Prior land use shapes the functional composition of tree-seedling communities along a tropical forest chronosequence

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Abstract

Tropical rainforests are highly threatened by deforestation, yet they have the potential to regrow naturally when left abandoned. To understand natural recruitment, it is essential to explore the recovery of tree-seedlings and their traits within the community assembly of secondary forests. Here, we studied the taxonomic and functional diversity as well as the composition of tree seedling communities in 39 plots along a chronosequence of forest recovery, ranging from 0 - 38 years after cacao production or pasture abandonment. We measured leaf traits related to the life strategy (acquisitive or conservative) of all tree-seedling species and determined the surrounding forest cover within a 500 m radius around each plot. Our results showed that the (1) abundance, species diversity, and functional diversity of tree seedlings were increasing, and that the seedling composition was becoming more similar to old-growth forests with increasing time since the onset of recovery, even if it was nowhere near the composition of primary rainforests. The (2) abundance of tree seedlings and their species diversity increased with increasing forest cover. Remarkably, (3) the functional composition of the communities on plots formerly used for pasture was characterized by acquisitive traits, while former cacao plots and old-growth plots were associated with conservative traits, highlighting the role of prior land use in seedling recruitment.

Synthesis: Our study showed that forest recovery is a complex and multifactorial process. Forest cover is a key factor accelerating natural forest recovery, while prior land use may limit functional recovery, potentially affecting ecosystem functioning.

Keywords: chronosequence, forest recovery, prior land use, seedling functional composition, tree-seedling dynamics, tropical forest succession.

1 INTRODUCTION

Land use change leads to a loss of biodiversity and threatens ecosystem functions and services that nature provides for humans (Isbell et al., 2017; Newbold et al., 2015). Especially in the neotropics, primary rainforests are often converted to agricultural land (Curtis et al., 2018; Newbold et al., 2020) which affects the quality and spatial structure of the remaining primary rainforests and reduces greatly landscape connectivity (Edwards et al., 2019). Yet, large amounts of these agricultural land areas are abandoned every year, allowing secondary forest recovery to start (Chazdon et al., 2016). Sixty percent of tropical forests are currently considered secondary forests (Lennox et al., 2018; Ritchie, 2021), and it is particularly important to understand the dynamics of forest recovery in order to provide important insights into conservation management (Arroyo-Rodríguez et al., 2017; Meli et al., 2017). In particular, little is known about the resilience of the forest, i.e. the speed at which the regrowing forest resembles its original state (Nimmo et al., 2015; Pimm, 1984).

Previous work on forest recovery has shown that the composition of plant species changes during secondary succession. In young secondary forests, early-successional species assemble rapidly (Van Breugel et al., 2007), driven by environmental filtering (Baldeck et al., 2013). This fast establishment of early-successional species is due to their acquisitive trait strategy, which includes high photosynthetic rates, rapid growth, and low investment in defense mechanisms. Traits such as high specific leaf area and thin and soft leaves foster establishment, survival, and growth under the hard early-succession conditions (Estrada-Villegas et al., 2020; Lebrija-Trejos et al., 2010; Poorter et al., 2021). In comparison, the regeneration of late-successional species is highly variable and strongly determined by environmental conditions (Chazdon, 2008; Chazdon et al., 2007; Mesquita et al., 2015; Norden et al., 2009; Peña-Claros, 2003).

As forests recover, light intensity and soil nutrients availability decrease with an associated shift from early-successional tree species to late-successional ones. These species have conservative resource-use strategies, which prioritize shadow tolerance and protection against damage at the expense of slow growth rate (Whitfeld et al., 2014), allowing plants to perform better in such environmental conditions (Lohbeck et al., 2013; Peña-Claros, 2003; Pinho et al., 2018; Schönbeck et al., 2015). This points at the crucial role of functional traits in forest regeneration (Boukili & Chazdon, 2017; Swenson et al., 2012).

Although some studies have looked at forest recovery along a chronosequence (Denslow & Guzman G., 2000; Reiners et al., 1994; Saldarriaga et al., 1988), few have compared recovery patterns in relation to local land use history based on different types of land use (Jakovac et al., 2021). Even less studies have focused on the recovery of tree-seedling communities (Denslow & Guzman G., 2000; Marín et al., 2009). Species and functional traits composition in regenerating forests is further influenced by the type, intensity and duration of their prior land use such as pasture or plantations (Chazdon et al., 2007; Günter et al., 2006). For instance, tree-seedling recovery on pastures is characterized by high light availability and strong competition with grasses, preventing late-stage and mature forest species to establish, and fostering then a long persistence of early-successional species (Palomeque et al., 2017; Pascarella et al., 2000; Rivera & Aide, 1998). Moreover, prolonged intensive use of agricultural land can lead to soil eutrophication (e.g. through cattle dung) and depletion of organic matter (e. g. nutrients washed away on bare soil), which can slow down or even stop forest recovery (Chazdon et al., 2007; Holl & Zahawi, 2014). In contrast, tree plantations, as cacao plantations, feature similar environmental conditions as forests. The closed canopy cover results in low light intensity and provides structural habitat characteristics for seed dispersing birds and mammals, facilitating the recruitment of late-successional species (Pascarella et al., 2000). Yet, the use of pesticides together with the intensive land use can weaken the resilience of the ecosystem, by altering or reducing soil micro- and macrobiotic communities, which, in turn, might reduce the nutrient availability for plants, and thus seedling establishment (Jakovac et al., 2021).

It has also been shown that the landscape matrix can modulate forest recovery (Boukili & Chazdon, 2017) with the proximity and cover of mature forest in the surrounding landscape influencing seed input and creating favorable micro-climatic conditions for seed germination (Mullah et al., 2011). For example, the composition of recovering seedling communities resembles those of old-growth forests much faster when being in close vicinity than in distant vicinity to forest remnants (Chazdon et al., 2009; Letcher & Chazdon, 2009). The influence of surrounding forest landscapes on tree-seedling recruitment is larger in early stages of succession, when seed input seems to be more important than forest prior land use than in later stages of forest recovery (Lu et al., 2016).

Despite knowing the main factors influencing forest regeneration, predicting the forest recovery is a highly uncertain and complex task (Norden et al., 2015). It is therefore essential to shed light on the multiple factors affecting succession at local scale, such as remaining forest, prior land use, light availability and forest recovery time, to increase the success of forest restoration.

In this study, we monitored tree-seedling recruitment along a chronosequence across a gradient of tropical rainforest recovery originating from former pastures and cacao plantations. Our study has the advantage of presenting both prior use types (cacao plantations and pasture) with an age gradient in the same region, allowing us to compare locally the effect of the forest prior land use. On 39 selected plots, we assessed the abundance, species diversity and composition of seedling communities and measured traits related to their life-history strategy (Specific Leaf Area (SLA), leaf thickness and toughness, and Leaf Dry Matter Content (LDMC)) to determine the functional diversity and composition. We expect that (1) seedling abundance, species diversity and functional diversity will gradually increase toward those values seen in old-growth forests as forest recovery progresses, with the diversity recovery differing with prior use as recovery is slowed down in pastures (Chazdon et al., 2007; Holl & Zahawi, 2014). Likewise, we predict (2) that the compositional similarity to old growth forests will recover more slowly on pastures than on cacao plantations, for both species and functional composition. Finally, we predict the community composition recovery to show (3) a shift in trait composition from acquisitive to conservative traits with regeneration time.

2 MATERIALS AND METHODS

2.1 Study site and plot design

Our study was conducted in the Chocó lowland tropical rainforest, Esmeraldas Province in Ecuador (Figure S1), as part of the REASSEMBLY research unit (Escobar et al., 2025). Mean annual temperature ranges from 22 – 23°C and the mean annual precipitation ranges between 3000–6000 mm, with dry seasons occurring in June-July and October-November. The elevation varies between 159 m and 615 m (Escobar et al., 2025). The study area was located within and around the forest reserves Canandé and Tesoro Escondido, comprising about 6,500 ha of evergreen old-growth forest, regenerating secondary forests either recovering from cattle grazing pastures or cacao plantations, as well as active pastures and cacao plantations. More detailed information on the study area can be found in Escobar et al. (2025).

We collected data in 39 plots comprising nine old-growth forest plots, eleven secondary forests originating from pastures, eleven secondary forests originating from cacao plantations, four active pastures and four active cacao plantations. Active plots were assigned to a recovery age of 0. The secondary forest plots depict a chronosequence, i.e. successional gradient of plots distributed between one and 38 years; with the oldest plot abandoned in 1985 and the youngest in 2022. Hereafter, active and secondary former pasture plots will be named pasture regeneration, and active and secondary former cacao plots will be referred to as cacao regeneration. To minimize spatial dependence, plots with the same age and prior land use were at least 200 m apart. The elevation of the plots ranged from 127 to 615 m with old-growth forests, on average located at the highest elevation (374 ± 30 m), followed by cacao regeneration (319 ± 35 m), pasture regeneration (308 ± 31 m), active pasture (205 ± 39 m), and active cacao plantations (205 ± 58 m). Our previous results suggest that there is no significant effect of altitude on the plot design (Escobar et al., 2025).

2.2 Tree-seedling monitoring and taxonomic response variables

We monitored tree-seedling recruitment on four 1 m^2 quadrants randomly placed within the 39 plots. We defined seedlings as all young plants (including palm trees), that grew from a seed or resprouted from a fallen branch and had a root-collar diameter (RCD) between 2 mm and 10 mm. All tree seedlings were tagged and identified to the lowest taxonomic level possible (species or morpho-species level). For this study, we used the data of the seedling communities to determine taxonomic diversity and composition per plot.

2.3 Leaf trait measurements and functional trait response variables

To determine the functional diversity of seedling communities along the chronosequence we collected seedlings of the most common species and morphospecies from the close surroundings of 32 out of the 39 plots covering all successional regeneration time and forest prior use (five plots on active cacao plantations, 18 secondary forests, nine old-growth forest plots). The functional traits were averaged per species and regeneration stage (forest prior use and age). No seedlings were collected inside our quadrants, to allow for monitoring replication. In total, we collected 290 individuals belonging to 46 (morpho-)species, with an average of four individuals per (morpho-)species.

We measured four morphological leaf traits on 3-6 leaves per seedling in the lab following Cornelissen et al. (2003): Specific leaf area (SLA, mm^2/mg), leaf thickness (mm), leaf toughness (N) and leaf dry matter content (LDMC, mg/g). These four traits have been shown to be related to a gradient from fast-growing/acquisitive to slow-growing/conservative strategies in trees (Chai et al., 2016; Lasky et al., 2014). While SLA of a species is positively correlated with leaf life span, potential growth rate and photosynthetic rate in tropical tree species (Poorter et al., 2004), LDMC, thickness and toughness are linked to leaf resistance towards physical hazards as well as to the relative water content and are therefore used as a proxy for plant water deficit (Castro et al., 2023; Frenette-Dussault et al., 2012). The four selected traits have also been related to the canopy-light regime and soil-nutrient availability (Hofhansl et al., 2021; Pinho et al., 2018), both environmental factors related to forest succession.

We determined the toughness and thickness of the leaves with the help of a penetrometer (1 digit accuracy, IMADA, Japan) and a micrometer (Mituyoto, Germany) respectively. The leaves were then weighed to obtain fresh mass (FM, g) per individual with a fine scale balance (±003 g, Kubei, China), including the petiole. After drying the leaves with silica gel (LLG-Labware), we measured leaf dry mass (DM, mg) and calculated LDMC (mg/g) as DM divided by FM. To calculate SLA, we scanned the leaves to calculate the leaf area (LA, mm^2) with a CanoScan LiDE 300 device (Canon INC., Germany). The resolution of the scan was set to 300 dpi. The leaf area was then calculated using images based on a semantic segmentation approach that employed deep learning. This was done with the aid of the DeepLabV3 model (L.-C. Chen et al., 2017) that utilized the ResNet101 backbone (He et al., 2015). The optimizer used was Adam (Kingma & Ba, 2017), while Focal Loss (Lin et al., 2018) was used for the loss parameter to account for class imbalance due to the smaller holes found within the leaf. In total, 169 images (out of 1167) underwent labeling during the training pipeline. In this labeling process, the images were classified manually to train the AI algorithm to recognize the leaf lamina shape, in order to count the number of pixels, equating the leaf area. To validate the precision of this method, we compared the results from the deep learning process with those that were obtained after calculating the LA of approximately 30% of the pictures using GIMP (The GIMP Development Team (2024), version 2.10.38). Lastly, we calculated SLA (mm^2/mg) as LA divided by DM.

2.4 Environmental variables

For each plot, we have information on the *regeneration time* (1 - 38 years) and *prior land use (pasture* or *cacao*). We classified as early secondary forest plots ranging from 0 to 12 years of recovery, late secondary forests as plots ranging from 19 to 38 years of recovery, and old-growth forest as plots with unknown age, but not known human use in the recent past. In addition, we assessed four environmental variables per plot that have been shown to influence the recovery of seedling communities: *elevation*, *forest cover*, *distance to forest* and *light availability*. Detailed information about our environmental variables can be found in Table S2. We determined *elevation* as proxy for differences in climatic conditions. Since the elevation gradient is small (400 meters approximately), we expected it to play a minor role in our study area, however, we still controlled for elevation in our models (Escobar et al., 2025). Using satellite data, we also assessed the *forest* *cover* within a 500 m radius around each plot and the linear *distance to the closest forest* as source of seed input. For more information on the landcover context data, please address Escobar *et al.* (2025). Finally, *light availability* was estimated on each plot by assessing the leaf area index (LAI) using the LICOR LAI 2200. After cross-correlating these variables, we excluded *LAI* and *distance to forest* from the models because they were highly correlated with *regeneration time* (Pearson correlation= 0.73) and *forest cover* in the 500 m radius (Pearson correlation= -0.61), respectively (Figure S2).

2.5 Statistical analysis

2.5.1 Response variables

All analysis were carried with the statistical software R (v 4.4.1) (R Core Team, 2024). Spatial autocorrelation was tested for all response variables with a Moran's I test, and no spatial correlation was found.

Tree-seedling abundance and diversity

We assessed tree-seedling abundance to determine any effect of abundance of individuals on the response of diversity to recovery age. This was calculated to avoid misinterpretations when observing effects on species diversity, since the small sample size due to the slow recovery of tree-seedlings did not allow us to perform rarefaction analysis.

As a measure of tree-seedling diversity, we assessed the Exponential Shannon-Index [exp(H_Shannon)] (Jost 2006). This was calculated using the function "diversity" from the package "vegan" (v. 2.6-6.1) (Oksanen et al., 2024). This transformation of the Shannon-Index determines the "true diversity" value, or the equivalent amount of equally common species to a specific Shannon-Index value.

Based on the functional trait measurements, we determined the functional diversity of the seedling communities. We calculated the functional diversity per plot using the multifunctional Rao's quadratic entropy index (RaoQ) (Botta-Dukát, 2005) which considers multiple traits and the species relative abundances. The functional diversity RaoQ was obtained with the function "dbFD" from the R package *"FD"* (Laliberté et al., 2014; Laliberté & Legendre, 2010).

Tree-seedling composition

To determine the similarity of species' composition between secondary forest plots and the surrounding old-growth forests, we calculated the Bray-Curtis dissimilarity between each secondary forest plot and all eleven old-growth forest plots. The mean value of Bray-Curtis dissimilarity was then extracted for each secondary forest plot. By transforming Bray-Curtis's dissimilarity into similarity (f(x)= 1- Bray-dissimilarity) we obtained our response variable, ranging from 0 to 1. The larger or closer to 1 the Bray-Curtis similarity score, the more similar the species communities from secondary forest plots were to the old-growth forest. Since this index relies heavily on the abundance of species, common species have a stronger impact on the metric. Thus, we assigned a value of 0 in the Bray-Curtis similarity score to the plots that had no individuals. To avoid exact zeros and run beta-regression models (for predictors and model explanation see below in "Statistical analysis" section), we added a value of 0.01 to all similarity scores.

We also determined the similarity of functional composition of the seedling communities in the secondary plots compared to the old-growth plots and we identified associations in the functional trait structure in the tree-seedling communities. To do so, the similarity in functional composition was based on the pairwise comparison of the “gower” distance of the Community Weighted Mean (CWM) per plot (Díaz et al., 2007), as further response property of forest recovery along the chronosequence. CWM represents the mean of the trait values in a community, weighted by the relative abundance of the species. It is often understood as the dominant trait value in a community, and it is a useful tool to compare communities to each other, or study how the functional composition of a community changes over time. The distance matrix was obtained with the *“cluster”* package (Maechler et al., 2022). As well as for similarity of species composition, we obtained the mean value of the distances of the secondary plots to every old-growth plot. We transformed the gower-distance into similarity of functional composition by subtracting it from 1.

Finally, we studied the functional structure association through a Principal Component Analysis (PCA) implemented with the base R package 'stats' (R Core Team, 2024). The PCA was performed on a plot-level functional composition matrix, which included the mean values of the four traits per plot: specific leaf area (SLA), leaf thickness, leaf toughness, and leaf dry matter content (LDMC). From the PCA, we extracted the scores of the first two axes as response variables: PC1 (scores from the first axis) and PC2 (scores from the second axis).

For the functional analysis, we excluded all the plots that had less than 75% of the individuals from the species sampled for functional traits, to minimize the effect of under-sampling and missing trait values in the analysis. Also, we excluded all plots that had no individuals due to their young age (11 plots). Furthermore, a further plot had to be omitted in the functional diversity (RaoQ) analysis due to less than three functionally species.

2.5.2 Ecological modelling

We ran linear models with all response variables (abundance, species and functional diversity, species and functional composition, as well as the two PC axis) and the four environmental variables as predictors (*elevation, forest cover, forest prior land use* (*cacao* or *pasture*) and *regeneration time*). We tested the interactions between *prior land use* and *regeneration time* to assess how land use influences forest succession. All numeric predictors were centered, *regeneration time* was square root transformed and old-growth forest plots were excluded from the analysis because we had no knowledge on the precise age of these plots.

To test our first hypothesis that species diversity and functional diversity will increase with *regeneration time*, we modeled the tree-seedling abundance (model 1, Table S1) and species diversity (model 2, Table S1) response to *regeneration time* according to *prior land use*, including *elevation* and *forest cover* effect in the analysis as covariates. The increase in functional diversity as succession progresses, required a third linear model (model 3, Table S1), with the RaoQ index modeled against the plot predictors.

We used a combination of two measures of similarity in composition to old-growth forest to address the second hypothesis stating that the similarity in composition will show stronger differences to the old-growth plots in *pastures* than in *cacao* plantations. Both Bray-Curtis similarity (similarity of species composition) (model 4, Table S1) as well as CWM similarity (similarity of functional composition) (model 5, Table S1) to old-growth forests were modeled against the environmental predictors. For the response variables: similarity of species composition, similarity of functional composition to old-growth forest and functional structure, the predictor *regeneration time* was modeled with a quadratic term. To test the third hypothesis about the trait shift from acquisitive to conservative traits, the functional trait structure per plot (PCA) was modeled. The first two axis, PC1 (model 6, Table S1) and PC2 (model 7, Table S1) were modeled with our four environmental predictors. We considered functional trait responses as high SLA and low LCMC, leaf thickness and toughness to be related with acquisitive strategies of tree seedlings, as found in previous literature (Lasky et al., 2014) while conservative strategies to be related to low SLA and high leaf thickness, toughness and LDMC.

To analyze our data, we selected different families based on the distribution of each response variable. For count data (abundance, Table S1), we used a negative binomial family to address overdispersion. For proportional data, ranging between 0 and 1 (similarity of species and functional composition, Table S1), we applied a beta regression. Continuous variables (species and functional diversity, as well as the functional structure, Table S1) were modeled using Gaussian families. Predictor significance was tested with an Anova test for normally distributed response variables (models 2,3, 6 and 7, Table S1), and a deviance Table for the non-normal ones (model 1, Table S1) using the "car" package (Fox & Weisberg, 2019). For the models 4 and 5 (Table S1) we tested the significance with the Wald-z test from the "summary" function in the "betareg" package (Cribari-Neto & Zeileis, 2010). We calculated the 95% confidence intervals for our estimates. All model residuals were evaluated to ensure that model assumptions were met, and potential model fit issues were assessed using the packages 'DHARMa' (Hartig 2022) and 'performance' (Lüdecke et al. 2021).

3 RESULTS

3.1 Tree-seedling abundance and diversity increase with recovery time along the chronosequence

Across our 39 study plots we recorded a total of 241 individuals (0 to 16 individuals per plot with one individual plot outlier with 49 individuals) belonging to 50 species and 16 morphospecies (0 to 11 species per plot). From these species, 8 were found in early secondary forests only, 15 established only in late secondary forests and 27 were found in old-growth forests only; 16 were intermediate species, found all over the regeneration gradient (Figure S3). Seedling abundance increased with increasing *regeneration time* (Table 1; Figure 1A) from a mean number of 0 individuals in active pastures and cacao plantations, to 4 individuals from 3 morphospecies in secondary forests and a mean number of 11 individuals and 7 morphospecies in the 8 old-growth plots. Likewise, the abundance of seedlings was also positively influenced by the *forest cover* within the 500 m radius (Table 1; Figure 1B). Neither the *prior land use* (Table 1) nor *elevation* had a significant effect (Table 1) on the recovery of seedling abundance.

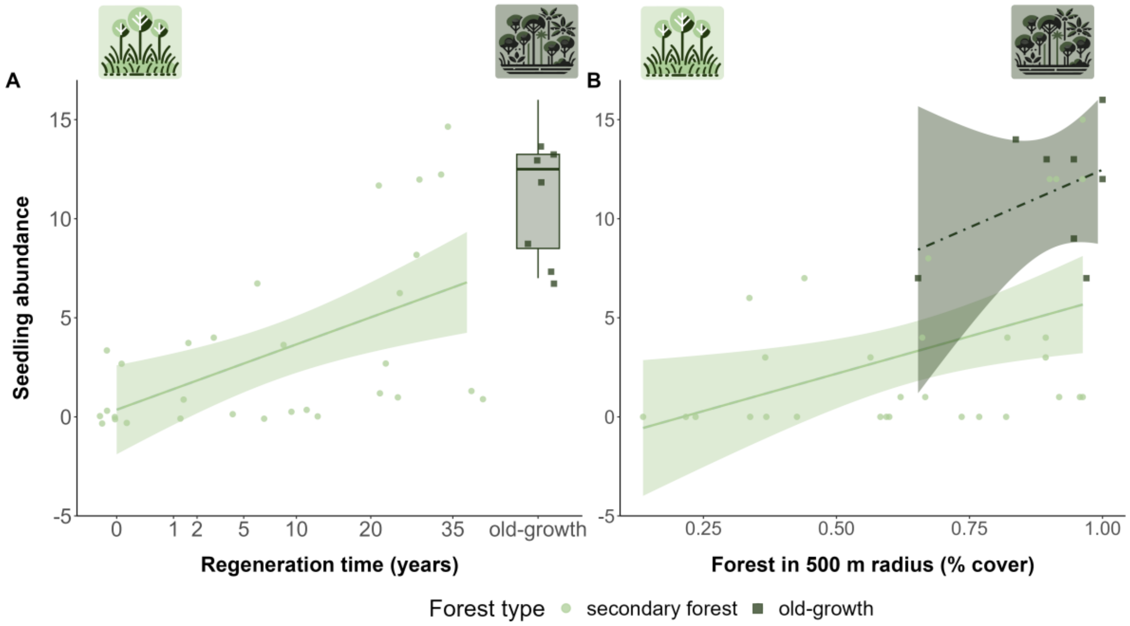

Figure 1. The influence of regeneration time (A) and forest cover within a 500m radius (B) on seedling abundance in 30 secondary forest plots (light green) and 8 old-growth forest plots (dark green). Regeneration time (A) was square root transformed. Green dots and regression line with confidence interval represent secondary forest plots. Continuous lines represent significant relationships ($p < 0.05$). Old-growth forest plots are plotted in dark green. Significance was based on linear models that included "elevation", the forest cover in the surrounding 500 m, prior land use and regeneration time as fixed factors. See Table 1 for statistical results. n = 30 plots.

Likewise, although species diversity also increased with increasing *regeneration time* (Table 1; Figure 2A) and marginally with *forest cover* (Table 1; Figure 2B) from 0 to 7 species, it did not reach up to the level of diversity of the old growth forests in the study area.

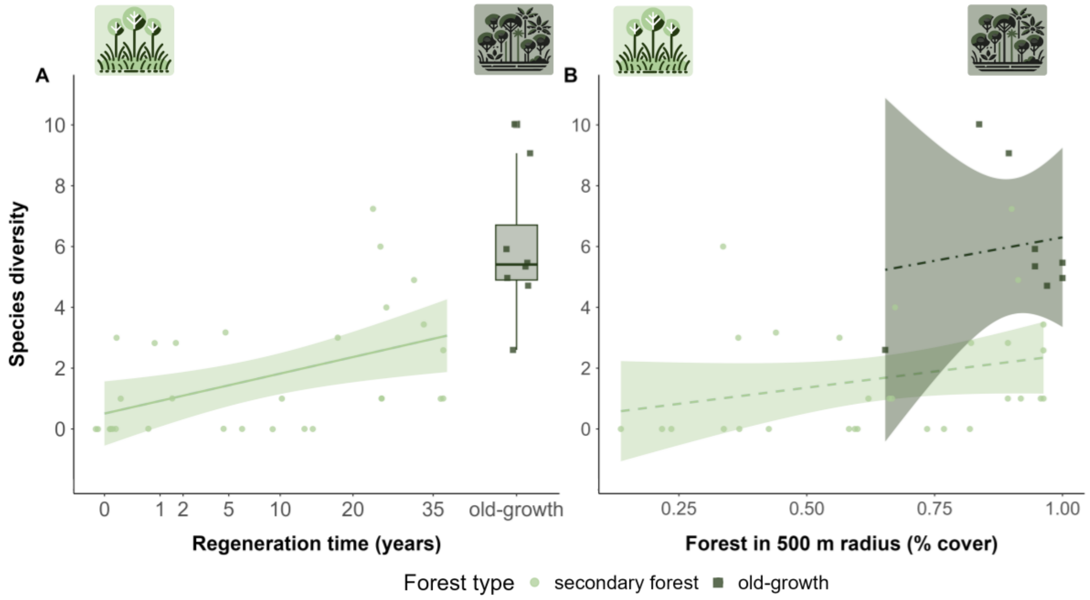

Figure 2. Relationship between seedling species diversity (exponential Shannon Index) and regeneration time (A) and amount of forest in the closest 500m (B), for 30 secondary forest plots in comparison with 8 old-growth forest plots. Regeneration time axis (figure A) was square root transformed. Green dots and regression line with confidence interval represent secondary forest plots. Continuous lines represent significant relationships ($p < 0.05$). Old-growth forest plots are plotted in dark green. Significance was based

on linear models with elevation, the forest cover in the surrounding 500 m, prior land use and regeneration time as fixed factors. See Table 1 for statistical results. n = 30 plots.

3.2 Functional seedling diversity increases with regeneration time along the chronosequence

The functional diversity ranged from a minimum of 0 to a maximum of 5.33 across plots (range for active pastures and cacao plantations: 0-1.25, for secondary forest: 0-5.33, and for old-growth forest: 0.47 to 3.84). The six plots with a functional diversity value of 0 ranged from 0 to 38 years with one plot originating from a previous cacao plantation and five from previous pastures.

Functional diversity (RaoQ) increased with increasing *regeneration time* (Table 1; Figure 3) and slightly decreased with *elevation* (Table 1).

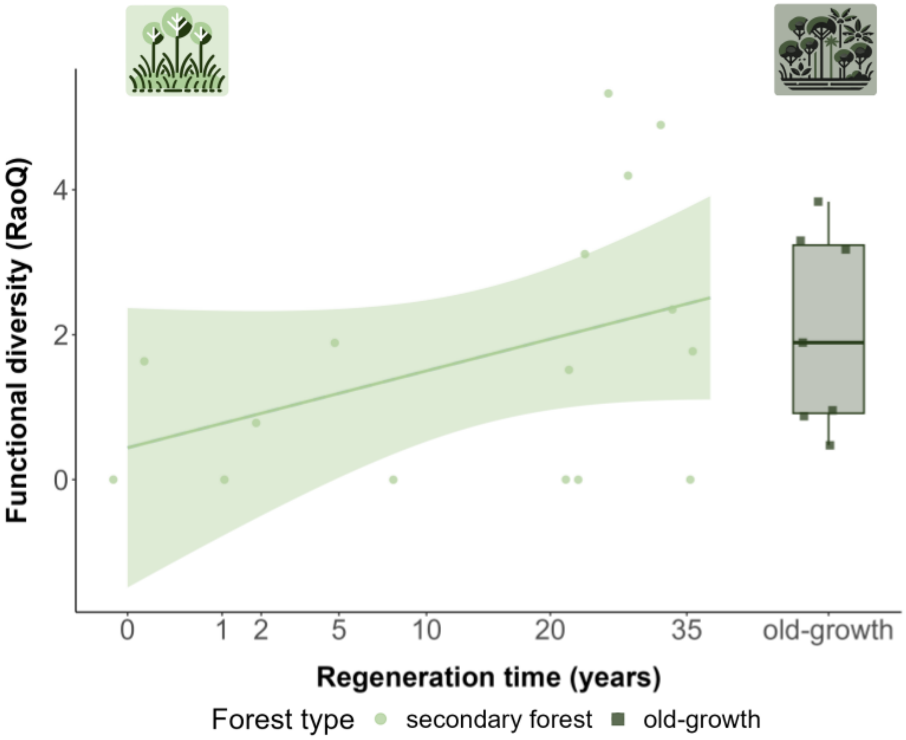

Figure 3. Relationship between functional seedling diversity (RaoQ Index) and regeneration time for 16 secondary forest plots (light green) in comparison to 8 old-growth forest plots (dark green). Regeneration time axis was square root transformed. Green dots and regression line with confidence interval represent secondary forest plots. Continuous lines represent significant relationships ($p < 0.05$) based on linear models with elevation, the forest cover in the surrounding 500 m, prior land use and regeneration time as fixed factors. See Table 1 for statistical results. n = 16 plots.

3.3 Similarity in species composition to old-growth forest increases with regeneration time

Species composition in our study area showed a high variability even among the old-growth forest plots (from 0.15 to 0.30). Similar to seedling abundance and diversity, the compositional similarity to old-growth forest increased with increasing forest *regeneration time* (Table 1; Figure 4).

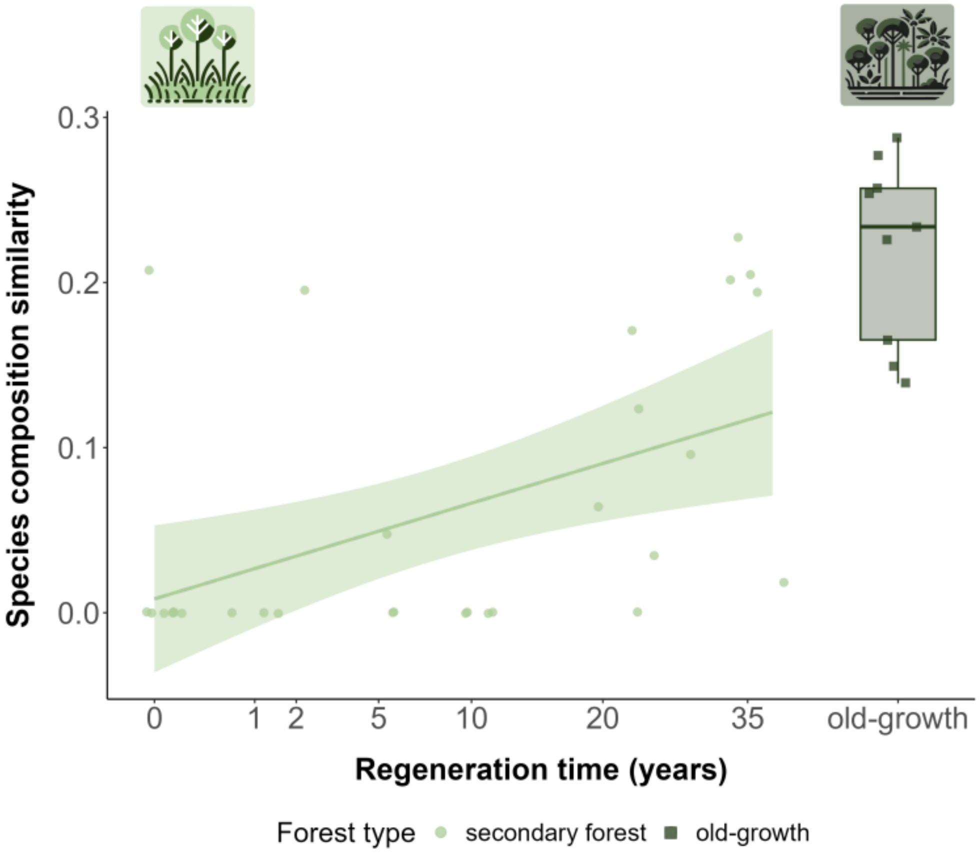

Figure 4. Relationship between species composition similarity to old-growth forests and regeneration time for 30 secondary forest plots in comparison with 8 old-growth forest plots. Significance was based on linear models with elevation, the forest cover in the surrounding 500 m, prior land use and regeneration time as fixed predictors. Regeneration time was square root transformed. Green dots and regression line with confidence interval represent secondary forest plots. Continuous lines represent significant relationships ($p < 0.05$). Old-growth forest plots are plotted in dark green. See Table 1 for statistical results. n = 30 plots.

3.4 Similarity in functional composition to old-growth forest increases with regeneration time, influenced by prior land use

In general, secondary forests show high levels of similarity of functional composition to old-growth forests, with values ranging from 0.53 to 0.85. The similarity in functional composition to old-growth forests differed by *former land use*, with pastures showing lower functional composition similarity than cacao plots (Table 1; Figure 5). When taking into account *regeneration time* depending on the *prior land use* (*pasture* vs *cacao*), there are strong differences in functional composition at early regeneration stages, however these differences get reduced with regeneration time, showing a tendency towards old-growth forest functional community, especially in former cacao plantations (Table 1; Figure 5).

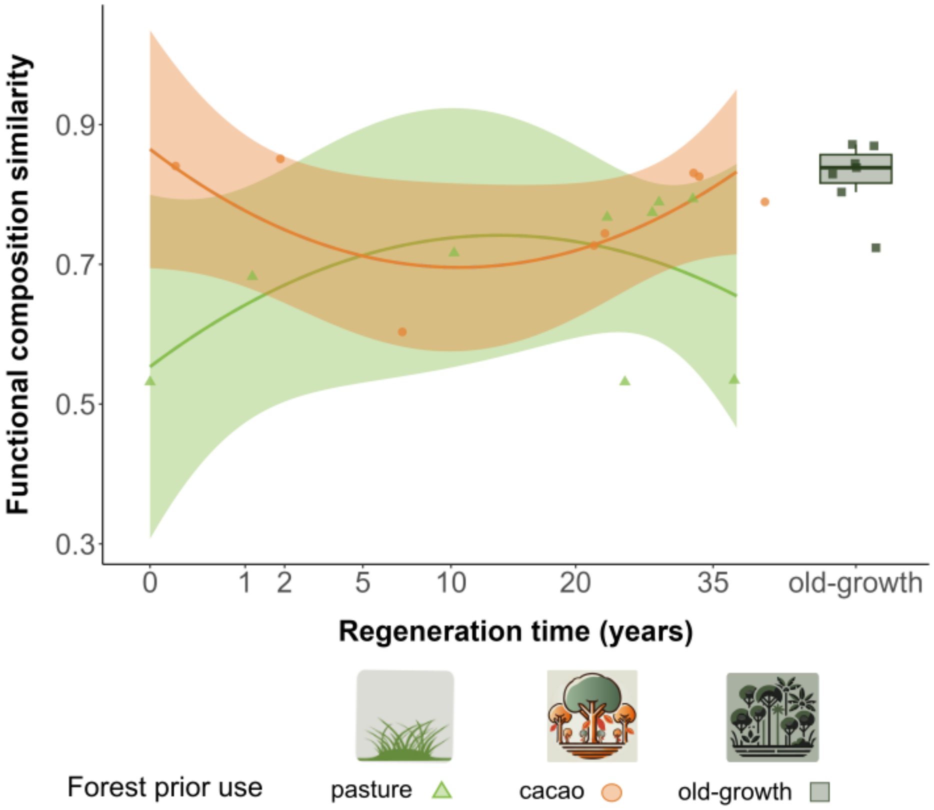

Figure 5. Similarity in functional composition similarity to old-growth forests in relation to prior land use (pasture or cacao) and to regeneration time. Regeneration time was quadratic transformed. Continuous lines represent significant relationships ($p < 0.05$). Old-growth forest plots are plotted in dark green. Significance was based on linear models with elevation, the forest cover in the surrounding 500 m, prior land use and regeneration time. See Table 1 for statistical results. n = 17 plots.

3.5 Functional trait structure across plots

The PCA based on functional traits revealed strong patterns of variation in the community-level functional structure of the tree-seedling among study plots, with the first two axis explaining 80% of the variation (Figure 6). The first axis was positively associated with LDMC and negatively with leaf toughness. This axis separated pastures from cacao and old-growth forest plots, showing a tendency toward higher LDMC and lower leaf toughness in the pasture plots. The second component showed a high positive loading in SLA and high negative loadings for leaf thickness, partly separating the three prior uses, with old-growth forest plots showing higher values of leaf thickness and lower SLA than cacao and pasture plots. When modeling leaf trait variation among plots, we found that, regardless of *regeneration time*, only *prior land use* significantly influenced the leaf trait distribution for the first PC axis, representing the variance in toughness and LDMC (Table 1, Figure 7). The second axis, which represented the relationship of SLA and leaf thickness, did not have any predictor significant (Table 1).

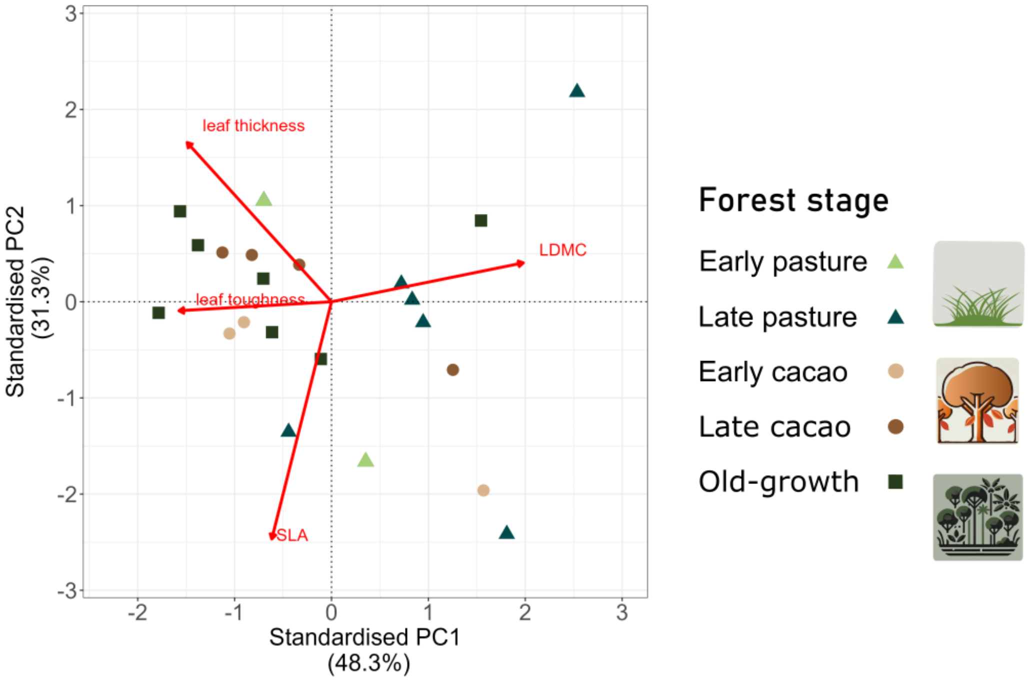

Figure 6. Tree-seedling functional composition structure of 22 plots along two Principal Component (PC) axes explaining 79.6% of the variance. The two axes separated the tree-seedling community plots based on traits related to acquisitive (high Specific Leaf area (SLA), low Leaf Dry Matter Content (LDMC), low leaf thickness and toughness) and conservative traits (low SLA, high LDMC, high leaf thickness and toughness). The percentages in the axes represent the explained variance for that axis. Plots with prior land use as pasture are depicted at the acquisitive side and old-growth forest at the conservative side. Regeneration time is shown in different color tones, with light color depicting early secondary forests (0 - 12 years), and darker colors depicting late secondary plots (19 – 38 years). Dark green is used for the old-growth forests. Prior land use is depicted by different symbols, i.e. triangles = pasture, circles = cacao and squares = old-growth forest plots. Although there is not a clear distribution pattern, pasture plots tend to be situated in the positive region of the PC1 (mean pc1 score = 0.95) and cacao together with old-growth are located towards the negative PC1 region (mean pc1 score = -0.50 and -0.66 for cacao and old-growth forests respectively).

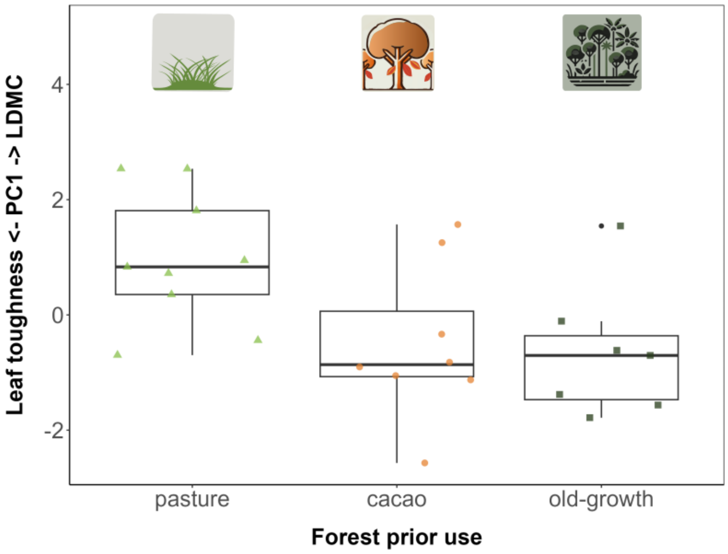

Figure 7. Functional structure variation for the traits related with the first Principal component (PC) axis according to prior land use (*pasture* or *cacao*). PC1 depicted the relationship between leaf toughness and Leaf Dry Matter Content (LDMC), with higher values of PC1 meaning high LDMC and low leaf toughness. Old-growth forest is shown as a comparison in the dark green boxplot. Former pastures were differentiated from cacao and old-growth forest for their high values in the

first PC axis.

Table 1. Results from general linear models Model results testing the response variables (models 1 to 7 in Table S1) against elevation, forest cover in the surroundings, prior land use and regeneration time. All continuous predictors were scaled, and regeneration time was root-transformed. Regeneration time was quadratic transformed in models 4 to 7. Depicted are the model estimates, their 95% confidence intervals, as well as the predictor significance and the fitness of the model explained variance. Due to the variation in the response variable distributions, the predictor significance and the fitness are based on different tests (Table S1). Significant predictors are marked in bold. Corresponding visualizations of the significant relationships are shown in Figures 1 to 5, and Figure 7.

Parameter

1.Tree-seedling abundance	**Estimates**	**95% CI**	**p-value**
Elevation	-0.542	-1.14 - 0.01	0.053
Forest cover (500 m)	0.756	0.20 - 1.34	**0.007**
Prior land use	-0.291	-1.22 - 0.63	0.650
Regeneration time (sqrt transformed)	0.740	0.03 - 1.49	**<0.001**
Prior land use : Regeneration time (sqrt transformed)	0.319	-0.63 - 1.29	0.509
Fitness of the model	0.432		

2.Tree-seedling species diversity	**Estimates**	**95% CI**	**p-value**
Elevation	-0.628	-1.34 - 0.09	0.688
Forest cover (500 m)	0.443	-0.26 - 1.15	0.057
Prior land use	0.040	-1.18 - 1.26	0.850
Regeneration time (sqrt transformed)	0.566	-0.41 - 1.55	**0.006**
Prior land use : Regeneration time (sqrt transformed)	0.811	-0.45 - 2.07	0.196
Fitness of the model	0.258		

3.Tree-seedling functional diversity	**Estimates**	**95% CI**	**p-value**
Elevation	-1.073	-2.23 - 0.09	0.066
Forest cover (500 m)	-0.231	-1.28 - 0.82	0.633
Prior land use	-0.351	-2.06 - 1.36	0.664
Regeneration time (sqrt transformed)	1.382	0.15 - 2.61	**0.023**
Prior land use : Regeneration time (sqrt transformed)	-0.415	-2.21 - 1.38	0.617
Fitness of the model	0.256		

4.Species composition similarity	**Estimates**	**95% CI**	**p-value**
Elevation	-0.210	-0.56 – 0.15	0.249
Forest cover (500m)	0.020	-0.33 – 0.37	0.909
Prior land use	-0.385	-0.65 – 1.42	0.467
Regeneration time (sqrt transformed)	0.552	0.12 – 0.99	**0.013**
Regeneration time (sqrt and quadratic transformed)	0.461	-0.27 – 1.20	0.221
Prior land use: Regeneration time (sqrt transformed)	-0.111	-0.46 – 0.68	0.702
Prior land use: Regeneration time (sqrt and quadratic transformed)	0.165	-0.66 – 0.997	0.696
Fitness of the model	0.524		

5.Functional composition similarity	**Estimates**	**95% CI**	**p-value**
Elevation	0.020	-0.20 – 0.26	0.796

Forest cover (500m)	0.065	-0.19 – 0.32	0.616
Prior land use	-0.175	-0.79 – 0.44	0.579
Regeneration time (sqrt transformed)	0.231	0.00 – 0.46	0.050
Regeneration time (sqrt and quadratic transformed)	-0.374	-0.81 – 0.07	0.096
Prior land use : Regeneration time (sqrt transformed)	-0.439	-0.86 – 0.02	**0.042**
Prior land use : Regeneration time (sqrt and quadratic transformed)	0.765	0.20 – 1.33	**0.008**
Fitness of the model	0.501		

6.PC1 (Toughness - LDMC)	**Estimates**	**95% CI**	**p-value**
Elevation	-0.328	-1.36 – 0.71	0.492
Forest cover (500m)	-0.536	-1.45 – 0.38	0.218
Prior land use	0.133	-2.18 – 2.45	**0.038**
Regeneration time (sqrt transformed)	1.004	-0.73 – 2.73	0.388
Regeneration time (sqrt and quadratic transformed)	1.339	-0.33 – 3.01	0.488
Prior land use : Regeneration time (sqrt transformed)	-0.890	-2.90 – 1.12	0.343
Prior land use : Regeneration time (sqrt and quadratic transformed)	-1.698	-3.70 – 0.31	0.088
Fitness of the model	0.251		

7.PC2 (Thickness - SLA)	**Estimates**	**95% CI**	**p-value**
Elevation	0.694	-0.24 – 1.63	0.130
Forest cover (500m)	-0.472	-1.33 – 0.38	0.250
Prior land use	0.291	-1.05 – 1.63	0.645
Regeneration time (sqrt transformed)	0.468	-0.52 –1.45	0.979
Prior land use : Regeneration time (sqrt transformed)	-1.136	-2.57 – 0.29	0.109
Fitness of the model	0.049		

4 DISCUSSION

In this study, we investigated the recovery of tree-seedling communities in tropical secondary forests as compared to old-growth forests, from a taxonomic and functional perspective. We considered multiple factors such as *elevation*, *forest cover*, leaf area index (*LAI)*, *prior land use* and *regeneration time*. We found evidence that both species' diversity and functional diversity of naturally recovering tree-seedling communities as well as their similarity to old-growth forest for both species and functional trait composition increased with *regeneration time*. The increase of tree-seedling abundance and species diversity was also enhanced by *forest cover*. Importantly, species and functional composition were shaped by *prior land use* with communities on previously used pasture dominated by acquisitive traits in contrast to old-growth plots which were associated with conservative traits.

4.1 Species diversity and functional diversity increase along the chronosequence

Our results confirm our first hypothesis that species diversity and functional diversity will gradually resemble those in old-growth forests with increasing time of forest recovery.
This aligns with the principles of community assembly. In young plots, we observed lower species and functional diversity, likely due to the harsh environmental conditions favoring specific functional traits that enhance species' ecological performance in this challenging environments (Buzzard et al., 2016; Violle et al., 2007). In contrast, in older forests, interspecific competition, as explained by the limiting similarity theory, promotes a greater diversity of functional traits. High functional diversity reduces the likelihood of mutual exclusion among species due to competition. These findings are consistent with our results, where functional diversity increases with forest age, eventually reaching levels comparable to those in old-growth forests (Roscher et al., 2013) .

Regeneration time is positively correlated with LAI. LAI is positively related to vegetation cover and thus negatively to light availability. Low light availability can influence seedling establishment in a species-specific way, with some species benefiting more than others from shade, being this particularly true for old-growth forest species (Schupp et al., 1989; Zipperlen & Press, 1996). But, in general, it facilitates the establishment of tree seedling by out-competing heliophilous species (Shirima et al., 2015). An increase in vegetation cover increases the probability of seed arrival, either through vertical seed rain (Reid et al., 2015) or attracting seed dispersers (Laborde et al., 2008). It also increases the seedling establishment rate, since it creates favorable microclimate conditions for seed survival, through the presence of leaf litter, improving soil conditions, such as organic matter content and soil moisture (Sayer, 2006). Vegetation cover also protects seedlings from intense solar radiation and heat stress (Logan et al., 2022), which improves the edaphic conditions and increases the chances for late stage-species seedling establishment and survival (Schupp et al., 1989).

The surrounding landscape, i.e., a high forest cover in the surroundings of the plots, improved the recovery of tree-seedling abundance and species diversity. This has been already found in other studies, where proportion of old-growth forest in the landscape drove increases in seedling diversity, especially in the first 30 years of recovery (Lu et al., 2016) and in locations with high forest cover in the landscape (above 60%)(Arroyo-Rodríguez et al., 2023). Forest cover directly or indirectly promotes several key ecological processes such as improvement of microclimatic conditions, provisioning of seeds (Leitão et al., 2010; Young et al., 1987), and enhancement of seed dispersal and seedling recruitment (Arroyo-Rodríguez et al., 2017).

4.2 Tree-seedling composition recovery with regeneration time is influenced by forest prior land use

Tree-seedling composition is specially affected by light availability. Even though shade can be beneficial for tree-seedling establishment, seedlings still need certain light availability to reach maturity. It has been described how both early and late successional species benefit from light availability at early stages of life. However, late successional species are more prone to survive in low-light environments (Schupp et al., 1989; Zipperlen & Press, 1996) since they are better adapted to the selective pressures from these environments (Chen et al., 2010). In our study we found that species and functional composition become more similar to old-growth forests with lower LAI in increasingly older forests. Nevertheless, shade-tolerance strongly differ also among late successional species (Montgomery & Chazdon, 2002) leading to a resource partitioning even in low light environments. This could be an explanation for the fact that even after 40 years of recovery, the tree-seedling community still differs from the community in old-growth forests.

Prior land use represents a multifaceted driver of ecological dynamics in secondary forests. The prior land use effects depend on multiple aspects, from differences in light regimes at the beginning of succession, which have been shown to affect seedling distribution even after several years in tropical forests (Nicotra et al. 1999), to the intensity of prior land use or land management, that can influence several processes, such as seed predation, seedling establishment, herbivory, competition, among others for decades (Jakovac et al., 2021). We found a significant influence of the prior land use in the tree-seedling composition, with former cacao plots becoming more similar to old-growth forest seedling communities with regeneration time, than former pasture plots. The influence of prior land use on functional similarity persists along the chronosequence, with pastures depicting a differentiated trajectory from cacao, and remaining different from old-growth forests independently of their abandonment time. Our results confirm other studies about prior land use that found different functional composition in secondary forests than in old-growth forests, since functional trajectories of forests with different prior land uses are less directional in tropical forests (Neto et al., 2019). This trend in community composition, together with the fact that similarity of functional trait composition seems to follow a different pathway for former pastures, points to an arrested succession in forests regenerating from pastures. Extreme environments, like those found in pastures, can filter for determined functional traits that allow the individuals to be more tolerant to the hard conditions. This pattern agrees with the Environmental filtering theory (Keddy, 1992), which suggest that abiotic conditions can restrict the species capacity to establish or survive in a certain environment, since in our study functional composition is showing a lower similarity to old-growth forests in former pastures, where the tree-seedling community tend to show acquisitive or fast growing functional trait associations.

Even though the presence of the nearest forests has a strong positive impact on the recovery of tree-seedling species diversity, this does not necessarily imply that it helps the seedling community in our study area to resemble those in old-growth forests, neither taxonomically nor functionally. This could be due to the fact that we did not consider the age of the surrounding forests, but only whether there was forest present. It is possible that the forest surrounding our plots have similar ages as the recovering plots themselves, and thus cannot act a source for late successional species, as shown already in other tropical regions (de la Peña-Domene et al., 2017; Toledo et al., 2020). This could also imply limited dispersal from older forests in the region, either because the distances are too large, or because late successional species cannot establish in younger forests. Previous studies found that the potential for natural regeneration increases in the vicinity of the forest edge, with the distance of 300 m being a threshold for this potential, especially in neotropical forests (Williams et al., 2024).

4.3 Functional trait structure shift influenced by forest prior land use

We found a compositional shift from acquisitive to conservative traits with regeneration time for leaf traits related to photosynthetic capacities and life strategy (SLA and leaf thickness). It has been already shown that early-successional species tend to be more responsive to resource availability, allowing them to perform better in the typically nutrient-rich environment in early succession (Báez & Homeier, 2017). Plant functional composition tends to adapt in response to the changing environmental conditions over time, typical in successional forests. This shift is characterized by an increase on conservative traits found in late successional species, such as higher leaf thickness and lower SLA.

The fact that prior use is of mayor importance in our results, points towards differentiated effects on functional structure between pastures and cacao plantations. The presence of grasses, especially exotic grasses like *Hyparrhenia rufa*, *Panicum maximum* or *Brachiaria*, are known to outcompete tree seedlings and reduce their survival and growth (Gunaratne et al., 2014; Holl, 1998; Ortega-Pieck et al., 2011). Our data supports these finding as the presence of the exotic African grass *Brachiaria sp*. seems to hamper the establishment of tree seedlings on active and formerly used pastures. In contrast, cacao plantations are dominated by trees that reduce the establishment of heliophilous grasses in the low light conditions underneath the cacao trees (Gerber et al., 2017; Shirima et al., 2015). Therefore low light conditions also foster the establishment of late-successional tree species by reducing the competition with grasses (Palomeque et al., 2017; Pascarella et al., 2000).

The turnover we found for species composition was, however, not mirrored by a turnover of morphological traits like leaf toughness and LDMC. For both leaf toughness and LDMC structure, former cacao plantations resembled old-growth forest seedling communities already in early stages of forest recovery, with tougher, thicker leaves and low SLA values than former pastures (see Figure 7). It is concerning to observe that we did not detect a trend towards a reduction in these functional differences over time, which can be a sign of how cattle grazing can lead to long term perturbations and even create a different successional pathway.

In regenerating tropical forests, leaf trait assemblages are strongly influenced by soil fertility, which exerts a negative effect on LDMC, and a positive one on leaf thickness, while SLA is not affected (Pinho et al., 2018). This is the same pattern that we found in our own analysis where tree-seedling communities in former pastures were characterized by higher LDMC and lower leaf toughness and thickness than cacao and old-growth forests. This suggests a lower soil fertility in the former pasture in our locality, which matches previous findings about the resilience of tropical abandoned pastures (Rasiah et al., 2004). Rasiah et al. (2004), found that former pastures do not show an improvement in the soil fertility conditions when compared with the local rainforests, even after 40 years of abandonment.

5 CONCLUSIONS

Our study highlights that not only the time since abandonment and former use of areas but also the surrounding context are important determinant shaping recovery of tree-seedling communities. Human disturbances such as forest clearance and prior land use can influence tree-seedling communities' decades after the perturbation, which can lead to different successional pathways in the most disturbed regions.

The causes behind this differential process could be abiotic conditions such as light availability but also biotic conditions such as seed dispersal and competition with herbaceous species. These factors can modulate the establishment and survival of tree seedlings on abandoned land. This suggests that, besides fostering seed input, the suppression of herbaceous vegetation and the recovery of the soil conditions seems to be an important determinant of passive restoration processes. Thus, human management actions can support forest recovery when the landscape context does not present sufficient forest cover.

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SUPPORTING INFORMATION

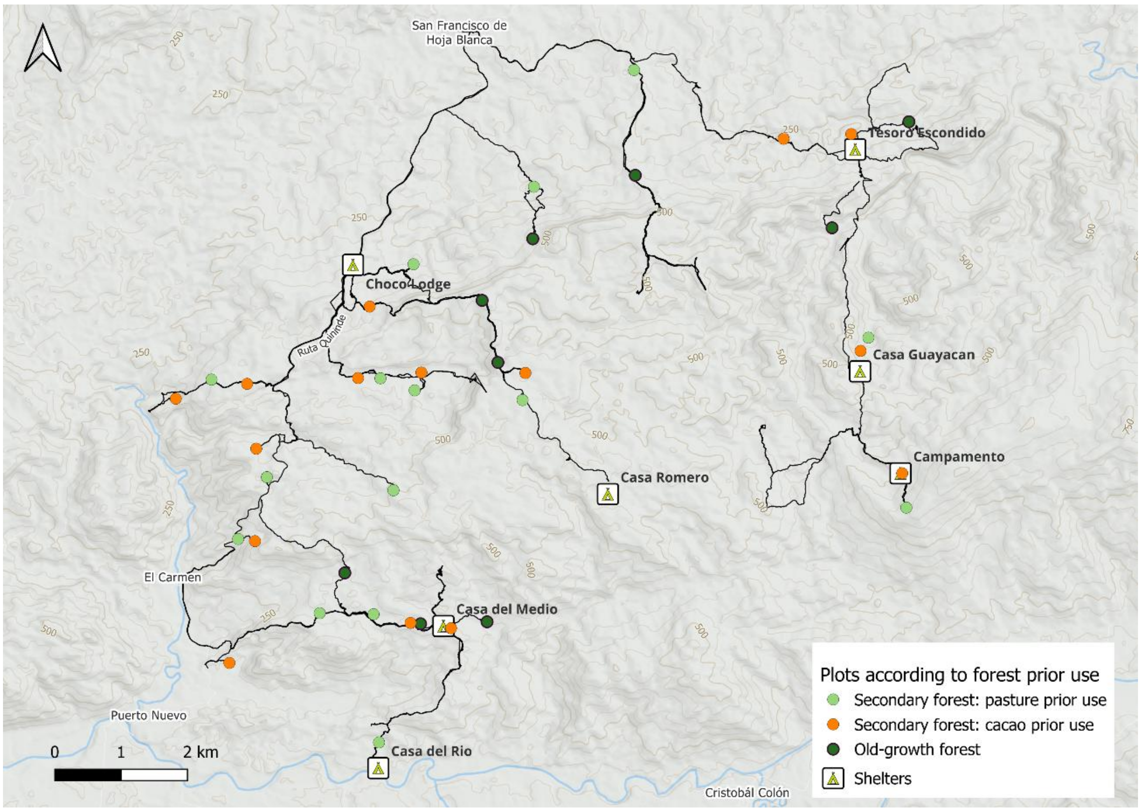

Figure S1. Map of Reassembly’s study area in Esmeraldas, Ecuador. The 39 plots are marked in light green dots for secondary forest plots, and dark green dots for old-growth forest plots.

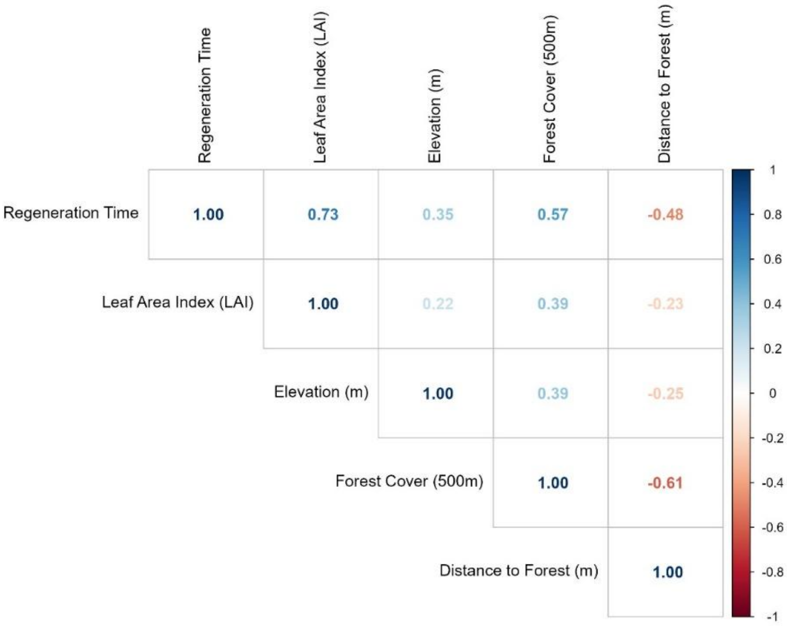

Figure S2. Correlation plot for our predictor metrics. Correlations were calculated with Pearson Correlation Index. All predictors exceeding 0.6 of correlation were excluded from our models.

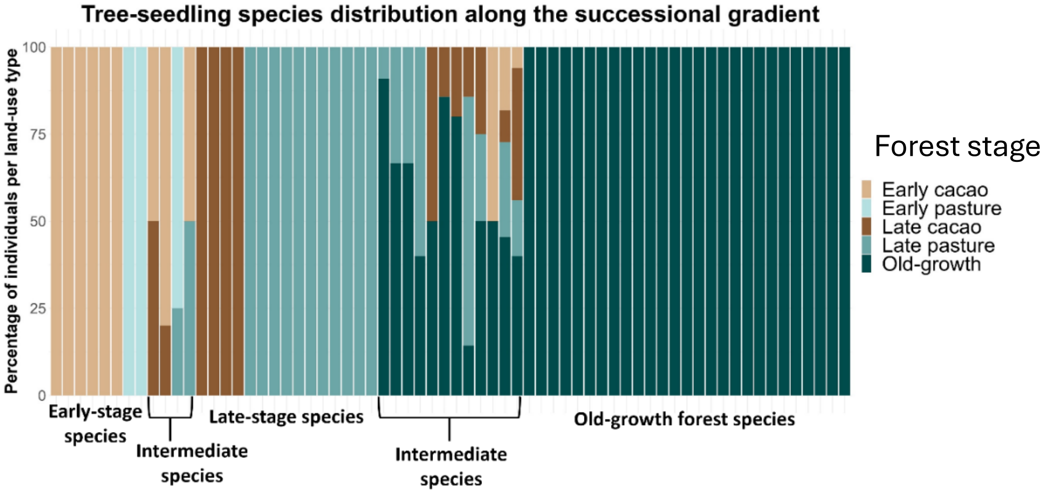

Figure S3. Species distribution along forest age gradient according to forest legacy. Each bar represents a species, and the color determines the proportion of the individuals found in every forest stage, thus, monochromatic bars are species that have only be found in a determined age and forest prior use.

Table S1. Family selected and R package used for every model according to the response variables. The number of observations per model refers to the number of plots included in the respective model and varies for functional response variables. For taxonomic response variables we used the whole data set. For functional response variables we exclude all plots with no individuals (11 plots) and plots with less than 75% of the community sampled for functional traits (2 plots). Functional diversity analyses excluded an extra plot since it did not achieve the requirement of counting with more than 3 functionally singular species.

	Response variable	Number of observations	Model family	Package	Fitness of the model variance	Predictor significance test
1	**Abundance**	30	Negative binomial	MASS (Venables & Ripley 2002)	McFadden's Pseudo R-squared (McFadden 1972)	Chi-square
2	**Species diversity**	30	Gaussian	lme4 (Bates *et al.* 2015)	Adjusted R-square (lme4 package)	F-statistic
3	**Functional diversity**	16	Gaussian	lme4 (Bates *et al.* 2015)	Adjusted R-square (lme4 package)	F-statistic
4	**Species composition similarity to old-growth**	30	Beta regression	betareg (Cribari-Neto & Zeileis 2010)	Pseudo R-square (betareg package)	Wald-z
5	**Functional composition similarity to old-growth**	17	Beta regression	betareg (Cribari-Neto & Zeileis 2010)	Pseudo R-square (betareg package)	Wald-z
6	**Functional structure (PC1)**	17	Gaussian	lme4 (Bates *et al.* 2015)	Adjusted R-square lme4 package)	F-statistic
7	**Functional structure (PC2)**	17	Gaussian	lme4 (Bates *et al.* 2015)	Adjusted R-square (lme4 package)	F-statistic

Table S2. Environmental predictors for our 39 plots. Leaf area index (LAI) is unitless. Forest cover is a percentage of forest coverage in 500 m circle surrounding our plots. The first two letters of the plot code stand for the legacy and status of the forest (CA: active cacao, CR: regenerating cacao; PA: active pasture, PR: regenerating pasture, OG: old-growth forest).

Plot	Elevation	Prior use	Forest type	LAI	Forest cover (500 m)	Distance to forest (m)	Abandonment year
CA60	440	cacao	secondary	0	0.59	17.96	2022
CA62	372	cacao	secondary	0	0.24	131.62	2022
CA63	240	cacao	secondary	6.03	0.56	143.88	2022
CA64	256	cacao	secondary	3.51	0.58	35.07	2022
CR02	400	cacao	secondary	4.33	0.89	36.42	2021
CR03	250	cacao	secondary	4.03	0.77	33.08	2018
CR04	560	cacao	secondary	6.3	0.96	29.42	1987
CR05	377	cacao	secondary	3.53	0.14	65.64	2011
CR06	397	cacao	secondary	6.41	0.37	28.97	2003
CR09	159	cacao	secondary	3.97	0.44	39.95	2017
CR10	347	cacao	secondary	6.82	0.92	25.04	1999
CR11	372	cacao	secondary	5.62	0.91	36.47	1992
CR13	311	cacao	secondary	3.45	0.82	38.53	2022
CR14	529	cacao	secondary	5.04	0.96	22.72	1985
CR17	450	cacao	secondary	4.65	0.60	49.12	2014
PA53	510	pasture	secondary	1.34	0.82	71.47	2022
PA54	207	pasture	secondary	0	0.43	92.25	2022
PA55	350	pasture	secondary	0	0.89	8.49	2022
PA57	375	pasture	secondary	3.67	0.22	16.37	2022
PR19	177	pasture	secondary	0	0.34	56.77	2017
PR21	560	pasture	secondary	6.67	0.96	21.17	1987
PR22	400	pasture	secondary	4.88	0.37	105.82	2011
PR23	415	pasture	secondary	2.94	0.62	30.92	2022
PR26	325	pasture	secondary	4.1	0.90	25.03	2001
PR27	214	pasture	secondary	4.59	0.67	50.20	1996
PR31	316	pasture	secondary	5.3	0.67	39.35	1999
PR32	339	pasture	secondary	6.21	0.34	174.45	1997
PR33	311	pasture	secondary	0	0.74	23.12	2022
PR34	615	pasture	secondary	3.98	0.96	24.54	1985
PR36	380	pasture	secondary	3.5	0.66	35.07	2014
OG38	535	old-growth	old-growth	5.91	0.97	0.00	NA
OG39	576	old-growth	old-growth	6.14	1.00	0.00	NA
OG41	389	old-growth	old-growth	6.83	0.95	0.00	NA
OG42	374	old-growth	old-growth	5.94	0.84	0.00	NA
OG45	362	old-growth	old-growth	6.11	0.90	0.00	NA
OG46	260	old-growth	old-growth	6.09	1.00	0.00	NA
OG47	450	old-growth	old-growth	6.53	0.65	0.00	NA
OG49	310	old-growth	old-growth	6.27	1.00	0.00	NA
OG52	225	old-growth	old-growth	7.78	0.95	0.00	NA