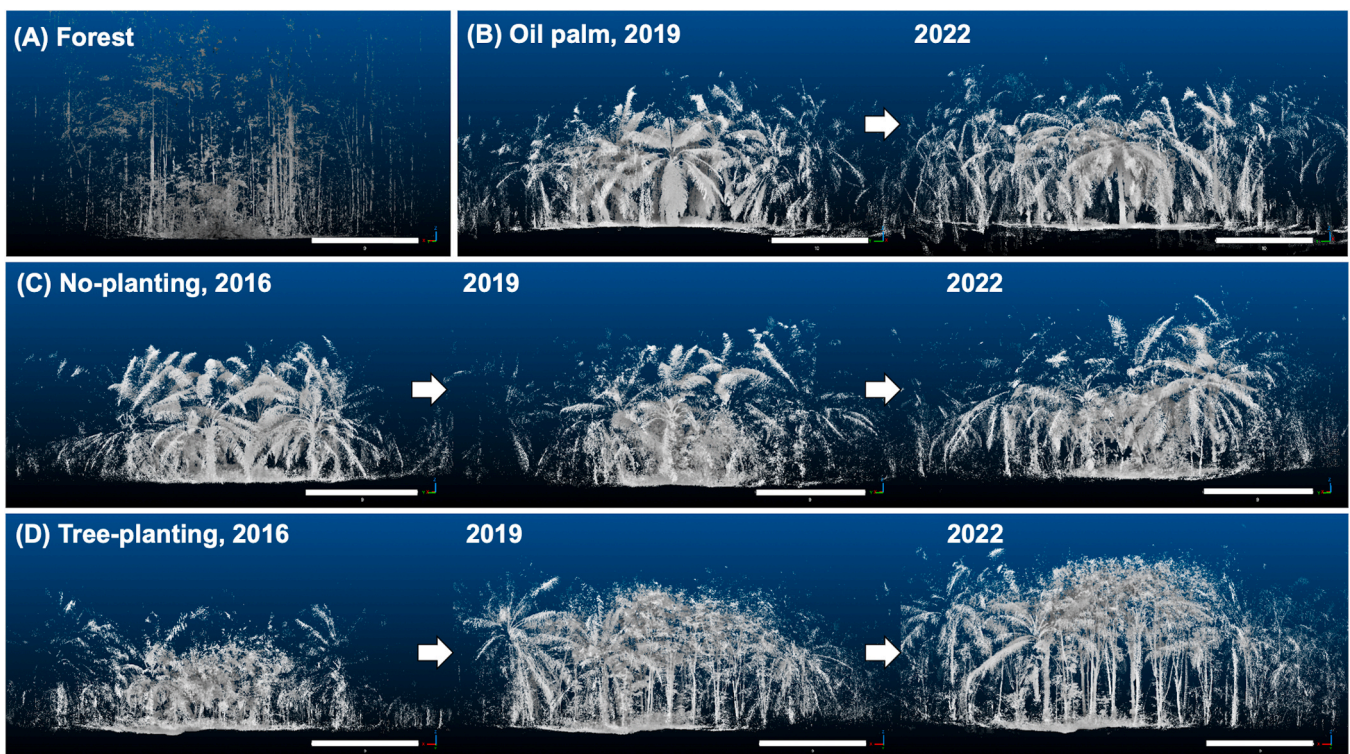

Fig. 2. 2D representations of exemplary 3D point cloud images from single scans from (A) a reference forest plot in 2016; (B) an oil palm plantation plot from 2019 to 2022; (C) a no-planting plot (1600 m^2) from 2016 to 2022; and (D) a tree-planting plot (1600 m^2) from 2016 to 2022. The white scale bar is 9 m for (A), (C), (D), and 10 m for (B).
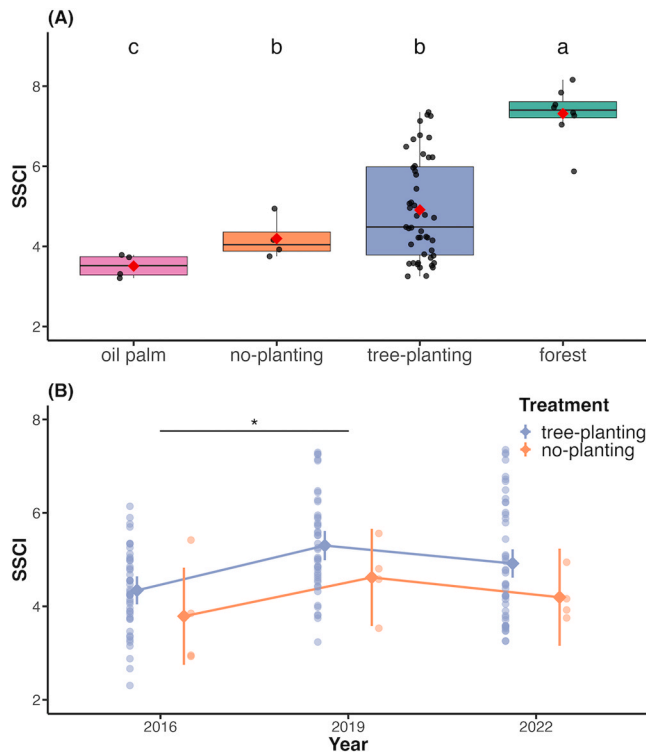
Fig. 3. (A) Box plot of SSCI nine years after tree planting (2022) across different treatments (oil palm plantation ($N = 4$), no planting (natural regeneration, $N = 4$), and tree planting ($N = 47$)) and forest (Harapan Rainforests, $N = 8$)). Different letters indicate significant differences among the means (red diamonds) (*p*-value < 0.05) according to a Tukey test following ANOVA. Black points represent values per plot. (B) Temporal trends in the relationships between SSCI and the experimental treatments (tree planting and no planting). Diamonds represent the predictions of a linear mixed effect model with 95 % confidence intervals. Points are observed plot values (tree-planting plots: $N = 48, 44, 47$ (2016–2022), no-planting plots: $N = 4$ (2016–2022)). Statistical significance (* *p*-value = 0.015) between 2016 and 2019 is based on Z-statistic.

two principal components captured variation across all variables well (76 %). The first component (PC1) represents closed, dense, and complex structures as it has strong positive correlations (factor loadings) with the SSCI (0.90), the MeanFrac (0.82), the UCI (0.81), and negative correlation with canopy openness (-0.53). On the other hand, the second axis (PC2) represents vertically stratified canopies as it is highly correlated with the ENL (0.97) and canopy height (0.92). Therefore, the reference forests showed higher structural complexity than the experimental plots. The trajectories in the PCA space indicated that tree-planting and no-planting plots, on average, similarly developed denser and vertically more stratified canopies (i.e., more structural complexity) between 2016 and 2019. In contrast, between 2019 and 2022, the trajectories in the PCA space indicated that vegetation, on average, became less dense but developed more vertically stratified canopies regardless of treatments, including oil palm plantation. There was a wider variation in the PC1 than the PC2, and many tree-planting plots reached similar levels of SSCI, MeanFrac, and UCI as the reference forests.

3.2. Effects of initially planted tree richness and plot area on the development of structural complexity

We did not find significant effects of initially planted tree richness and its interaction with year on SSCI (initially planted tree richness: Chi^2 = 0.824, df = 1, *p*-value = 0.364; initially planted tree richness × year: Chi^2 = 3.802, df = 2, *p*-value = 0.148) (Fig. 5A, Tables S3, S4). We also did not find significant effects of plot area and its interaction with year on the SSCI (plot area: Chi^2 = 0.000, df = 1, *p*-value = 0.982; plot area ×
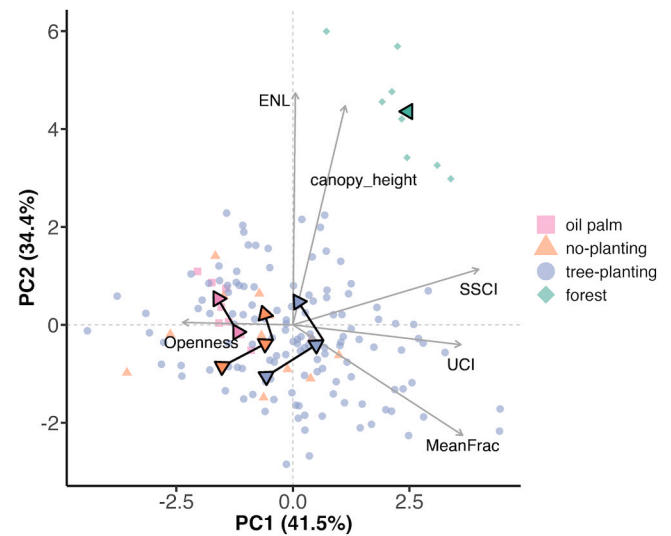

Fig. 4. Biplot of a PCA of different structural characteristics based on TLS: SSCI, ENL, MeanFrac, UCI, canopy height (canopy_height; m), canopy openness (Openness; %). The arrows with heads filled with a color indicate the trajectories of the mean scores of each treatment (oil palm plantation (pink), no planting (natural regeneration, orange), and tree planting (light blue)) in the PCA space from 2016 to 2022 (2016–>2019–>2022). Oil palm plantations lacked data in 2016. The green triangle is the mean score of reference forest plots in 2016 (Harapan Rainforests). Symbols represent values per plot in the PCA space ($N = 167$). All variables were scaled to zero mean and unit variance before the PCA.

year: Chi^2 = 1.222, df = 2, *p*-value = 0.543) (Fig. 5B, Tables S3, S4). These results remained qualitatively unchanged after accounting for the mortality of planted trees (i.e., realized planted tree richness) (Figure S2, Tables S5, S6). Although we found a weak indication of the interaction effect between realized planted tree richness and year (Chi^2 = 5.508, df = 2, *p*-value = 0.064), the effect did not increase over time (Tables S5, S6).

Nine years after tree planting, planted tree species showed varying performance (Table S7). *A. pauciflorum* and *P. canescens* showed low mortality rates (5.7–16 %), while *D. polyphylla*, *D. zibethinus*, and *R. leprosula* showed high mortality rates (> 90 %). *P. speciosa* showed a moderately high mortality rate (60 %). Not only planted trees but also oil palms became taller (Fig. 2D, Table S7). The emptied spaces due to the deaths of planted trees were filled up by naturally regenerated woody plants (Table S8). In tree-planting plots, on average, regenerated woody plants made up 38 % of the total basal area. According to the PCA of different structural characteristics based on TLS and manual inventory data from tree-planting plots, after nine years, different vegetation components (oil palms, planted trees, naturally regenerated woody plants) were related to different structural characteristics (Figure S3). The basal area of regenerated woody plants was strongly correlated with the SSCI ($\rho = 0.56$, *p*-value < 0.001) and the MeanFrac ($\rho = 0.58$, *p*-value < 0.001) (Figure S4). The mean meristem height of oil palms was moderately positively correlated with the ENL ($\rho = 0.45$, *p*-value = 0.0015) and canopy height ($\rho = 0.49$, *p*-value < 0.001) (Figure S5). Lastly, the basal area of planted trees showed the strongest negative correlation with canopy openness ($\rho = -0.50$, *p*-value < 0.001) among considered inventory indices (Figure S6).

4. Discussion

Our results show that tree planting and natural regeneration treatments promoted structural complexity by creating denser and more complex structures than the conventional oil palm plantation. Tree-planting plots tended to show greater structural complexity than no-
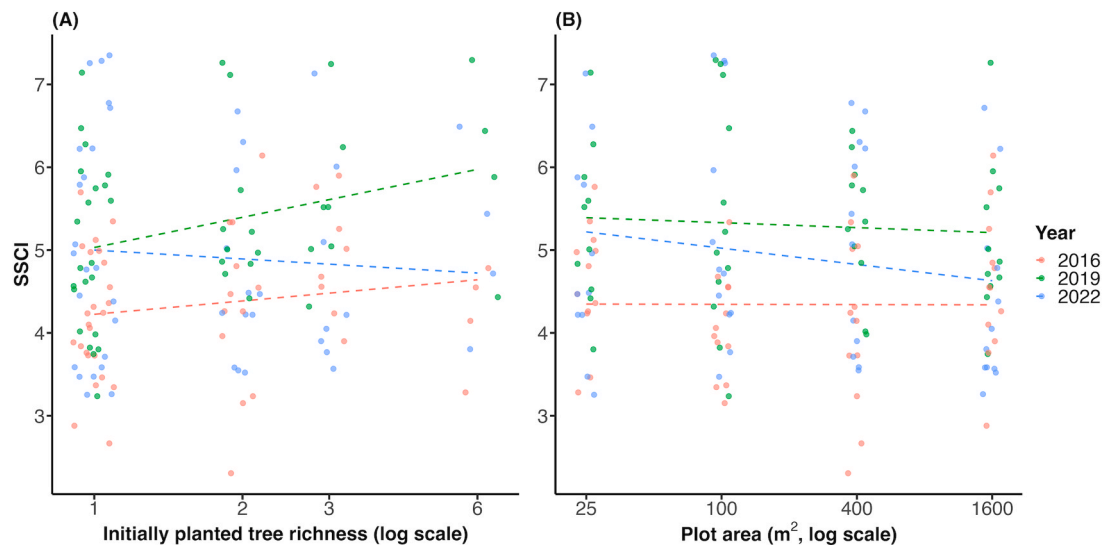
Fig. 5. Temporal changes in the relationships between SSCI and experimental treatments ((A): initially planted tree richness; (B): plot area) in tree-planting plots. The dotted lines indicate non-significant relationships (*p*-value > 0.05) (marginal effects at the mean) found in the linear mixed effect model. Initially planted tree richness and plot area were log-transformed in the model. Points are observed values per plot (*N* = 48, 44, 47 (2016–2022)).

planting plots (i.e., natural regeneration only). However, oil palms still dominated heights during the nine years of the study period, and the temporal changes of structural complexity between plots with or without a tree planting treatment were not significantly different. We also found that the initially planted tree richness and plot area did not significantly affect the development of structural complexity. Nine years after tree planting, the size of naturally regenerated woody plants was an important factor of structural complexity, while planted trees were not directly associated with structural complexity.

4.1. Effects of tree planting on the development of structural complexity

We found that nine years after establishment, tree-planting plots had, on average, 40 % higher SSCI than the conventional oil palm plantation and 67 % SSCI compared to the reference forests. Meanwhile, no-planting plots showed 20 % higher SSCI than the oil palm plantation (Fig. 3 A). Therefore, the SSCI increased in the following order: the oil palm plantation < no-planting plots < tree-planting plots < the reference forests. However, the effect of tree planting on the SSCI was not significantly different from that of no-planting. Therefore, we did not statistically confirm the hypothesis that tree planting promotes the development of higher structural complexity than no planting (H1). However, we attribute the insignificant difference in the SSCI to the large variation in the SSCI of tree-planting plots. The SSCI of tree planting plots varied between the mean SSCIs of the oil palm plantation (SSCI = 3.51) and the reference forests (SSCI = 7.32). Furthermore, disturbance-tolerant seed dispersers, such as macaques and civets (Lindsell et al., 2015), observed at our study site, may have enhanced the overall potential for natural regeneration despite the limited forested area (Paterno et al., 2023) (Table S8). This may have reduced the effect of active tree-planting on structural complexity compared to passive no-planting (Silva et al., 2017), given that most species regenerating in the experiment are animal-dispersed (Paterno et al., 2023).

According to a previous study investigating the SSCI of primary forests across biomes (Ehbrecht et al., 2021), nine years after establishment, the complexity of tree-planting plots was, on average, comparable to Palearctic tropical moist broadleaf forests (SSCI = 5). The complexity of no-planting and control plots was comparable to Afrotropic tropical woodlands (SSCI = 4) (Fig. 3 A). Also, tree-planting and no-planting plots, on average, seemed to show higher SSCI (> 4) than similarly young (non-oil palm) agroforests in Brazil, presented in

Steinfeld et al. (2024). This is likely because oil palms are more structurally complex than herbaceous crops due to the palms' height and large fronds (Luskin and Potts, 2011; Zemp et al., 2019) (Fig. 2B,C,D, Table S7).

The trajectories of structural complexity of tree-planting plots tended to show more complex structures with closed canopies and dense vegetation compared to no-planting plots and the conventional oil palm plantation (Figs. 3B, 4). However, the temporal changes of the SSCI between tree-planting and no-planting plots were not significantly different (Fig. 3B, Table S1), and the directions of changes in vegetation structure space were similar among agroforestry plots and the oil palm plantation (Fig. 4). Hence, we also did not find support for the hypothesis that tree planting changes structural complexity more rapidly than no planting (H2).

The decreasing tendency in structural complexity from 2019 to 2022 (Figs. 3B, 4, Table S2) suggests the development of single-layer canopies with lower plant materials (e.g., twigs and leaves) in the understory (Fig. 2B,C,D). This is because SSCI is also influenced by the vegetation density around the scanner (i.e., the MeanFrac) (Ehbrecht et al., 2017). For instance, Stiers et al. (2018) found a non-monotonic relationship between the SSCI of European beech forests and ages, where the increase in SSCI stopped at an early stage of succession, and SSCI steadily decreased due to the formation of a single-layer canopy until the decay and regeneration phase. Unlike structural attributes (e.g., maximum stem diameter) (Poorter et al., 2021), structural complexity considers the 3D arrangement of above-ground plant biomass and is not necessarily related to the accumulation of plant biomass (Ehbrecht et al., 2021; Seidel and Ammer, 2023). Thus, the temporal development of the structural complexity of agroforests is not necessarily a monotonic increase.

4.2. Effects of initially planted tree richness on the development of structural complexity

Intra- and interspecific species differences in crown architectures and physiological traits, such as shade tolerance, promote complementary growth of forest canopies, resulting in high structural complexity (Ehbrecht et al., 2021; Ishii et al., 2004; Williams et al., 2017). However, we did not find significant effects of initially planted tree richness and its interaction with year on the SSCI (Fig. 5A, Table S3) even after accounting for mortality of planted trees (i.e., realized planted tree

richness) (Figure S2A, Table S5). These results contradicted our hypotheses of a positive effect of initially planted tree richness on structural complexity (H3) and that this effect would intensify over time (H4).

In contrast, Perles-Garcia et al. (2021) found an increasing initially planted tree richness effect on the SSCI over time in a subtropical tree diversity experiment in China, where tree richness promoted the ENL (i. e., canopy vertical stratification). One possible reason we did not see a positive effect of initially planted tree richness is that our plots experienced rapid dynamics of planted trees and naturally regenerated woody plants (Tables S7, S8), as observed in early succession on abandoned tropical agricultural lands (Holl et al., 2020; Van Breugel et al., 2007). This may explain why tree-planting plots showed large variations in the SSCI (Fig. 3). Another possible reason is that the oil palms still dominated the heights (Fig. 2D, S5, Table S7), and the canopies of well-growing planted trees (*A. jiringa* and *P. canescens*) likely occupied a similar space as oil palms during the study period (Fig. 2D, Table S7) (Zemp et al., 2019). These potential reasons may also explain why the directions of changes in vegetation structure space were similar among the oil palm plantation, no-planting, and tree-planting treatments (Fig. 4), and the temporal changes of the SSCI between tree-planting and no-planting treatments were not significantly different (Fig. 3B, Table S1).

The large variation in the SSCI of tree-planting plots suggests that the outcomes of tree planting regarding structural complexity at the local scale are uncertain. However, the heterogeneity of structural complexity would increase biodiversity at the landscape scale because of the contrasting responses of organisms to different habitats (Azhar et al., 2015; Montoya-Sánchez et al., 2023; Reiss-Woolever et al., 2023). Accordingly, during the first five years of the experiment, Zemp et al. (2023) found varying responses of taxa to the structural complexity of the tree islands, resulting in an insignificant effect of structural complexity on multi-taxa diversity. However, in the future, structurally more complex tree islands may increase the share of forest-dependent taxa (Grass et al., 2020) due to enhanced structural similarity with forests.

4.3. Effects of plot area on the development of structural complexity

In contrast to our expectation that plot area positively affects structural complexity (H5) and that the effect strengthens over time (H6), we did not find significant effects of plot area and its interaction with year on the SSCI in tree-planting plots (Fig. 5B, Table S3). Our results indicate that structural complexity looking from the center of a plot was not necessarily dependent on the plot area during the study period. This suggests that even small tree islands (25–100 m^2) in a monoculture oil palm plantation can increase structural complexity at the local scale. However, small tree islands would only have a relevant connectivity effect for wildlife if the management of the surrounding oil palm plantation is also reduced to promote understory vegetation (Iddris et al., 2023). Also, it is worth mentioning that plot area is important for biodiversity, as the island biogeography theory predicts (MacArthur and Wilson, 1963). During the first five to six years of the experiment, tree island size had direct and indirect positive effects on biodiversity (Paterno et al., 2023; Zemp et al., 2023).

4.4. Drivers of structural complexity nine years after tree planting

The size of regenerated woody plants was strongly positively correlated with the SSCI and the MeanFrac nine years after establishment (Figures S3, S4). Meanwhile, oil palms positively affected the ENL and canopy height (Figures S3, S5). Structural indices of planted trees were mainly negatively associated with canopy openness (Figures S3, S6). Thus, our results indicate that regenerated woody plants drove current structural complexity by increasing vegetation density below oil palm canopies (Stiers et al., 2018) while well-growing planted trees promoted closed canopies. In contrast, Zemp et al. (2019) found that three years

after establishment, planted trees drove structural complexity. Thus, we posit that planted trees initially increased structural complexity by enhancing density (Fig. 4) (Zemp et al., 2019), later facilitated natural regeneration (Paterno et al., 2023), and consequently, the regenerated woody plants increased current structural complexity. Therefore, we argue that sustaining vegetation density below oil palm canopies is an effective way to increase the structural complexity of oil palm landscapes.

5. Conclusion

We quantitatively analyzed the development of the structural complexity of experimental oil palm agroforests, which were implemented as tree islands within a conventional monoculture oil palm plantation. Our results indicate that local structural complexity did not depend on plot area during the study period. Thus, creating even small tree islands in a monoculture oil palm plantation can increase structural complexity locally. Our results also indicate that the combination of planting trees and natural regeneration promoted structural complexity by enhancing density compared to the monoculture oil palm plantation and natural regeneration only. However, oil palms still drove canopy height and vertical stratification nine years after tree planting. Hence, our results suggest that sustaining vegetation density below oil palm canopies is a key strategy to increase the structural complexity of oil palm landscapes.

CRediT authorship contribution statement

Holger Kreft: Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Gustavo Brant Paterno:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Tatsuro Kikuchi:** Writing – original draft, Methodology, Formal analysis, Conceptualization. **Fabian Brambach:** Writing – review & editing, Investigation, Data curation. **Bambang Irawan:** Project administration, Methodology. **Leti Sundawati:** Project administration, Methodology. **Dirk Hölscher:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Martin Ehbrecht:** Writing – review & editing, Methodology. **Delphine Clara Zemp:** Writing – review & editing, Investigation. **Dominik Seidel:** Writing – review & editing, Supervision, Software, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data and R codes that support the findings of this study are available from GRO.data: https://doi.org/10.25625/1L7VDU.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122182.

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