Recovery of forest structural complexity during secondary succession in the tropics

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Abstract

Forest structural complexity is an essential determinant of forest ecosystem functions and biodiversity. The natural dynamics of structural complexity of tropical forests remain largely unexplored, especially for naturally regenerating forest during secondary succession. Better understanding the trajectories of forest structural complexity recovery is crucial to inform the development of forest landscape restoration strategies and to predict the reassembly of ecological networks during secondary succession. Here, we investigate the recovery of forest structural complexity during secondary succession following land use abandonment in a human-modified landscape in Ecuador. We employ a terrestrial laser scanning-based index of forest structural complexity to quantify three-dimensional vegetation structure of agricultural lands (cacao plantations and pastures), naturally regenerating sites, and primary old-growth forests along a chrono-sequence of secondary succession. We find that sites recovering after land use abandonment attain levels of forest structural complexity comparable to old-growth forest within 40 years. Changes in forest structural complexity along the successional gradient follow a saturating pattern, with rapid increases in the first years and only minor potential for further increases after 40 years. Increasing tree species diversity during secondary succession is identified as a major driver of the recovery of forest structural complexity. Using a structural equation modelling approach, we find that effects of tree species diversity on forest structural complexity are mediated by its effects on vertical stratification, as the effective number of canopy layers increases with increasing recovery age. Our results suggest that passive restoration is a suitable strategy to restore forest structural complexity in human-modified landscapes.

Keywords: 3D forest structure; diversity-complexity relationships; forest landscape restoration

Introduction

Secondary tropical rainforests recovering from anthropogenic disturbance comprise approximately half of the world's total tropical rainforest area (FAO 2015). Secondary rainforests have been shown to play a crucial role in restoring ecosystem functioning and significantly contribute to the sequestration of atmospheric CO_2 and biodiversity conservation (Hérault & Piponiot, 2018; Poorter et al., 2016). Predicting recovery trajectories of recovering tropical rainforests is subject to a high degree of uncertainty, as the recovery of several forest attributes, such as species diversity, species composition, forest structure and ecosystem functioning, depends on past land use type and intensity (Hordijk et al., 2024; Zemp et al., 2023), as well as several environmental factors, such as proximity to remnant forests, soil properties, seed rain and species interactions (Chazdon, 2003; Norden et al., 2015; Poorter, Rozendaal, et al., 2021). A better understanding of recovery trajectories is crucial for actively or passively restoring biodiversity, forest structure, and ecosystem functioning in formerly forested, human-modified tropical landscapes (Aleeje et al., 2025).

Different forest attributes recover at different paces. While soil attributes or species diversity may recover within a few decades (Aleeje et al., 2025; Poorter, Craven, et al., 2021; van der Sande et al., 2024), other attributes, such as biomass and species composition may take more than a century to attain values comparable to old-growth forests (Escobar et al., 2025; Lennox et al., 2018; Poorter, Craven, et al., 2021). The recovery trajectory of different forest attributes, such as biomass, soil attributes, taxonomic or functional diversity have received some attention (Poorter, Rozendaal, et al., 2021; van der Sande et al., 2022; Veldkamp et al., 2020). However, we are still far from being able to generalize how tropical forest ecosystems recover structurally and functionally. In this light, understanding how forest structural complexity recovers during secondary succession is of particular interest, because it strongly influences ecosystem functions, such as productivity and carbon sequestration (Gough et al., 2019; Gough, Atkins, et al., 2021; Ray et al., 2023) as well as biodiversity, by defining habitat quality and niche space (Knuff et al., 2020; Wildermuth et al., 2024).

Forest structural complexity is defined by vegetation density and the heterogeneity of plant material distribution in three-dimensional space (*sensu* Atkins et al., 2018; de Conto et al., 2024; Ehbrecht et al., 2021; Gough et al., 2019). The structural complexity of forests is determined by several biotic and abiotic factors and their interactions. While the global variation of forest structural complexity is largely determined by climate, at local-scale, variations are predominantly controlled by site conditions as well as the natural and anthropogenic disturbance regime (Ehbrecht et al., 2021). The level of forest structural complexity that can be attained under specific site conditions and disturbance regimes is then determined by the successional stage and the associated tree species composition (Juchheim et al., 2020). It depends on the tree species´ complementarity in crown architectures, tree size diversity and functional diversity (Ehbrecht et al., 2021). In this context, several studies have pointed to a positive relationship between tree species diversity and forest structural complexity (e.g. Coverdale & Davies, 2023; Perles-Garcia et al., 2021; Zemp et al., 2023). Forest stands composed of tree species with varying functional and morphological traits may promote the formation of multiple canopy-layers as well as a more efficient occupation of available space and thereby show higher levels of forest structural complexity. While the formation of multiple canopy layers results in a more heterogeneous distribution of biomass in three-dimensional space, an efficient occupation of available canopy space determines overall vegetation density. The interplay of biomass distribution and vegetation density then determines the level of forest structural complexity. Describing forest structural complexity as a function of plant material distribution and vegetation density in a three-dimensional space is underpinned by several studies that used three-dimensional laser scanning data to quantify complexity using different indices, such as the stand structural complexity index (SSCI, Ehbrecht et al., 2017), box-counting-dimension (Db, (Seidel, 2018), canopy rugosity (Atkins et al., 2018) and space-borne metrics like the Waveform Structural Complexity Index (WSCI, de Conto et al., 2024).

In anthropogenically altered forest ecosystems, both biomass distribution and vegetation density and thus structural complexity, are strongly determined by land use type and management practices (Ehbrecht et al., 2017; Soto et al., 2024; Willim et al., 2022). Land use or management effects on structural complexity have been widely studied, mostly by comparing different land use systems or different types of management, with and without undisturbed forests as reference systems. The impacts of forest management or other land-uses on formerly forested lands on forest structural complexity have been investigated for boreal coniferous forests (Aalto et al., 2023; Põldveer et al., 2021), temperate broadleaved forests (e.g. Asbeck & Frey, 2021; Soto et al., 2024; Willim et al., 2022), temperate coniferous forests (e.g. Juchheim et al., 2020; Seidel et al., 2016), tropical moist broadleaf forests (Ehbrecht et al., 2021; Milodowski et al., 2021; Rosen et al., 2024), or tropical agroforestry systems (Kikuchi et al., 2024; Steinfeld et al., 2024). Both positive and negative impacts of management on structural complexity have been reported. Whether management has positive or negative effects on forest structural complexity depends on the management practices and their intensity (i.e. enrichment planting vs. logging, selective logging or partial harvests vs. (partial) clear-cutting), as well as the selected reference a certain land use system or forest type is compared to. For instance, enriching monocultural cash crop plantations, such as oil palm plantations, increases complexity by planting trees (Kikuchi et al. 2024, Zemp et al., 2019). Management practices focusing on e.g. timber harvesting often result in lower levels of forest structural complexity compared to unmanaged or late-successional stages of primary forests, but may also increase forest structural complexity in the mid- to long-term by accelerating the establishment of natural regeneration (e.g. Soto et al. 2024, Willim et al. 2022).

Compared to the well-studied effects of land use, management or disturbances on forest structural complexity, much less is known about the natural dynamics of structural complexity in general, and in particular about the development of structural complexity during succession. For instance, Gough et al. (2021) showed that the development of forest structural complexity followed a sigmoidal trend over a period of 200 years in temperate forest ecosystems, with a short period of slow recovery of forest structural complexity in the first years, followed by longer periods of constant increase in complexity over time and, reaching a saturation after around 150 years. For human-modified tropical landscapes, an in-depth understanding of forest structural complexity dynamics and its drivers is lacking, as most knowledge on the structural recovery of tropical rainforests is based on single structural attributes, such as above-ground biomass, canopy height or basal area (e.g Aryal et al., 2024; Nytch et al., 2023; Oberleitner et al., 2021).

Here, we investigate the recovery of forest structural complexity during secondary succession and test whether changes in forest structural complexity along the successional trajectory are driven by changes in tree diversity. To quantify forest structural complexity, we employ a widely used, terrestrial laser scanning-based index of forest structural complexity (SSCI) and conduct tree inventories along a chrono-sequence of tropical forest succession after land use abandonment in a Neotropical lowland rainforest landscape in Ecuador. Additionally, we sample forest structural complexity and tree diversity in old-growth forests as reference sites. We first hypothesize that forest structural complexity increases over time, but follows a saturating pattern. Thus, we expect an asymptotic relationship between SSCI and recovery age. Second, we hypothesize that the recovery of forest structural complexity is driven by increases in tree diversity along the successional gradient. To test how recovery age and tree diversity drive forest structural complexity, we employ a structural equation modelling approach.

Methods

Study site

This study was conducted in the neotropical lowland rainforest of the Canandé watershed of the Chocó-Region, located in the province of Esmeraldas in North-Western Ecuador (see Fig. 1). Mean annual precipitation was reported to range between 4000-5000 mm per year, while mean annual temperature ranges between 21° to 25°C (Escobar et al., 2025). The topography of this region is shaped by the foothills of the Andes. The elevation of the plots ranges from 159 m to 615 m above sea level, with vegetation types randomly distributed across this range. The research area is mainly marked by old-growth forest, recovering secondary forest, cacao plantations and pastures. Active land use in this area is mainly characterized by smallholders managing cacao plantations and cattle pastures. Actively managed cacao plantations are characterized by small stands of cacao trees systematically arranged, with rarely any other vegetation present. Actively grazed cattle or horse pastures are mainly characterized by tall grasses up to 1.5 meters, some thickets and occasionally large remnant trees from former forest cover. This study was conducted within the frame of the *Reassembly* project, which is an interdisciplinary research unit to study the restistance, resilience and functional recovery of rainforest ecosystems. For further details, see (Escobar et al., 2025).

A total of 56 experimental plots have been established in a forest reserve owned by the *Fundación Jocotoco* and the *Tesoro Escondido* Reserve. These plots represent a chrono-sequence of secondary succession following land use abandonment, utilizing a space-for-time approach. In total, 10 plots were established in active agriculture, 30 plots in recovering sites after land use abandonment, and 16 plots in primary old-growth forest. The plots are randomly distributed within an area of 140 km^2 and differ in their current land use status (see Fig. 1). The recovering plots comprise former agricultural land left to regenerate naturally without the influence of active restoration interventions. They can be further characterized by their historical land use (cacao plantation or pasture) and their stage of succession (time since land use abandonment, termed “recovery age” in the following). Abandoned cacao plantations are characterized by small- to mid-sized cacao trees with mostly dense vegetation in the lower levels during the first years of recovery. Later recovery stages are marked by mixed stands and larger cacao trees.

Abandoned pastures characterized by mixed stands of small pioneer species and dense ground vegetation in the young stages of recovery. Later recovery stages are characterized by larger trees and less dense ground vegetation. The recovery age of the plots ranges from 0 to 39 years.

The age of reference old-growth forest plots is unknown. Each plot is arranged in a square shape with a side length of 50 meters (2500 m^2), except for five plots, where plot size had to be adjusted to 20 x 20 meters (400 m^2) due to practical reasons resulting from active land use. The distribution of the vegetation type along the measured 56 plots is shown in **Fehler! Verweisquelle konnte nicht gefunden werden.**.

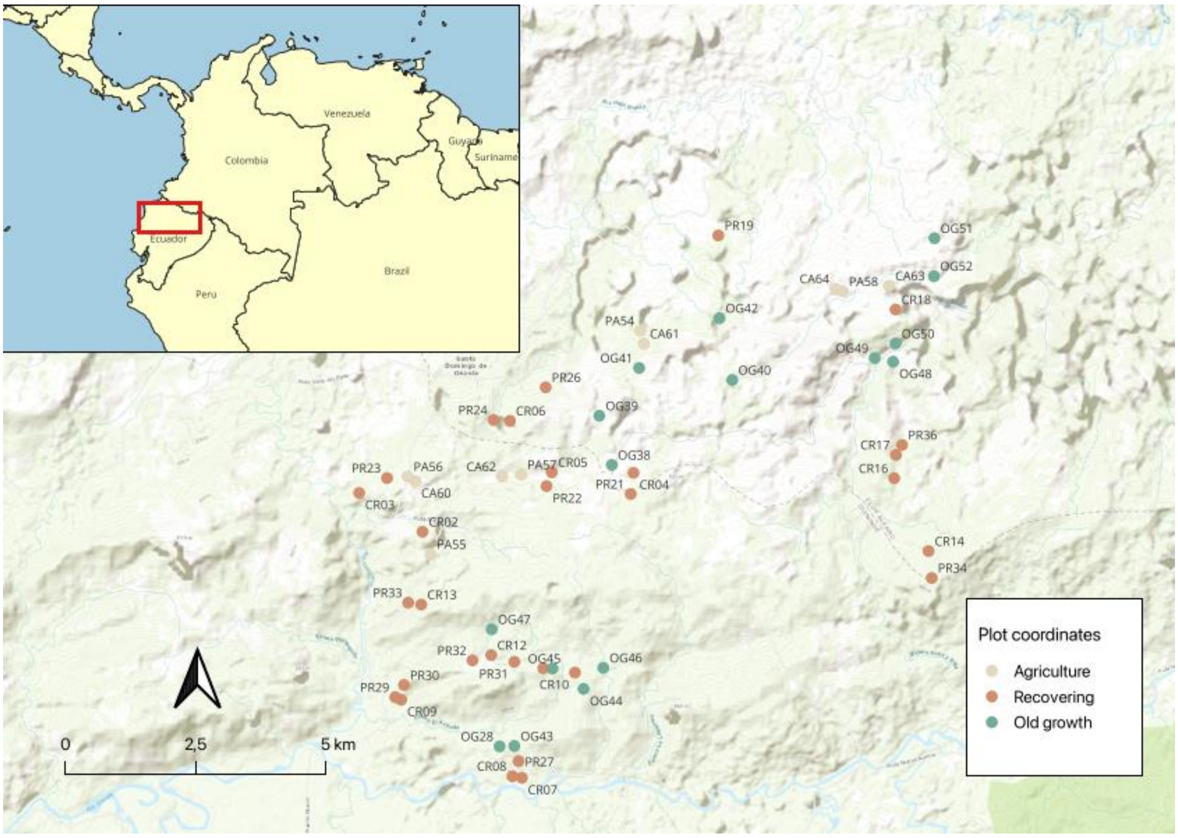

Figure 1. Map of the study area with plot locations and elevation above sea-level (m).

Quantification of forest structural complexity

At each plot, forest structural complexity was quantified based on single terrestrial laser scans, which were conducted using a Faro Focus M70 (Faro Technologies Inc., Lake Mary, USA) terrestrial laser scanner in November 2023. Scans were systematically distributed across a plot, with one scan made in the center and the other four scans towards the corners with a diagonal distance of ≈ 21 m from the center (see Fig. 2). The terrestrial laser scanner was mounted on a tripod at a height of 1.3 m. The area was scanned with a field of view of 360° horizontally and 300° vertically with an angular step width of ≈ 0.035°. The maximum scan distance of this device reaches up to 70 m. Where big trees or inaccessibility due to dense vegetation, ponds or steep slopes did not allow for setting up the scanner, the nearest possible area within the plot was used. The resulting three-dimensional point cloud was then used to calculate the stand structural complexity index (SSCI) following Ehbrecht et al. (2017, 2021).

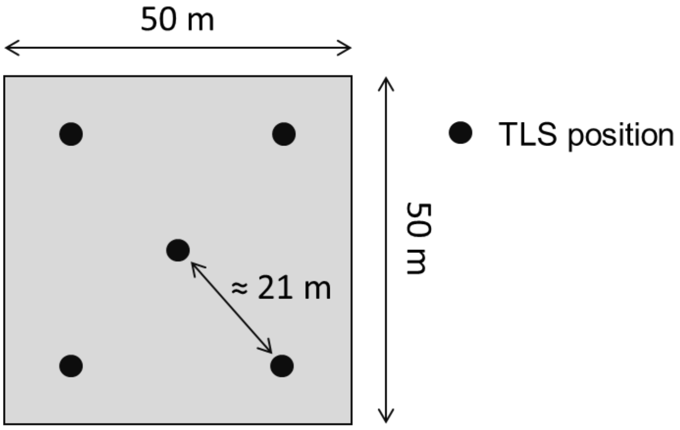

Figure 2. Distribution of single terrestrial laser scans within each plot.

Scan data was processed using the hardware-specific software FARO SCENE (Faro Technologies Inc., Lake Mary, USA, v.7.1.1.81). Point clouds were then exported as text file in .xyz-format. The .xyz-files were then been imported to R to calculate the stand structural complexity index (SSCI) for each scan using the publically available R-code by Ehbrecht et al. (2021, GitHub-Link). The SSCI is based on two components: (1) the mean fractal dimension of cross-sectional polygons derived from the point cloud (MeanFrac) and (2) the effective number of layers (ENL) (Ehbrecht et al., 2016). The cross-sectional polygons represent slices through the point cloud for 1280 azimuthal directions with the scanner position being the center for each polygon. Polygons are constructed by connecting points of the point cloud along the hemisphere for each azimuthal direction. For each polygon, the shape complexity is then calculated based on a modified perimeter-area-ratio following McGarigal & Marks (1995, for details see Ehbrecht et al. 2021). The resulting 1280 fractal dimension values are then aggregated to a mean fractal dimension (MeanFRAC) as a measure of structural complexity. The MeanFRAC index increases with increasing canopy space filling and can be interpreted as a proxy for vegetation density. As the fractal dimension is a scale-invariant measure of complexity, MeanFrac values are scaled using the effective number of layers (ENL) to take stand height and vertical stratification into account. ENL is based on the concept of Foliage Height Diversity, introduced by MacArthur & MacArthur (1961), and quantifies the number of layers that are effectively occupied by foliage and woody components. Here, the inverse Simpson-Index is applied to the vertical distribution of points binned in 1 m-thick layers. As such, ENL quantifies the distribution of canopy elements in three-dimensional space and be interpreted as measure of vertical foliage distribution. SSCI is then calculated following equation 1:

$$\mathrm{SSCI} = \mathrm{MeanFrac}^{\ln(\mathrm{ENL})} \quad \text{(eq. 1)}$$

The SSCI value for each plot was then calculated as the mean SSCI based on the SSCI values derived from the five scans per plot. For detailed information on the SSCI calculation see Ehbrecht et al. (2017, 2021). SSCI has been used in several studies as a measure of vegetation complexity, incl. (Kikuchi et al., 2024; Perles-Garcia et al., 2021; Ray et al., 2023; Soto et al., 2024; Willim et al., 2022)

Assessment of tree species diversity

At each plot, a tree census was conducted between February 2022 and July 2023, whereby each tree with a circumference ≥ 25 cm at 1.3 m above the ground (dbh ≥ 7.95 cm) was recorded, including palms and lianas (Escobar et al., 2025). A total of 7542 cultivated and non-cultivated trees were surveyed, from which 7408 trees (> 98 %) were identified to species or genus level. We identified 539 tree species and morphospecies within the census. Tree species diversity was then estimated based on coverage-based rarefied species using the iNEXT package. To investigate the role of tree diversity in shaping forest structural complexity, we focus on the diversity of dominant tree species using Hill number q = 2 for all analyses.

Statistical analyses

All data analyses were conducted using the statistical software environment R, version 4.3.3 (R Development Core Team 2024). Differences of SSCI between the vegetation types and their significance have been tested with an analysis of variance (ANOVA) and a subsequent TukeyHSD post-hoc test. To test how forest structural complexity changes along the successional gradient from actively managed cacao plantations and pastures to late-successional stages, SSCI as well as both of its components were first regressed against recovery age. Data from old-growth forest plots was used as reference. For SSCI, we tested a linear model with a log-transformation of recovery age, a generalized additive model (*mgcv*-package (Wood, 2023)) and an asymptotic, non-linear least squares regression model (*nls2* package (Grothendieck & Team (nls), 2024)). For ENL, we tested a linear and log-linear model. For MeanFRAC, we tested a linear model only, as no clear trend was apparent in the data. Afterwards, the Akaike Information Criterion (AIC) values of the models have been compared and the model with the lowest AIC value was selected as the best fitting model. In figures, only regression lines for the best fitting model are shown.

From a mechanistic perspective, recovery age can be considered an indirect driver of forest structural complexity. We hypothesize that effects of recovery age on forest structural complexity are mediated by increasing tree species diversity and tree size (canopy height) along the studied-chrono-sequence, whereby canopy height determines the three-dimensional canopy space (niche space) that can be occupied by canopy elements. Tree species diversity is then hypothesized to determine niche occupation and therewith canopy space filling as well as vertical stratification. To investigate whether effects of recovery age on forest structural complexity are mediated by tree species diversity and canopy height, we employ a structural equation modelling approach, in which we test the effects of those predictors on the above-mentioned components of SSCI, namely ENL and MeanFRAC, using the *piecewiseSEM* package (Lefcheck et al., 2024). Additionally, we tested whether tree species diversity ($q = 2$) explained the residuals of models explaining the structural metrics as a function of recovery age. We thereby aimed to test whether tree species diversity affects three-dimensional forest structure regardless of recovery age. We set a significance level of $p < 0.05$ for each analysis. Residuals of all regression models were tested using the *DHARMa* package (Hartig et al., 2024). Residuals diagnostics are presented in the Supplementary Information (Fig. SI 3 and Fig. SI 4).

Results

Forest structural complexity (SSCI) increases from active agriculture to recovering sites to old-growth forest and significantly differs between the three vegetation types (Fig. 3a, $p < 0.01$). A similarly increasing pattern can be observed for ENL, whereas no significant differences between agriculture and regenerating sites could be detected (Fig. 3b, $p = 0.10$). For MeanFRAC, we did not find significant differences between the three vegetation types (Fig. 3c, $p > 0.21$).

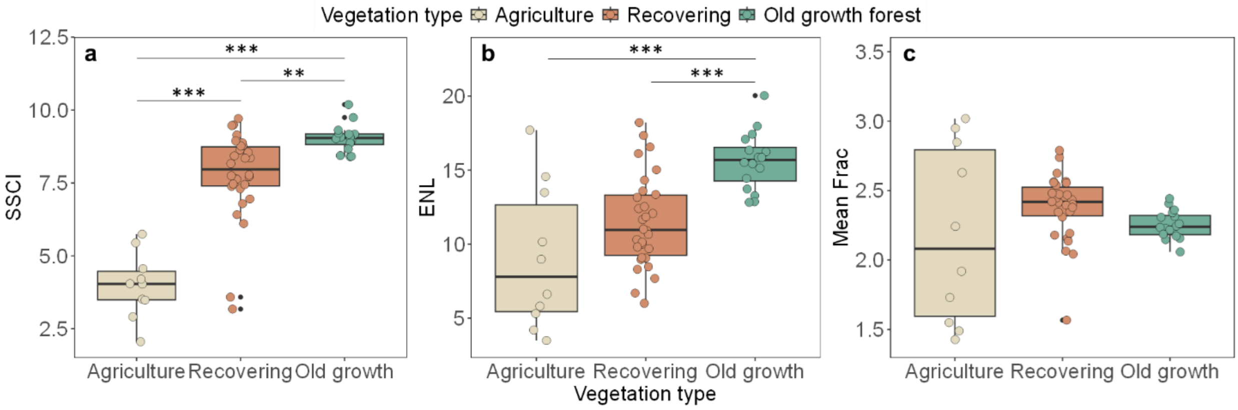

Figure 3. (a) Forest structural complexity (SSCI), (b) vertical stratification (ENL) and (c) vegetation density (MeanFRAC) of agricultural, recovering and old-growth forest plots, respectively.

Table 1. Model type, response variable (structural metrics), (log-transformed) predictor, adjusted R^2, AIC and p-value of models used to predict 3D stand structure as a function of recovery age

Model	Response	Predictor	Adjusted R^2	AIC	p-value
lm	SSCI	log(Recovery age)	0.72	126.49	< 0.001
nls	SSCI	Recovery age	0.72	128.64	< 0.001
gam	SSCI	Recovery age	0.69	131.85	< 0.001
lm	SSCI	Recovery age	0.54	145.79	< 0.001
lm	ENL	Recovery age	0.26	210.06	< 0.001
lm	ENL	log(Recovery age)	0.2	213.03	0.002
lm	MeanFRAC	Recovery age	< 0.01	40.49	0.65

Forest structural complexity positively correlates with recovery age ($p < 0.001$), which explained 72% of variation in SSCI. The best model is a linear model with a logarithmic predictor (Fig. 4a, Tab. 1). SSCI increased sharply in the first years of recovery, then the shape of the curve starts to flatten out from the fifth to tenth year after reaching mean values of 6 to 7. At a recovery age of about 20 years, SSCI doubled its value (mean SSCI ≈ 8) and levels similar to old growth forest are reached after 40 years of recovery (mean SSCI ≈ 9). ENL increased linearly with recovery age with no apparent saturation at higher recovery age (Fig. 4b). MeanFRAC showed no significant correlation with recovery age (Fig. 4c).

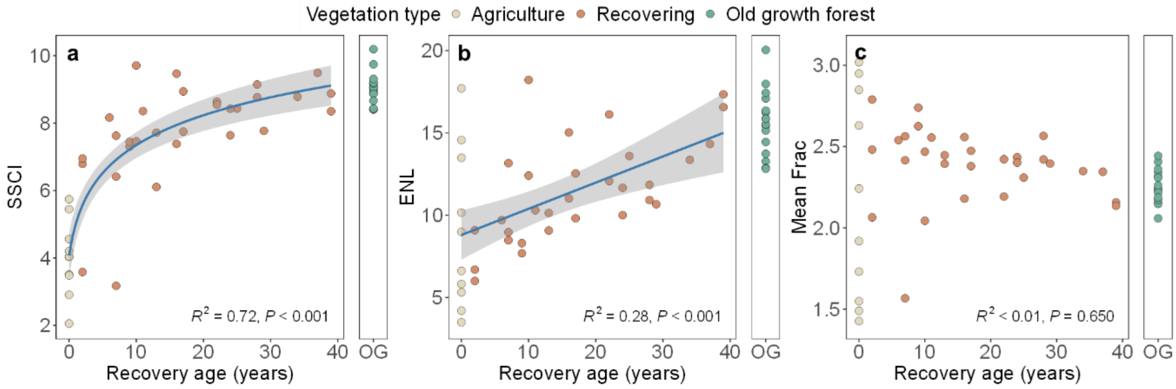

Figure 4. Relationships between (a) forest structural complexity (SSCI), (b) vertical stratification (ENL), (c) vegetation density (MeanFRAC) and recovery age. Values of old-growth forest plots are plotted for comparison.

We hypothesized that the correlation between recovery age and forest structural complexity is mediated by the effects of tree species diversity on the components of SSCI. With increasing recovery age, tree species diversity and canopy height are increasing, which has been already shown by Escobar et al. (2024) for the same plots. By employing a structural equation model, we found that effects of tree species diversity on forest structural complexity are mediated by its effects on vertical stratification, as quantified by ENL, whereas no significant effects on vegetation density, quantified by MeanFRAC, nor direct effects were found (Fig. 5). Canopy height had both direct and indirect effects on SSCI with ENL as mediator.

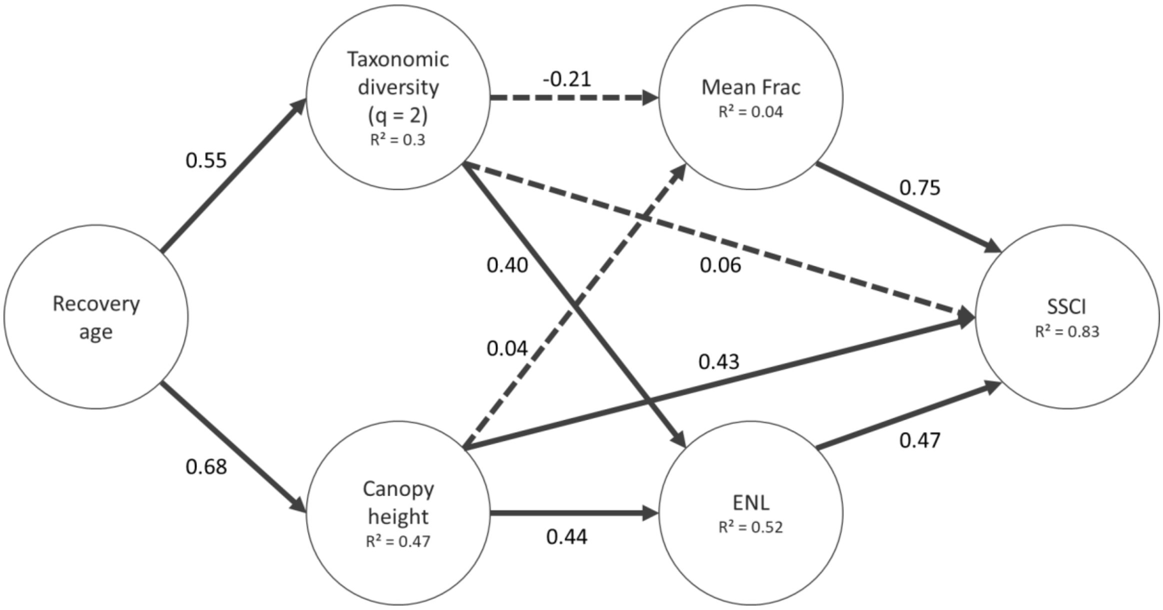

Figure 5. Piecewise structural equation model relating variation in forest structural complexity (SSCI) to tree species diversity and canopy height effects, mediated by vertical stratification (ENL) and vegetation density (MeanFRAC) and driven by recovery age. Solid lines indicate significant effects, dashed lines indicate non-significant relationships. Figures represent standardized effect sizes.

Additionally, we tested whether the residuals of models predicting SSCI, ENL and MeanFRAC as a function of recovery age could be explained by tree species diversity (q = 2) (Fig. 6). We thereby aimed to test whether there is an effect of tree species diversity on each of the structural metrics regardless of recovery age. We found a significant correlation between tree species diversity and the residuals of the model predicting ENL as a function of recovery age (Fig. 6b). Correlations between tree species diversity and the residuals of the SSCI (Fig. 6a) and MeanFRAC model (Fig. 6c) were not significant.

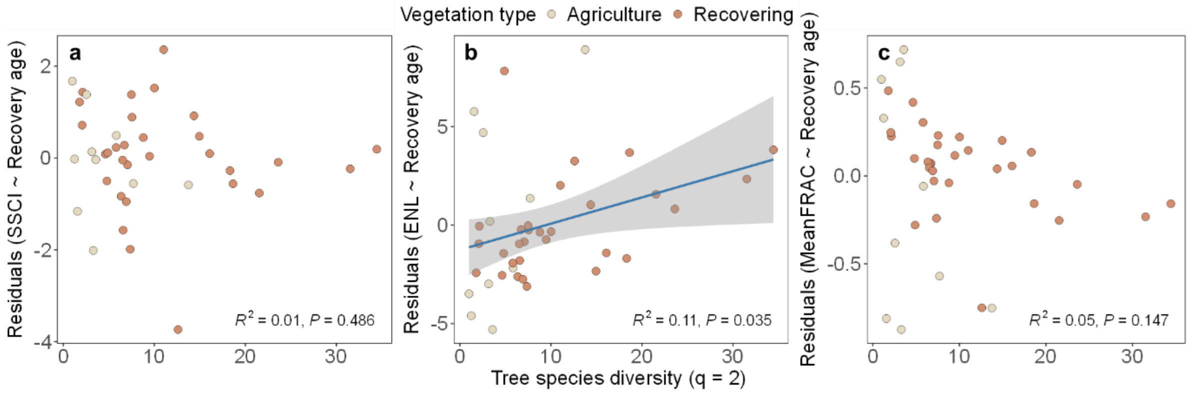

Figure 6. Relationships between tree species diversity and the residuals of models used to predict (a) forest structural complexity (SSCI), (b) vertical stratification (ENL) and (c) vegetation density (MeanFRAC) as function of recovery age.

Discussion

We assessed forest structural complexity of recovering Neotropical lowland rainforest along a successional gradient using a space-for-time substitution approach. We hypothesized that the structural recovery along the successional gradient for the studied tropical rainforest follows a saturating model, characterized by an asymptotic curve. However, the most suitable model identified describes the relationship between recovery age and SSCI with a logarithmic function, suggesting continued (minimal) growth potential in late successional stages. Following an initial sharp increase in forest structural complexity during the early years of forest recovery, the successional dynamics start to slow down in the mid-stage of the chrono-sequence. Later, the curve begins to flatten, indicating that once a certain level is reached, continued, but marginal increases in forest structural complexity can be expected in subsequent time periods. During forest recovery, the variance of SSCI values appears to decrease with increasing age and stabilize at comparable levels towards late successional stages. Approximately 40 years after the initiation of forest recovery, forest structural complexity has attained levels comparable to those identified for the old-growth forest plots (mean SSCI ≈ 9). This indicates a rapid recovery of forest structural complexity in comparison with temperate forest ecosystems, which were reported to attain levels of forest structural complexity similar to old-growth forests after around 150 years (Gough, Bohrer, et al., 2021). Contrary to the recovery trajectory reported for temperate forest ecosystems, we did not observe a sigmoidal pattern of structural recovery. It is important to note that similar forest structural complexity does not equate to a fully developed old-growth forest, as other structural attributes, such as biomass, tree species composition, and certain ecosystem functions are still recovering and may require much longer time to reach pre-disturbance levels (Aryal et al., 2024). For instance, Escobar et al. (2024) show that for the same plots, above-ground biomass and tree species richness have not yet reached levels comparable to old-growth forests. In a meta-analysis on tropical forest recovery, compiled from chrono-sequence data from 2275 plots in the Neotropical lowland rainforest and West Africa, Poorter, Craven, et al., (2021) reported a recovery time of around 60 years for the forest's structural heterogeneity to resemble that of old growth forests. In this study, structural heterogeneity was quantified as tree size variability using the Gini-coefficient. Even though the Gini-coefficient of tree sizes does not directly quantify the complexity of three-dimensional forest structure, it has shown to closely correlate with SSCI (Ehbrecht et al. 2021), because a heterogeneous plant material distribution in three-dimensional space as well as higher vegetation density can only be realized through a high variability of tree sizes and associated greater canopy packing. Against this background, the recovery pace of forest structural complexity in our study is similar to what has been observed in other tropical landscapes. Furthermore, after 40 years of recovery, SSCI values are comparable with old-growth tropical rainforests of other realms, such as Indo-Malayan or Oceanian rainforests (Ehbrecht et al., 2021).

We hypothesized that the increase of forest structural complexity with recovery age is mediated by the effects of tree diversity and size on vegetation density and increasing heterogeneity of biomass distribution in three-dimensional space. The structural equation modelling approach employed here suggests that increases of forest structural complexity with recovery age are driven by an increase in the effective number of canopy layers (ENL), i.e. by increasing vertical stratification, resulting in a more heterogenous distribution of foliage and woody components in three-dimensional space. We did not find significant effects of tree diversity on MeanFRAC, a proxy for vegetation density. These finding suggests that the increase in tree diversity along the recovery trajectory is associated with a more efficient occupation of different forest strata by tree species with varying functional and morphological traits. This finding is further supported by the correlation between tree diversity and the residuals of the recovery age-ENL model, which suggests that tree diversity drives vertical stratification regardless of recovery age. We did not find significant correlations between residuals of the recovery age-SSCI model or the recovery age-MeanFRAC model, which suggests that the effects of tree diversity on three-dimensional forest structure are solely driven by tree diversity effects on vertical stratification, and not by tree diversity effects on vegetation density. Successional theories state that the establishment of early-successional pioneer trees after land use abandonment is followed by the establishment of mid- to late successional species along the recovery trajectory (Poorter et al., 2023). Early-, mid- and late-successional species differ in their functional traits (Manhães et al., 2022). While early-successional species are often light demanding species, late-successional species have to be more shade-tolerant in order to be able to thrive in lower strata beneath an otherwise closed-canopy forest. Thus, a multi-layered canopy may develop along the recovery trajectory where light-demanding species occupy upper canopy layers and shade-tolerant species mid- to lower canopy layers, resulting in a higher effective number of canopy layers. In late-successional stages, canopy openness and tree height marginally changed (see Fig. SI 1), whereas ENL continued to increase at similar rates. This suggests the formation of additional canopy layers by climax tree species emerging from the understory, resulting in the characteristic vertical stratification of tropical rainforests. The assumption that increases in vertical stratification along the recovery trajectory are driven by greater functional diversity is supported by other studies that reported increases in functional diversity with recovery age. Surprisingly, we did not detect changes in vegetation density with recovery age. However, the slightly lower MeanFRAC-values of old-growth forest in comparison with recovering forest may suggest that vegetation density might decrease as succession continues. As dominant trees mature, competition for light and belowground resources can result in insufficient resource availability for trees of lower canopy strata, which might lead to a less dense understory vegetation (Matsuo et al., 2024). Similar results have been reported for other old-growth forests (Ehbrecht et al. 2021).

Positive effects of tree diversity on forest structural complexity were further reported for temperate broadleaved forests (Juchheim et al., 2020), savannas (Coverdale et al., 2024), tropical tree diversity experiments (Perles-Garcia et al., 2021; Ray et al., 2023; Zemp et al., 2019) and tropical agroforestry systems (Steinfeld et al., 2024). So far, evidence of positive tree diversity effects was lacking for naturally regenerating tropical forests. By reviewing diversity-complexity relationships, Coverdale & Davies, (2023) suggest that effects of tree diversity on forest structural complexity usually follow a saturating pattern. At higher levels of tree diversity, additional species may not increase forest structural complexity further due to functional redundancy as soon as the available niche space is fully occupied. Even though we find a saturating relationship between tree diversity and forest structural complexity in our study (see Fig. SI 2), we cannot draw robust conclusions from this relationship because the tree diversity-SSCI relationship is confounded by recovery age in a univariate regression.

With increasing interest in forest recovery after agricultural use and the goal of restoring biodiversity and ecological functionality by promoting forest stand structural complexity, the need for adequate management practices is growing. Future studies, efforts or experiments on forest recovery under similar conditions may refer to results from this study, as a comparison with natural succession dynamics can be employed to evaluate the success of assisted management approaches and the impact of implemented techniques on the development of forest structural complexity.

With its hyper-diverse and evergreen tree communities, tropical rainforests are among the forest types with the highest SSCI values worldwide (de Conto et al., 2024; Ehbrecht et al., 2021). In addition to trees, other vegetation groups in the rainforest should be focused on further research when assessing stand structural complexity. The uniquely high occurrence of epiphytes and lianas in tropical rainforests and their effects have not been extensively considered in SSCI evaluations to date. Given that these plant groups establish themselves in highly specialized niches on tree surfaces, their impact on the structural complexity of the forest would be of particular interest.

Overall, our results suggest that passive restoration is an effective tool to restore forest structural complexity after land use abandonment, allowing a structural recovery within time frames of at least 40 years. However, the recovery trajectory strongly depends on the colonization success by pioneer tree species, which in turn depends on a vital seed bank and/or seed dispersal from adjacent intact forests and subsequent recruitment success. This questions whether our findings hold for other human-modified tropical landscapes, where landscape fragmentation, limited seed dispersal, or colonization of abandoned sites by grasses or shrubs might hinder the recovery of forest structural complexity in comparable time frames.

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Conflict of interest statement

The authors declare no conflicts of interest

Data availability statement

The data and code used in this study will be made available upon acceptance of the study in a peer-reviewed journal.

Author contributions

ME and NB conceptualized the study. ME wrote the first draft and analyzed the data. TL collected the data and contributed to data analyses and manuscript writing. SE contributed data and contributed to manuscript writing. DD, MJE and JGA contributed equally to manuscript revisions.

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Supplementary Information

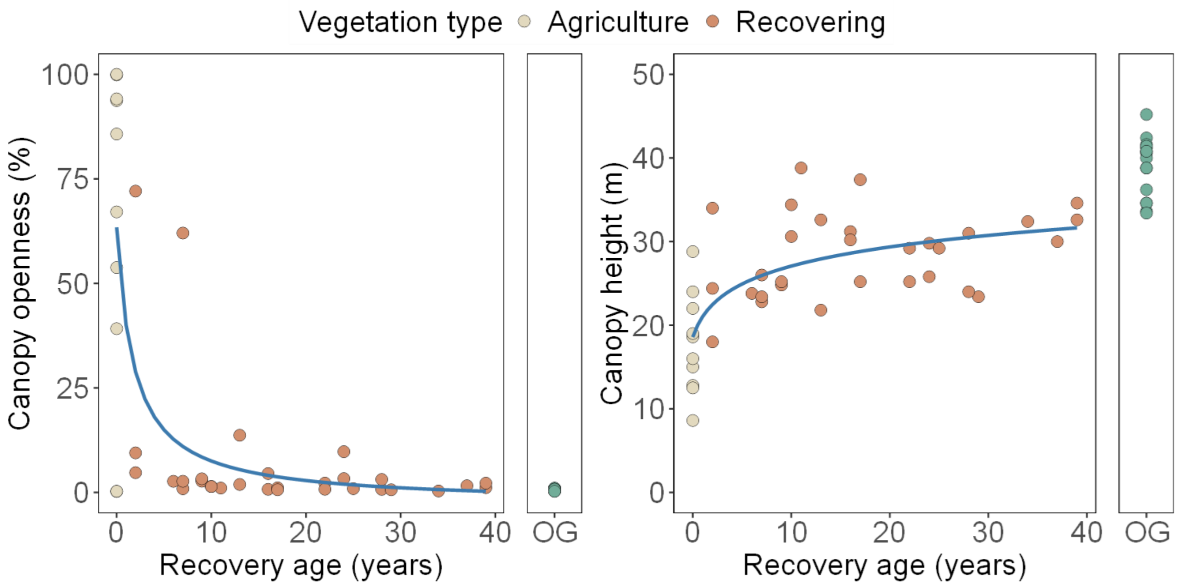

Figure SI.1. Canopy openness (*left*) and canopy height (*right*) as a function of recovery age. Canopy openness was modelled using a negative exponential asymptotic function. Canopy height was modelled with a log-linear model. Values for old-growth forest are shown for comparison, respectively.

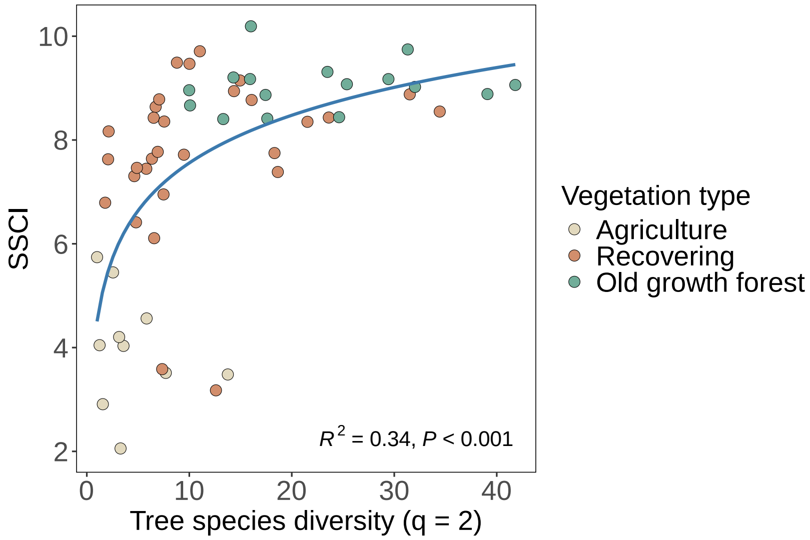

Figure SI.2. Relationship between forest structural complexity (SSCI) and tree species diversity (q = 2).

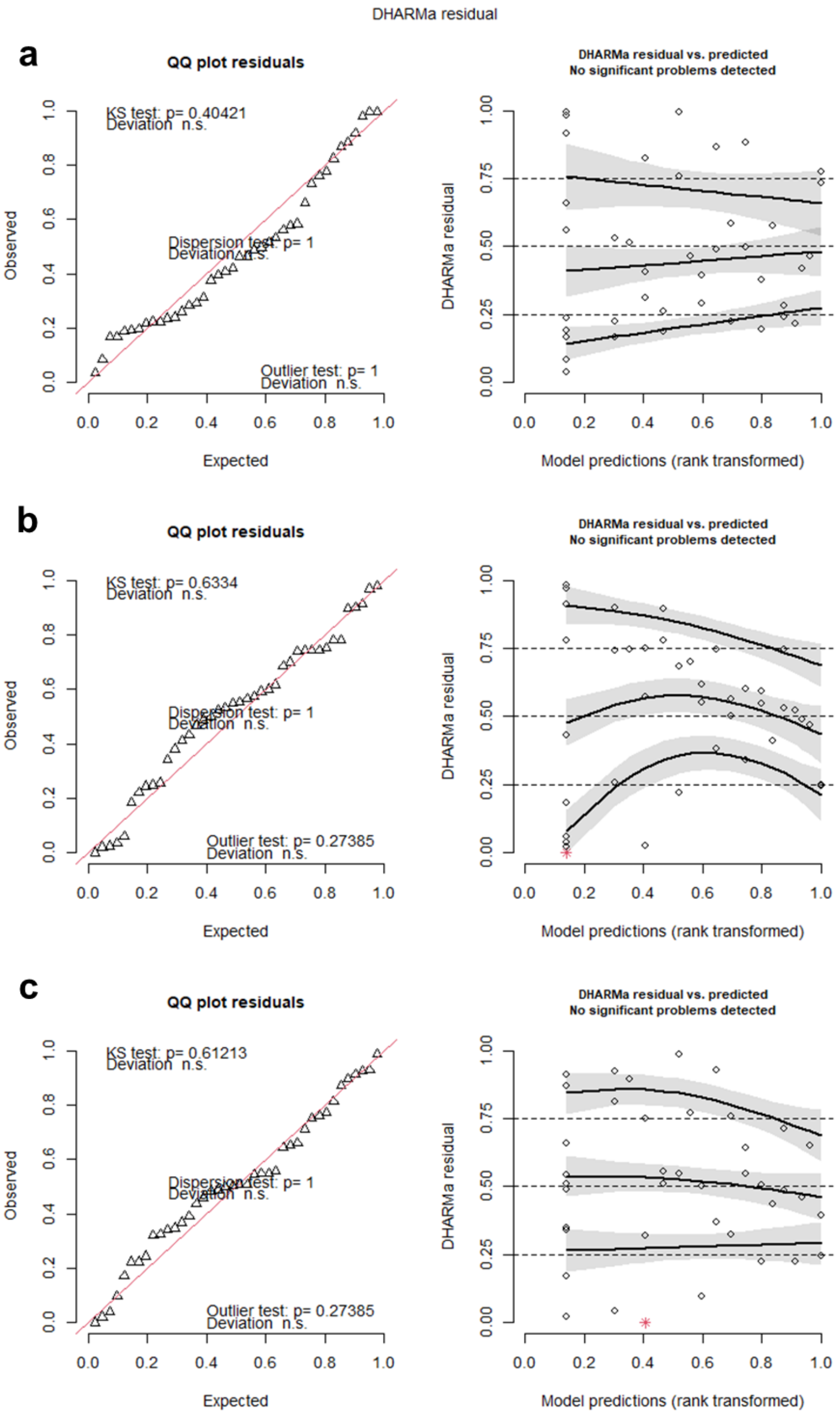

Figure SI.3. Residual diagnostics for models explaining (a) forest structural complexity (SSCI), (b) vertical stratification (ENL) and (c) vegetation density (MeanFRAC) as a function of recovery age.

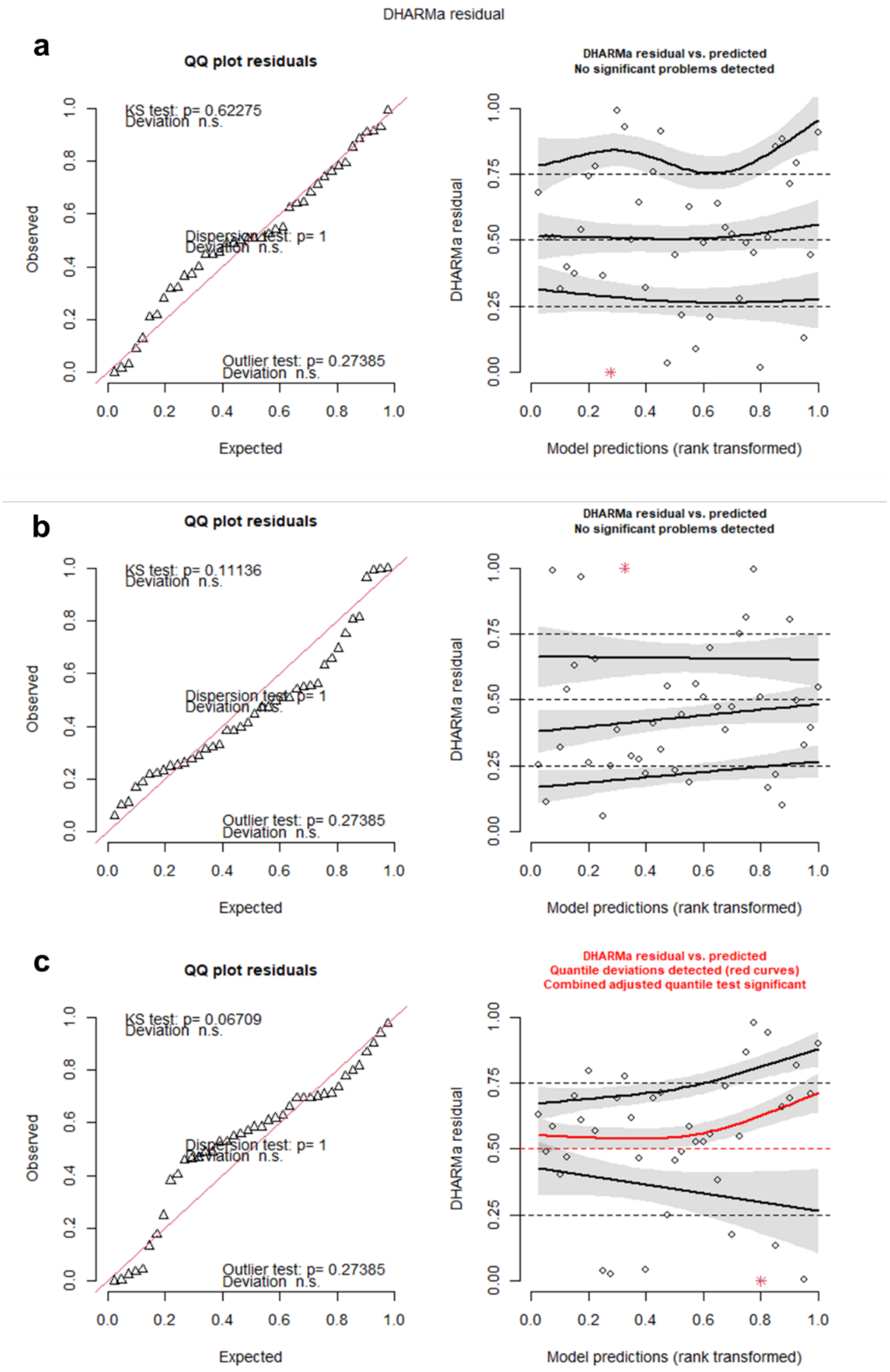

Figure SI.4. Residual diagnostics for models explaining the residuals of recovery age effects on (a) forest structural complexity (SSCI), (b) vertical stratification (ENL) and (c) vegetation density (MeanFRAC) as a function of tree species diversity.