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RESEARCH ARTICLE

All Reforestation Methods Can Support Tropical Tree Diversity Recovery, but Drivers and Species Composition Vary

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ABSTRACT

Tropical landscapes are undergoing rapid transformation due to human activities and global change. Forest restoration has emerged as a key strategy to mitigate biodiversity loss and climate warming. However, a standardized assessment of how different restoration methods contribute to biodiversity recovery and conservation remains lacking. Here, we present the first comprehensive comparison of tree diversity restoration and the drivers of recovery across five main reforestation methods (naturally regenerating forests, biodiverse restoration plantings, short- and long-rotation tree monocultures, agroforests) relative to three reference systems (agropastoral lands, degraded and conserved forest remnants). Tree inventories were conducted in 519 plots (900 m^2 each) across two forest types (rainforest and seasonally dry forest) in the Atlantic forest of São Paulo state, Brazil, encompassing over 39,000 trees and 869 species. We found that: (1) all reforestation methods except short-rotation monoculture plots supported tree diversity recovery. In the rainforest, conserved remnant plots maintained the highest average Shannon diversity (Hill $1 = 29 \pm 14$), while naturally regenerating forests and restoration plantings approached the diversity of degraded remnant plots (15 ± 5). In seasonally dry forest, biodiverse restoration plantings and agroforests reached diversity levels comparable to conserved remnants (15 ± 6). Additionally, (2) recovery was influenced by forest age, climate (water availability), soil fertility, and landscape context, though the relative importance of these factors varied by method. Climate and landscape context were more influential for recovery in naturally regenerating forests, while soil conditions played a greater role in biodiverse restoration plantings. Lastly, (3) species composition in naturally regenerating forests most closely resembled that of conserved remnants. Conversely, restoration plantings and agroforests exhibited high compositional overlap across sites, reducing overall species richness. Our findings underscore the wide variation in

biodiversity outcomes among and within reforestation methods, emphasizing that goals and strategies must align with local conditions to maximize benefits in complex tropical landscapes.

1 | Introduction

Tropical forests harbor the highest tree diversity on Earth (Cazzolla Gatti et al. 2022), but are degrading and disappearing rapidly due to logging, agricultural expansion, and commodity production (Curtis et al. 2018; Guo et al. 2022). In response, global interest in reforestation, the recovery of tree cover on previously forested lands, has increased (Chazdon 2008; Koch and Kaplan 2022; Romanelli et al. 2022). This shift is reflected in major international initiatives, such as the Bonn Challenge, which aims to restore 350 million hectares by 2030, and the Kunming-Montreal Global Biodiversity Framework, which commits countries to ambitious restoration targets (Bell-James and Watson 2025). The potential for reforestation is substantial (Brancalion et al. 2019): global reforestation potential was recently estimated at 195 million ha (Fesenmyer et al. 2025) and in an earlier estimate, it was calculated that 215 million ha in the tropics could regenerate naturally (Williams et al. 2024), an area larger than Mexico. However, not all restoration pledges automatically lead to biodiversity benefits (Brancalion et al. 2025; Martin et al. 2021).

Reforestation remains a broad concept that can include active interventions, such as tree planting, and passive approaches like natural regeneration (Busch et al. 2024; Chazdon and Uriarte 2016; Chazdon et al. 2025; Crouzeilles et al. 2017; Holl and Aide 2011; Williams et al. 2024). Historically, reforestation efforts have prioritized carbon sequestration, forest products, or soil protection (Martin et al. 2021; Schubert et al. 2024; Veldkamp et al. 2020). More recently, efforts increasingly include approaches aimed at restoring native forest conditions, such as biodiverse restoration plantings and natural regeneration (Cole et al. 2024; Holl and Aide 2011). Each of these methods can play a role in achieving conservation and restoration goals across highly human-modified landscapes in the tropics (Chazdon and Uriarte 2016; Gopalakrishna et al. 2024; Holl 2017; Rodrigues et al. 2009), where forests often compete with other land uses such as agriculture and timber production. Many factors should be considered when deciding on a reforestation strategy. Importantly, both ecological and socioeconomic factors must be balanced, accounting for trade-offs and competing land-use demands (Aguirre-Gutíerrez et al. 2023; Rodrigues et al. 2009; Strassburg et al. 2019), and evaluating conservation outcomes of reforestation strategies under different circumstances (Brancalion et al. 2019; Erbaugh et al. 2020; Vancine et al. 2024). This calls for a strategic, context-specific approach that considers both the 'how' (method and implementation) and 'where' (site-specific biophysical conditions) of reforestation, to maximize biodiversity outcomes.

However, despite numerous pledges and growing global investment, we still lack a standardized, field-based assessment of how different reforestation methods contribute to biodiversity recovery. This gap is urgent to address, as terms like 'forest restoration', 'tree planting', and 'forest landscape restoration' are often used interchangeably but refer to diverse practices with differing impacts (Brancalion et al. 2025). Most evidence on biodiversity recovery comes from meta-analyses (Hua et al. 2022; Meli et al. 2017; Reid et al. 2018; Romanelli et al. 2022) or studies focusing on specific methods (Poorter, Craven, et al. 2021; Prieto et al. 2022; Rozendaal et al. 2019), often omitting systems like agroforests or monocultures. These systems can support considerable biodiversity (Hua et al. 2022; Simões et al. 2024; Wurz et al. 2022) but are underrepresented in research, partly because their primary objectives do not always align with the restoration of natural ecosystems (Gama-Rodrigues et al. 2021; Simões et al. 2024). However, agroforests have been used extensively to restore degraded forest areas while creating livelihood opportunities at the same time, and are frequently included in reforestation commitments, especially in less economically developed countries (Kalame et al. 2011; Wurz et al. 2022). At the same time, tree monocultures are expanding rapidly to supply wood and a broad range of forest products to the market, but have also been demanded to reduce their pressure on the environment and support biodiversity conservation and ecosystem services provisioning (Simões et al. 2024). To inform better restoration planning, we thus need a field-based comparison across a range of reforestation approaches, stand ages, and environmental contexts, particularly in diverse and fragmented tropical landscapes.

To address this gap, we present a large-scale, standardized assessment of tree diversity across all major reforestation methods. Our dataset includes > 39,000 trees from 869 species sampled across 519 plots (each 900 m^2), representing five reforestation methods: naturally regenerating forests (NatReg), biodiverse restoration plantings (Rest), short-rotation tree monocultures (< 10 years; Mono10−), long-rotation tree monocultures (≥ 10 years; Mono10+), and agroforests (AF; Figure 1). We separate short- and long-rotation tree monocultures because they represent very different systems: short-rotation monocultures represent a higher management intensity and short rotation cycles. Long-rotation monocultures, on the other hand, represent a lower management intensity and a longer rotation cycle, which can leave room for more biodiversity. Because detailed management information was not available for all forests, we decided that an age cutoff was the most appropriate way to distinguish between these systems that are likely to differ in their biodiversity value. These reforestation methods are compared to three reference systems: two types of remaining natural forest remnants (conserved and degraded forest remnants; ConFor and DegFor) and a third representing a highly human-modified system (agropastoral lands; AgroPast). Table 1 summarizes reforestation methods and reference systems.

The plots span broad climatic gradients, diverse surrounding landscape context, and varying soil properties (see Table S2 for the ranges per reforestation method). Including this broad range of reforestation types is critical because nearly half of the Bonn Challenge pledges involve monoculture plantations (Lewis et al. 2019), and most tree planting initiatives globally

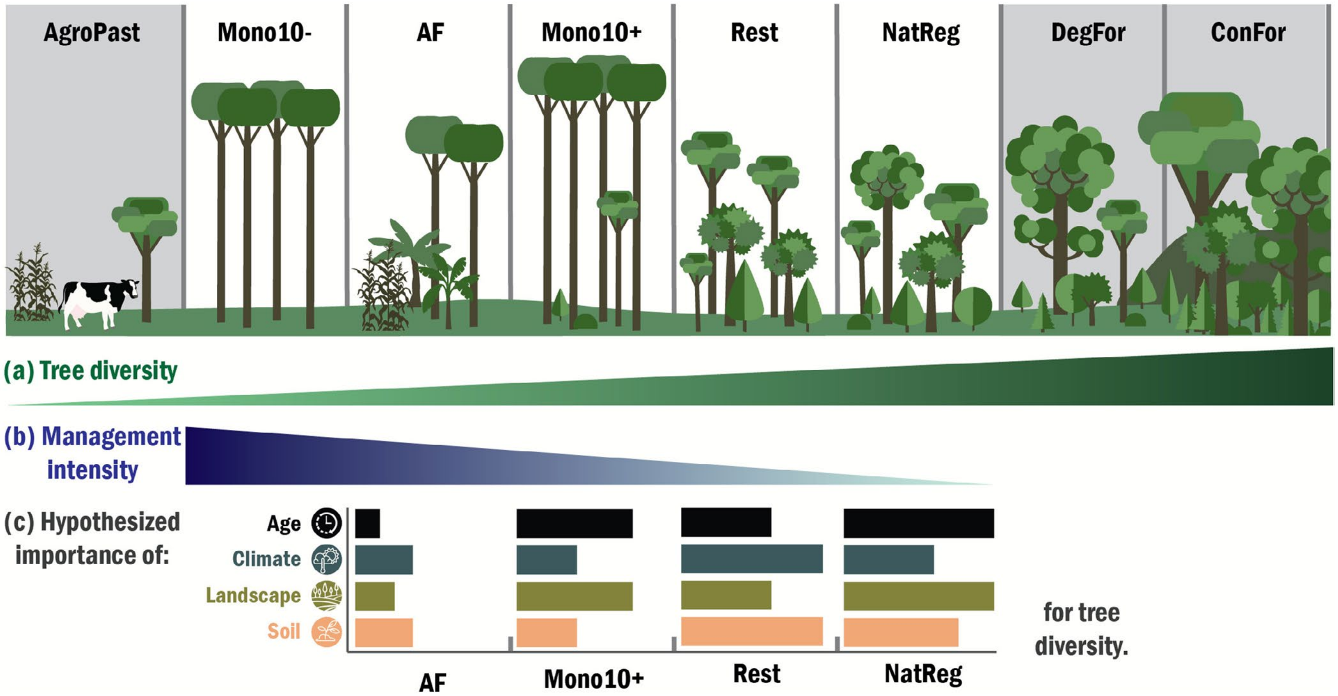

FIGURE 1 | Schematic visualization of the reforestation methods (white background) and reference systems (gray background), ordered by (a) a hypothesized increase in tree diversity and (b) a decreasing management intensity for the reforestation methods. For four reforestation methods, (c) we present hypotheses regarding the relative importance of drivers of tree diversity recovery (RQ2); short-rotation tree monocultures were excluded due to insufficient diversity for this analysis. AF, Agroforestry systems; AgroPast, Agropastoral lands; ConFor, Conserved forest remnants; DegFor, Degraded forest remnants; Mono10, Short-rotation tree monocultures (< 10 years); Mono10+, Long-rotation tree monocultures (≥ 10 years); NatReg, Naturally regenerating forests; Rest, Biodiverse restoration plantings. Please refer to Table 1 for details on the different reforestation methods. Reforestation methods are visualized at 10–30 years of age and can be more diverse and dense than depicted here schematically.

prioritize species with utilitarian values (Martin et al. 2021; Schubert et al. 2024). We divided the plots by forest type (rainforest and the seasonally dry forest), as floristic differences exist between them, which impact the diversity levels (Eisenlohr and De Oliveira-Filho 2015; Morellato and Haddad 2000; Oliveira-Filho and Fontes 2000).

We use this dataset to ask: (1) how do different reforestation methods compare with each other and with reference systems in terms of tree diversity (focusing on Shannon diversity, Hill 1)? (2) how do stand age, climate, soil properties, and landscape context shape patterns of tree diversity recovery? and (3) do the reforestation areas reach the species composition of old growth forests? Our study encompasses a gradient of expected levels of diversity (Figure 1a) and management intensity (Figure 1b), ranging from intensively managed, short-rotation monoculture plantations to minimally managed natural regeneration. Furthermore, we expect that the relative importance of diversity drivers (stand age, climate, soil, and landscape) will vary depending on the reforestation method (Figure 1c). Specifically, in systems fully reliant on natural seed sources to reestablish tree cover (e.g., natural regeneration) or to incorporate additional species in the system (e.g., monocultures), variables that facilitate species arrival, such as landscape context and stand age, will be more influential (Timmers et al. 2025). In contrast, in systems where a diverse set of species is actively planted or maintained (e.g., restoration plantings and agroforests), factors supporting species survival, such as climate and soil conditions, will play a more prominent role. Additional details regarding our hypotheses for each driver are provided in Section 2 (Methods).

While reforestation can deliver a range of objectives and ecosystem services, including carbon sequestration, water retention, and commodity production (Griscom et al. 2017; Ngo Bieng et al. 2021), our focus here is on tree diversity, a key indicator of ecological recovery. Diverse tree communities promote faster recovery of biomass, canopy cover, nitrogen fixation, and enhance resilience to climate variability (Blondeel et al. 2024; Poorter, Craven, et al. 2021; Schnabel et al. 2019; Veryard et al. 2023). In tropical regions in particular, the potential wins of biodiversity recovery are high due to their high levels of endemism, high local species diversity (Koch and Kaplan 2022; Newmark et al. 2017) and high fragmentation (Banks-Leite et al. 2014; Newmark et al. 2017). In these contexts, reforested areas can provide critical habitat for endangered species and improve connectivity between remnant forest patches (Cerullo et al. 2024).

We focus on the Brazilian Atlantic Forest, which is recognized as one of the most diverse and threatened conservation hotspots globally, with over 80% of endemic tree species threatened with extinction (de Lima et al. 2024; Sloan et al. 2014). It is also considered a restoration hotspot, as it is the tropical forest ecosystem with the highest concentration of areas that maximize both restoration opportunities and restoration feasibility (Brancalion et al. 2019). Within the Atlantic Forest, we focused our research on São Paulo state, Brazil. This region has been heavily shaped by human activities for centuries, resulting in highly fragmented

TABLE 1 | Description of the reforestation methods and reference systems and the number of plots sampled. The reforestation methods form a gradient in expected tree diversity (from low diversity in AgroPast to high diversity in ConFor) and management intensity (from high intensity in AF to low intensity in NatReg), following Figure 1.

Agropastoral lands (AgroPast): areas currently used as croplands or pastures located as close as possible to reforestation sites, selected to represent similar climate conditions in which the reforested areas were established and developed. The complete sampling protocol was employed in these areas, but tree cover was absent or very little (some pasture areas may have isolated trees). 13 plots in the rainforest, 42 in seasonally dry forest
Short-rotation monocultures; < 10 years of age (Mono10−): forests established by systematic planting of commercial trees and < 10 years old. They are usually employed using regular spacing at planting (3 × 3 or 3 × 2 m spacing) and intensive management (soil preparation, weeding with herbicide spraying, fertilization, control of leaf cutter ants, and understory clearing). These sites were mostly plantations of eucalyptus (92.8%), but also included plantations of pine trees (3.6%) and some native species (3.6%). The forests within this category are the short rotation forests (mean age 3.73 ± SD 2.22 years), representing typical industrial monoculture plantations for pulp production. 6 plots in the rainforest, 24 in seasonally dry forest
Agroforests (AF): forests established through the combined cultivation of crops and planting and/or natural regeneration of trees—either native or exotic. Silvopastoral systems were not included. This includes crops such as fruit trees, bananas, and coffee. In some cases, crops were cultivated only at the earlier stages of the agroforest development and were absent at the time of sampling, as the site was not used for agroforestry anymore, whereas in other plots crops were grown permanently and were present at the time of sampling. Thus, this reforestation method is quite complex and heterogeneous, including a broad range of production systems. 17 plots in the rainforest, 26 in seasonally dry forest
Long-rotation monocultures; ≥ 10 years of age (Mono10+): forests established like Mono10−, but older in age. These forests represent longer rotation plantations managed to favor biodiversity and ecosystem services, usually referred to as “close to nature” forestry, or even abandoned plantations. There are fewer eucalyptus (52%) plantations in this category, and more pine trees (18%), as well as other exotics (9%), native species (14%), or a mixture of exotic and native species (7%). This category also includes forests established in harvested eucalyptus plantings through secondary succession, in which resprouting eucalyptus and recolonizing native trees grow together. These forests may or may not have been subject to understory clearing, which enabled native species regeneration, and includes older (mean age 33 ± SD 20 years) and lower density forest stands. 12 plots in the rainforest, 75 in seasonally dry forest
Biodiverse restoration plantings (Rest): forests established by systematic planting of nursery-grown native trees, often employing 3 × 2 m spacing, soil preparation, weeding with herbicide spraying or by rowing, fertilization, and control of leaf cutter ants. Projects usually include 30–80 species. Maintenance stops once the planted trees are established, usually after 3 years, and other trees then regenerate in the area. We were not able to distinguish between planted and naturally regenerated trees so the sampled vegetation is a mixture of these two origins. 27 plots in the rainforest, 132 in seasonally dry forest.
Naturally regenerating forests (NatReg): forests established through the spontaneous recolonization of trees in abandoned lands. Usually, these forests are established on marginal lands for agriculture, mostly extensive pastures, and without human intervention. 22 plots in the rainforest, 45 in seasonally dry forest
Degraded forest remnants (DegFor): forests found within productive landscapes, as close as possible to reforestation plots, and historically exposed to one or more degradation sources such as logging, fires, and cattle grazing. We ensured that these plots had not been completely cleared in recent decades, based on remote sensing data (since 1985), aerial photographs from 1962 when available, or earlier land-use information when available. They were included in the survey as a reference condition for reforestation in human-modified landscapes. Six plots in the rainforest, 29 in seasonally dry forest
Conserved forest remnants (ConFor): forests with no known record of degradation, either in public or private protected areas, with a management plan for biodiversity conservation. They were included as a reference condition for the full potential of ecosystem diversity, structure, and functioning when human disturbances are minimal. 22 plots in the rainforest, 24 in seasonally dry forest

forests with small, isolated remnants surrounded by forest plantations, large areas of agriculture, and pasture (Tambosi et al. 2014; Vancine et al. 2024). At the same time, it also encompasses the largest remaining continuous tract of Atlantic Forest. As a result, it has been the focus of several conservation and reforestation initiatives. São Paulo state's broad edaphoclimatic and landscape gradients present a unique opportunity to evaluate the relative contributions of climate, soil, and landscape conditions on reforestation biodiversity outcomes. As such, it is a model system to answer these types of questions.

2 | Materials and Methods

2.1 | Reforestation Types and Reference Systems

We selected the five most commonly used reforestation methods and three reference systems (Figure 1, Table 1). Two references represent the remaining forests in the landscape (conserved and degraded forest remnants; ConFor and DegFor), and a third represents a highly human-modified system (agropastoral lands; AgroPast; Table 1).

The dataset consists of 519 plots of 900 m^2 each, established between July 2019 and July 2023, covering a broad range of climate conditions (Table S2). Unfortunately, it was not possible to obtain information on the varied management interventions for every plot (e.g., previous land use, list of planted species, weeding method, amount and type of fertilizers used), as most of this information was not recorded by owners and managers, and interventions were done years or decades ago. To address this limitation, we prioritized sampling a large number of plots distributed across major socio-ecological gradients (e.g., neighboring land uses, soil and climate types, and varied planted species). This approach allowed us to achieve a comprehensive, yet feasible, assessment of variation in reforestation methods. We tested the overlap in climate variables, soils, and landscape configuration across all plots using a PCA and found a strong overlap between reforestation methods and reference systems, indicating no fundamental bias in any of the explanatory variables (Figures S5 and S6).

2.2 | Plot Selection

To select target regions, we first mapped known reforestation sites and initiatives across the tropical Atlantic Forest in São Paulo state, focusing on the dominant rainforest (Ombrophilous) and seasonally dry (Semideciduous) forest (Eisenlohr and De Oliveira-Filho 2015; Oliveira-Filho and Fontes 2000). We then contacted landowners or managers to identify sampling opportunities that maximized coverage of reforestation methods, reference conditions, and climate variability. For each selected region, we obtained or delineated polygons for each reforestation site or reference condition and randomly placed a 30 × 30 m field plot within each polygon. Using 900 m^2 plots allowed us to balance sampling effort and spatial replication, thereby enabling robust comparisons of relative patterns of tree diversity recovery across methods. However, we acknowledge that this relatively small plot size may underestimate total species richness at larger spatial scales.

For each reforestation site, we interviewed local managers and landowners and reviewed project files to gather information on reforestation year, previous land use, and fire history. As an observational, noncontrolled study, our sampling of reforestation methods was not fully balanced, leading to some methods being under- or over-represented across regions. For example, reforestation plantings were more common inland, in the seasonally dry Atlantic Forest, characterized by low native forest cover, drier climates, and flatter terrain, while naturally regenerated forests were sampled more near the coast under wetter climate conditions, in rainforests. Still, we covered large climate gradients in all reforestation methods (Figures S5 and S6). Table S2 summarizes all variables and their measured ranges by reforestation method.

2.3 | Data Collection

In every 900 m^2 plot, we measured and identified all tree stems > 5 cm in diameter to species level in the field. The 5 cm DBH cutoff was chosen to be small enough to catch newly establishing trees in reforestation sites, for which a larger cutoff would not be appropriate (such as 10 cm DBH, employed in old-growth forests in the Amazon), and to match the standard cutoff used in restoration studies, thus allowing for a comparison with our results. If identification in the field was not possible, vouchers were collected, and individuals were identified in the lab by botanists. When species-level identification was not possible, we assigned individuals to genus (6330 individuals) or family (129 individuals). Only 1251 out of the 39,042 inventoried individuals remained fully undetermined (3.2%).

Stand age of every plot was determined through a two-step approach. First, we obtained information from interviews with land managers and project records, providing the most precise data. This was recorded for 44% of the plots. For the remaining 56%, we used plot coordinates and all available aerial or high-resolution satellite Landsat images from 1984 to 2023, identifying the onset of forest growth with the *npphen* package (Chávez et al. 2022), which detects temporal anomalies in NDMI vegetation index (Normalized Difference Moisture Index). By first defining the annual phenological baseline from the time series per site, this method detects the year in which a change in this cycle occurs, which was recorded as the year in which regrowth started. This approach allowed us to estimate plot age in all reforestation types in a standardized way. As such, it matches the particularities in our study design better, with small plots and several reforestation types compared to alternatives such as MapBiomas.

Average climatic variables per site were calculated using daily summaries from Xavier et al. (2022), based on plot locations and climate data from 1961 to 2019 (Xavier et al. 2022). Mean annual precipitation (mm/year) was calculated as the average total yearly precipitation. Mean daily maximum temperature (°C) was calculated as the average of all daily maxima across years. Mean annual climatic water deficit (CWD, mm/year) was calculated as the difference between potential evapotranspiration and rainfall when evapotranspiration exceeded rainfall; otherwise, CWD was set to zero. CWD values were then averaged across years. Mean annual solar radiation (MJ/m^2) was calculated as the average total yearly solar radiation per plot.

We characterized the surrounding landscape variables using landscape information from Mapbiomas collection 7.1, which relies on 30 × 30 m Landsat images. We used data from the year 2019, when we started field data collection. All landscape analyses were conducted in QGIS version 3.32.3. We calculated the abundance of the most dominant land uses in a 5 km radius around the centroid of every plot, including the percentage of pasture, sugarcane, fruit or coffee plantation, plantation for wood production (mostly eucalyptus and pine), and non-plantation forest, as labeled by Mapbiomas. If the site was located in a forest, we calculated the core area of the forest fragment by first calculating the total fragment area and then subtracting an area of (20 m × the plot perimeter (km)), assuming an edge effect of 20 m (Harper et al. 2024; Vancine et al. 2024). This approach accounted for the fact that long and thin fragments have a much larger edge area compared to spherical fragments, and this can affect biodiversity (Vancine et al. 2024). We also calculated the distance of the plot centroid to the forest edge. We calculated the total size of the largest forest patch that occurred within the 5 km radius around the plot, also considering its forest area outside of the radius (Arroyo-Rodríguez et al. 2020). We calculated the distance to the closest forest patch as the shortest distance between the plot perimeter and the edge of the nearest forest fragment. We calculated the distance to the closest water body as the distance from the plot centroid to the nearest water source (river, lake) based on the data provided by the Brazilian Foundation for Sustainable Development (FBDS; https://geo.fbds.org.br/SP/). We calculated the number of preceding years with fire as the total number of years that a fire occurred within a 1 km radius from the plot centroid as recorded by Mapbiomas between 1985 and 2019, assuming these were the fires that may have affected the plots. Lastly, we calculated the total road length within a 1 km radius using the plot centroid and OpenStreetMap using data from the year 2023.

For the soil variables, we took 3 soil samples at 0–10 depth in each plot that made up one composite sample for the site. Samples were transported to the lab to measure clay content (%, Bouyoucos method), total sum of bases (mmol/dm^3, sum of K^+, Ca^{2+}, and Mg^{2+}, where K^+ was extracted using the ion exchange resin method, while Ca^{2+} and Mg^{2+} were extracted by the 1 mol/L KCl method), phosphorous content (mg/dm^3, through ion exchange resin), organic matter content (g/dm^3, through colorimetry), bulk density (g/cm^3, core method), and pH (in 0.01 M $CaCl_2$) (Cèsar Teixeira et al. 2017).

We then assessed the distribution of these variables across all eight plot types to ensure that no specific forest type was confined to areas with a particular climate or landscape context, thereby minimizing potential bias. To do so, we ran two PCAs using all climate, soil, and landscape variables of each plot: one for the rainforest (Figure S5) and one for the seasonally dry forest (Figure S6), using the *FactoMineR* package (Lê et al. 2008). We also calculated the minimum, mean, and maximum value of each predictor variable per forest type (Table S2).

2.4 | Data Analysis

2.4.1 | Diversity Across Reforestation Methods

Using the plot inventories, we calculated Hill 0, 1, and 2 using the *HillR* package (Li 2018). As data was not normally distributed, we tested for differences between reforestation methods and reference systems using the Kruskal-Wallis test using the *ggpubr* package (Kassambara 2023). We applied a pairwise Wilcoxon post hoc test with a significance cutoff of $p < 0.007$ (0.05/7) to account for multiple comparisons.

2.4.2 | Drivers of Diversity Recovery

To evaluate how stand age, climate, soil, and landscape factors influence biodiversity recovery, we focused on Shannon diversity (Hill 1), which incorporates both species richness and relative abundances. Unlike measures of richness or evenness alone, Shannon diversity is less affected by the presence of rare species or the dominance of a few individuals. This makes it particularly suitable for assessing diversity in smaller plots and across systems that differ a lot in dominance structure, as was found in the different reforestation methods.

We used a Structural Causal Modeling Framework to evaluate the relative importance of the drivers of diversity recovery (Arif and MacNeil 2023; Dee et al. 2023; Pearl 2009; Pinho et al. 2024; Siegel and Dee 2025). To do so, we first constructed a causal diagram (DAG; Figure S2) to assess the total causal effect of each predictor variable. This DAG represents our hypotheses regarding factors influencing tree diversity (grouped hypotheses shown in Figure 1, interactions shown in Figure S2). We expected tree diversity to increase with site age across all methods, especially in the least managed reforestation methods (Rozendaal et al. 2019). For climate, we expected a positive association with total annual precipitation (mm/year) (Rozendaal et al. 2019) and negative associations with maximum temperature (°C/day), climatic water deficit (CWD; mm/year), and total annual radiation (MJ/m^2/year), as these factors influence species establishment and survival (Poorter, Rozendaal, et al. 2021; Poorter et al. 2024).

For soil variables, we hypothesized that fertile soils with high water retention potential would promote species establishment and survival (Soong et al. 2020; van der Sande et al. 2018; Zhao et al. 2017), thereby enhancing diversity. Specifically, we expected positive associations with clay content, soil organic matter, sum of bases, phosphorus content, and pH (up to 7 in our plots), and a negative effect of bulk density (Soong et al. 2020; van der Sande et al. 2022). However, we recognize that successional changes may also influence soil fertility, as soil properties can evolve during forest restoration, and these may thus be results of succession as well as drivers of recovery (van der Sande et al. 2022; Veldkamp et al. 2020).

Regarding landscape factors, we anticipated positive associations between diversity and indicators of greater forest cover in the surrounding landscape (Rozendaal et al. 2019), including shorter distance to the nearest forest patch (km), larger patch area (ha), greater core forest area (ha), and higher proportion of non-plantation forest (%). These variables represent potential seed sources, facilitating species arrival (Timmers et al. 2025). We also expected higher diversity in plots closer to water and further from forest edges, supporting both species arrival and survival. Conversely, we hypothesized negative associations with landscape features that result in reduced native forest cover, such as higher proportions of sugarcane, tree monoculture, and fruit or coffee plantations or pasture in the surrounding area (%). Similarly, we expected that indicators of increased human disturbance, including total road length within a 1 km radius (km) and the number of years with fire over the past 40 years in the vicinity of the plot (1 km), would negatively affect diversity (Pivello et al. 2021).

After developing the DAG diagram, we tested the testable implications for each of the reforestation methods for which we wanted to test associations with biodiversity recovery (NatReg, Rest, Mono10+, and AF) and confirmed that the DAG was consistent with the data. We applied the so-called 'backdoor criterion' to the DAG using the *daggity* package (Ankan et al. 2021), resulting in a minimal set of control variables for each variable for which we wanted to estimate its association with diversity (Pinho et al. 2024). This approach allowed us to condition the

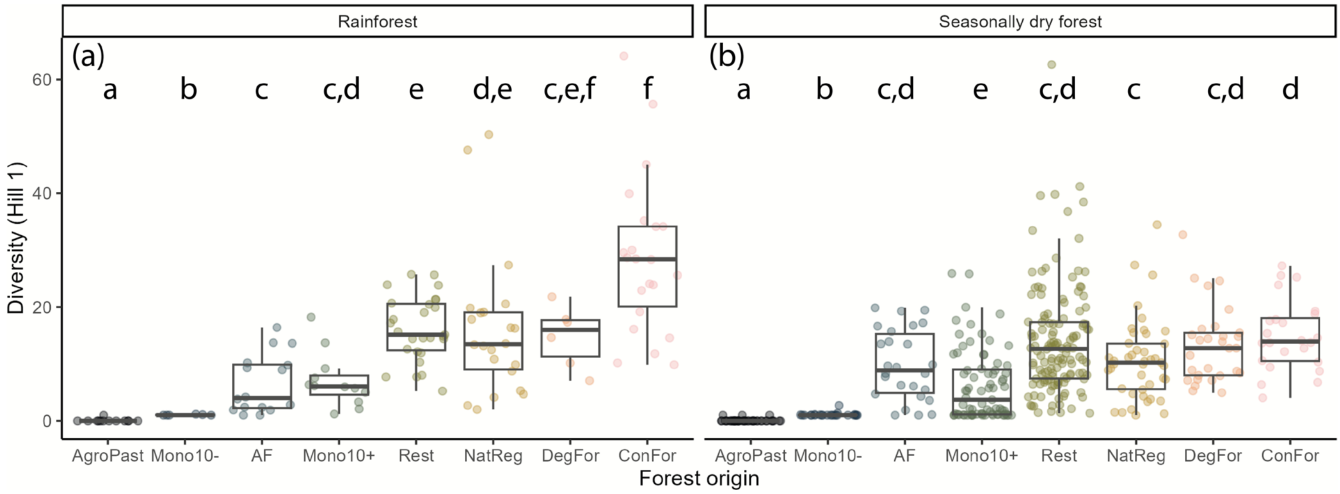

FIGURE 2 | Tree species diversity per reforestation method and reference system. Dots show tree diversity (Hill 1 = Shannon diversity) per 900 m^2 plot across (a) rainforest and (b) seasonally dry forest, summarized in boxplots. Letters indicate significant differences between groups based on Kruskal–Wallis and pairwise Wilcoxon tests, where $p < 0.007$ is regarded as significant to account for multiple comparisons (=0.05/7). Differences were tested separately within the rainforest and seasonally dry forest. We did not control for age or any other explanatory variable in this analysis. AgroPast, Agropastoral lands; Mono10−, Short-rotation tree monocultures (<10 years); AF, Agroforestry systems; Mono10+, Long-rotation tree monocultures (≥10 years); Rest, Biodiverse restoration plantings; NatReg, Naturally regenerating forests; DegFor, Degraded forest remnants; ConFor, Conserved forest remnants. For additional metrics on species richness (Hill 0) and evenness (Hill 2), see Figure S1.

statistical models on control variables based on the DAG, which closed any non-causal paths between the exposure and outcome variable (see Arif and MacNeil 2023 for more information on DAG analyses). This led to the equations in the Table S1.

Before fitting the models, we transformed most variables to reduce skewness in their distributions: Hill 1, Daily maximum temperature, Total annual precipitation, Total road length, Distance to closest forest patch, Percentage of pasture and plantation, Distance to forest edge, Area of largest nearby patch, Forest fragment core area, Distance to water, P concentration and sum of bases were transformed (log or power transformations). All variables were standardized by subtracting the overall mean and dividing by 2× the standard deviation. We then fitted each model separately for the four reforestation methods (NatReg, Rest, Mono10+, and AF) to test the total effect of the predictor variables on diversity within the forest types. We did not perform this analysis for the conserved and degraded forest remnants (ConFor, DegFor) because the processes determining diversity are not about arrival but about the loss of species in those forests. Additionally, we did not perform it for the agropastoral lands and the short-rotation tree monocultures either because there was too little variation in tree diversity across plots. We found a maximum of one tree species in the plots of agropastoral lands, and in the short-rotation tree monoculture plots, we found a maximum of four species, with 66% of the short-rotation tree monoculture plots consisting of only one species.

We fitted the linear models using forest type (rainforest and seasonally dry forest) as a fixed effect because they varied in maximum biodiversity levels (Figure 2). There was no spatial autocorrelation in the models with forest type as fixed effect (Moran's I, $p > 0.05$, *DHARMa* package (Hartig 2022)). For each model, we calculated the standardized effect size, standard error, and partial R^2 of each predictor to quantify the direction and magnitude of its effect on diversity.

2.4.3 | Species Composition

To test the overlap in species across plots, we used rarefaction curves by reforestation method and reference forest for the rainforest and seasonally dry forest using the *BiodiversityR* package (Kindt and Coe 2005). Additionally, we calculated Bray-Curtis vegetation dissimilarity for the full dataset (rainforest and seasonally dry forest combined) with the vegdist function of the *vegan* package (Oksanen et al. 2020) and visualized these in a PCoA using the *ape* package (Paradis and Schliep 2019). We removed individuals from the main monoculture species (*Eucalyptus* spp., *Pinus* spp., *Acacia* spp.) before calculating the dissimilarity because we were more interested in the composition of newly arriving species, and otherwise these individuals had a strong effect on the dissimilarity between plots. The PCoA, including these individuals is shown in Figure S4 for comparison. These approaches (rarefaction and PCoA) are less sensitive to plot-level under-sampling of rare species (which may happen when smaller plot sizes are used) compared to more formal quantification of beta diversity into turnover and nestedness components. They allowed us to visualize community turnover at the landscape scales, as well as to compare this between different forest types. All the analyses described above were performed in R v.4.4.1 statistical software (R Core Team 2024).

3 | Results

3.1 | Comparing Tree Diversity Among Reforestation Methods and Reference Systems

Tree taxonomic species richness varied a lot across the 519 plots, ranging from a single species in monoculture plantations to 82 species in a conserved rainforest remnant (see Figure S1 for species richness). Additionally, there was a large variation in

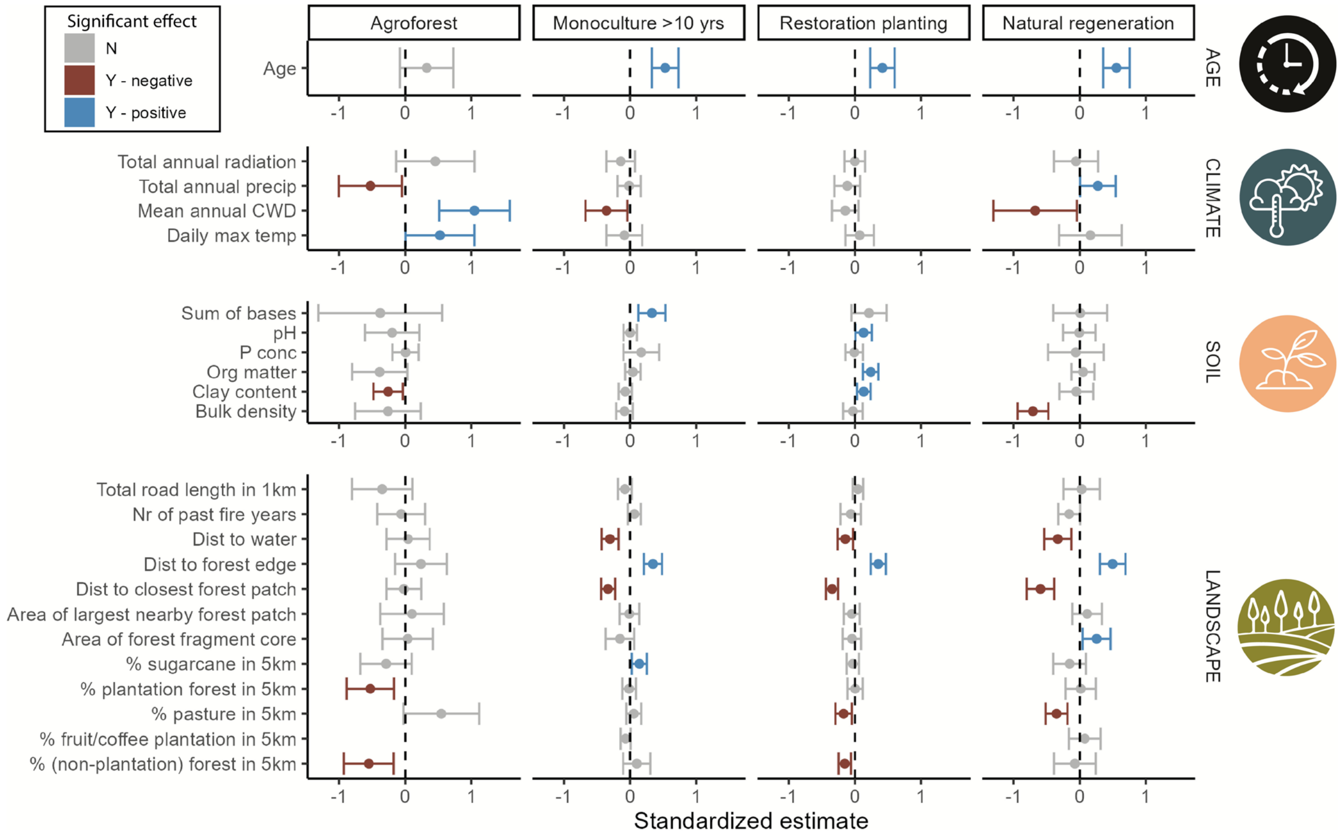

FIGURE 3 | Standardized coefficients of the predictors of diversity across reforestation methods. Predictors are grouped by category: Age, Climate, Soil, and Landscape. Each point represents the standardized effect size of an individual predictor variable, with error bars denoting the 95% confidence interval (CI). Color coding indicates whether CI overlaps zero, where no overlap indicates a significant association with diversity (Hill 1; brown = significant & negative, blue = significant & positive, gray = not significant). Forest type (rainforest/seasonally dry forest) was included as fixed effect in all models. Please refer to Table S1 for the full set of models as derived from the DAG (Figure S2). We did not perform this analysis for short-rotation tree monocultures because their low diversity precluded robust analyses. Rest and Agroforest plots did not have enough variation in fruit/coffee plantation percentage for this analysis. CWD, Climatic Water Deficit. The individual regressions for age are highlighted in Figure S3.

Shannon diversity (Hill 1) within each reforestation method: reforestation method itself only accounted for 43% of the variation in tree diversity in the rainforest and 17% in the seasonally dry forest (Kruskal–Wallis η, excluding Mono10− and AgroPast due to their low diversity).

In the rainforest, we found a mean tree diversity in the conserved remnant plots (mean Hill 1 of 29 ± 14) that was similar to the degraded remnant plots and higher than all reforestation methods plots (Figure 2a). The tree diversity found in naturally regenerating forest plots (16 ± 13) was similar to the biodiverse restoration planting plots (16 ± 6), while both supported diversity levels similar to those of degraded remnant plots (15 ± 5). In contrast, long-rotation monoculture plantation plots (≥ 10 years.; 7 ± 5) and agroforest plots (6 ± 5) exhibited lower diversity, with the lowest tree diversity values in short-rotation tree monoculture plots (1 ± 0.5) and agropastoral land plots (0 ± 0).

In the seasonally dry forest, many of the reforestation methods reached diversity values comparable to those of conserved forest remnants (Figure 2b). Restoration plantings supported some of the highest diversity among all reforestation methods (Figure S1, mean Hill 1 of 14 ± 10). Interestingly, even the agroforestry plots (10 ± 6), on average, exhibited diversity levels like that of conserved remnants (15 ± 6), highlighting the potential of various reforestation strategies to restore biodiversity in seasonally dry environments.

3.2 | Drivers of Diversity Recovery

Since reforestation method only accounted for 17%–43% of the variation in tree diversity, we considered other variables that can influence diversity and are commonly associated with forest recovery, including stand age, climate, soil, and landscape characteristics (Figures 1c, 3). We formulated hypotheses regarding these drivers (described in detail in the Methods section, visually summarized in Figure 1c), which guided our causal modeling framework to assess the relative influence of each driver (please refer to Figure S2 for the DAG) (Arif and MacNeil 2023; Dee et al. 2023; Pearl 2009; Pinho et al. 2024; Siegel and Dee 2025).

Tree diversity increased with stand age for three reforestation methods (long-rotation tree monocultures, restoration plantings, and naturally regenerating forests), but not in agroforests (Figure 3 and Figure S3). Additionally, plots maintained a higher diversity when located farther from the forest edge, closer to water bodies, and nearer to patches of natural forest, again with the exception of agroforestry plots, where these associations were not significant. Certain variables showed no

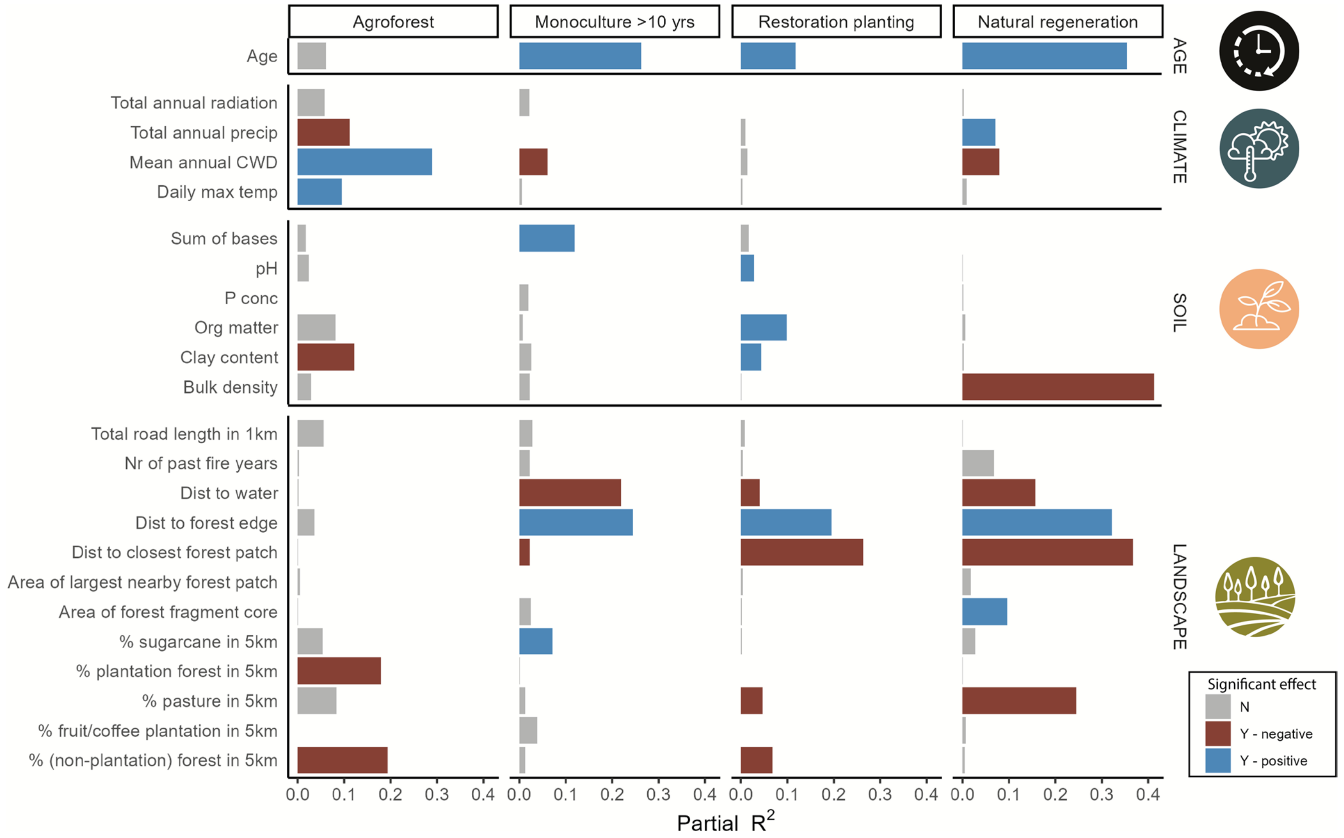

FIGURE 4 | Partial R^2 values of predictor variables across reforestation methods. Each bar corresponds to the partial R^2 of a single predictor variable from Figure 3, representing the proportion of diversity variance explained by that variable. Color coding follows Figure 3, indicating if the variable is significantly associated with diversity (brown = yes & negative, blue = yes & positive, gray = no). Results are grouped by reforestation method. Note that the partial R^2s can sum up to more than one because they represent multiple independent regressions (models and results are included in Table S1).

significant association with diversity across all reforestation types: total road length within a 1 km radius, a proxy for human access, had no measurable effect, nor did the number of years with fire over the past 40 years.

Other associations differed among the reforestation methods. A favorable surrounding landscape for species arrival strongly increased biodiversity in naturally regenerating forests (larger effect sizes and higher partial R^2 values, Figure 4 and Table S1). In these naturally regenerating forests, diversity was higher in larger patches and lower in areas where a high proportion of the surrounding area was pasture. The most influential predictor was the distance to the closest forest patch, again showing the importance of nearby forest remnants for diversity recovery during natural regeneration. Additionally, naturally regenerating forests exhibited the strongest positive association between diversity and age among all reforestation methods (Figure S3): these forests can have a high diversity (Figure 2), but recover more gradually compared to other methods.

We did not find significant effects of climate on tree diversity in the biodiverse restoration plantings. In contrast, a greater number of soil variables were positively associated with higher diversity (Figure 3). Compared to naturally regenerating forests, landscape variables also had a smaller impact on biodiversity in the restoration plantings, as reflected by lower effect sizes and partial R^2 values (Figure 4).

We found similar associations of age, climate, and landscape with diversity in long-rotation tree monocultures and natural regeneration plots, although the effects were less strong in the long-rotation tree monocultures. Plots closer to water, further from the forest edge, and closer to the closest forest patch were associated with higher tree diversity in these reforestation types.

Agroforestry plots showed the strongest associations between tree diversity and climate variables (Figures 3 and 4), whereas we had expected the weakest associations here because this is the most managed reforestation method (Figure 1c). Surprisingly, diversity was negatively associated with total annual rainfall and positively associated with both total radiation and climatic water deficit, which contrasted with the patterns found in naturally regenerating forests.

3.3 | Overlapping Tree Composition for Old and Newly Established Forests

Species rarefaction curves show that the largest overall number of tree species was found in the conserved rainforest remnant plots (Figure 5). The curve was not yet flattening, indicating limited overlap in species across the plots. In both the rainforest and seasonally dry forest plots, the species accumulation curve of restoration plantings started flattening much faster than the naturally regenerating forest and the conserved and degraded forest remnants. This finding indicates that biodiverse restoration plantings have a higher species similarity across plots. Agroforestry plots had the lowest number of tree species and the highest similarity across plots.

These findings were supported by the principal coordinate analysis (Figure 6), where plots were positioned on the first two axes based on their similarity in species composition. For visualization, we show the rainforest and seasonally dry forest plots first separately and then together, but these results are based on the same dissimilarity values as calculated from the full dataset. Only a subset of restoration planting plots overlapped in species composition with conserved and degraded forest remnants. In fact, restoration plantings were more similar between

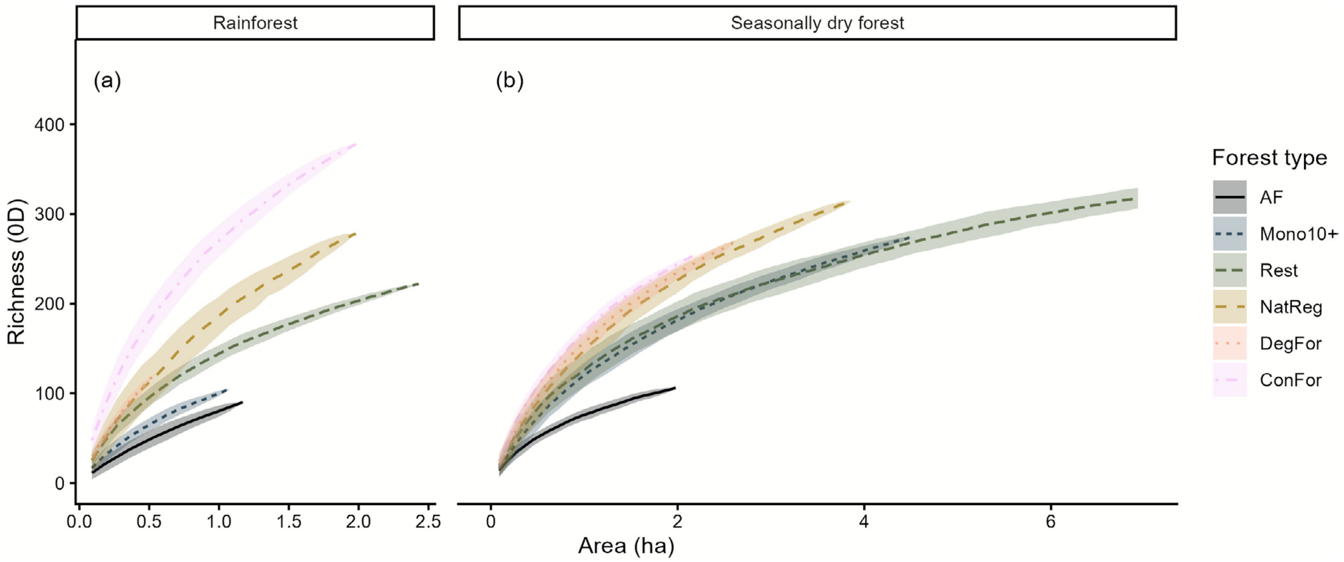

FIGURE 5 | Species rarefaction curves for the (a) rainforest and (b) seasonally dry forest, stratified by reforestation method or reference system. Species-area relationships are depicted through sample-based rarefaction curves. Each point represents the cumulative number of observed species as a function of the number of sampled plots. The dots indicate mean species rarefaction, while the error bars indicate the 95% confidence intervals derived from random permutations of sampling order. The curve for Rest in the Seasonally dry forest was cut off at 7 ha to show details for all forest types (continued until 12 ha). Forest abbreviations follow Figure 1. We did not perform this analysis for short-rotation tree monocultures and agropastoral lands due to their low diversity.

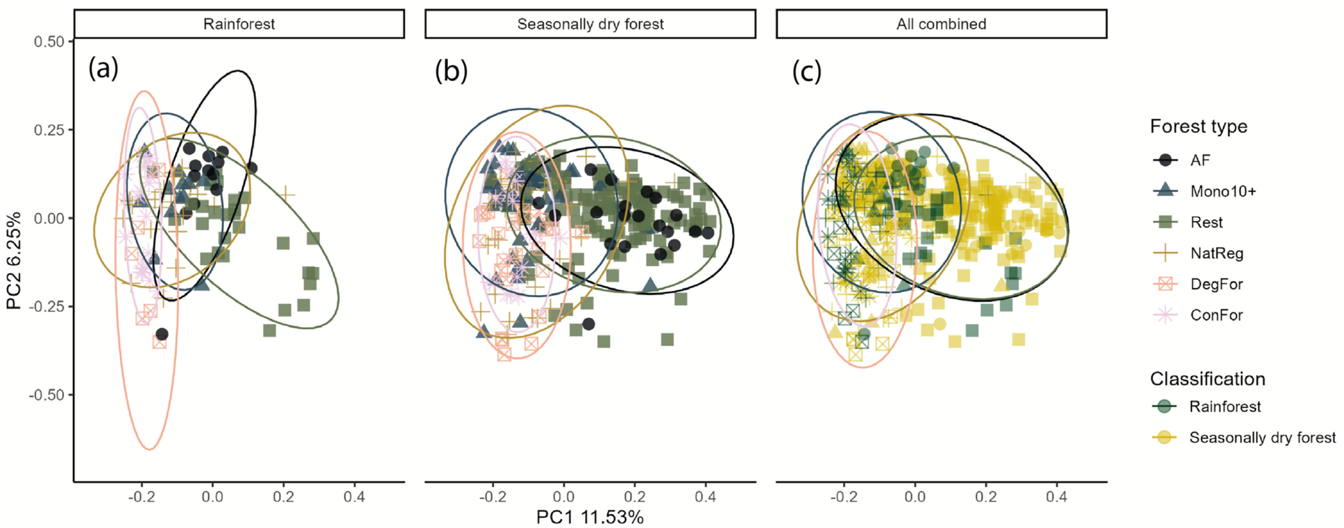

FIGURE 6 | Principal Coordinate Analysis (PCoA) of species composition overlap among forest plots based on Bray–Curtis dissimilarity indices. Each point represents an individual forest plot, with inter-point distances reflecting the degree of species composition similarity. Plots are shown for (a) rainforest, (b) seasonally dry forest, and (c) both classifications combined. Color in A and B indicates the reforestation method or reference system, whereas color in C indicates forest classification. The ellipses represent the 90% confidence regions around each group. Individuals of the main monoculture species (*Eucalyptus* spp., *Pinus* spp., *Acacia* spp.) were removed to focus on new growth in the Mono10+ plots rather than emphasizing their dissimilarity based on the high abundance of these species. A version of this plot including those species can be found as Figure S4. Note that the distances were calculated using the full dataset; therefore, relative positions of points remain consistent across all panels. Forest abbreviation follows Figure 2. We did not include short-rotation tree monocultures and agropastoral lands in this analysis due to their low diversity.

the rainforest and seasonally dry forest than compared to most of the conserved and degraded forest remnants, as seen by the strong overlap of the green and yellow reforestation plots in the combined plot (Figure 6c). Species composition in naturally regenerating forest plots overlapped the most with conserved and degraded forest remnants in both the rainforest and seasonally dry forest plots.

4 | Discussion

We explored patterns of tree diversity in the highly modified tropical landscapes of the Atlantic Forest of Southeastern Brazil using a large, standardized dataset of 519 inventory plots (900 m^2 each) spanning five reforestation methods and three reference ecosystems. Our results showed that: (1) all reforestation methods can support diversity conservation, with diversity values approaching those of conserved and degraded forest remnants, especially in the seasonally dry forest. The exception was short-rotation tree monoculture plantation plots, which showed low tree diversity, but among long-rotation tree monoculture plantations, we did find a diverse set of tree species. Despite these overall trends, we found (2) substantial variation in tree diversity within each reforestation method that was influenced by age, landscape, soil, and climate (Chazdon et al. 2025; Timmers et al. 2025). The surrounding landscape played a stronger role in naturally regenerating forests, compared to landscape and soil characteristics in restoration plantings. Lastly, (3) rarefaction curves and PCoA analysis showed that naturally regenerating forests supported the largest overall species pool, and their species composition was most similar to conserved forest remnants.

4.1 | Diversity Recovers With Time, but Composition Outcomes Lag Behind

Age had a strong positive effect on diversity across all reforestation methods except in agroforestry systems (Figure 3 and Figure S3), likely due to the gradual arrival and establishment of new species and the active management of the regenerating vegetation, with weeding and thinning favoring selected, utilitarian species in the agroforestry systems (Poorter, Craven, et al. 2021; Rozendaal et al. 2019). However, both the effect of age and the proportion of variance it explained were lower in more intensively managed forests (Rest and Mono10+) compared to other reforestation methods (Figure 4). Although many reforestation methods achieved high levels of diversity (Figure 2), the species composition of agroforests and restoration plantings showed the least overlap with conserved and degraded forest remnants (Figure 6). These results are consistent with previous studies on natural regeneration, which found that even when species richness in secondary forests approaches that of old-growth forests, it takes much longer for their species composition to converge (Poorter, Craven, et al. 2021; Rozendaal et al. 2019). We did find that naturally regenerating forests supported more species across plots, even though their plot-level diversity was lower than that of similarly aged, biodiverse restoration plantings. Moreover, their species composition was more similar to that of conserved forest remnants plots. Therefore, naturally regenerating forests have greater potential to contribute to landscape-scale biodiversity conservation at the regional level.

When interpreting these results, it is important to note that our plot size was relatively small (900 m^2), which thus captures only a subset of local tree diversity. As a result, these diversity metrics should be interpreted as comparative indicators rather than as full estimates of complete local diversity. Accordingly, our analytical strategy prioritized patterns of species composition across plots and forest types over absolute within-plot richness. To address our objective of evaluating compositional differentiation across a large number of plots distributed over a broad geographic extent (> 500 plots across São Paulo State), we used species accumulation curves and ordination (PCoA) as complementary tools. These approaches are less sensitive to plot-level undersampling and still allow for a visualization of community turnover at landscape scales across the different forest types.

4.2 | The Importance of Landscape for Diversity Recovery

Surrounding landscape had a strong effect on biodiversity recovery for all reforestation methods (Figure 3) (Arroyo-Rodríguez et al. 2020; Poorter et al. 2024; Timmers et al. 2025). Proximity to forest and water increased species diversity, possibly because of a higher abundance of seed trees and seed-dispersing animals near forests, and the presence of forests near waterbodies, as riparian forests are protected by law in Brazil (Chazdon 2008; Hordijk et al. 2024; Timmers et al. 2025; van Breugel et al. 2019; Zhu et al. 2025). A larger area of surrounding pasture was associated with lower diversity. The importance of the landscape context for biodiversity recovery was also reflected in the variables related to tree establishment and growth (Figure 3 and Figure S2). Biodiversity was lower close to the forest edge, and when pasture dominated in the surrounding landscape, probably because of competition with grasses and browsing by cows, as most forests were not protected from cattle entry. For naturally regenerating forests, we also found greater diversity in larger forest fragments that provide a larger diversity of seed trees and dispersers, and a better habitat quality. Together, these results underscore the importance of a high-quality matrix for biodiversity recovery (Arroyo-Rodríguez et al. 2020; Timmers et al. 2025).

We found some specific differences in the variables associated with higher tree diversity between reforestation types (Figure 3). In biodiverse restoration plantings, we found no association with climate variables and a reduced dependence on landscape context for biodiversity recovery, possibly because planting and management practices mitigate these effects (through fertilization, irrigation, soil preparation, etc.). The intentional introduction of diverse species could make these plots less reliant on natural species arrival during the early stages of establishment, while landscape importance may increase over time as more species come in. Additionally, we found the counterintuitive effect that diversity in the biodiverse restoration plantings was lower when the percentage of natural forest cover in a 5 km radius was high, although with a small effect size (Figure 3). This pattern might reflect a potential bias in restoration methods. Common restoration protocols employed in the region consider that the need to plant a higher diversity of tree species is lower when restoration sites are closer to forest remnants, as tree diversity could be reestablished spontaneously under the shade of the fewer tree species planted. However, our results indicate that this assumption may not always be valid in this context.

Natural regeneration occurred more often in areas with high forest cover, where active interventions are not needed. We did, however, find a strong association between diversity and distance to closest patch in three of the four reforestation methods, but none with the size of that patch, indicating that a closer forest patch is beneficial for diversity recovery, regardless of its size.

In long-rotation tree monocultures, the generally weaker associations between diversity and age, climate, and landscape variables compared to naturally regenerating forests may indicate that production trees moderate microclimatic extremes, thereby reducing environmental filtering. Nevertheless, the importance of distance to water, forest edges, and nearby forest patches highlights the continued role of both species arrival and post-establishment survival in shaping diversity outcomes within this reforestation approach.

Lastly, the agroforestry systems exhibited the strongest associations between tree diversity and climate, contrary to expectations given their relatively high management intensity. The unexpected negative association between diversity and total annual rainfall, coupled with positive associations with radiation and climatic water deficit, suggests that agroforestry diversity patterns may be shaped by spatial variation in system composition and management rather than by direct climatic effects alone. For example, wetter regions are often dominated by banana-based agroforests, where dense litter and canopy structure may inhibit tree recruitment, whereas agroforests in drier regions more frequently include coffee or mixed fruit systems that allow greater natural regeneration. In addition, higher disease pressure in wetter environments may incentivize managers to maintain lower tree densities. Together, these patterns indicate that heterogeneity in agroforestry system types and management practices along climate gradients may play a stronger role in determining diversity outcomes than climate per se.

There was no available information on land use before forest establishment for many of our plots, which is an important factor in shaping the early stages of forest succession (Hordijk et al. 2024; Jakovac et al. 2021; Poorter et al. 2024). Our findings show that forests surrounded by land currently used for pasture had lower biodiversity, and active interventions may be needed to improve diversity recovery in those areas (Rodrigues et al. 2011). This pattern may reflect both direct negative effects of land use in the surrounding landscape, such as through pesticide use, cattle grazing, and trampling (Pivello et al. 2021), lower availability of seed trees and dispersal agents (Rozendaal et al. 2019), and indirect effects of intensive previous land use in these plots, through legacies on the soil properties and the local ecosystem (Hordijk et al. 2024).

4.3 | Informing Reforestation Practice

Our findings provide crucial insights into the relative effectiveness of various reforestation methods in recovering tree diversity. This is essential for guiding reforestation planning and optimizing biodiversity conservation efforts in human-modified tropical landscapes. Especially in these landscapes, natural ecosystems compete with other land uses, such as food and timber production, and it is important to avoid leakage effects of restoration and conservation projects, where conservation in one location inadvertently results in forest conversion to other uses elsewhere (Arroyo-Rodríguez et al. 2020; Cerullo et al. 2024).

First, we clearly show that even more intensively managed reforestation methods can play a role in biodiversity conservation. We found long-rotation tree monocultures and agroforests supporting high levels of tree diversity (Scales and Marsden 2008; Simões et al. 2024; Tavares et al. 2019), especially compared to agropastoral land uses and short-rotation monocultures, even when these reforestation methods do not have biodiversity as their main priority. With a management that allows for other species to arrive and establish, they can thus contribute to biodiversity conservation in addition to more natural-like systems, such as biodiverse restoration plantings and natural regeneration (Simões et al. 2024). However, we found that the species composition of restoration plantings and agroforests did not show much overlap with conserved and degraded forest remnants (Figure 6). Furthermore, rarefaction curves for biodiverse restoration plantings and agroforests started flattening much earlier than those of conserved and degraded forest remnants and naturally regenerating forests in both the rainforest and seasonally dry forest, and thus support a smaller regional species pool (Figure 5), probably because a similar set of up to 80 species is planted statewide (De Almeida et al. 2025; Vidal et al. 2020). This approach may inadvertently limit the ecological uniqueness of individual reforestation plots compared to natural forests (De Almeida et al. 2025; Holl et al. 2022). Incorporating an even more site-specific species selection could enhance the ecological outcomes of reforestation efforts and better mimic the complexity of natural forests, thus avoiding biotic homogenization (Holl et al. 2022). In contrast, natural regeneration supported a larger regional species pool and is more likely to result in a forest with a species composition similar to natural forests.

Second, we show that the surrounding landscape is crucial when assessing the most desirable reforestation options (Crouzeilles et al. 2017; Holl and Aide 2011), as some areas may be more or less suited for some reforestation methods (Tambosi et al. 2014). In areas with very few remaining forest fragments or far from water bodies, natural regeneration will be slow, and biodiverse restoration plantings may be more successful in such marginalized areas. When feasible, planning restoration methods at a landscape scale will ensure that land uses can be targeted to where they are likely to be most successful. This can include long-rotation monoculture plantations, as plantations alone already covered 4% of the state in 2023, and they are often located in areas close to natural forest remnants, thus showing high potential for diversity recovery if management permits (Simões et al. 2024; Tavares et al. 2023).

Ultimately, the choice of reforestation method should depend on the expected outcomes and the local conditions: the ‘why’ and the ‘where’. Although naturally regenerating forests had higher overall tree diversity and biodiverse restoration plantings had higher plot tree diversity than other reforestation methods, they are not ecologically and economically feasible everywhere, so production-driven reforestation methods such as long-rotation tree monocultures may perform complementary conservation roles (Simões et al. 2024). However, it was also clear that the species composition of native forests is unique, especially in the rainforest. These findings support the importance of a multi-pronged strategy (Aguirre-Gutíerrez et al. 2023; Rozendaal et al. 2019), where (1) conserved and degraded forest remnants are protected, even when their area may be small (Arroyo-Rodríguez et al. 2022), (2) naturally regenerated forests are promoted wherever feasible socio-ecologically (Chazdon et al. 2024, 2025), (3) biodiverse restoration plantings are established in critical areas for biodiversity and ecosystem services, but in which natural regeneration is not viable (Chazdon et al. 2024), and (4) productive forests such as monoculture plantations with long rotation periods and agroforests are planted whenever economically feasible (Arroyo-Rodríguez et al. 2020; Kalame et al. 2011). The combined outcomes of these varied reforestation methods are likely superior to the prioritization of one or another method. However, the pros and cons of these methods, and there were marked differences among them, should be carefully considered in determining the location and total area to be reforested by each method (Smith et al. 2023).

Future research should explore the conservation value of restored forests in greater depth by examining the specific species present, their ecological roles, and their threatened status. A critical question is whether these reforestation methods support species that are classified as threatened or endangered, and thus whether they are actually contributing to preventing species extinctions, complementing the conservation role of conserved forest remnants. Moreover, it is essential to assess whether restored forests harbor significant diversity in taxa beyond trees, such as understory plants, fungi, and animal communities. Lastly, including a comparison of carbon sequestration potential would be valuable in addition to these measures of diversity, to complement this comparison of the different restoration methods. These studies would not only clarify the ecological contributions of reforestation efforts but also guide improvements in reforestation strategies.

Author Contributions

Laura E. Boeschoten: conceptualization, writing – original draft, investigation, methodology, visualization, writing – review and editing, formal analysis. **Joannès Guillemot:** conceptualization, writing – review and editing, methodology. **Juliano van Melis:** conceptualization, data curation, writing – review and editing. **Lourens Poorter:** supervision, project administration, writing – review and editing, funding acquisition. **Ricardo R. Rodrigues:** investigation, funding acquisition, writing – review and editing, resources, supervision, project administration. **Frans Bongers:** conceptualization, supervision, resources, project administration, writing – review and editing, funding acquisition. **Paulo G. Molin:** investigation, funding acquisition, writing – review and editing, resources, supervision, project administration. **Marielos Peña-Claros:** supervision, project administration, writing – review and editing, funding acquisition, resources. **Vinicius C. Souza:** writing – review and editing, investigation, data curation. **Cássio A. P. Toledo:** writing – review and editing, investigation, data curation. **Patrick Faria Fernandes:** writing – review and editing, investigation, data curation. **Marcelo P. Ferreira:** writing – review and editing, investigation, data curation. **Angélica F. Resende:** writing – review and editing, investigation, data curation. **Laura H. P. Simões:** writing – review and editing, investigation, data curation.**Catherine Torres de Almeida:** writing – review and editing, investigation, data curation. **María Uriarte:** writing – review and editing. **Pedro H. S. Brancalion:** conceptualization, investigation, supervision, resources, project administration, writing – review and editing, funding acquisition, methodology.

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Conflicts of Interest

P.H.S.B. and R.R.R. are partners at re.green, a forest restoration company.

Data Availability Statement

The data that support the findings of this study are openly available on Zenodo at https://doi.org/10.5281/zenodo.18244527.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb70721-sup-0001-Supinfo.pdf.