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Tropical forest succession increases tree taxonomic and functional richness but decreases evenness

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Abstract

Aim: Successional changes in functional diversity provide insights into community assembly by indicating how species are filtered into local communities based on their traits. Here, we assess successional changes in taxonomic and functional richness, evenness and redundancy along gradients of climate, soil pH and forest cover.

Location: Neotropics.

Time period: Last 0–100 years.

Major taxa studied: Trees.

Methods: We used 22 forest chronosequence studies and 676 plots across the Neotropics to analyse successional changes in Hill's taxonomic and functional diversity

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of trees, and how these successional changes vary with continental-scale gradients in precipitation, soil pH and surrounding forest cover.

Results: Taxonomic and functional richness and functional redundancy increased, while taxonomic and functional evenness decreased over time. Functional richness and evenness changed strongly when not accounting for taxonomic richness, but changed more weakly after statistically accounting for taxonomic richness, indicating that changes in functional diversity are largely driven by taxonomic richness. Nevertheless, the successional increases in functional richness when correcting for taxonomic richness may indicate that environmental heterogeneity and limiting similarity increase during succession. The taxonomically-independent successional decreases in functional evenness may indicate that stronger filtering and competition select for dominant species with similar trait values, while many rare species and traits are added to the community. Such filtering and competition may also lead to increased functional redundancy. The changes in taxonomically-independent functional diversity varied with resource availability and were stronger in harsh, resource-poor environments, but weak in benign, productive environments. Hence, in resource-poor environments, environmental filtering and facilitation are important, whereas in productive environments, weaker abiotic filtering allows for high initial functional diversity and weak successional changes.

Main conclusion: We found that taxonomic and functional richness and functional redundancy increased and taxonomic and functional evenness decreased during succession, mainly caused by the increasing number of rare species and traits due to the arrival of new species and due to changing (a)biotic filters.

KEYWORDS

community assembly, evenness, Hill numbers, richness, tropical forest

1 | INTRODUCTION

Community assembly is the process in which species are filtered from the regional species pool to compose the local community (Diamond, 1975). Community assembly theories aim to understand which species co-occur and why (Poorter et al., 2023; Weiher et al., 1998). Such processes are often inferred from taxonomic diversity and species distributions, but such species-based approaches provide little insight into why species are filtered out because they cannot infer underlying mechanisms of community assembly. In contrast, the functional trait approach has the potential to turn community assembly into a more mechanistic and predictive science because traits are related to plant functioning and plant responses to the abiotic and biotic environment (Garnier et al., 2016; Keddy & Laughlin, 2021; McGill et al., 2006). The trait distribution in the community (i.e. functional diversity) should therefore provide insights into dominant assembly mechanisms at play (Vellend, 2016). Many studies have compared communities and their functional diversity across environmental gradients (Pakeman, 2011; Spasojevic & Suding, 2012), but a more direct test would be to follow community assembly during succession.

Here, we advance community assembly theory by synthesizing 22 chronosequence studies across the Neotropics and evaluate (1) whether long-term successional changes in taxonomic and functional diversity are predictable or stochastic (Norden et al., 2015) and (2) how community assembly varies across continental scale gradients in resource availability (water and soil fertility) and forest cover.

Community assembly is generally thought to be driven by three filters (dispersal, abiotic and biotic) that jointly operate at different spatial scales (Keddy & Laughlin, 2021). Dispersal filters determine which species from the regional species pool are able to reach a site. Dispersal can be deterministic (i.e. depending on the species' dispersal traits) and/or stochastic (i.e. a chance process), as time increases the chance for seeds to arrive (Dent & Estrada-Villegas, 2021; Hubbell, 2001). Abiotic filters determine the type of species that are able to establish given the local abiotic conditions. Strong abiotic filtering would restrict the trait distribution in the community to the trait range that is compatible with the abiotic conditions (Cornwell et al., 2006; Weiher et al., 1998). Biotic filters refer to interactions between organisms, such as competition, facilitation, mutualism, parasitism and predation (MacArthur & Levins, 1967).

Secondary forest succession on abandoned agricultural lands provides an ideal study system to test assembly theories because it is 'community assembly in action' (Lebrija-Trejos et al., 2010). Assembly starts nearly from scratch in terms of tree biomass and diversity as most woody vegetation has been removed, while the vegetation regrows rapidly (Poorter, Craven, et al., 2021) because of legacies of seeds and stumps in the soil and ample space and light availability. Early in succession, high irradiance and hot and dry conditions may provide strong abiotic filters, leading to low species and functional diversity (Bhaskar et al., 2014). Later in succession when vegetation builds up, more benign microclimatic conditions may allow a larger number of species (Rozendaal et al., 2019) with wider trait ranges to establish (Poorter, Rozendaal, et al., 2021), or could lead to competitive exclusion and reduce the number of species and the trait range. Increased competition and limiting similarity (i.e. limited trait overlap to increase co-existence between species) among species and increased biotic filtering due to density-dependent pests (Lebrija-Trejos et al., 2014) and pathogens (Bever et al., 2015) may prevent species from becoming very dominant and therefore cause more even species abundance (i.e. taxonomic evenness), more even distribution of species abundance across trait space (i.e. functional evenness) and a lower functional redundancy. The few local-scale studies that evaluated changes in functional diversity (FD, i.e. the distribution of traits within a community) during secondary succession found mixed results; some studies indeed found an increased FD during succession (Craven et al., 2018; Lohbeck et al., 2012), but others found no change (Bhaskar et al., 2014) or a decrease for small trees (Sanaphre-Villanueva et al., 2016).

One reason for these contradictory results might be that community assembly proceeds in fundamentally different ways in resource-poor versus resource-rich environments, and depends on the landscape context that determines the available seed sources. For example, in resource-poor environments such as dry regions or on poor soils, taxonomic and functional diversity may be low and increase slowly because of strong abiotic constraints. Under these conditions, the early stages of succession may be driven more by facilitation than by competition (Batterman et al., 2013; Menge & Sutherland, 1987) as increasing plant biomass improves understory microclimates and increasing soil carbon improves soil fertility, while the later stages of succession may be limited by the relatively small pool of species and functional traits successful under relatively resource-poor conditions. In contrast, in resource-rich environments such as wet or fertile sites, a larger species pool and more benign environmental conditions may lead to faster species growth and turnover rates and more competition. This, in turn, would lead to a faster increase during succession in taxonomic and functional diversity and a higher finally obtained diversity (Falster et al., 2017; Kohyama, 1993).

Here, we focus on three aspects of functional diversity: (1) functional richness, which indicates the total functional trait variation in the community; (2) functional evenness, which indicates how evenly the species abundances are distributed across the trait space of the community (Mason et al., 2005) and (3) functional redundancy, which

indicates the degree to which species overlap in their functioning (i.e. their traits) (Dick, 2023). During succession, species accumulate (Rozendaal et al., 2019) and the functional richness may increase (Lohbeck et al., 2012; Whitfeld et al., 2014). The increase in functional richness may become slower over time as newly added species have less chance to further increase the trait space. Therefore, functional redundancy may increase during succession. Taxonomic richness may increase faster than functional richness. Furthermore, the accumulation of species may lead to more inter-specific competition and limiting similarity, leading to higher functional evenness within the community (Villéger et al., 2008). If functional diversity increases independently of the increase in species diversity, then this may indicate that species face competition and therefore occupy a wider and more evenly distributed trait space.

To assess successional changes in functional diversity and how this is explained by taxonomic diversity, we evaluate two questions for functional and taxonomic diversity. First, how do taxonomic and functional diversity (i.e. richness and evenness, and for functional traits, also the redundancy) change during succession? We expect taxonomic and functional richness and functional redundancy to be initially low due to relatively high irradiance and temperature early in succession that lead to abiotic filtering and low taxonomic and functional richness. Taxonomic and functional richness would increase over time due to arrival of more and later successional species and milder conditions later in succession that lead to higher richness. Taxonomic and functional evenness would also increase over time because increased biotic filtering due to competition would reduce the abundance of dominant species and result in higher evenness. Changes in functional diversity would largely be explained by changes in taxonomic diversity because adding species to a community most likely also increases the functional diversity of that community. Functional redundancy would increase over time because the number of species increases more rapidly than the trait volume. Second, how do successional changes in taxonomic and functional diversity depend on climate, soil and surrounding landscape forest cover? We expect that taxonomic and functional richness and evenness and functional redundancy will increase more quickly over time under conditions that speed up growth, space filling and competition such as high rainfall (higher productivity and a longer growing season), high soil fertility (higher productivity) and high surrounding forest cover (more seed input and a high diversity of old-growth forest species). Conversely, taxonomic and functional richness and evenness and functional redundancy will increase more slowly under resource-poor conditions and low surrounding forest cover.

2 | METHODS

2.1 | Chronosequence sites

We used data from 22 lowland Neotropical chronosequence sites (Appendix S1). The sites cover large gradients in climatic and soil conditions across the Neotropics (Appendix S2). Across all sites,

precipitation varied from 640 to 4100 mm/year and dry season climatic water availability varied between -1225 and 0 mm/year. Soil pH varied between 4.9 and 7.4, and surrounding forest cover (within a 1-km radius) varied between 0% and 100%.

2.2 | Plots

We used a chronosequence approach to infer long-term trends in succession, because few studies have actually monitored succession over a longer (>20 years) time period. Chronosequences use a space-for-time substitution to infer succession, and assume that all plots within a chronosequence had similar starting points and will follow similar trajectories, which is not necessarily the case (Walker et al., 2010; Norden et al., 2015), though successional patterns from dynamic studies are similar to those of chronosequence studies to a large extent, especially over wider spatial and time scales. Within each site, multiple forest plots of different ages since agricultural abandonment (0–100 y) were used. The plot sizes were consistent within chronosequence sites but varied among chronosequences between 0.02 and 1 ha (median = 0.1 ha). The sites had a median of 17 secondary forest plots (range 6–274), providing a total of 676 secondary forest plots (Appendix S2). In all plots, individual trees, shrubs and palms with a minimum stem diameter at breast height of 5 cm were measured and identified to species.

2.3 | Trait data

We focused on four functional plant traits that are important for light, water and nutrient conservation and use and for the heat balance of the plant (Díaz et al., 2015; Poorter, Rozendaal, et al., 2021). Specific leaf area (SLA; cm^2/g) is the fresh leaf area per dry mass and represents the amount of biomass investment for light capture. High values indicate large but thin leaves that capture more light, but may have a lower leaf lifespan (Poorter et al., 2009). Leaf area (LA; cm^2) is the fresh surface area of the leaf, and high values indicate not only efficient light capture and out-shading of neighbours, but also reduce convective heat cooling and, hence, a higher dependency on transpirational heat cooling, which results in either overheating or more water loss (Wright et al., 2017). Leaf nitrogen concentration is the amount of nitrogen per unit dry plant mass (in %), and high values are related not only to high photosynthetic efficiency but also to higher palatability and is therefore associated with lower leaf lifespan (Wright et al., 2004). Wood density is measured as the dry mass divided by the fresh wood volume (g/cm^3). High values indicate slow volumetric growth, but high resistance against environmental hazards such as droughts, pests, pathogens and wind (Chave et al., 2009). We chose these four traits because they represent important plant stem and leaf functions, because they capture the main global strategy spectra of plant form and function (Díaz et al., 2015) and they were available for most species at our sites.

Trait data were locally collected in all sites for the most abundant species. SLA and LA were sometimes based on the whole leaf including rachis and sometimes on leaflets (in the case of compound leaves). To correct for these differences, we estimated SLA based on the whole leaf for all species using the formula provided by Poorter, Rozendaal, et al. (2021). For LA, we only included data for the whole leaf. Correlations between the four species-level traits were weak (Appendix S3).

2.4 | Gap filling of trait data

Functional diversity metrics depend strongly on the completeness of the trait data (Pakeman, 2014). To increase the coverage of traits and to obtain similar trait coverage between plots and sites, we performed gapfilling of missing trait data (see details in Appendix S4), based on trait coordination and phylogenetic conservatism. We gap-filled SLA for 30% of the species and 11% of the stems (median across sites), LA for 72% of the species and 25% of the stems, leaf nitrogen concentration for 46% of the species and 18% of the stems and wood density for 42% of the species and 17% of the stems. These concern the rarest species of the plots that are usually not included in trait measurements.

2.5 | Diversity metrics

The main aim of this study was to understand successional changes in taxonomic and functional diversity. We also assessed how taxonomic diversity affects functional diversity (Monge-González et al., 2021) and if successional patterns in functional diversity are still found when statistically correcting for taxonomic diversity. We used the first two Hill numbers to quantify taxonomic diversity and evenness and functional diversity, evenness and redundancy. We used Hill numbers because they provide a mathematically coherent family of metrics, referred to as qD , which makes all diversity measures directly comparable (Chao et al., 2014; Jost, 2006). Hill numbers differ in their sensitivity to relative abundances and indicate the 'effective number of species', i.e. the number of equally abundant species required to obtain the observed value of (functional) diversity. For example, if a community has a Hill 5D diversity of 5, then it means that 5 equally abundant species are needed to obtain the observed value of diversity. For functional Hill 5D diversity this would be 5 functionally distinct species (i.e. 5 'virtual functional groups') (Chao et al., 2019). The first Hill number (0D) equals the number of species present and is insensitive to relative abundances, and the second Hill number (1D) equals the exponentiated Shannon–Wiener diversity index and weights species by their relative abundances. Hill numbers are equal if all species (or functional groups) have equal abundance. Hill numbers diverge as relative abundances diverge, with ${}^0D > {}^1D$. We use 0D to quantify taxonomic (0D_t) and functional (0D_f) richness and ${}^1D/{}^0D$ to quantify taxonomic (${}^1D_t/{}^0D_t$) and functional (${}^1D_f/{}^0D_f$) evenness

[henceforth referred to as 'Hill's evenness', where values close to 0 indicate a very uneven community and a value of 1 indicates an even community (Hill, 1973), Appendix S5]. Finally, we quantify functional redundancy as $1 - \text{functional richness}/\text{taxonomic richness}$ following Dick (2023). Large values of functional redundancy (i.e. close to 1) indicate that functional richness is low relative to taxonomic richness (i.e. many species contribute little to functional richness). Note that Hill diversity values are expressed on a continuous scale and do not need to be integer values.

We determined taxonomic and functional richness (0D) and diversity (1D) using the estimate3D function of the iNEXT.3D package based on a Gower functional distance matrix and a similar coverage between samples (see next section), using the default FDtype='AUC' (area under the curve of the tau profile). The parameter tau determines the threshold of functional distinctiveness between any two species and can range between 0 (no distinctiveness between species, so each species forms its functional group) and 1 (high distinctiveness, so all species are lumped into one functional group and FD reduces to 1). Using this approach, functional diversity is calculated at different values of tau and a relationship is constructed between functional diversity and tau. The area under this relationship provides a functional diversity value integrated over all possible values of the threshold of functional distinctiveness for each sample plot. Note that species with similar dissimilarity between two functional groups might be lumped in both groups. See correlations between Hill numbers in Appendix S6.

2.6 | Standardization of taxonomic and functional diversity for sample coverage

Diversity values strongly depend on sampling effort (i.e. on the number of individuals and area sampled). In species-rich tropical forests, small sample areas (such as those used in this study) are missing many of the rare and infrequent species that occur in the true assemblage (estimated from the asymptotic value of the rarefaction curve), so values of sample coverage are often below the maximum value of 1 (Chao & Jost, 2012). Sample coverage is the fraction of the total number of individuals in the assemblage (including individuals from the undetected species) that belong to the observed species represented in the sample. It is therefore an objective measure of sample coverage at the individual level. For example, if in an assemblage (i.e. a community) 50 species are present, but if in a sample plot only 20 species are found, and those 20 species represent 60% of all the individuals in the assemblage, then the sample coverage is 60%. To correct for differences between plots in sample coverage, we standardized the taxonomic and functional diversity metrics by using a 'sample coverage' (Chao et al., 2021) of 0.77, which was the median sampling coverage found across all plots in the dataset (Appendix S7). Appendix S8 shows the correlations between functional and taxonomic richness and between functional and taxonomic evenness.

2.7 | Environmental data

To assess how successional changes in functional and species diversity depend on local environmental conditions, we quantified for each chronosequence site its climate using cumulative dry season water deficit (CWD), its soil fertility using soil pH in water as a proxy, and its isolation using forest cover in the surrounding landscape. CWD describes the cumulative water deficit during the dry months and soil pH is positively associated with relatively basic soils, a high cation exchange capacity [i.e. a positively charged cation such as calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+) and potassium (K^+)] and, hence, with plant-available cations (Veldkamp et al., 2020). Throughout the article, we refer to climatic water availability instead of climatic water deficit because climatic water deficit is expressed in negative numbers, where high values (close to zero) indicate high water availability. Forest cover is estimated in a 1-km radius, as this influences propagule availability of old-growth species and the diversity of dispersal agents (see details in Appendix S9 and distributions of data in Appendix S10).

2.8 | Statistical models

For each of the two taxonomic diversity and two functional diversity metrics and for functional redundancy, we fitted a linear mixed model with successional age and three environmental variables (climatic water availability, soil pH and surrounding forest cover) as predictors. All response and predictor variables were scaled to assess their standardized effects, by subtracting the mean and dividing by its standard deviation. We also included the interactions between environmental variables and stand age (i.e. successional age) to assess how environmental variables influence the successional changes in taxonomic and functional diversity. Sites can vary strongly in how diversity changes during succession due to biogeographical and historical reasons. We therefore included chronosequence site as a random intercept to account for the nested design of plots within sites, and we included a random slope of stand age per chronosequence site to allow sites to have varying changes in the diversity index over time. Models with random intercepts and slopes had a better fit (i.e. lower AIC) than models with only random intercept, and we therefore used random slope mixed effects models for all diversity variables. In the two models for functional diversity, we also included the effect of the corresponding taxonomic species diversity measure as a predictor variable to be able to assess the changes in functional diversity independent of the changes in species diversity. That is, for the model of functional richness, we included taxonomic richness, and for the model of functional evenness, we included taxonomic evenness. The changes in taxonomic and functional diversity could be linear or non-linear (e.g. asymptotic or modal) through time. To test which shape gave the best fit, we ran each model 3 times, including (1) only the linear effect of stand age, (2) the \log_{10} -transformed stand age (prior to scaling) or (3) the linear and quadratic effect of stand age. For all functional and species

diversity metrics, the model with \log_{10} -transformed stand age had the lowest AIC value, and we therefore present only those results (Appendix S11). Mixed effects models were run with the nlme package (Pinheiro & Bates, 2016). All analyses were performed in R version 3.6.1 (R Team, 2019).

3 | RESULTS

Across secondary forest plots, estimated taxonomic richness (Hill 0D at a sampling coverage of 0.77) per plot is on average 11.2 species (Figure 1a) and functional richness is on average 2.4 distinct functional 'groups' (Figure 1c). Functional evenness is generally higher (mean=0.80; Figure 1d) than taxonomic evenness (mean=0.63; Figure 1b). Relative functional redundancy is on average 0.67 (Figure 3).

Stand age had a positive effect on taxonomic and functional richness (Figure 1a,b) and functional redundancy (Figure 3), indicating that they increase during succession. Stand age had a weaker and marginally significant ($p=0.08$) positive effect on functional richness when the model statistically controlled for taxonomic richness (i.e. the standardized regression coefficient β declined from 0.48 to 0.16,

Figure 1c), indicating that a large part – but not all – of the successional increase in functional richness was caused by the successional increase in taxonomic richness. Stand age also had a positive effect on abundance-weighted taxonomic and functional diversity metrics (Hill numbers 1D and 2D , Appendix S12), indicating that the diversity of dominant species increases with plot age in successional chronosequences. In contrast, stand age had a negative effect on taxonomic and functional evenness (Figure 1d–f), indicating that evenness decreased during succession (Figure 1b,d), though evenness was still high (>0.75). The standardized effect of stand age on functional evenness was weaker when the effect of taxonomic evenness was taken into account, indicating that the successional decline in functional evenness is largely – but not fully – driven by the successional decline in taxonomic evenness (effect size of taxonomic evenness on functional evenness >0.7).

Climatic water availability (CWA), pH and forest cover had, in general, no independent effect on taxonomic and functional diversity (Figure 2). This indicates that variation in diversity across sites (i.e. the intercepts) generally did not depend on these environmental variables. CWA showed a significant negative interaction with stand age for functional richness when statistically controlling for taxonomic richness (Figure 2c, dots below the dashed line), and pH

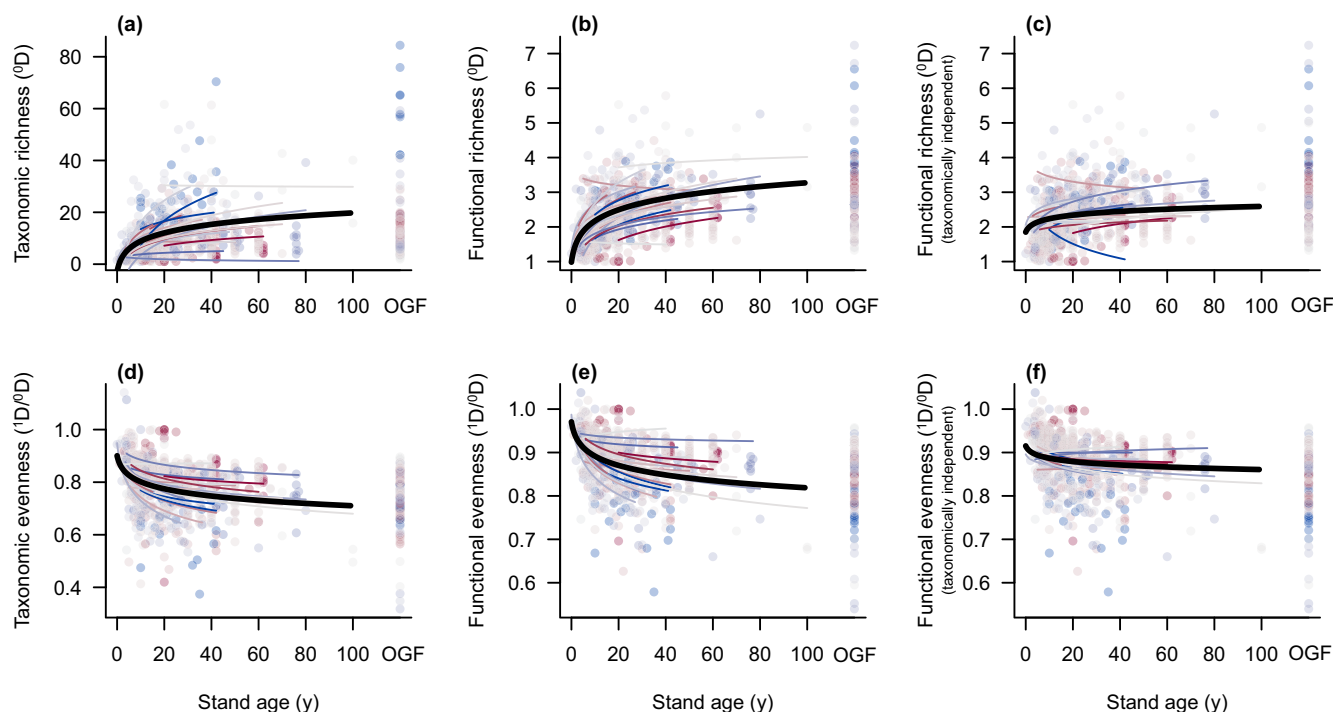


FIGURE 1 Scatter plots of stand age against richness (upper row) and evenness (lower row) for Neotropical secondary forests (22 chronosequence sites and 676 forest plots). Predicted lines are shown for (a) taxonomic richness, (b) functional richness, (c) functional richness when correcting for the effect of taxonomic richness and for (d) taxonomic evenness, (e) functional evenness and (f) functional evenness when correcting for taxonomic evenness in the model. The black line shows the predicted mean effect of stand age on taxonomic and functional diversity. The coloured lines show the predicted regression lines for each of the chronosequence sites, derived from their random slopes in the mixed effects models. Individual dots indicate individual plots (colour-coded according to the sites). The sites are coloured based on their climatic water availability, from wettest (dark blue) to driest (dark red). Dots at 'OGF' are old-growth forest plots, which were not included in the regression models but are shown here for illustrative purpose. Taxonomic and functional richness and evenness are based on Hill numbers (see Methods).

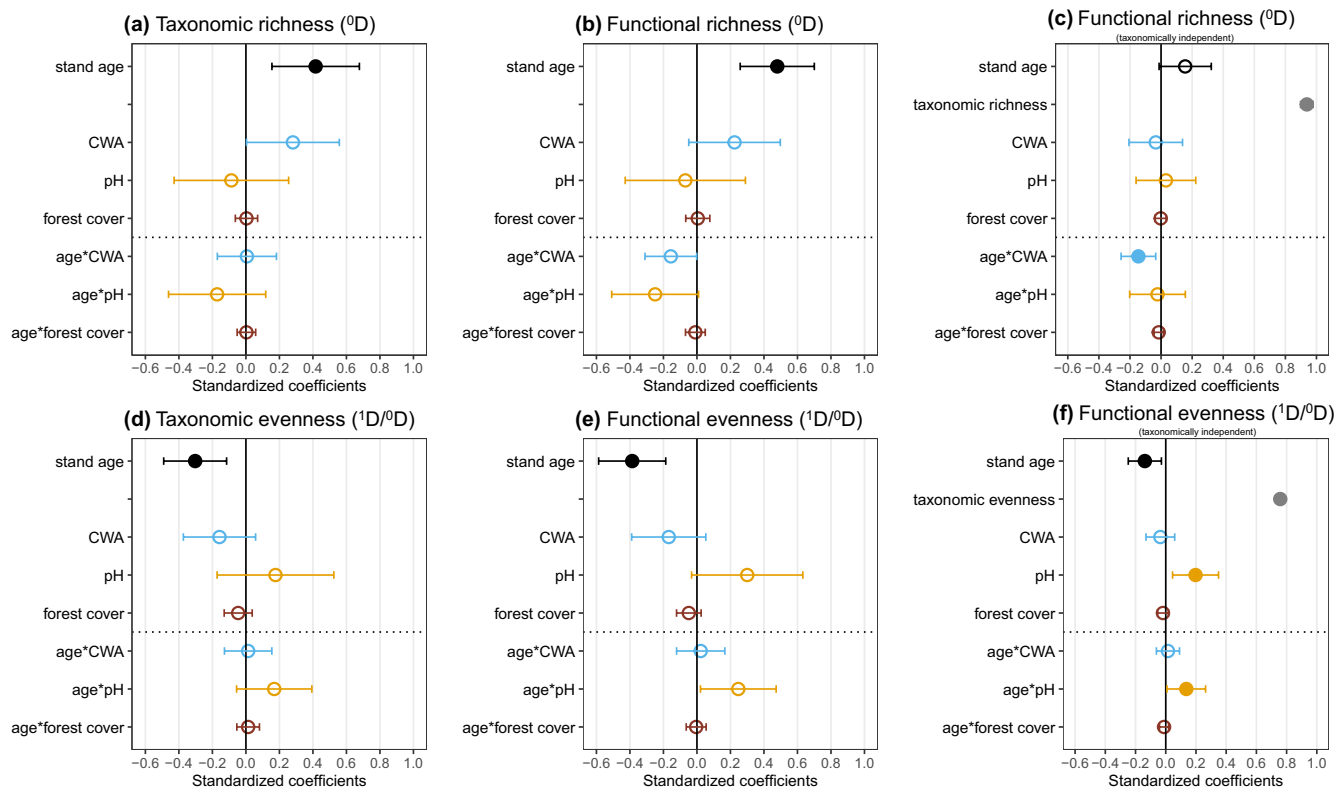


FIGURE 2 Standardized regression coefficients (with 95% confidence intervals) of stand age, environmental factors and their interactions (below the dashed lines) on taxonomic and functional richness (top row) and taxonomic and functional evenness (bottom row) across Neotropical secondary forests. The effects of stand age (black), species richness or evenness (grey), climatic water availability (CWA; blue), pH (yellow), forest cover (brown) and the interactions between the latter three and stand age on (a) taxonomic richness, (b) functional richness without correcting for taxonomic richness and (c) with correcting for taxonomic richness, (d) taxonomic evenness and (e) functional evenness without and (f) with correction for taxonomic evenness. Filled dots represent significant coefficients and open dots represent non-significant coefficients. All functional and taxonomic richness and evenness metrics are based on Hill numbers and standardized based on an equal of 0.77 of sample coverage. The analysis is based on 22 chronosequence sites and 676 forest plots.

showed a significant positive interaction with stand age for functional evenness when statistically controlling for taxonomic evenness (Figure 2f). CWA and pH also showed a negative interaction with stand age for functional redundancy (Figure 3b). This means that at high resource availability (i.e. at high CWA for functional richness, Figure 4a, and at high pH for functional evenness, Figure 4b) the effect of stand age on functional diversity metrics is close to zero, whereas at low resource availability the effect of stand age is positive for functional richness and negative for functional evenness (Figures 2c,f and 4). These interactive effects were not found for functional richness and evenness when not controlling for, respectively, taxonomic richness and evenness, indicating that the patterns of uncorrected functional diversity are mainly driven by taxonomic diversity. Patterns were similar for abundance-weighted taxonomic and functional diversity (i.e. 1D and 2D , Appendix S12).

4 | DISCUSSION

We analysed successional changes in taxonomic and functional diversity and found that, in general, richness increased and evenness

decreased over time. After statistically controlling for taxonomic diversity, the successional changes in functional richness and evenness were strongest in resource-poor environments (dry, nutrient poor), where they started closer to zero (for richness) and one (for evenness) and changed over time, and weak or absent in resource-rich environments. Functional redundancy increased during succession, also most strongly in resource-poor environments. We first discuss general successional patterns in diversity (4.1 and 4.2), then how they are modified by the environment (4.3), and finally what this means for community assembly of secondary forests (4.4).

4.1 | Richness increases during succession because of species arrival and environmental change

Taxonomic richness (Hill number 0D) increased considerably during succession from 1 species/plot at 1 year to ca. 20 species/plot after 100 years (Figure 1a), as indicated by the overall prediction line based on all Neotropical sites (cf. Derroire et al., 2016; Rozendaal et al., 2019). The abundance-weighted diversity (Hill 1D and 2D) also increased during succession (Appendix S12). Taxonomic richness is

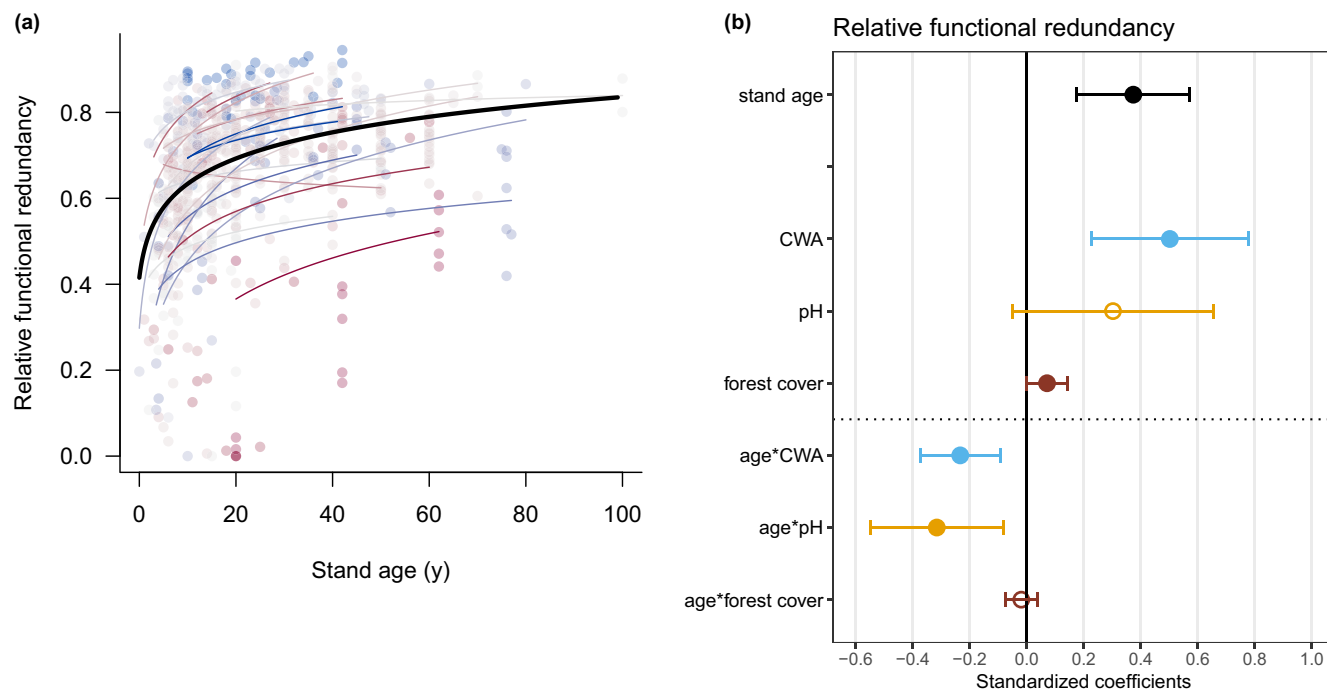


FIGURE 3 (a) Relationship between functional redundancy and stand age and (b) standardized regression coefficients (with 95% confidence intervals) of stand age, environmental factors (CWA = climatic water availability, pH, surrounding forest cover) and their interactions on functional redundancy. Filled dots represent significant coefficients and open dots represent non-significant coefficients. Functional redundancy is expressed in a relative way and varies from 0 (no functional redundancy) to 1 (maximal functional redundancy). In (a), the black line shows the predicted mean effect of stand age on relative functional redundancy for the overall model. The coloured lines show the predicted regression lines for each of the chronosequence sites, derived from their random slopes in the mixed effects models. Individual dots indicate individual plots (colour-coded according to the sites). The sites are coloured based on their climatic water availability, from wettest (dark blue) to driest (dark red).

initially close to zero because nearly all woody vegetation has been removed for agricultural use. Subsequently the resprouting and dispersal filter play a role, as initially richness steeply increases due to the re-sprouting stumps and the germination of pioneers from the soil seedbank and dispersal, followed by a slower accumulation of species due to the gradual dispersal and arrival of seeds of later successional species (Martínez-Ramos et al., 2021), and increased space and light limitations (Lebrija-Trejos et al., 2011; Matsuo et al., 2021). The pool of later successional species is generally larger than the pool of early-successional species, which may further lead to increased taxonomic richness during succession. Also, at the initial stage of succession many species may establish because early canopy closure by pioneer species improves microclimatic conditions (Lebrija-Trejos et al., 2011), thus facilitating the establishment of generalists and later successional specialists (Rüger et al., 2023).

Functional richness increases strongly during tropical forest succession (Figure 1b; cf. Becknell & Powers, 2014; Bhaskar et al., 2014; Craven et al., 2018; Makelele et al., 2021; Whitfeld et al., 2014). Changes in functional richness are partly caused by increases in taxonomic richness (Figure 1c; cf. Lohbeck et al., 2012; Monge-González et al., 2021), as functional richness increased with succession to a lesser extent after accounting for taxonomic richness (Figure 2c, $\beta = 0.16$, $p = 0.082$ vs. $\beta = 0.48$, $p = 0.002$ without accounting for taxonomic richness). This suggests a sampling effect, where

an increase in the number of species leads to a chance of adding species with more extreme trait values and, hence, an increase in the occupied trait space. We also find increases in *functional redundancy* (Figure 3). This agrees with studies showing functional redundancy is low in early-successional forests (Lohbeck et al., 2012), but high in late-successional and old-growth forests (Bu & Ding, 2014; Monge-González et al., 2021). Increasing functional redundancy during succession indicates that taxonomic richness increases more rapidly than functional richness, because new species lead to little or no increase in the multivariate trait space. Each additional species has a reduced chance of contributing to functional richness, leading to increased functional redundancy during succession (Figure 3). Such increased functional redundancy may increase forest resilience to disturbances such as extreme climatic events, as functional overlap between species buffers the impact of the loss of a few species on community-level ecosystem processes.

Besides the sampling effect, however, community assembly mechanisms (i.e. deterministic processes) also play a role, which can be seen from the taxonomically independent successional increases in functional richness (marginally significant, Figures 1c and 2c). First, during succession, light-demanding, early-successional species remain present in the forest canopy (Peña-Claros, 2003; Rüger et al., 2023) or are maintained in gaps. At the same time, the build-up of vegetation and shading leads to the establishment of

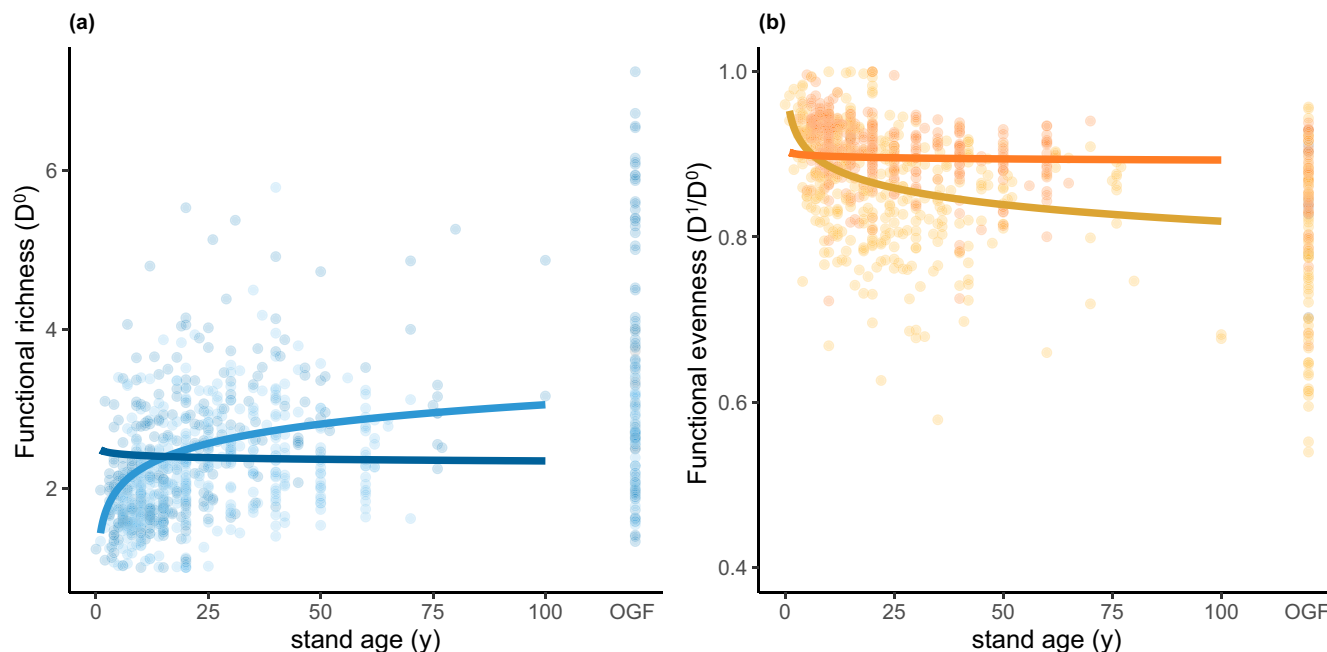


FIGURE 4 Scatter plots of stand age and (a) functional richness and (b) functional evenness, showing the interaction effect of (a) stand age \times climatic water availability (CWA) for functional richness and of (b) stand age \times pH for functional evenness. These interaction effects were significant in the regression models (see blue and yellow dots in Figure 2c,f). Light blue line shows the prediction at a CWA of -800 mm/year and dark blue line at a CWA of -200 mm/year. Light blue dots are dry plots (CWA < -505 mm/year) and dark blue dots are wet plots (CWA > -505 mm/year). Light orange line represents the prediction at a pH of 5 and dark orange line at a pH of 7. Light orange dots are low-pH plots (pH < 6.3) and dark orange dots are high-pH plots (pH > 6.3). The predicted lines are at representative 'high' and 'low' CWA and pH values in the dataset. Dots at 'OGF' are old-growth forest plots, which were not included in the regression models but are shown here for illustrative purposes. Prediction lines were calculated while setting all other variables at their mean.

shade-tolerant, late-successional species with different trait values in the forest understory (Müller et al., 2021), which leads to an increase in the occupied functional trait space. Second, generally milder abiotic conditions (e.g. cool, humid, shaded) and, third, greater vertical abiotic heterogeneity in later successional stages (Lebrija-Trejos et al., 2011; Matsuo et al., 2021) may allow a larger number of functional types to establish and co-exist (Falster et al., 2017; Kohyama, 1993). Taxonomic and functional richness of old-growth forests are higher than old secondary forests (Figure 1a,c), indicating that recovery takes longer than the time frame assessed here.

4.2 | Evenness decreases during succession because of increased filtering of dominant species and a large tail of rare species

Taxonomic evenness is determined by species number and relative species abundances. In contrast to the expectations (Odum, 1969), taxonomic evenness declined from 0.88 after 1 year to 0.75 after 100 years as indicated by the overall prediction based on all Neotropical sites (Figure 1d). This indicates that, counterintuitively, later successional forests have low evenness because of a combination of few dominant species and a large tail of rare species (ter Steege et al., 2013). Studies using Hill's evenness also find decreasing evenness during succession (Chazdon et al., 2023), whereas site

studies that use other taxonomic measures of evenness (i.e. Pielou's evenness) find that taxonomic evenness remains constant (Bauters et al., 2019) or increases during succession (Bazzaz, 1975; Derroire et al., 2016; Makelele et al., 2021; Mora et al., 2015). These contrasting results depend on how evenness is calculated; Pielou's evenness puts relatively more emphasis on dominant species [by using \ln -transformed diversity as $\ln(D^1)/\ln(D^0)$]. In contrast, our measure of Hill's evenness weighs all species proportional to their abundance. As a result, the accumulation of rare species (e.g. singletons and doubletons) leads to a more uneven abundance distribution and lower Hill's evenness over time (Figure 1d) (Tuomisto, 2012). We indeed find that, in contrast to Hill's taxonomic evenness, Pielou's taxonomic evenness generally increases during succession (Appendix S13 and S14). This indicates that the evenness of dominant species (which receive more weight in Pielou's evenness) increases during succession, whereas the evenness of the whole community (i.e. the Hill's evenness) declines due to a strong increase in rare species. The increase in rare species during succession may be largely caused by the larger pool of later successional species compared to the smaller pool of early-successional species (Hubbell, 2005).

Functional evenness (i.e. Hill's functional evenness) also decreased during succession (Figure 1e), and more weakly when accounting for taxonomic evenness (Figure 1f), from ca. 0.92 at 1 year to ca. 0.88 after 100 years (Figure 1e, f). This indicates that the distribution in traits becomes slightly more uneven during succession. As

for taxonomic evenness, this decrease is caused by relatively faster increase in functional richness (0D) than abundance-weighted functional diversity (1D) with forest age, leading to a decrease in $^1D/^0D$.

We had predicted that functional evenness would increase with succession because of increased biotic filtering and density-dependent processes such as pests (Lebrija-Trejos et al., 2014), pathogens (Bever et al., 2015) and competition. In the shaded and humid understory, pests and pathogens are more abundant and have a stronger impact, potentially leading to functionally more diverse and even communities in such humid than in drier environments (Harms et al., 2000). Additionally, competition among neighbours may lead to increased limiting similarity during succession (MacArthur & Levins, 1967) and therefore an increase in functional evenness. However, increased competition during succession could also lead to dominance by a few competitive species, leading to reduced overall evenness. Contrary to these predictions, the observed decrease in functional evenness suggests that increased filtering may lead to a convergence in trait values of the dominant species (Lasky et al., 2014) towards values that are most successful given the prevailing (a)biotic conditions, and/or may cause competitive exclusion of some other species with sub-optimal trait values. At the same time, a long tail of rare species with different trait values manages to establish and survive due to small-scale heterogeneity in abiotic conditions. As the successional decrease in functional evenness may be more strongly driven by the rare species, it is more likely that decreases in functional evenness are caused by processes such as increased small-scale heterogeneity, which may lead to higher trait variation among rare species. Functional evenness of dominant species, however, may actually increase (see also discussion of taxonomic evenness) due to increased shading, which selects for shade-tolerant species with similar trait values that can compete successfully under-shaded conditions (Kunstler et al., 2016; Lebrija-Trejos et al., 2014). This is supported by the successional increase in functional redundancy (Figure 3), suggesting that most newly added species are functionally similar to the already established species. Other successional tropical forest studies also find evidence for increased abiotic filtering by light or soil nutrients over time (Craven et al., 2018). Similarly, studies in temperate forests found that competitively dominant species had very similar trait values (Kunstler et al., 2012; Mayfield & Levine, 2010).

Most studies that assess functional evenness or other abundance-weighted functional diversity indices (e.g. Rao's quadratic entropy and functional divergence) did not find any changes during succession (Bhaskar et al., 2014; Makelele et al., 2021; Müller et al., 2021; Whitfield et al., 2014). Functional dispersion (Fdis) is the only index assessed by these studies that does show successional changes. Fdis is the abundance-weighted distance of species from the centroid of trait space and emphasizes trait differences among dominant species. On abandoned pastures in Panama, Fdis increased briefly during the first 7 years of succession and saturated afterwards (Craven et al., 2018). In contrast, on abandoned intensively-used and fertilized sugarcane plantations in Brazil, Fdis declined over succession, probably because of a decline in soil fertility and an increase in

the filtering for species with similar, conservative trait values (Pinho et al., 2018). This latter study is in line with our results, as it shows that filtering increases during succession especially in resource-poor environmental conditions, leading to convergence of traits of the dominant species. Differences with other studies can also be due to the use of null models or because they did not correct for taxonomic evenness (Figure 2f). By accounting for taxonomic richness, we show that functional evenness does not only decrease over time because taxonomic evenness decreases, but probably also because of a combination of trait convergence in dominant species due to increased filtering effects, and trait divergence in rarer species due to increased environmental heterogeneity (Lasky et al., 2014).

4.3 | Functional diversity changes strongly with forest age in harsh conditions but remains constant in benign conditions

Successional trajectories of taxonomic and functional diversity varied surprisingly little with environmental conditions, as indicated by the few significant interactions between forest age and the environmental drivers (Figure 2). Only for functional redundancy (Figure 3), and when functional diversity was corrected for successional changes in taxonomic diversity, we found that under harsh environmental conditions functional richness, evenness and redundancy changed strongly, whereas under benign environmental conditions they changed little (Figure 4). In dry areas with low climatic water availability, functional richness and functional redundancy start closer to zero and increase with forest age, whereas in wet areas functional richness starts at higher values but remains constant over time (Figure 4a). Similarly, low pH (and thus nutrient poor) sites show a stronger decrease in (taxonomically corrected) functional evenness, whereas fertile, high pH sites show no or weak changes (Figure 4b). Under harsh site conditions, the establishment of early pioneer species may facilitate the establishment of later successional species by improving microclimatic conditions (e.g. less drought and heat stress due to more shading) (Lebrija-Trejos et al., 2010), leading to functional richness increase. The even faster increase in taxonomic richness, however, leads to an increase in functional redundancy during succession (Figure 3). The idea that strong initial abiotic filtering quickly reduces in harsh sites is supported by changes in the community-weighted mean trait values in dry forests from conservative to more acquisitive (Lohbeck et al., 2013; Poorter et al., 2019; Poorter, Rozendaal, et al., 2021). The reduced filtering during succession in harsh sites may also provide an advantage for species that are relatively more acquisitive (e.g. fast growers). If such species then become more dominant, it would result in a decrease in functional evenness and an increase in functional redundancy. Although in productive sites competition for light increases over time, competition for water and/or soil nutrients may be weaker and lead to initial strong biotic competition and limiting similarity, which may remain relatively constant or decrease during succession. These conditions would result in high initial functional richness and

evenness and weak changes during succession. Contrary to functional richness and evenness, changes in taxonomic richness and evenness during succession did not depend on site conditions, indicating that these effects mainly determine the type (i.e. traits) of species and, hence, the richness and dominance of functional traits in the community.

The forest cover surrounding the sites did not affect the recovery of taxonomic and functional diversity. We expected that higher forest cover would facilitate and speed up recovery due to higher influx of seeds from old-growth forest species (Arroyo-Rodríguez et al., 2023; Pérez-Cárdenas et al., 2021). Possibly, recovery is more strongly determined by seeds present in the soil seedbank and resprouting of remaining stumps or roots than by influx of new seeds (Jakovac et al., 2021). Forest cover may also have weak effects because of methodological reasons; we estimated forest cover at one moment in time, but the surrounding forest cover may have been larger at the time of abandonment of the older plots in the chronosequence than at the more recent time of abandonment for the younger plots, as most landscapes have experienced forest loss over time. Alternatively, not only forest quantity but also forest quality is important; seeds of new species with different trait values (i.e. old-growth forest species) are mainly originating from surrounding old-growth forest remnants (Sloan et al., 2016), while our forest cover index included both secondary and old-growth forests, which captures the potential seed input from species from different successional stages.

4.4 | Perspectives and conclusions

Functional diversity indices are intriguing because they enable the quantification of biological complexity from a functional point of view. Yet, complexity does not necessarily enhance understanding. For example, it may be the individual traits rather than the combinations of multiple traits, or a different set of traits, that are relevant for community assembly in different communities and over succession. Moreover, it is difficult to infer community assembly processes from the patterns, as all community assembly mechanisms (dispersal limitation, abiotic filtering, priority effects, facilitation, mutualistic relationships, pests, pathogens and competition) operate simultaneously, and their individual effects on the observed functional diversity are hard, if not impossible, to disentangle (van Breugel et al., 2024). Furthermore, understanding the underlying mechanisms and testing the relative importance of assembly processes require a quantification of the filters, traits and vital rates. For the filters, this requires the identification and quantification of successional changes in dispersal context (landscape, identity and abundance of seed sources and dispersal agents), disturbances (e.g. fire), abiotic conditions (resources, microclimate) and biotic conditions (abundance and identity of symbiotic mutualists such as mycorrhizae, pests, competitors and the facilitative role of early-successional species) (Poorter et al., 2024). For the traits, this requires going beyond the soft traits that underlie the global spectrum of plant form

and function (e.g. plant height, specific leaf area, seed size and wood density; Díaz et al., 2015), and measuring those hard traits (Craven et al., 2015; Oliveira et al., 2021) that are really functional given the local ecological conditions. For the vital rates, this requires monitoring the performance (recruitment, growth, survival) of individuals and replacement of species longitudinally over time (e.g. Lasky et al., 2014). Unravelling community assembly may require from us as much work and time as it does for plants to participate in the community assembly process.

Yet, our continental-wide synthesis of successional patterns in functional diversity allows generalizations and inferences about the most important mechanisms at play and has advanced understanding of succession in three ways. First, functional richness, functional redundancy (this study) and individual trait ranges (Poorter, Rozendaal, et al., 2021) increase consistently during succession independent of the changes in taxonomic richness, suggesting an important role of increased environmental heterogeneity and reduced abiotic filtering during succession. Second, in general, functional evenness declines during succession. This suggests that biotic pressures such as competition lead to convergence of trait values of dominant species towards late-successional, shade-tolerance traits, while simultaneously allowing a large tail of rare and functionally distinct species to establish and survive due to increased abiotic heterogeneity. Third, successional pathways in functional diversity proceed in fundamentally different ways in resource-poor environments versus resource-rich environments, suggesting that abiotic filtering and facilitation are important assembly processes during early succession in resource-poor environments, whereas in resource-rich environments abiotic constraints are relaxed and cause higher initial functional diversity with little further change over time. Hence, despite the complexity of functional diversity, our study has increased our mechanistic understanding of community assembly during succession of secondary forests across the Neotropics, where we found that increasing number of rare species and traits drive changes in diversity and richness.

AUTHOR CONTRIBUTIONS

The study was designed by MTvdS, LP and FB; data management was done by CCJ, DMAR and MTvdS; data analyses were carried out by MTvdS; drafts were written by MTvdS and LP; intense discussions were held with MTvdS, LP, GD, MMES, ML, SCM, RB, MvB, JMDR, SMD, CCJ, HP, DMAR, DC, FMA, PBr and FB. They, together with JSA, PBA, JB, BF, RGC, JLHS, DK, SL, EMS, RM, CRG, LSV, LPU and GWF provided comments multiple times and contributed data, and FSA, JLA, FA, VB, GALC, JC, RC, GC, MDMV, BdJ, ELT, VdSM, DD, SDW, EDG, YRFN, VG, JH, RL, OL, EVSBS, HMT, MMR, JAM, SOG, ASA, MT, MU, JW and KZ commented at least once and contributed data.

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CONFLICT OF INTEREST STATEMENT

None.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supplementary Material of this article (Appendix S16).

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