



Functional recovery of tropical forests: The role of restoration methods and environmental conditions

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ABSTRACT

Forest and landscape restoration strategies influence the recovery of plant functional traits, which in turn shape ecosystem processes. To understand how traits respond to restoration and environmental conditions, we assessed the functional recovery of three forest restoration types in Brazil's Atlantic Forest: natural regeneration, high-diversity restoration plantations (20–60 species), and unmanaged tree monocultures. Across 285 plots aged 1–76 years, we quantified seven leaf and stem traits for over 500 species. For each plot, we calculated community mean trait values and three functional diversity indices. The three restoration types showed contrasting successional patterns. Natural regeneration and restoration plantations shifted from acquisitive to conservative resource-use strategies with site age, while monocultures moved in the opposite direction. Restoration plantations exhibited the highest functional richness. Soil conditions (sand content and sum of bases) influenced trait composition and diversity, whereas climate and landscape context had smaller effects. In 20-year old sites, most traits in natural regeneration and restoration plantations approached 90 % of forest remnants values. In contrast, unmanaged monocultures recovered slowly, with only half of the traits reaching this threshold in 40-year old sites. Our findings show that restoration methods and site conditions jointly shape functional recovery. Natural regeneration tends to align with forest remnant traits, restoration plantations speed up early recovery but may diverge over time, and monocultures require active interventions to enhance outcomes. Recognizing these functional trajectories is key to improving biodiversity conservation and ecosystem resilience in tropical forest restoration.

1. Introduction

Forest and landscape restoration efforts can help mitigate deforestation, land degradation, and climate change by restoring forest cover

and the ecosystem services it provides in deforested and degraded landscapes (Sabogal et al., 2015). Forest landscape restoration initiatives have gained significant momentum globally through initiatives such as the Bonn Challenge – which accumulated over 210 million

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hectares of pledges from over 60 countries, the Trillion Tree Campaign, and the United Nations Decade on Ecosystem Restoration (Brancalion and Holl, 2020). These initiatives do not simply aim only at increasing tree cover, which could be easily done by establishing industrial monocultures of exotic species (Lewis et al., 2019); they also aim to support the long-term recovery of forest functions (e.g., carbon sequestration, nutrient cycling, and water regulation). Given that functional traits influence plant growth and survival and shape ecosystem dynamics (Grime, 1998; Tilman et al., 1997), they have been used to evaluate restoration performance. In this study, we focus on changes in functional traits to provide insights into how restored forests develop over time under different restoration strategies and environmental conditions.

Forest restoration in the tropics varies along a passive-active restoration continuum, ranging from the spontaneous colonization of the target area (e.g. natural regeneration) to the active introduction of trees in plantations (e.g. restoration plantations), including intermediary situations in which active planting and natural regeneration are parts of a restoration approach (e.g., unmanaged tree monocultures) (Chazdon et al., 2024). Each of these methods has different implications for forest recovery, particularly in terms of species composition and trait dynamics over time (Carlucci et al., 2020; Martínez-Garza et al., 2013; Toledo-Aceves et al., 2021; Werden et al., 2022). Natural regeneration, unmanaged tree monocultures, and restoration plantation are usually implemented in different conditions, resulting in different starting points, environmental filters, and successional pathways. There is limited knowledge, however, about how restored forests recover their functional attributes over time under various restoration methods and environmental conditions (Brouwer et al., 2024). Preliminary studies show that active and passive restoration methods result in different functional attributes, such as a higher proportion of biotic dispersed species and more later successional species in plantations, although largely depending on the planted species (Toledo-Aceves et al., 2021).

Beyond the choice of restoration method, the recovery trajectory of restored forests is also shaped by environmental conditions that influence species establishment, growth, and functional composition over time. Environmental conditions such as climate, landscape characteristics, and soil properties significantly influence the pace and trajectory of forest recovery (Boukili and Chazdon, 2017; Poorter et al., 2023; Wiczyński et al., 2019). Water availability is a particularly important driver of functional composition and the trajectory of succession in secondary forests (Poorter et al., 2021b; Poorter et al., 2019). Landscape characteristics, such as connectivity to nearby forests, fragmentation, and habitat quality, shape the composition and distribution of species during succession and the recovery process (Safar et al., 2022). Moreover, soil properties, including structure, acidity, and nutrient availability, play an important role in determining the success of restoration efforts by influencing plant growth and ecosystem functioning (Pinho et al., 2018; van der Sande et al., 2018).

Here, we ask (1) how three different restoration methods (natural regeneration, unmanaged monocultures, and restoration plantations) differ in functional composition and functional diversity, (2) how functional attributes develop over time under different environmental conditions, and (3) whether these restored forests recover toward forest remnants values.

We expected natural regeneration to begin with fast-growing, light-demanding pioneer species that facilitated the efficient acquisition and utilization of resources such as nutrients, water, and light, thereby supporting growth and reproductive success. In contrast, we expected restoration plantations to include a mix of early- and later-successional species, as these were typically selected to represent multiple functional groups or to target specific functions such as nitrogen fixation, and were introduced simultaneously at the start of the project (Rodrigues et al., 2009). In unmanaged tree monocultures—such as those dominated by *Eucalyptus* spp. and *Pinus* spp.—we hypothesized that remnant crop trees would remain dominant, alongside a regrowing native understory

composed of species with conservative resource-use traits adapted to lower light availability. We also expected that communities in resource-poor environments (limited in light, nutrients, and water) would express more conservative traits and exhibit lower functional richness (Wiczyński et al., 2019). Over time, we anticipated that the outcomes of all restoration methods would converge and gradually recover toward conditions observed in forest remnants (Brouwer et al., 2024). However, we hypothesized that restoration plantations would recover more rapidly than the other methods due to controlled species selection focused on establishment success, fast growth, and high survival rates. Conversely, we expected unmanaged monocultures to take longer to approach forest remnant conditions, as commercial species such as pine or eucalypt were likely to occupy the niche of several late-successional, emergent native trees with more diverse functional attributes.

2. Methods

2.1. Study region

We focused on the Atlantic Forest of São Paulo state, southeastern Brazil, a heavily fragmented and human-modified tropical (and sub-tropical) forest but with prominent restoration initiatives. Forest remnants in most parts of this region show a decline in biomass and species (de Lima et al., 2020). In the Atlantic Forest, landowners are required by the Native Vegetation Protection Law to have at least 20 % native forest cover on their lands and Areas of Permanent Protection (e.g., riparian buffers, water springs, steep slopes), resulting in landscapes with natural regeneration and restoration plantations (more details in (Brancalion et al., 2016)). Complementary, monoculture tree plantations, mostly of eucalypts and pine trees, have been established for timber production, but have been historically abandoned in marginal production areas, especially in slopes, and in properties with legal deficits of native vegetation. These are typically older plantations that were previously harvested or left unmanaged, but have since developed a closed canopy formed by remnant crop trees and the regrowth of native vegetation. As consequence, the new forests of this region are a heterogeneous mosaic of patches established by different methods and in different biophysical contexts, with different ages. Forest landscape restoration has been practiced for decades in this region, using natural regeneration, high-diversity restoration plantations, and other restoration methods (Rodrigues et al., 2009). This region is characterized by a large biophysical gradient, that used to be covered with evergreen and semi-deciduous (sub-) tropical forests (Fig. 1A). The coldest and hottest average mean temperature ranges from 15 to 27 °C and average annual precipitation from 1100 to 2800 mm/yr (de Souza Rolim and Lucas, 2016). The presence of multiple restoration methods (Fig. 1B), a range of forest landscapes, and a large biophysical gradient make this area an excellent testing ground for our research. We studied three restoration methods: natural regeneration on pastures, natural regeneration under unmanaged monocultures, and high diversity restoration plantations (detailed description in sup. Mat. and Fig. 1B). In addition, we used as reference sites remnant forest patches with no previous record of conversion to alternative land uses or major levels of disturbance (hereafter referred as forest remnants). However, it does not mean that these forests express the best conservation situation or pristine ecosystems, as they are mostly embedded in highly modified landscapes and are subjected to several human-mediated disturbances as edge effects, dispersal limitation, cattle entry, among others.

2.2. Chronosequence sites

We used a chronosequence approach to describe long-term successional trajectories in functional composition for each of the three restoration methods. Chronosequences use a space-for-time substitution, by establishing plots in forest patches with different ages since abandonment (in the case of natural regeneration and unmanaged

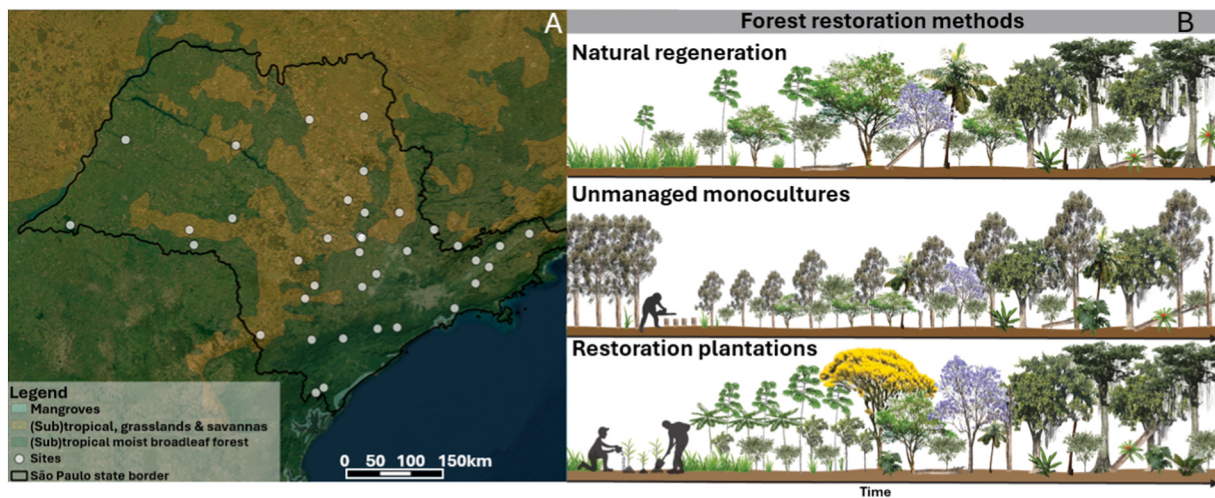


Fig. 1. A) Map of São Paulo State, Brazil. Tropical and subtropical forest (green) and savanna biomes (yellow) with the 29 chronosequence study sites (dots). B) Illustration of succession in three restoration methods: natural regeneration (passive), unmanaged tree monocultures (passive), and restoration plantations (active), showing distinct differences in starting points, species and development over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

monocultures) or tree planting (in the case of restoration plantations). Chronosequences assume that all sites experienced similar starting conditions and followed a similar successional trajectory, which is often not the case (Angert, 2024). Although this approach does not track changes within the same sites over time and is inherently correlative rather than causal, to date few restoration plots have been monitored over time. To account for potential environmental variability, we designed our sampling strategy to represent a range of biophysical gradients and spatial-temporal heterogeneity in the study area (Table S3, Fig. 1A). For each of the three restoration methods we compiled a chronosequence by establishing 211 plots at 29 forest sites in São Paulo State, Brazil (Fig. 1A, Fig. 1B), and in addition we established 74 plots in forest remnants which we included in the results figures as reference values, i. e., these were not part of the chronosequence analysis. In total this study encompasses 285 plots.

2.3. Plot data

We established 30×30 m plots in 38 natural regeneration areas, 44 in unmanaged tree monocultures, and 129 plots in restoration plantations (Table S1). The age of the forest patch where the plots were located was calculated using all available Landsat satellite images from 1984 to 2023, and the *nphen* R package to detect vegetation anomalies (Chávez et al., 2023). When plots were older than satellite imagery (<1984), we used interview data from landowners, when available. Forest age varied from 1 to 76 years across sites (mean $17.01 \pm \text{SD } 14.53$). In each plot all trees, palms, ferns, and shrubs ≥ 5 cm stem diameter at breast height (at 1.3 m, dbh) were measured and identified to species level. Across plots, on average, 96.3 % of stems were identified to species level (range 72.9 to 100.0 %). To assess how changes in community-weighted mean traits (CWM) and functional diversity (FD) depend on local environmental conditions, we quantified for each plot its local environmental characteristics (Table S3). Water availability (or in this case, deficit) was calculated as average annual climatic water deficit CWD (mm year^{-1}) for the period 1993–2022, following the method of (Campanharo and Silva Junior, 2019). As a proxy for forest connectivity and fragmentation, distance from the centre of each plot to nearby forest fragment in meters was calculated using MapBiomass forest cover (Souza et al., 2020). Distance was taken from the year at the start of regrowth, or in the case of plots where regrowth was older, we took distance to nearby forests in the year 1984 (to coincide with Landsat data)). Three soil samples were taken per plot at 0–10 cm depth and combined to create a

composite sample for particle size analysis and chemical analysis (Fig. S2). Principal component analysis was used to determine the soil variables that explained most variation, resulting in soil sum of bases (Na, K, Ca and Mg), soil sand content and potential soil acidity ($\text{H} + \text{Al}$) (Fig.S1, & Fig.S2). Mean, standard deviation, minimum and maximum values of environmental drivers are presented in Table S3. We tested differences in environmental conditions among restoration methods using an ANOVA (Fig. S3).

2.4. Trait data, CWM and FD

We focused on seven traits; specific leaf area (SLA), leaf dry matter content (LDMC), wood density (WD), leaf nitrogen content (LNC), nitrogen fixing ability (N-fixation), proportion of biotic dispersal (biotic dispersal), and proportion of deciduousness (Evergreen), related to resource use and adaptations to biophysical conditions (Table S4). These are traits that shape plant responses to the environment and impact the recovery of forest ecosystem functions such as carbon, water, and nutrient cycling. Traits were collected in all sites, covering most of the environmental and floristic gradients in the study region. We measured traits for 528 species for 3–7 individual trees per species following standardized protocols based on (Pérez-Harguindeguy et al., 2013). We selected well exposed branches with fully expanded, undamaged, and (partially) sunlit leaves. Deciduousness, nitrogen fixation, and biotic dispersal data were derived from TRY (Kattge et al., 2020), NodDB (Kattge et al., 2020; Tedersoo et al., 2018), and TreeCo (de Lima et al., 2020) databases, trait data that was missing was imputed based on phylogenetic distances (more details in Sup. Mat.). Community trait averages (the community-weighted mean; CWM) were calculated based on the trait values and weighted by the basal area of each species in each plot, including remnant commercial crop trees. Furthermore, for a subset of 199 plots, three functional diversity (FD) indices (richness, evenness, and divergence, Table S4) were calculated based on the four continuous traits in our dataset (SLA, WD, LDMC, and LNC) using the *FD* package in R (see Sup. Mat. for more details about CWM and FD calculations). Plots included in this analysis had data for all four traits.

2.5. Statistical analyses

For each restoration method, functional recovery was analyzed by regressing CWM and functional diversity indices against stand age. CWM values of forest remnant plots were not included in the regression

analysis but were used as a reference. In addition, we used linear mixed models to assess how CWM trait values and diversity indices were affected by possible drivers using a model consisting of proxies related to resource availability (climatic water deficit, soil sum of bases), soil conditions (soil sand content, soil potential acidity), time since establishment and its interaction with restoration method (more details in sup. Mat.; Table S6 model structures). We tested for multicollinearity using the Variance Inflation Factor (VIF) function in R, and all predictor variables had VIF values below the commonly accepted threshold (<5), indicating no strong multicollinearity. To compare the recovery of functional attributes between restoration methods we calculated for each site the percentage of recovery of an attribute compared to forest remnant values. Mean forest remnant functional attribute values (CWD and FD) were corrected for climatic water deficit, soil sand content, sum of bases, and potential acidity. Because attribute values can be smaller or larger than forest remnant values, we calculated the Kullback-Leibler

divergence, which calculates a proportion of recovery, this was then multiplied by 100 to convert it to percentages (following the method of (Poorter et al., 2021b)). The results of this analysis should be interpreted as relative trends rather than direct measurements of recovery speed, as our chronosequence approach does not track individual sites over time. All models were fitted in R (R Core Development Team, 2011) using the lme4 package (Bates et al., 2007) and glmmTMB package (Brooks et al., 2017).

3. Results

3.1. Effects of restoration method and age

Restoration method and site age both significantly influenced functional traits and diversity, with several traits also showing significant interactions between these factors (Figs. 2, 3, 4; Table S5, Fig. S5). Four

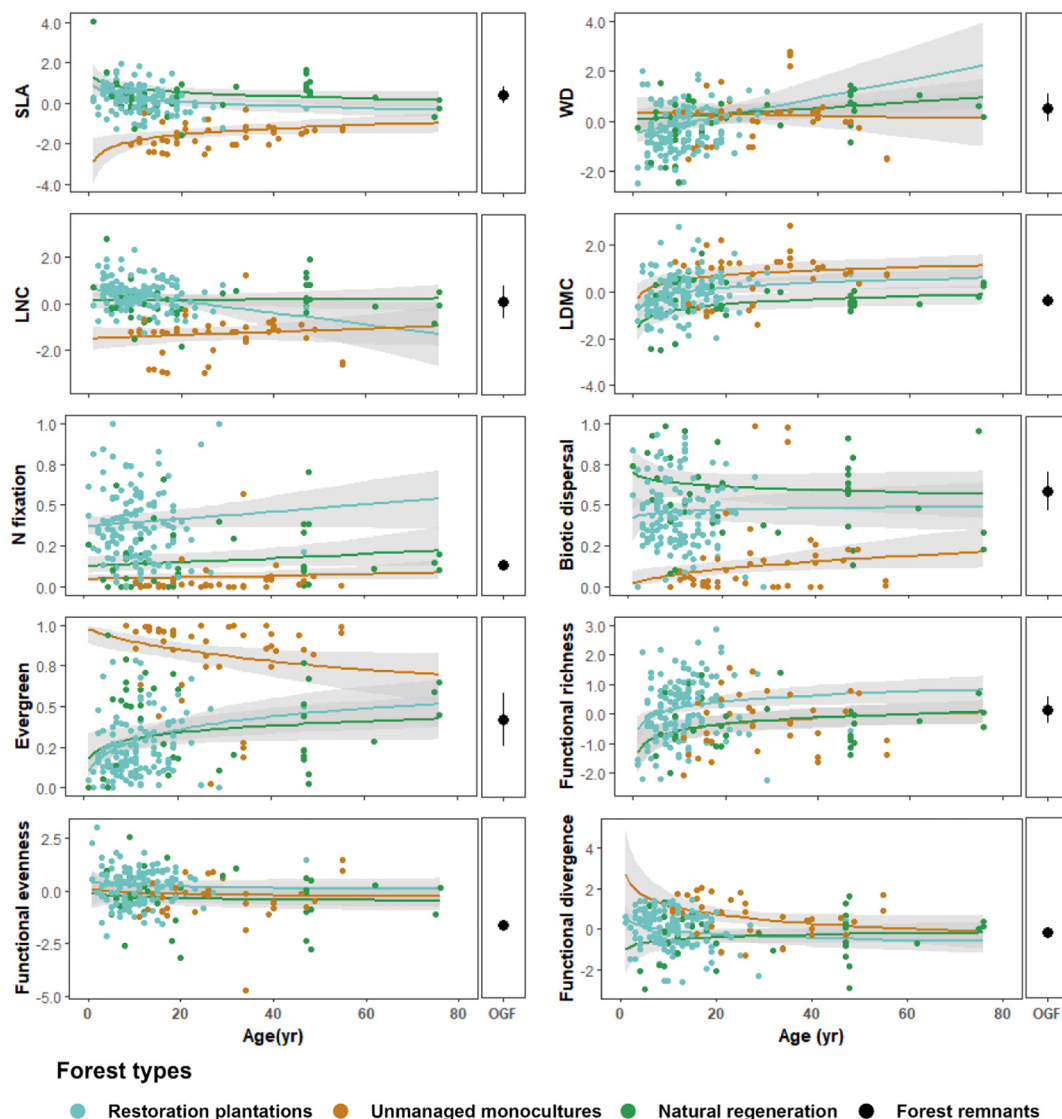


Fig. 2. Recovery of Community Weighted Mean (CWM) functional trait values and Functional diversity (FD) indices with time since regeneration started. CWM trait values were calculated by weighting by basal area, FD by weighting by abundance. All attributes were standardized except proportional data (N-fixation, Biotic dispersal, and Evergreen). Dots indicate CWM or FD values of individual plots. Each line and colour represent the model prediction for a different forest type (blue = restoration plantations; orange = unmanaged monocultures; green = natural regeneration). Grey areas show bootstrap confidence intervals. Other predictors (Fig. 3, Table S5) used in the models were kept constant at the mean. Forest remnants reference mean values for illustrative purposes (black dot in right panel) were based on models that corrected for climatic water deficit, soil sand content, soil sum of bases and potential soil acidity. N.B. The green line of natural regeneration overlaps the orange line of unmanaged monoculture in the functional richness subpanel. SLA = specific leaf area; WD = wood density; LDMC = leaf dry matter content; LNC = leaf nitrogen content. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

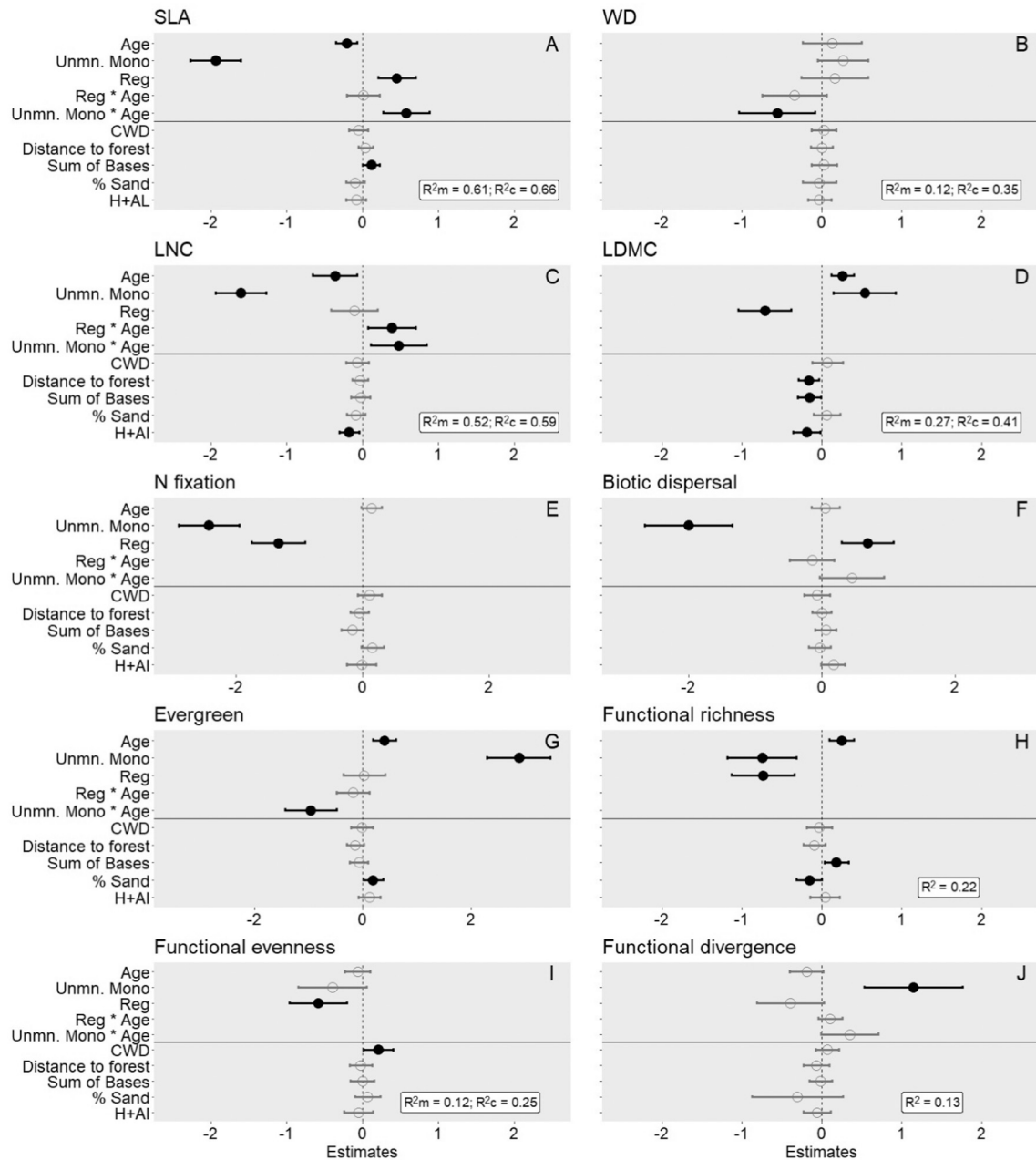


Fig. 3. Standardized biophysical drivers of Community Weighted Mean functional trait values and Functional Diversity indices. Significant ($p < 0.05$) predictors are colored black, nonsignificant predictors that remained in the model are grey and, predictors that did not remain in the model after averaging are empty. Restoration plantations are the reference factor, coefficients of unmanaged monocultures and natural regeneration show the relative change in relation to restoration plantations. R^2_m for fixed effects only and R^2_c for fixed and random effects together are shown, or only R^2 in case the random effect was omitted from the model. For mixed effect beta regression models, no reliable (pseudo) R^2 can be calculated, so we do not show these (i.e. for the N-fixation, biotic dispersal and evergreen models). SLA = specific leaf area; WD = wood density; LDMC = leaf dry matter content; LNC = leaf nitrogen content.

traits—SLA, WD, LNC, and proportion of evergreen species—exhibited significant interactions between restoration method and age, indicating that successional trajectories varied by restoration approach. For example, SLA decreased with age in natural regeneration and restoration plantations, but increased in unmanaged monocultures ($\beta = 0.58$). WD declined over time only in unmanaged monocultures ($\beta = -0.56$), while remaining stable in the other two methods. LNC increased with age in natural regeneration and monocultures ($\beta = 0.39$ and 0.47 , respectively), but declined in plantations. Similarly, the proportion of evergreen species decreased significantly with age in unmanaged monocultures ($\beta = -0.96$), with no consistent pattern in the other methods.

When averaged across ages, restoration methods differed markedly in CWM traits and functional diversity. Natural regeneration had the highest SLA and biotic dispersal, intermediate N-fixation, and lowest functional evenness. Restoration plantations showed highest N-fixation and functional richness, and intermediate values for SLA, LDMC, and biotic dispersal. Unmanaged monocultures had the highest LDMC, evergreenness, and functional divergence, but the lowest SLA, LNC, N-fixation, and biotic dispersal. WD did not differ significantly across restoration methods.

Across all restoration types, several traits also showed consistent successional trends with age. Specifically, SLA ($\beta = -0.21$) and LNC ($\beta = -0.37$) decreased, while LDMC ($\beta = 0.26$), evergreenness ($\beta = 0.40$),

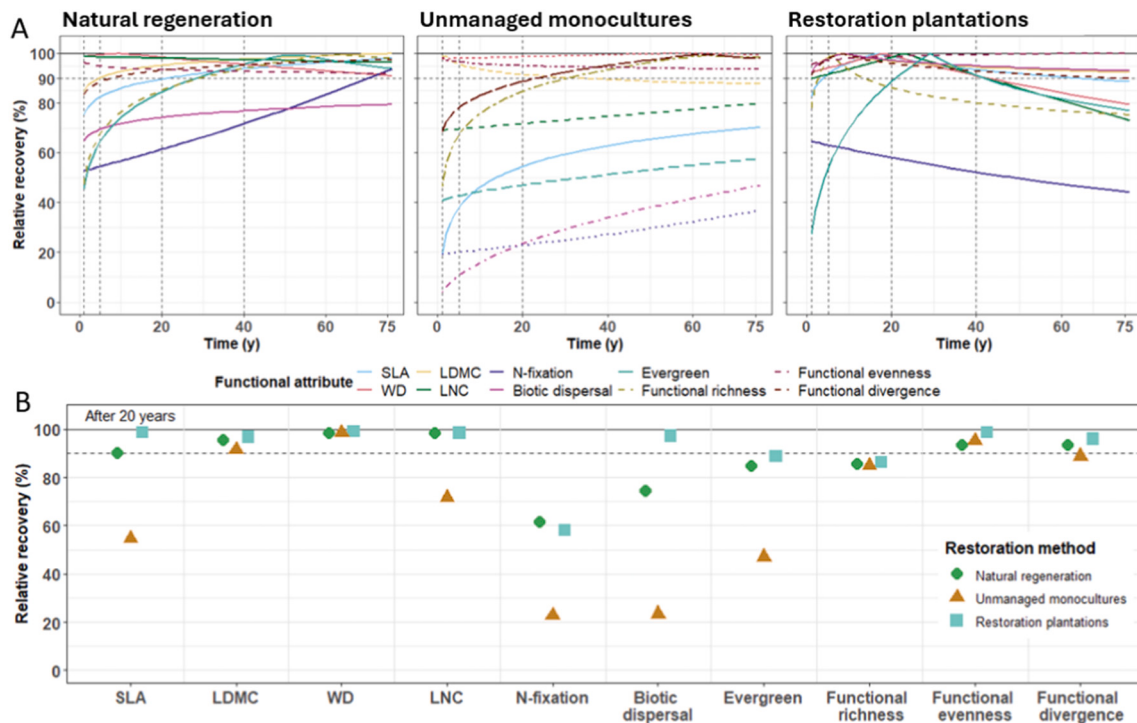


Fig. 4. A) Predicted relative recovery (in percentages) of functional attributes to forest remnants values per restoration method. Percentage similarity to forest remnants mean value was calculated using the Kullback-leibler divergence. Colors show functional attributes, solid lines are CWM traits and dashed colored lines are functional diversity indices. Vertical black dashed lines mark at time (y) = 1, 5, 20 and 40, corresponding to time intervals of panels in Fig. 4B and S6. The horizontal black dashed line indicates 90 % of forest remnants values. B) Predicted relative recovery (mean in percentages) of functional attributes to forest remnants values per restoration method at stand age = 20 (recovery at years 1, 5 and 40 are shown in fig. S6). Colors show restoration method. Dashed line shows 90 % of mean forest remnants value. SLA = specific leaf area; WD = wood density; LDMC = leaf dry matter content; LNC = leaf nitrogen content.

and functional richness ($\beta = 0.25$) increased with site age (Figs. 2, 3; Table S5). Other traits only showed age-related changes in interaction with restoration method.

3.2. Effect of environmental factors and restoration method

Environmental factors varied across restoration methods, though no consistent pattern of differentiation was observed (Fig. S3, S4, S5 Table S3). Naturally regenerating sites were located on soils with lower sand content, while unmanaged monocultures occurred on more acidic and nutrient-poor soils. Additionally, unmanaged monocultures were located closer to forest remnants. However, a PCA of soil variables (Fig. S1 & S2) revealed substantial overlap across regeneration methods, suggesting that abiotic conditions do not fully explain functional differences among restoration methods.

Environmental drivers also had an effect on CWM traits and functional diversity (Fig. 3, Table S5). Soil conditions particularly sum of bases, sand content, and acidity, had significant relationships with five of the twelve evaluated traits, while water availability and landscape context influenced only one trait each. Higher soil fertility (sum of bases) was associated with higher SLA ($\beta = 0.11$) and functional richness ($\beta = 0.18$), but lower LDMC. More acidic soils were associated with lower LNC and LDMC ($\beta = -0.18$; -0.19). Water deficit was positively associated with functional evenness ($\beta = 0.20$), and plots farther from forest remnants showed slightly lower LDMC ($\beta = -0.16$).

3.3. Recovery of forest remnants attributes

Restoration plantations and natural regeneration showed higher similarity to forest remnants compared to unmanaged monocultures, though the extent of convergence varied by trait (Fig. 4, S6). In sites older than 20 years, over half of the functional attributes in restoration

plantations and natural regeneration—except for the proportion of evergreen trees, nitrogen fixation, biotic dispersal, and functional richness—had reached >90 % similarity to forest remnants (Fig. 4B). In contrast, unmanaged monocultures showed slower convergence, with three attributes (LDMC, WD, and functional evenness) surpassing 90 % similarity in sites older than 20 years. In sites older than 40 years, all restoration methods had increased in similarity to forest remnants (Fig. S6), but some traits started to diverge after initial convergence patterns. For example, in restoration plantations, N-fixation exceeded forest remnants, while SLA, LNC, WD, and functional richness began to diverge from forest remnants. In unmanaged monocultures, LDMC also deviated from forest remnants.

4. Discussion

We studied differences in functional attributes as a function of site age, environmental drivers and restoration method. Restoration showed to be an important driver, as starting points and functional recovery trajectories differed among methods. We found that functional traits shifted with site age in all restoration methods, but the speed of recovery varied. Recovery to forest remnants reference values was faster for restoration plantations and natural regeneration, whereas unmanaged monocultures were considerably slower in recovery.

4.1. Restoration methods matter: different starting points and trajectories

Our models show that there are distinct patterns among restoration methods (Fig. 3, S4 & Table S5). Functional attributes of natural regeneration and restoration plantations showed the expected natural successional pathway, from traits related to an acquisitive resource-use strategy (high SLA, LNC, low LDMC) that take advantage of the available light and nutrients, toward more conservative resource-use strategies

with increased site age that allow them to conserve limiting resources and survive under low-resource conditions (Meiners et al., 2015; Poorter et al., 2019). In contrast, unmanaged tree monocultures have relatively more conservative resource-use traits, which can be explained by dominance of remnant and resprouting *Eucalyptus* spp. (34 plots), and *Pinus* spp. in few cases (10 plots), both characterized by having low SLA, LNC and high LDMC. While native regenerating species within these monocultures often resemble natural regeneration forests in functional traits (Brouwer et al., in review; Simões et al., in review, Simões et al., 2024), remnant crop trees were included in our analysis because they influence overall community composition. In older unmanaged monocultures, as native species establish, the tree community may shift toward more functionally acquisitive (higher SLA, higher LNC, lower WD), suggesting a transition away from functional dominance by remnant crop trees, as the native vegetation typically has more acquisitive traits compared to remnant crop trees. This shift suggests that unmanaged monocultures eventually support recovery, albeit more slowly than other methods.

Restoration plantations were associated with the highest proportion of nitrogen-fixing species (36 %) compared to natural regeneration (19 %) and unmanaged monocultures (3 %) (Figs. 2,3 & S5). In passive restoration methods, N-fixers are typically more dominant in early succession when there is sufficient light to support the rhizobial symbionts with carbohydrates (Lau et al., 2012) (Lau et al., 2012). In Brazil, standard practice in restoration plantations is to plant many trees of legume N-fixing species such as *Inga* spp., *Erythrina* spp., and *Anadenanthera* spp., as they grow fast and help outcompeting invasive grasses (Chae et al., 2011). However, species selection in restoration plantations is often driven by nursery availability rather than ecological planning possibly because these species are easier to collect and have cheaper seed (de Almeida et al., 2024; Vidal et al., 2020).

Biotic dispersal was more common in natural regeneration communities (58 %) than in restoration plantations (44 %) and unmanaged monocultures (15 %) (Figs. 2, 3 & S5). This suggests that natural regeneration relies more on frugivores and may face stronger limitations in the establishment of abiotic-dispersed species. In contrast, restoration plantations may compensate for such limitations by planting abiotically dispersed species, which are often preferred due to lower seed costs (Brancalion et al., 2018). Their dominance reduces the relative abundance of animal-dispersed species. Additionally, restoration plantations are often isolated from forest remnants, further limiting animal-dispersed species (Molin et al., 2018). These patterns may hinder successional development and reduce contributions to restoration success and biodiversity conservation (Leighton Reid, 2015; Silva & da Silva and Tabarelli, 2000). To address this, planting more animal-dispersed species, particularly large-seeded ones, has been proposed (Elliott et al., 2023; Brancalion et al., 2018). Alternatively, thinning dense stands could improve understory light and habitat heterogeneity, although evidence from the region suggests that higher aboveground biomass enhances regeneration of animal-dispersed seedlings by suppressing grasses (Brancalion et al., 2019a).

Unmanaged monocultures contained a greater proportion of evergreen species (Figs. 2,3 & S5), probably because their shaded understory prevented the regenerating of many native canopy trees, many in seasonally dry forests, which have a high proportion of deciduous and semideciduous species. The dominance of evergreen *Eucalyptus* spp. and *Pinus* spp. species influences water use and competition dynamics, particularly in semi-deciduous forests where some tree species shed leaves seasonally to conserve water (Hasselquist et al., 2010). This could have implications for local hydrology, as deep-rooted evergreens can affect stream flow and compete with native vegetation for water (de Ferraz et al., 2019).

4.2. Restoration methods differ strongly in functional diversity

Functional richness tended to increase with site age and was highest

in restoration plantations, despite their younger average age (Figs. 2 & 3). This likely reflects the intentional planting of a mix of early- and later-successional species with distinct traits. While high functional richness suggests broader resource use, it is worth noting that restoration efforts often rely on a limited pool of species. For example, a recent study in the Atlantic Forest found that restoration plantations commonly use the same set of 423 species—just 8 % of the regional flora (de Almeida et al., 2024). In contrast, second-growth forests may accumulate functional diversity more gradually through natural regeneration. Low functional richness in unmanaged monocultures is likely due to dominance by a single crop species.

Lower functional evenness in natural regeneration suggests that certain functional groups may dominate during early succession, limiting trait diversity and niche complementarity, a pattern also observed in naturally regenerating secondary forests in the Neotropics (Lohbeck et al., 2012). This may indeed be the case as the majority of the natural regeneration plots measured in this study were younger than 30 years. As succession progresses, functional redundancy may become more important, potentially leading to greater ecosystem stability in later stages of natural regeneration (van der Sande et al., 2024). This aligns with studies showing that later-successional forests tend to exhibit greater trait convergence and redundancy (Muscarella et al., 2016).

In contrast, restoration plantations generally exhibited greater trait redundancy compared to natural regeneration due to species selection, as planted species often share similar functional attributes to optimize survival and growth in degraded environments, even if being selected to represent different functional groups (Rodrigues et al., 2009). Higher functional divergence in unmanaged monocultures may be the result of strong functional contrast between remnant crop trees in the overstory and the regenerating native vegetation in the lower forest layers (Lebrija-Trejos et al., 2011; Wills et al., 2017; Simões et al., in review). Higher functional divergence indicates a higher degree of niche differentiation among the most abundant species within a community, the most abundant species (*Eucalyptus* spp.) are very dissimilar and weakly compete with regrowing native species (Mouchet et al., 2010).

4.3. Recovery of functional attributes to forest remnants is quickest in restoration plantations and natural regeneration

Restoration plantations showed greater similarity to forest remnants because a diverse community is planted, reaching 90 % of forest remnants functional trait values in 20-year old sites. This aligns with functional trajectories found in restoration sites where species from multiple functional groups were planted (Manhães et al., 2022). In the same direction, natural regeneration showed similarity to forest remnants after 20 years, which adheres to a natural successional trajectory (Fig. 4B). This pattern has been observed in secondary tropical forests, where functional composition shifts progressively toward late-successional traits over decades (Poorter et al., 2021a, 2021b). Recovery for some attributes tended to be faster in active restoration plantings compared to passive restoration (Shoo et al., 2016), whereas others suggest that natural regeneration has more success when evaluating more attributes, including bird and invertebrate diversity (Crouzeilles et al., 2017). Unmanaged monocultures showed slower convergence, because remnant crop trees dominate the stands for such a long time, requiring 40 years to reach similar levels for half of the assessed traits (Fig. S6). A global study has shown, however, that native woody species tend to regenerate under tree monoculture and harbor a substantial fraction of diversity (Simões et al., 2024).

As restoration plantations age, they may diverge from forest remnant values, likely due to the overrepresentation of certain traits, such as high nitrogen fixation rates (de Almeida et al., 2024). This suggests that functional recovery is not a linear process, and some traits may continue to shift beyond initial convergence. Planted trees may take decades to be replaced by spontaneously recolonizing species, and the system may take time to stabilize at a final, less variable steady state. However,

uncertainty increases for predictions beyond 20 years, as older restoration sites were underrepresented in our dataset. These findings underscore the importance of species selection in restoration planning. If the objective is to restore a compositionally similar native forest, species with traits aligned to natural reference ecosystems should be prioritized. Conversely, if specific functional outcomes—such as soil fertility enhancement or suppression of invasive grasses—are desired, the intentional inclusion of N-fixers or evergreen species may be more effective.

4.4. Community traits and diversity are only partially explained by environmental drivers

Restoration method had a stronger effect than environmental drivers on functional attributes, possibly because the effects of environment were overruled by the restoration method. Sum of bases, a measure for fertility, was related to lower LDMC, but higher functional richness. Soil fertility has been shown to be important for these traits in several places (Jager et al., 2015; Pinho et al., 2018), likely because these attributes are more related to the efficient use of resources. Sand content was associated with higher proportion of evergreen species but lower functional richness, which may be explained by better performance (in terms of dominance) of *Eucalyptus* spp. that can be deep-rooted to access the groundwater in sandy soils (Christina et al., 2017). Lastly, soil acidity was associated with LNC and LDMC. Impoverished acidic soils are likely to induce strong nutrient limitations to plant growth and may lead to more conservative leaves (low LNC) (Jager et al., 2015), but unexpectedly LDMC also was lower, which may be more driven by light availability than soil acidity (Goud and Roddy, 2022).

Of the environmental drivers, soil (especially sand content, and sum of bases) had the strongest relation, while water availability and landscape context had weaker relations, possibly because the gradients in climatic water deficit (−42.4–2.2 mm/yr) and distance to nearby forests (0–893 m) were not large enough. Alternatively, the relation with sand (which correlates negatively with sum of bases) may also indicate an effect of water deficit. In São Paulo state, local variation in vegetation types, especially from seasonal semideciduous forests to “Cerrado” woodlands, savannas, and grasslands, are essentially determined by soil, as all these vegetation types can be found side by side, across continuous gradients or with abrupt changes in some cases, in the same climate. These results suggest that underlying differences in environmental factors among plots did not contribute much to the observed recovery trends, and that site differences may not have strongly influenced the choice of restoration method, contrasting with the positive site selection bias observed in previous studies (Reid et al., 2018).

4.5. Implications for restoration

Our results emphasize that different restoration approaches lead to distinct successional pathways and functional trait trajectories, careful planning is needed to balance ecological outcomes with socio-economic considerations. Therefore, it is crucial for decision-makers and restoration practitioners to select the appropriate restoration method, as it significantly influences successional pathways and functional attributes' recovery.

All three restoration methods led to some level of functional recovery, but at different rates. Based on our findings, we recommend to: 1) *Favor natural regeneration when feasible* – It achieves relatively quick recovery toward forest remnant values and may support the establishment of functionally diverse forests at a much lower economic cost (Brancalion et al., 2019b). 2) *Use restoration plantations strategically*, – They are beneficial in areas where natural regeneration is unlikely (e.g., degraded pastures, highly fragmented landscapes), but species selection should be diversified to prevent homogenization and ensure long-term ecological integrity and biodiversity conservation (Brancalion et al., 2019a; Holl et al., 2022). Diversify locally and regionally. 3) *Manage*

unmanaged monocultures to accelerate recovery – Although they eventually recover toward forest remnant values, their transition can be slow. Harvesting exotic species could accelerate succession and generate financial returns from timber, making this a viable, cost-effective restoration strategy.

CRediT authorship contribution statement

Rens Brouwer: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marielos Peña-Claros:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Frans Bongers:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Lourens Poorter:** Writing – review & editing, Validation, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Joannès Guillemot:** Writing – review & editing, Methodology. **Danilo R.A. Almeida:** Writing – review & editing, Methodology, Data curation. **Catherine Torres de Almeida:** Writing – review & editing, Methodology, Data curation. **Angélica F. Resende:** Writing – review & editing, Methodology, Data curation. **Laura H.P. Simões:** Writing – review & editing, Methodology, Data curation. **Natália M. Ivanauskas:** Writing – review & editing, Data curation. **Renato A. Ferreira de Lima:** Writing – review & editing, Methodology, Data curation. **Vinicius Castro Souza:** Writing – review & editing, Data curation. **Cássio A.P. Toledo:** Writing – review & editing, Data curation. **Miguel Cooper:** Writing – review & editing, Methodology, Data curation, Conceptualization. **José Guedes Fernandes Neto:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Mathieu Decuyper:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Paulo G. Molin:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Ricardo R. Rodrigues:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Pedro H.S. Brancalion:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: PHS Brancalion and RR Rodrigues are partners at Re.green, a restoration company. Further, the authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111269>.

Data availability

The data that support the results in this study will be made available at an online depository (DRYAD).

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