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Soil factors rather than stand age drive tree phylogenetic diversity along Amazon Forest succession

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ABSTRACT

Understanding the phylogenetic diversity and structure of woody communities can explain how deterministic or stochastic processes drive a forest community assembly. This study assessed the tree community's phylogenetic diversity and structure during secondary succession after shifting cultivation (SC) in the Northern Amazon Forest. We hypothesized that soil-mediated filtering, rather than habitat filtering based on stand age and neutrality-based stochastic processes, determines phylogenetic diversity and structure of woody community along Amazon Forest succession after SC. We used forest inventory data from 45 plots across three sites representing second-growth forests (SG) having stand ages after shifting cultivation (e.g., 5, 10, 15, and 20 years old) and an old-growth reference forest (> 100 years old, OG). We tested different linear mixed-effects models to determine the main effects of soil-mediated filtering (i.e., nutrients and soil texture) and stand age on phylogenetic metrics. Phylogenetic diversity (PD) showed a significant difference between SG and OG: the highest PD was found in OG, whereas the lowest PD was found during the initial successional stage. We found a trend of phylogenetic structure promoted by soil attributes; the variability of soil texture mainly explained most of the variation of phylogenetic diversity and structure. Stand age did not demonstrate a significant influence on phylogenetic metrics across any of the tested models. Higher soil fertility may favor the growth of species from multiple distant clades, increasing phylogenetic diversity and reducing phylogenetic clustering. However, SC may affect the fertility content in silt soils of OG and generate soils with a high proportion of sand and low fertility in SG. Thus, our study demonstrates that soil-mediated abiotic filtering shapes the phylogenetic structure and diversity of tree communities along Amazon forest succession due to deterministic processes rather than stand age and neutrality-based stochastic processes.

1. Introduction

Second-growth forests regrowing after disturbances represent important stages in the recovery of biodiversity and ecosystem services (Poorter et al., 2016; Rozendaal et al., 2019; Villa et al., 2021). Therefore, where vegetation can regenerate spontaneously, it may represent a passive restoration method (Holl and Aide, 2011; Holl, 2017). The comparison between SG and OG suggested that regenerated areas shelter higher tree species diversity, due to the coexistence of light-demanding pioneer species and shade-tolerant species from advanced

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successional stages (Chazdon, 2014; Rozendaal et al., 2019; Coelho et al., 2022). Most studies on tropical forest restoration using a chronosequence approach to compare different successional stages of SG and OG focused on changes in the taxonomic diversity of tree communities after disturbance (Jakovac et al., 2015; Mukul and Herbohn, 2016; Rozendaal et al., 2019). However, a most straightforward and purely taxon-based approach does not consider ecological differences between species diversity and forest succession, which may have biased conclusions about the processes underlying forest community assembly (Purschke et al., 2013). The relative importance of successional habitat and environmental filtering along forest succession can be inferred by assessing the phylogenetic relatedness among tree species based on phylogenetic community analysis (i.e., Purschke et al., 2013; Kleinschmidt et al., 2020; Maza-Villalobos et al., 2020; Diniz et al., 2021).

Studies in human-modified tropical landscapes are revealing the effects of disturbances on the phylogenetic diversity and structure of tree communities (Pausas and Verdú, 2010; Tucker et al., 2017; Santo-Silva et al., 2018). The phylogenetic structure of a community reflects the average level of differences among co-occurring species by measuring their relatedness (Webb et al., 2002; Cavender-Bares et al., 2009). It can be used as a backbone for two major types of hypotheses to explain the processes of plant community assembly: niche-based deterministic hypotheses (NDH) and neutrality-based stochastic hypotheses (NSH) (Webb et al., 2002; Cavender-Bares et al., 2009; Qian et al., 2013, 2020). NDH propose that abiotic filtering (e.g., habitat and soil conditions) increases under environmental stress and resource-limited scenarios, whereas biotic filtering (e.g., competition) increases with the decrease in environmental stress and wider resource supply (Götzenberger et al., 2012; Swenson and Enquist, 2007; Violle et al., 2011).

According to NDH, environmental filtering tends to favor the selection of species with more similar functional traits and niches, which leads to phylogenetic clustered communities (Cavender-Bares et al., 2009; Baraloto et al., 2012; Gastauer and Meira-Neto, 2014), while factors like competition would cause phylogenetic overdispersion due the exclusion of close relatives (Webb et al., 2002; Cavender-Bares et al., 2004; Violle et al., 2011). Conversely, NSH suggests that phylogenetic and functional differences between species are unimportant and plant community assembly is shaped by neutral processes, such as temporal niche dynamics, dispersal limitation, and ecological drift (Hubbell, 2001; Kelly and Bowler, 2009; Ge et al., 2021; Zhou et al., 2021). Under NSH, therefore, the phylogenetic structure of a community is expected to not differ from the null expectation of a random structure (Webb et al., 2002; Kembel and Hubbell, 2006).

Both types of hypotheses (NDH and NSH) have been tested to evaluate the drivers of secondary succession in plant communities and disentangle the changes in the relative importance of deterministic (biotic and abiotic filtering) and neutral mechanisms for the successional processes (Swenson et al., 2012; Arroyo-Rodríguez et al., 2015; Maza-Villalobos et al., 2020; Martínez-Ramos et al., 2021). Previous studies have shown that abiotic filtering may have a major role in the phylogenetic clustering of tree communities during the early successional stage, while the relevance of biotic filtering (i.e., biotic interactions, such as competition) increases during the late-successional stage (e.g., Letcher, 2010, Letcher et al., 2012; Diniz et al., 2021; Martínez-Ramos et al., 2021). However, there are scenarios (e.g., disturbance-phase) where deterministic processes operate simultaneously in species selection and can counteract one another and enhance a balance on their forces as assembly drivers. This might occur along secondary forest successions (Maza-Villalobos et al., 2020) and generate a random phylogenetic structure (Webb, 2000; Soliveres et al., 2012).

As an example of environmental filtering from soil features, higher organic matter and silt content increase total exchangeable bases and soil's field capacity, reducing several habitat constrictions (e.g., low nutrient and drought stress), limiting plant growth, and increasing phylogenetic diversity (Gastauer et al., 2017). However, diversity can also decrease above certain soil fertility levels in forests due to resource use from the interspecific competition (Peña-Claros et al., 2012). On the other hand, the inverse-texture hypothesis suggests that highly productive fine-textured soils (high clay contents) in humid regions tend to suffer from lacking drainage, while coarse-textured soils in arid or dry regions have a lower ability to maintain water availability during dry seasons (Sala et al., 1988). Despite the importance of the above-mentioned soil attributes, further research is needed to understand how they, combined with stand age, affect tree community assembling and phylogenetic diversity along tropical forest successions after anthropogenic disturbance. This kind of information will provide valuable insights for evaluating the effectiveness of the transition of traditional to more sustainable forest management practices in phylogenetic diversity.

The Amazon Forest is the most extensive, biodiverse, and carbon-dense sink in the world while providing essential ecosystem services (i.e., climate regulation, carbon cycling, and food resources) for human well-being (Sullivan et al., 2017; Mitchard, 2018; Villa et al., 2020, 2021). However, human-induced land-use changes (i.e., disturbance by logging, agriculture, forest fires, and forest fragmentation) are the main drivers causing the loss of biodiversity and ecosystem functioning in this forest (Lewis et al., 2015; Villa et al., 2018a, 2020; Pontes-Lopes et al., 2021). Among these pressures, shifting cultivation (SC) is the most common traditional farm system, which was probably sustainable for nomadic indigenous populations for centuries (Bush et al., 2015; Villa et al., 2021). Currently, the non-traditional shifting cultivation is a consequence of cultural changes of indigenous communities inducing local-scale expansion and intensification of land use (Heinimann et al., 2017; Villa et al., 2020, 2021). Hence, understanding the drivers underlying the biodiversity along Amazon forest succession after anthropogenic disturbances is critically relevant to gathering management, restoration, and conservation strategies. However, studies evaluating the effects of soil (physical and chemical) properties on the phylogenetic diversity and structure of plant communities regrowing along secondary forests succession remain scarce.

This study assesses the tree community's phylogenetic diversity and structure during secondary succession after SC in the northern Amazon forest. We used forest inventory data from 45 plots across three sites representing SG with different stand ages after shifting cultivation (5, 10, 15, and 20 years old) and an OG (> 100 years old). We established two main research questions: i) How do phylogenetic diversity and structure of tree communities change along successional stages? ii) What are the effects of soil properties and stand ages on phylogenetic structure and diversity of tree communities? We hypothesized that soil-mediated filtering rather than habitat filtering based on stand age and neutrality-based stochastic processes determines the phylogenetic diversity and structure of woody community along Amazon forest succession after SC. Thus, we expected that deterministic processes represented by soil-mediated filtering predominate and promote phylogenetic clustering of woody communities' during early successional stage, whereas biotic filtering (e.g., competitive interactions) gains higher importance during late-successional stage leading the assembly of communities in which the phylogenetic overdispersion predominates. Finally, we expected that harsh soil properties conditions, rather than habitat type, during the early successional stage impose a strong abiotic filtering effect on phylogenetic diversity and structure.

2. Material and methods

2.1. Selection of study sites and forest plots

The studied areas are in two Piaroa indigenous communities (Gavilán and Sardi) in the Cataniapo River basin, municipality of Atures, Amazon State, Venezuela (5°32′28 S, 67°24′13 E, Fig. 1). Both communities were established 60 years ago in the Cataniapo basin, belong to the Piaroa ethnic group, and maintain traditional SC based on *cassava* crop (*Manihot esculenta* Crantz) (Villa et al., 2018a). The region's climate

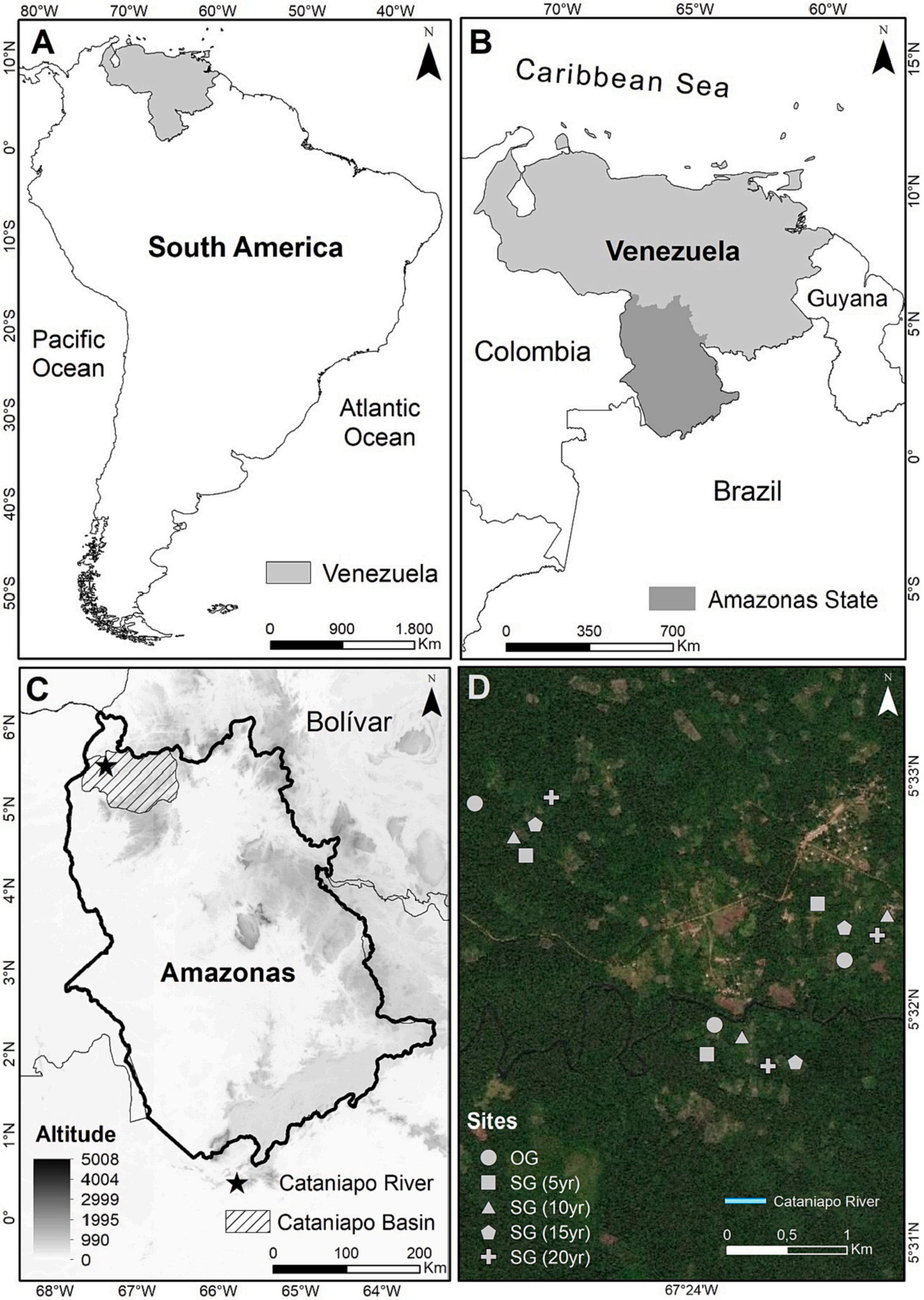

Fig. 1. Localization of the study area and sampling plots concerning South America (A), Venezuela (B), Amazonas State (C), and the Cataniapo basin (C and D) showing the distribution of second-growth forest and old-growth forest patches sampled (symbols) The second growth (SG) forest patches sampled at different successional stages (5, 10, 15, and 20 years old) and old-growth forests (OG, 100 years old) are indicated. Adapted from Villa et al. (2021).

is classified as a rainy tropical system, with dry season between December and January, mean annual rainfall of 2700 mm, and mean annual temperature of 28 °C. The predominant soil types are Oxisols (Latosols) and Ultisols (Argisols), with low cation exchange capacity and nutrient content and high acidity levels. The vegetation is dominated by semi-deciduous and old-growth lowland forests with SG patches (Villa et al., 2018a, 2018b).

Semi-structured interviews, with open and qualitative questions about different aspects related to forest management and shifting cultivation dynamics, were conducted with owners (Villa et al., 2018b). The land-use history and stand age of each forest patch were used to select three sites containing a mosaic of OG and SG. At each site, we selected four SG with different stand ages (5, 10, 15, and 20 years of natural regeneration) after a single cycle of traditional shifting cultivation and one old-growth forest (> 100 years old) (Fig. 2D). From January 2009 to December 2012, three plots (each 20 m × 50 m = 1000 m^2) were established for each SG and OG in each site, totalizing 45 plots (= 4.5 ha) (Fig. 2C). Sampling sites and forest plots were identified with the assistance of local farmers and experts.

2.2. Forest inventory

In each plot, all trees with diameters at breast height (DBH) ≥ 5 cm were identified to the species level and tagged for measurement. One specimen of each species was collected, identified by comparison with specimens of the Julian Steyermark Herbarium of Puerto Ayacucho (Ministry of the Environment, Amazonas State, Venezuela), and classified according to the Angiosperm Phylogeny Group (APG - Angiosperm Phylogeny Group IV, 2016).

2.3. Soil nutrients and texture

In each plot, we collected three samples of topsoil (0–10 cm depth) evenly distributed within the plot to obtain one composite sample for chemical and physical analyses. Measurements of soil properties were carried out in the Soil Analysis Laboratory of the National Institute of Agricultural Research, following regular protocols (Gilabert de Brito et al., 2015). The soil pH was determined in water. Acidic components ($H^+ + Al^{3+}$) were extracted with $Ca(OAc)_2$ 0.5 mol L^{-1} buffered to pH 7.0 and quantified via titration with NaOH 0.0606 mol L^{-1}. Exchangeable cations were extracted in KCl 1 mol.L^{-1}, and determined via atomic absorption spectroscopy (Ca^{2+} and Mg^{2+}) and titration with NaOH

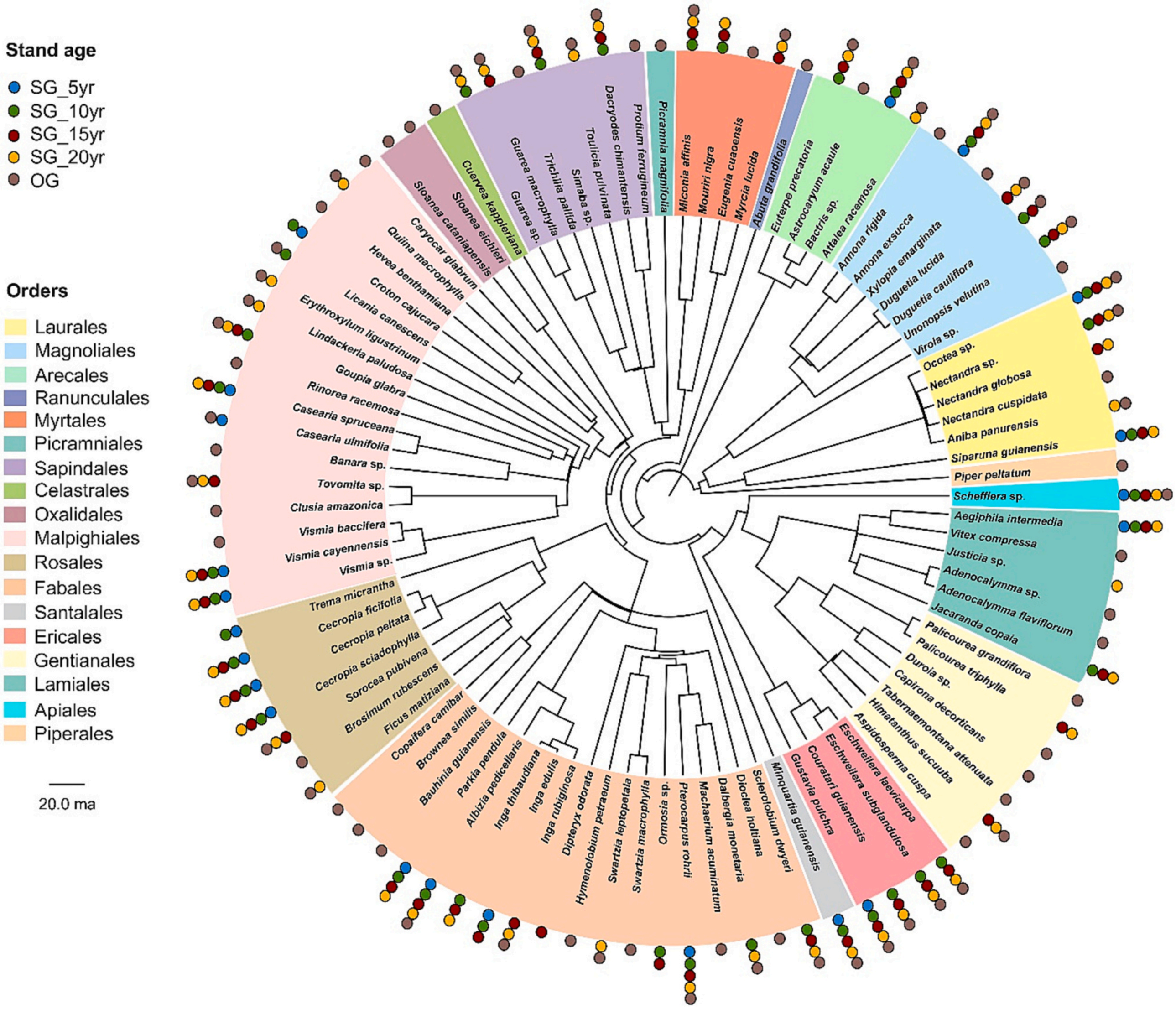

Fig. 2. Phylogenetic tree in the second-growth forest (SG) and old-growth forest patches (OG) sampled. Phylogenetic divergence scale is indicated in millions of years (Myr).

(Al^{3+}). The available phosphorus (P), Na^+, K^+, Fe, Cu, Mn and Zn were extracted with Mehlich-1, and quantified using inductively coupled plasma optical emission spectrometry (ICP-OES). The remaining P (P-rem) was obtained using a fine air-dried soil sample containing 60 mg L^{-1} of P (KH_2PO_4) and determined by photo colorimetry. Effective cation exchange capacity (ECEC) was calculated by determining the sum of cations (Ca^{2+}, Mg^{2+}, Na^+, K^+, and Al^{3+}). In contrast, the total cation exchange capacity (CEC) was estimated using the bases of sum (BS) and potential acidity ($H^+ + Al^{3+}$). We determined the bases saturation index (V) and Al saturation index (m). Organic C was determined by the Walkley-Black method without heating. The organic matter (OM) content was estimated by multiplying organic C by 1.724 (OM = Walkley-Black C × 1.724). Sodium Saturation Index indicates the proportion of soluble sodium concerning total cation exchange capacity. Granulometric analysis (clay, silt, coarse, and fine sand contents) was performed using the pipette method.

2.4. *Data analyses*

All analyzes were performed in the R program 4.2.1 (R Core Team, 2020), using different packages. For phylogenetic analyses, we used two R packages, the V.PhyloMaker to reconstruct our phylogenetic tree by pruning our list of species to the mega-tree GBOTB.extend (Jin and Qian, 2019), and the "*picante*" package to calculate the phylogenetic diversity and structure metrics (Kembel et al., 2010). We used the 'ggstatsplot' package (Patil, 2022), which is an extension of ggplot2 package (Hadley, 2015), for creating graphics with details from statistical tests included in the information-rich plots themselves (Patil, 2022).

The principal component analysis was performed using the "*FactoMineR*" package (Husson et al., 2017); then, synthetic variables were extracted using PCA axes following soil properties.

We used linear mixed-effects models (LMMs) to test the main effects of stand age and soil properties on different phylogenetic metrics, while including forest patches and plots as random effects, using the "lme4" package (Bates et al., 2019). Further, we employed the multi-model criteria selection for the mixed models using 'MuMIn' package (Barton, 2017). We also used the estimates of the predictors' coefficients in all models to interpret parameter estimates on a comparable scale using the "jtools" package (Long, 2020). To draw the graphs illustration in this study, we used the 'ggplot2' package (Hadley, 2015).

2.4.1. *Phylogenetic diversity and structure analysis*

We built a phylogenetic tree based on the mega-tree GBOTB.extend, which encompasses calibrated phylogenetic data for 74,533 vascular plant species (Jin and Qian, 2019). We used the function *phylo.maker* under evolutionary scenario 3 for creating a data frame of the mega-tree GBOTB.extended using the function build.nodes.1, which extracts the largest cluster's root and basal node information at the genus or family level (Jin and Qian, 2019). The scenario 3 binds the phylogenetic information for a genus by including a new tip between the family root node and basal node to the midway point of the family branch (Qian et al., 2013). Therefore, the scenario 3 tends to favor the reconstruction of phylogenies with most of the species phylogenetically resolved.

With the resultant reconstructed phylogeny, we calculated metrics related to phylogenetic diversity (PD) and dispersion (MPD - mean pairwise phylogenetic distance, and MNTD – mean nearest taxon distance) and their standardized effect size (ses) to evaluate the evolutionary relationships of the tree species in the forest types (SG and OG). For evaluating phylogenetic diversity, i.e., the sum of the branch lengths of a phylogenetic tree connecting all species in a community (Faith, 1992), we computed the Faith's PD (expressed in millions of years, Myr). We analyzed the phylogenetic dispersion with the metrics MPD and MNTD as indicators of structure patterns in the community assembly (i.e., clustering and overdispersion). MPD and MNTD are complementary; MPD estimates the average phylogenetic distance between all co-occurring species in the entire phylogeny (i.e., from the older clades and nodes to the shallower ones), while MNTD is more sensitive to capture phylogenetic distances between the taxon sharing closer evolutionary history (i.e., shallower clades and nodes towards the terminals of the phylogeny) (Webb, 2000; Webb et al., 2002, 2008). The higher the values of PD, the higher the phylogenetic diversity; the higher the values of MPD and MNTD, the higher the phylogenetic overdispersion. Then, we computed the ses (standardized effect size) for PD, MPD, and MNTD to normalize the influence of the natural correlation with species number (richness), comparing the observed values with the ones derived from random communities (Swenson, 2014). For that, we used an unconstrained null model (Kembel and Hubbell, 2006) under 10,000 randomizations with the algorithm 'phylogeny.pool' of the "*picante*" package (Kembel et al., 2010, 2015). This null model operates by generating null (random) communities by drawing species from the entire pool of species (95 species) with equal probability of being included in the null communities (Swenson, 2014). Significant negative values of sesMPD and sesMNTD indicate phylogenetic clustering, while significant positive values indicate phylogenetic overdispersion. Congruently, significant negative values of sesPD indicate lower phylogenetic diversity and positive values higher phylogenetic diversity than the expected by chance. We calculated PD, MPD, MNTD and their ses' values using the functions ses.pd., ses.mpd, and ses.mntd, respectively, of the "*picante*" package (Kembel et al., 2010).

2.4.2. *Principal component analysis*

We summarized soil variables by scores of the axes of principal component analysis (PCA, Fig. S1 from Supplementary material). To avoid the substantial presence of correlated soil attributes, we considered the first axis of PCA as the proxies for soil fertility (PCA1f) and variability in soil texture (PCA1t) (Villa et al., 2018a; Schmitz et al., 2020). Therefore, we defined the first PCA axis for soil fertility (PCA1f) and texture (PCA1t) variables (Figs. S2 and S3).

2.4.3. *Statistical analyses*

Firstly, we checked the data distribution based on the normality assumption using formally Shapiro-Wilk tests and visually Q-Q (Quantile-Quantile) plots (Crawley, 2013). Then, we checked the independence of the data between groups and within each group (forest types by successional stage), which was collected from a representative and randomly selected portion of the total population. Finally, we tested the homogeneity of variances using Bartlett's test based on an assumption that the variances of the different groups should be equal in the populations (i.e., homoscedasticity).

To address the first question, 'How do phylogenetic diversity and structure of tree communities change along sucessional stages?', we compared the average of the phylogenetic metrics among forest stand ages by applying a Kruskal-Wallis (for non-normally distributed data) and one-way ANOVA (for normally distributed data). We used a Kruskal-Wallis test to compare PD, MPD, sesMPD, MNTD and sesMNTD between stand age followed by a posteriori Dunn's test (Dinno 2017). Conversely, to compare the average of sesPD among forest types we applied a One-way ANOVA; the pairwise differences between stand age were outlined by applying multiple comparisons of means based on Tukey's post hoc test (HSD = 0.05), using the "car" package in the software R (Fox et al., 2017).

2.4.4. *Linear mixed-effects models*

To address the second question, 'What are the effect of soil properties and stand age on phylogenetic structure and diversity of tree communities?', we tested the influence of soil physical properties (PCA1t), chemical properties related to soil fertility (PCA1f), and stand age on phylogenetic metrics (ses.PD, ses.MPD and ses.MNTD) using linear mixed-effects models (LMMs). The PD and standardized effect size for MPD and MNTD were selected as response variables in separate models to dilute the influence of their natural correlation with non-standardized metrics. For these models, the predictors regarding the fixed effects were represent by two continuous explanatory variables (chemical and physical properties of soils) and one variable factor (i.e., stand ages). Forest patches and plots were considered as a random effect (1|Patch: plot) in all models. The residuals distributions attesting for quality and predictive performance of models were mainly evaluated by eyes according to their distributions in the Q-Q plots and histogram of raw residuals (Fig. S4); therefore, the Gaussian error distribution was corroborated (Crawley, 2013). Previously, we selected out the predictor variables using Spearman correlation to avoid collinearity ($r \geq 0.7$ was considered as non-acceptable collinearity; Dormann et al., 2013). Then, we tested separate LMMs (Fig. S5 from SM). Finally, we applied a multimodel selection approach based on Akaike Information Criterion (AIC) to evaluate the best models reflecting relationships between the phylogenetic (target) and soil and stand age variables (predictors). We applied the 'dredge' function in the MuMIn package and the best model was considered the one with $\Delta AICc = 0$, which is equally parsimonious in the overall fit and explanatory quality (Burnham et al., 2011; Matos et al., 2017; Barton, 2017).

3. Results

Altogether, 95 tree species belonging to 76 genera and 48 families were sampled across all 45 plots, which are grouped according to succession stages (Fig. 2). The richest family were Fabaceae (14 species), followed by Annonaceae (6), Lauraceae (5), and Lecythidaceae (5). Specifically, the 36 plots from the SG contained 86 species, 45 genera, and 38 families, whereas the nine old-growth forest plots contained 74 species, 52 genera, and 46 families.

The difference of phylogenetic diversity (PD) between SG and OG forests was significant (Fig. 3A). More specifically, the highest PD was found in OG, whereas the lowest PD was found in the initial successional stage, 5 years after disturbance (Fig. 3A). No significant differences were observed between plots with 10, 15, and 20 years of stand age (Fig. 3A). Significant differences in ses.PD were also observed between SG and OG, with OG having more significant positive values (Fig. 3B). However, MPD and ses.MPD showed a similar pattern between SG and OG forests (Fig. 4A and B), with higher values in the OG forests, but close to zero indicated possible neutrality. Differences were observed for ses.PD,

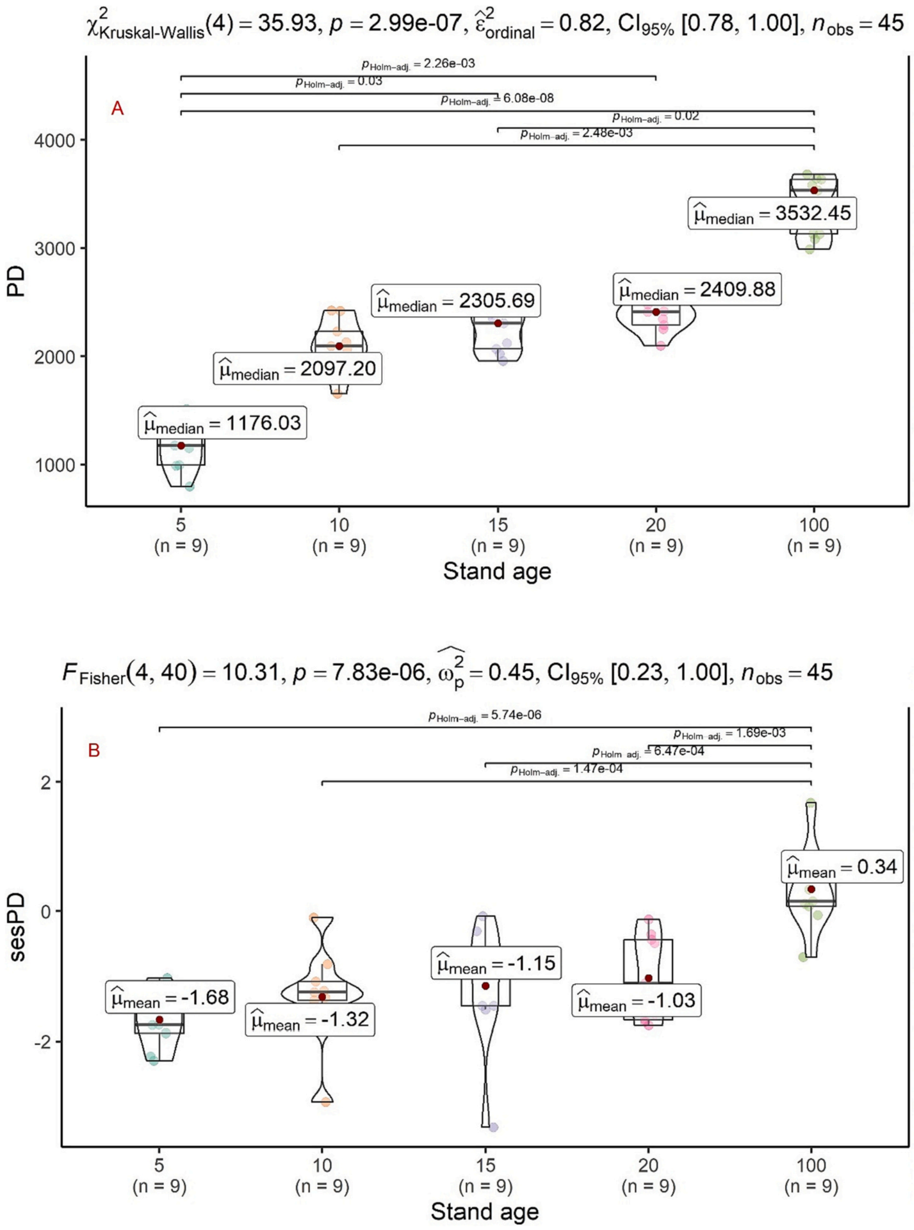

Fig. 3. Comparisons of the phylogenetic diversity and dispersion metrics between the second-growth forests (SG) along the distinct ages of succession (5, 10, 15, and 20 years old) and the old-growth forest (OG). Phylogenetic diversity (PD) (A), ses.PD, standard effective size of phylogenetic diversity (B). The mean value (red point) is presented for different stand age (5, 10, 15, and 20 years old) and in an old-growth forest (OG). The values above horizontal brackets indicate the p-values (Dunn test, $P < 0.05$) of the significance of the comparisons between stand ages. The estimated effect size and confidence interval (CI) level are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

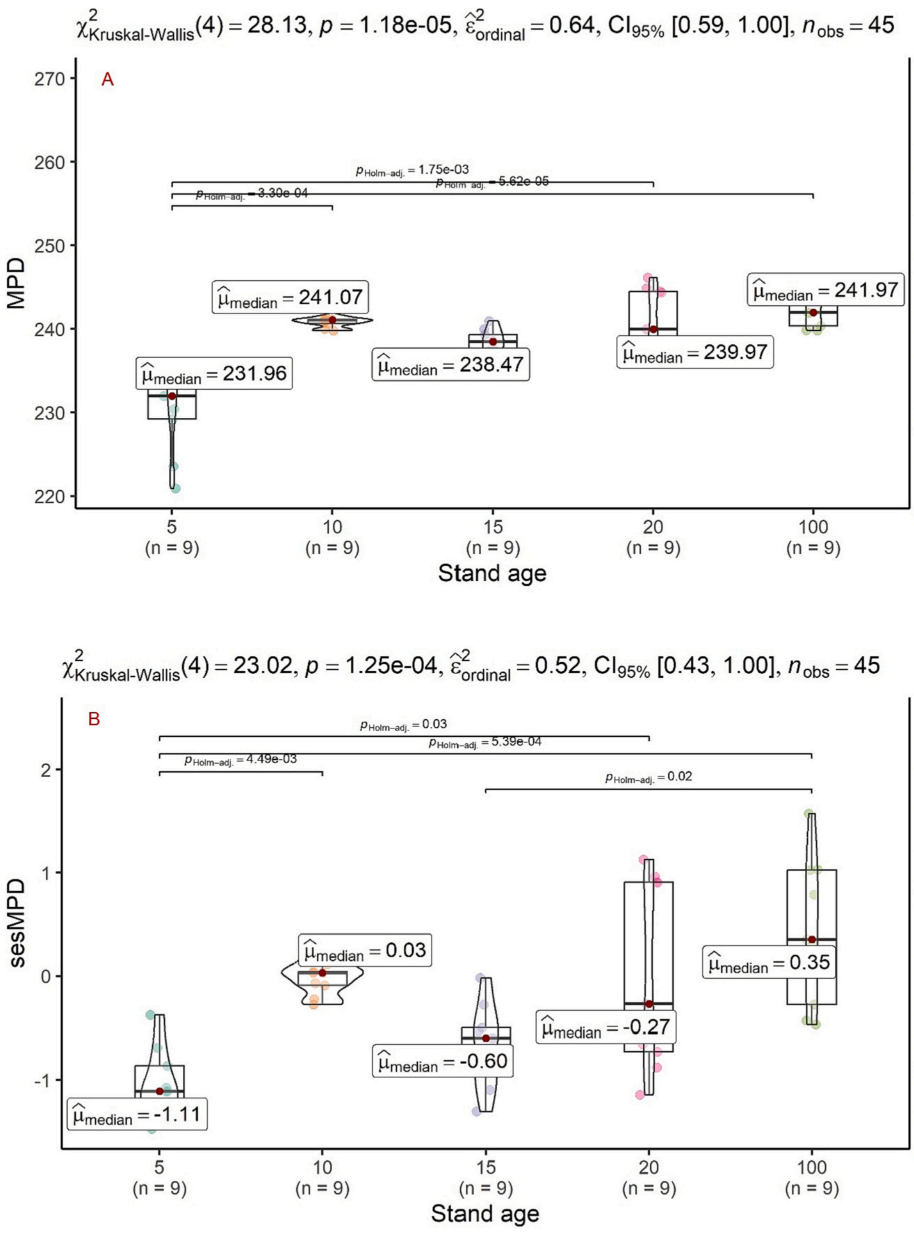

Fig. 4. Comparisons of the mean pairwise distance (MPD) (A) and standard effect size of MPD, ses.MPD (B) between the second-growth forests (SG) along the distinct ages of succession (5, 10, 15, and 20 years old) and the old-growth forest (OG). The mean value (red point) is presented for different stand age (5, 10, 15, and 20 years old) and in an old-growth forest (OG). The values above horizontal brackets indicate the *p*-values (Dunn test, $P < 0.05$) of the significance of the comparisons between stand ages. The estimated effect size and confidence interval (CI) level are indicated(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

where 5 and 15 years of stand age showed significant negative values (i.e., significant lower phylogenetic diversity), whereas 10 and 20 years of stand age showed values close to zero, and OG forests showed the positive values (Fig. 3B). In contrast, MNTD did not differ significantly among most of the forest types (Fig. 5A). Meanwhile the sesMNTD did not differ among SG forests having 5 to 20 years after disturbance (Fig. 5B), and a phylogenetic clustering was observed for the SG forests having 5 years after disturbance compared to OG forests close to zero (Fig. 5B).

From the best model selection approach (ΔAIC < 2), we found that variation of phylogenetic diversity and structure was mainly explained by the variability of soil texture (PCA1t), which consistently explained more variation in the different phylogenetic metrics and across all tested models (Fig. 6; Table 1). The PD was significantly and positively influenced by the PCA1t (LMM, Estimate = 0.51, $t = 6.67$, $p = 0.001$), which explains 61% of their variation (Fig. 6A). Moreover, we detected that variation of ses.MPD was significantly and positively affected by PCA1t (LMM, Estimate = 0.21, $t = 3.04$, $p < 0.009$) and PCA1f (LMM, Estimate = 0.13, $t = 3.15$, $p < 0.007$), which together explain 88% of variation (Fig. 6B and C; Table 1). According to the best models, the variability of soil texture (PCA1t) was the main predictor with the strongest positive effects on ses.MNTD (LMM, Estimate = 0.42, t = 6.6, p = 0.001) explaining 73% of variation (Fig. 6D, Table 1). Stand ages did not demonstrate significant influence on the phylogenetic metrics across any tested models (Table 1). The random intercepts of the models demonstrated the largest variance of the random effects of patch and plot of the forest sites for the main effect of soil fertility on sesPD and the smallest variance for the main effect of stand age on sesPD (Table 1).

4. Discussion

In this study, we evaluate the relative importance of soil properties and stand age on phylogenetic diversity metrics, we found that the phylogenetic metrics are context-dependent after disturbances caused by shifting cultivations in forests (Kraft et al., 2015). We corroborate the hypothesis that tree communities show phylogenetic clustering in initial successional stages, whereas old-growth forests show phylogenetic neutrality probably due to the alternated forces of action, from abiotic to

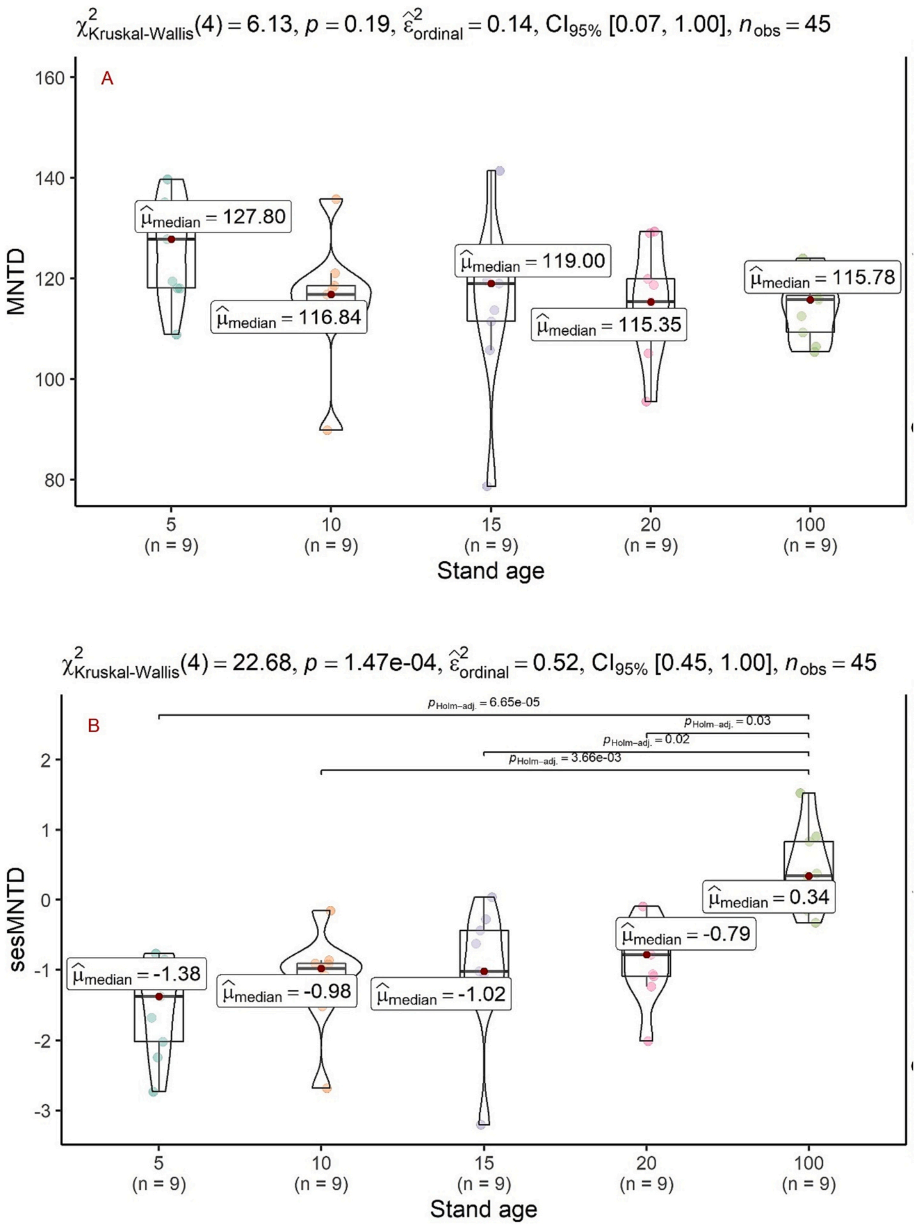

Fig. 5. Comparisons of the mean nearest neighbor distance (MNTD) (A), and standard effective size of MNTD, ses.MNTD (B) between second-growth forests and old-growth forest patch (OG). The mean value (red point) is presented for different stand age (5, 10, 15, and 20 years old) and in an old-growth forest (OG). The values above horizontal brackets indicate the p-values (Dunn, $P < 0.05$) of the significance of the comparisons between stand ages. The estimated effect size and confidence interval (CI) level are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

biotic filtering, during succession. In addition, our study demonstrates that both soil-mediated filtering and neutrality-based stochastic process can determine phylogenetic structure of SG. However, we infer that the observed change from clustered to random phylogenetic structure is shaped by the relative role of environmental filtering (e.g., deterministic processes by soil constrictions) compared to limiting similarity during succession, as reported for late-successional stage of tropical forests (e.g., Letcher, 2010; Letcher et al., 2012). Thus, environmental filtering and deterministic processes may be important when the harsh ecological condition after shifting cultivation promotes higher species turnover through colonization and regrow.

Overall, our study supports the hypothesis that phylogenetic structure and diversity of tree community along Amazon forest succession is predominantly shaped by deterministic processes such as soil-mediated filtering and competition, rather than stand ages and neutrality-based stochastic processes (Kraft et al., 2015). Moreover, early-successional soil conditions work as an environmental filter, determining phylogenetic clustering of woody communities, whereas biotic factors would contribute to reduce this clustering in OG forests. Thus, our results support the general assumption that soil is a key factor for plant diversity components (i.e., taxonomic, functional, and phylogenetic) at local scale in multiple ecosystems (Villa et al., 2018b; Campos et al., 2021; Gastauer et al., 2017).

The impact of environmental (abiotic) and biotic filtering and stochastic processes on the phylogenetic diversity and structure of woody communities along Amazon forest succession is still poorly known. Although studies have shown that stand age can represent a strong predictor of diversity in plant communities during tropical forests successions (Becknell and Powers, 2014; Villa et al., 2018b), our results highlight the opposite. Soil-related properties were the most important predictors to explain phylogenetic diversity, probably because more phylogenetically-distant species can coexist by using soil resources in different ways and thus occupy the niche space (Cavender-Bares et al., 2009; Ulrich et al., 2014). Hence, environmental filtering may be more important than stand age mainly during early successional stages, probably due to the negative impact of SC practices on soil properties (Kraft et al., 2015, Ulrich et al., 2016).

Most studies evaluating soil-mediated filtering on phylogenetic

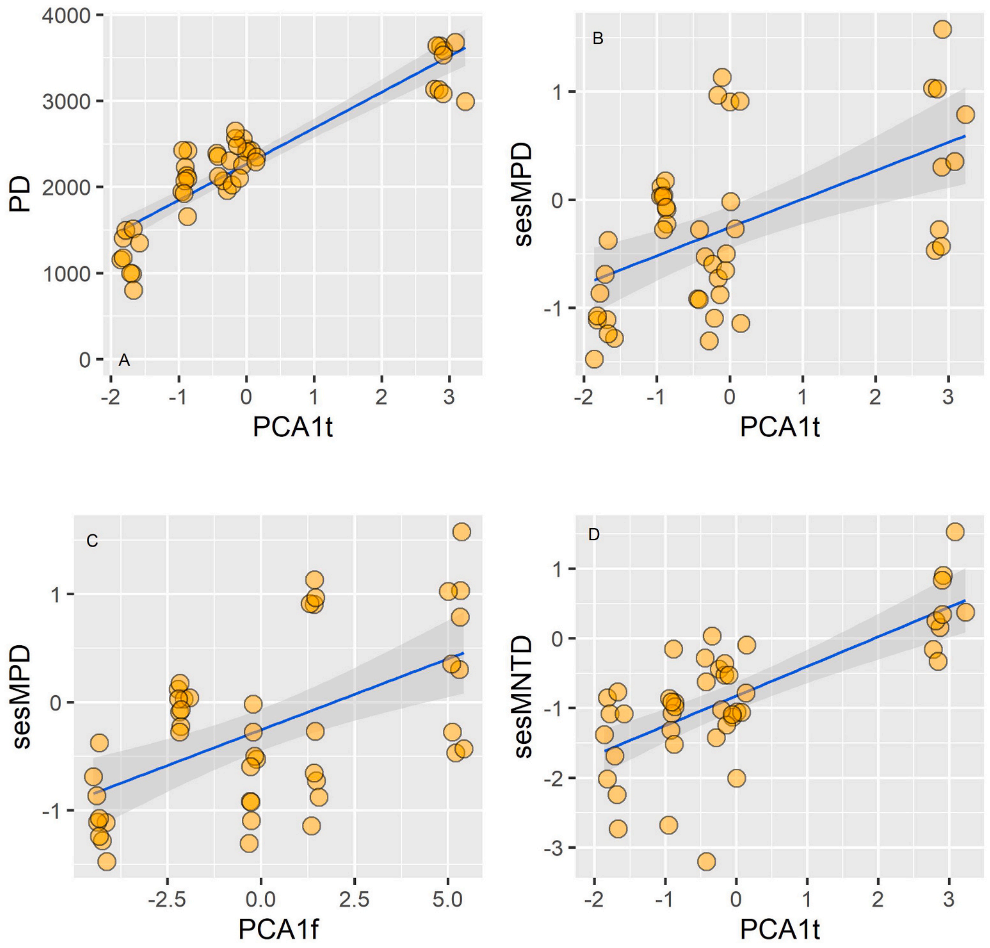

Fig. 6. Relationships between the soil attributes (PCA1f and PCA1t) and phylogenetic metrics (PD, sesMPD and sesMNTD). PD: phylogenetic diversity (A); ses.MPD: standard effect size of mean pairwise distance); (B-C); ses.MNTD: standard effective size of mean nearest taxon) (D). PCA1f (variability of nutrients content related soil fertility); and PCA1t (variability of physical properties related to soil texture). Solid lines represent the models' fitted (predicted) values and the shaded polygons the 95% confidence interval associated with the modeled predictions.

Table 1
Best selected (ΔAIC < 2) linear mixed models (LMM) based on tree global models explaining the relationships between the phylogenetic metrics (response variables; sesPD, sesMPD and sesMNTD) and soil (PCA1f and PCA1t) and stand age as predictors.

Model	Response variable	Explanatory variable	R^2	Randon effects	Fixed effects	Likelyhood	AICc	ΔAIC	AICcWt
Model 1	PD	~PCA1t	0.80	0.72	0.91	−46.10	101.2	0.0	0.61*
Model 2		~ PCA1f	0.72	0.71	0.45	−45.91	103.4	2.15	0.25*
Model 3		~ Stand age	0.47	0.12	0.23	−47.92	103.4	2.22	0.14
Model 4	sesMPD	~PCA1t	0.68	0.53	0.95	−39.63	88.3	0.0	0.50*
Model 5		~ PCA1f	0.48	0.48	0.39	−39.83	88.7	0.40	0.38*
Model 6		~Stand age	0.38	0.21	0.16	−39.49	90.5	2.25	0.12
Model 7	Ses.MNTD	~PCA1t	0.72	0.50	0.87	−45.14	99.3	0.0	0.73*
Model 8		~PCA1f	0.67	0.48	0.46	−46.29	101.6	2.31	0.18
Model 9		~Stand age	0.41	0.37	0.27	−45.10	101.7	2.46	0.10

The response variables are indicated: sesPD, standardized effect size of phylogenetic diversity; ses.MPD, standard effect size of mean pairwise;ses.MNTD: standard effective size of mean nearest taxon. The explanatory variables are indicated: PCA1f (variability of nutrients content related soil fertility); PCA1t (variability of physical properties related soil texture). Was used separate univariate LMMs models after tested the explanatory variables collinearity. AICc, Akaike criterion corrected for small samples (AICc); ΔAICc, the difference between the AICc of a given model and the best model was considered as ΔAIC = 0); AICcWt, Akaike weights (based on AIC corrected for small sample sizes). Models with significant effects (*) are indicated.

diversity and structure of plant communities have shown a low phylogenetic diversity and phylogenetic clustering under higher stress due to the nutrient's deficit for plant growth (Campos et al., 2021; Gastauer et al., 2017). Higher soil fertility (i.e., organic matter content, nutrients, and total exchangeable bases) may promote plant growth, which can increase phylogenetic diversity (Gastauer et al., 2017) and reduce phylogenetic clustering (Miazaki et al., 2015). Our results sheds light on the importance of soil texture to the phylogenetic diversity and structure after shifting cultivations in Amazon forests, indicating the role of context-dependency in successional stages of restoration. Among the influential contextual factors, the slash and burn practices might have affected the soil's physical and chemical properties before the farming crop phase (Are et al., 2009; Thomaz, 2009) since the increasing in fuel material (i.e., aboveground biomass) for burning may intensify the fire and damage the topsoil properties and functions (Are et al., 2009; Thomaz, 2009; Thomaz, 2013; Thomaz et al., 2014).

The impact of slash and burn can drive the trajectory of secondary forest succession by reducing the recovery of vegetation and properties related to soil fertility and texture (Villa et al., 2018a), which in turn changes the richness and phylogenetic diversity of tree communities (Purschke et al., 2013). For instance, after slash and burn, the ash incorporates nutrients available for opportunistic species (e.g., annual crops) for a short period due to degenerative effects on soil physical properties, with low ability to retain nutrients and fertility (Certini, 2005; Wuest et al., 2005). In addition, bare soils (i.e., with low vegetation cover of annual crops) quickly loses nutrient through the erosion caused by the direct impact of precipitation and runoff (Cerdà and Doerr, 2008; Thomaz, 2013). As an outcome, most soil nutrients are leached out soon after the abandonment due to the high sand content and rainfall in tropical regions (Hattori et al., 2019), and then runoff and soil loss can decrease exponentially from the burned phase to the early successional stages of SG (Thomaz, 2013). Such a soil degradation process affects the fertility content in silt soils of old-growth forest and let soils in SC with a high proportion of sand and low fertility (Hattori et al., 2019). However, under unstable conditions, the reduction of nutrient content can be different between clay-rich and sandy soils (Hattori et al., 2019).

Our study reveals that agricultural practices, rather than successional age, are probably the main cause of changes in the patterns of phylogenetic diversity during forest recovery. The phylogenetic diversity increased with increasing soil nutrients and improved soil texture, and this specific effect seems to be stronger in the later successional stages (e.g., old-growth forests). These results might be related to the fact that sites having high availability of soil nutrients may harbor diverse species through the availability of niche space in species-rich forests (Brown, 2014). However, biotic filtering (e.g., competition) be more intense in the late sucessional stages than in early ones, whereas the opposite trend might be true for environmental (abiotic) filtering (Letcher et al., 2012). The environmental conditions change throughout the succession, that is, the soils are already more fertile in advanced sucessional stages and therefore no longer represent such a restrictive filter. Meanwhile, species selected under degraded soils in early sucessional stages may be less competitive in OGF, therefore, the environmental filter should not be the same throughout succession until later stages . However, we found that, while stand age did not influence phylogenetic diversity, phylogenetic diversity between SG and OG forests were significantly different. These results indicate that soil properties over time, rather than increasing the time span of stand age alone, shapes the phylogenetic diversity of trees in Amazon forests. Perhaps differences in age are not revealed over a period of 20 years, but over 50 years, for example, especially if we consider the regeneration strategy of tree species, even pioneer ones, must exceed a few decades.

Although the environmental filtering emerges as the main driver of phylogenetic diversity in the studied Amazonian forest, we have to consider that relatedness is also dependent upon the functional attributes of the species. Thus, not necessarily communities holding a high phylogenetic diversity will show a high functional diversity (Cadotte et al., 2011). One can stick on the expectation that closely related species are usually ecologically similar and so they have more chances of co-occurrence (Cadotte et al., 2009). However, it can be also expected that closely related species compete strongly due to their ecological similarity, limiting their coexistence (Berntson and Wayne, 2000; Godoy et al., 2014). Suppose that phylogenetic structure and diversity patterns in our study is also an outcome of competitive interactions, the SG forests are occupied by phylogenetically close species in nutrient-limited sites probably because of the effects of the disturbances by shifting cultivations. Conversely, phylogenetically distant species sites occupy the nutrient-rich old-growth forests by having succeed in overcoming the environmental and biotic filtering processes through time (Cavender-Bares et al., 2009; Kraft et al., 2015).

Our results allow us to resume that the induced changes by shifting cultivation may affect the relative importance of the ecological processes (i.e., deterministic, and stochastic process) and their associated factors (i.e., abiotic and biotic) along secondary succession, which determine phylogenetic diversity and structure at a local scale. Overall, our findings refute that tree communities during early stages after disturbance are more likely to be composed of more closely related species than distantly-related species (Verdú and Pausas, 2007, Ding et al., 2012). We anticipate that our study will better promote further research on disturbance intensity and frequency to assess patterns of phylogenetic diversity and structure in these tree communities.

4.1. Implications for forest management and conservation

Traditionally, SC occupy small areas (0.1–0.8 ha) and have short cycles of agriculture (1–3 years), followed by fallow periods (i.e., natural regeneration) when the system is abandoned, representing a sustainable agricultural system in Amazonas region for a long time (Bush et al., 2015; Villa et al., 2017, 2021). However, agricultural intensification and forest degradation can alter patterns of phylogenetic diversity in tree communities at a landscape scale (e.g., Santo-Silva et al., 2018), which can be assessed based on phylogenetic diversity and structure metrics to predict vulnerability to local taxa loss and biotic homogenization. Then, under this approach, it can be inferred that both sustainable soil management and diversity of tree species would allow the conservation of taxa at a local scale, avoiding species loss with forest degradation.

Most studies have demonstrated that stand age is the main predictor of species richness and soil fertility (Becknell and Powers, 2014; Villa et al., 2018b; Poorter et al., 2016). Furthermore, successional habitat filtering by stand age and soil-mediated filtering can simultaneously determine soil resource availability and temporal changes in species richness and phylogenetic diversity, thus regulating the successional trajectories (Letcher et al., 2012; Arroyo-Rodríguez et al., 2015; Villa et al., 2018b; Rozendaal et al., 2019; Kleinschmidt et al., 2020). Initial soil properties (i.e. low soil fertility and high sand proportion) during early-successional conditions (i.e. 5–20 years old of stand age) filter commonly fast-growing and light-demanding pioneer species that colonize communities immediately after disturbance (Chazdon, 2014; Villa et al., 2018b, 2019). Then, replacing SG species with old-growth species is found to dominate young secondary and mature forests (Chazdon, 2014; Poorter et al., 2016). Thus, tree species regeneration strategies (i.e., light-demanding pioneers and shade-tolerant trees) are also related to successional habitat filtering and soil-mediated filtering along forest regeneration (Kleinschmidt et al., 2020; Villa et al., 2021). This succession pattern corroborates that when the environmental filters and habitat types are acting with higher strength, species with similar attributes, suitable for those conditions, are sorted predominantly during community assembly (Götzenberger et al., 2012; Kraft et al., 2015).

A growing body of studies on tropical forest recovery are analyzing the changes of stand-age-dependent forest attributes, such as biotic (i.e., tree community diversity, composition, and structure) and abiotic factors (i.e., chemical, and physical soil properties), in secondary succession compared to old-growth forests without disturbances (Poorter et al., 2016; Rozendaal et al., 2019). However, Amazon forest restoration strategies depend critically on integrative approaches (i.e., Dubey et al., 2020; Villa et al., 2021) and the understanding of multiple dimensions of diversity in tree communities (i.e., beyond species number), which can reveal the high conservation value in human-modified tropical landscapes forests (Pausas and Verdú, 2010; Tucker et al., 2017; Santo-Silva et al., 2018). We presume that sustainable soil management (organic agriculture, agroforestry) as the main predictor can determine the conservation of tree species diversity (taxonomic, functional, and phylogenetic).

5. Conclusions

This study outlines the relative importance of soil-mediated filtering versus the direct effect of stand age in shaping phylogenetic diversity and structure of woody community along Amazon forest succession after shifting cultivation. We argue that both soil-mediated filtering and neutrality-based stochastic processes can determine phylogenetic structure of SG forests. Our study also shows that stand age is not the direct determinant of tree phylogenetic diversity during tropical forest succession, but further studies are needed to disentangle the mechanisms underlying tree phylogenetic diversity over time and forest succession. By reducing land-use intensification with permanent sustainable management systems at the landscape scale, it is possible to mitigate the degradation of physical and chemical soil properties and, consequently, reduce deforestation of new forest areas for shifting cultivation, maintaining a pool of species in old-growth forests and SG forest at different sucessional stages.

CRediT authorship contribution statement

Pedro Manuel Villa: Conceptualization, Methodology, Software, Writing – original draft. **João Augusto Alves Meira-Neto:** Conceptualization, Methodology, Writing – review & editing. **Écio Souza Diniz:** Software, Writing – review & editing. **Arshad Ali:** Writing – review & editing. **Andreza Viana Neri:** Writing – review & editing. **Sebastião Venâncio Martins:** Conceptualization, Methodology, Writing – review & editing. **Prímula Viana Campos:** Methodology, Software, Writing – review & editing. **Herval Vieira Pinto-Junior:** Writing – review & editing. **Jamerson Souza da Costa:** Methodology, Software, Writing – review & editing. **Alex Josélio Pires Coelho:** Writing – review & editing. **Francielli Bao:** Writing – review & editing. **Graziela de Araújo Lima:** Writing – review & editing. **Alessandro Rapini:** Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Pedro Manuel Villa reports financial support was provided by Global Environment Facility. Pedro Manuel Villa reports a relationship with National Council for Scientific and Technological Development that includes: funding grants.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2023.106915.

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