

Multiple dimensions of taxonomic tree diversity reveal complementary effects of environmental filtering and land-use legacy in an urban Atlantic Forest

Marjory Cristina de Magalhães-Fernandes

marjorycmagalhaes@gmail.com

Universidade Federal de Juiz de Fora

Fabício Alvim Carvalho

Universidade Federal de Juiz de Fora

Lisandra Mendes Louzada-Camilo

Universidade Federal de Juiz de Fora

Marcelly de Souza Ventura

Universidade Federal de Juiz de Fora

Alex Josélio Pires Coelho

Universidade Federal de Juiz de Fora

Alice Cristina Rodrigues

Universidade Federal de Viçosa

Elpidio Inácio Fernandes Filho

Universidade Federal de Viçosa

Jamerson Souza da Costa

Universidade Estadual de Feira de Santana

Ronaldo de Araújo Ibiapina

Universidade Estadual de Feira de Santana

Pedro Manuel Villa

Universidade Federal de Juiz de Fora

Research Article

Keywords: Hill numbers, secondary succession, species composition, tree dominance, restoration ecology

Posted Date: August 20th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10504326/v1>

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Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Urban Ecosystems on October 17th, 2026.
See the published version at <https://doi.org/10.1007/s11252-026-02153-7>.

Abstract

The Brazilian Atlantic Forest is a highly diverse ecosystem that has been extensively fragmented by human activities, making secondary urban forests important for biodiversity conservation. However, the influence of environmental filtering and land-use legacies on taxonomic diversity during forest regeneration remains poorly understood. We evaluated tree community diversity along environmental gradients under contrasting management histories in an urban secondary forest in Juiz de Fora, Brazil. Three regenerating communities with a common origin as shaded coffee agroforestry systems were sampled: second-growth forest after silvicultural management (SGAM), second-growth forest after enrichment with *Euterpe edulis* (SGAE), and second-growth forest under natural regeneration (SGA). Phytosociological, topographic, soil, and litter data were analyzed using Hill numbers ($q = 0, 1, 2$) through iNEXT.3D and iNEXT.beta3D, Principal Component Analysis (PCA), Non-metric Multidimensional Scaling (NMDS), and Generalized Linear Mixed Models. PCA revealed edaphic and elevation gradients, whereas NMDS showed significant differences in species composition. Species richness ($q = 0$) was highest in SGAE and SGA, while dominance-weighted diversity ($q = 1$ and 2) was greater in SGAE and SGAM. Species richness increased with elevation, effective cation exchange capacity, sand content, and litter carbon-to-nitrogen ratio, but decreased with clay content, whereas management history showed little influence. In contrast, abundance-weighted diversity was primarily driven by management history, but also increased with litter carbon-to-nitrogen ratio and elevation. These findings indicate that environmental filtering shapes species richness, whereas land-use legacies have persistent effects on community structure, highlighting the importance of multidimensional approaches for evaluating and restoring secondary urban tropical forests.

1 Introduction

Tropical forests harbor the highest levels of terrestrial biodiversity and play a central role in regulating global climate and biogeochemical cycles, particularly through carbon storage and nutrient dynamics (Eguiguren et al. 2020; Villa et al. 2021). Within this context, the Brazilian Atlantic Forest represents one of the most biologically diverse yet critically threatened ecosystems worldwide, having experienced extensive deforestation and land-use conversion since the colonial period (Myers et al. 2000; Ribeiro et al. 2009; Arruda et al. 2025). Consequently, only a small fraction of its original extent remains, largely distributed in highly fragmented landscapes dominated by secondary forests (Rosa et al. 2021). These forests, once considered of limited ecological value, are now recognized as key components for biodiversity conservation, carbon sequestration, and ecosystem resilience, particularly as they regenerate over time (Barlow et al. 2007; Matos et al. 2020; Coelho et al. 2026). Within increasingly urbanized landscapes, these secondary forest remnants have become disproportionately important as reservoirs of native biodiversity, providers of ecosystem services, and natural infrastructure that enhances climate regulation, human well-being, and ecological resilience in cities (Aronson et al. 2017; Livesley et al. 2016). Despite this growing recognition, most ecological studies in tropical systems have historically focused on old-growth forests, resulting in a limited understanding of the processes governing biodiversity patterns in secondary forests, especially in human-modified landscapes where

environmental heterogeneity and land-use legacies interact in complex ways. This knowledge gap is particularly critical in urban forest remnants, where past land-use history, environmental heterogeneity, and long-term management frequently interact to shape community assembly and influence restoration outcomes, yet remain poorly integrated within studies of urban forest ecology (Aronson et al. 2017).

Environmental filtering is widely recognized as a fundamental mechanism for plant assembly communities, particularly in species-rich tropical ecosystems (Kraft et al. 2015). Soil physicochemical properties serve as primary abiotic filters that shape species establishment, growth, and persistence by mediating variation in nutrient availability, pH, texture, and aluminum toxicity (John et al. 2007; Quesada et al. 2009). In urban forest remnants, these edaphic gradients may be further modified by historical land use, habitat fragmentation, and past management interventions, creating heterogeneous environmental conditions that influence long-term regeneration trajectories (Kowarik 2018; Aronson et al. 2017). These edaphic conditions play a central role in community assembly by acting as environmental filters that favor species with specific functional traits, thereby shaping both species richness and taxonomic composition (Kraft et al. 2015; John et al. 2007). However, the effects of soil properties on biodiversity are not unidirectional, as shifts in resource availability and soil chemistry can either promote species coexistence or intensify competitive exclusion depending on successional context and resource dynamics (Paoli et al. 2006; Long et al. 2012). While increased fertility and organic matter may enhance resource availability and promote species coexistence, they may also accelerate competitive exclusion by favoring fast-growing, dominant species, particularly in early successional stages (Paoli et al. 2006; Long et al. 2012). Furthermore, successional dynamics are often accompanied by gradual shifts in soil characteristics, with early-stage secondary forests typically associated with nutrient-poor, sandy substrates, and later stages exhibiting increased fertility and clay content (Freitag Kramer et al. 2025; Valente et al. 2025). Understanding how these environmental gradients interact with historical management is therefore essential for predicting long-term community assembly and for improving restoration and adaptive management strategies in urban tropical forests.

In addition to soil properties, topographic gradients play a critical role in structuring tropical plant communities by generating fine-scale environmental heterogeneity (Rodrigues et al. 2019; Campos et al. 2022). Variations in elevation, slope, and landscape position generate fine-scale environmental heterogeneity, ultimately structuring species distributions and local abundance patterns (Rodrigues et al. 2019; Russo et al. 2005). In urban forest remnants, these topographic gradients often interact with historical land-use practices and localized management interventions, creating complex environmental mosaics that influence regeneration dynamics and biodiversity patterns (Kowarik 2018; Aronson et al. 2017). These gradients mediate key ecological processes, including niche differentiation, stress tolerance, and asymmetric competition, which collectively structure patterns of species coexistence and community assembly across spatial scales (Russo et al. 2005; Irl et al. 2015; He et al. 2023). The interaction between edaphic and topographic variation generates a heterogeneous mosaic of microhabitats that promotes high beta diversity by enhancing spatial turnover in species composition in regenerating secondary forests (Rodrigues 2020; John et al. 2007; Kraft et al. 2015). Such environmental heterogeneity may be particularly important in fragmented urban landscapes, where relatively small

changes in topography can interact with past disturbances to generate contrasting community assembly trajectories. However, despite the recognized importance of these environmental drivers, their combined effects across multiple dimensions of taxonomic biodiversity remain underexplored, particularly when considered alongside the legacy effects of past land use. Addressing this gap is essential for understanding how environmental filtering and historical contingency jointly influence biodiversity patterns and for supporting conservation and restoration strategies in urban tropical forests.

Land-use history is an additional, and often overriding, driver of community assembly in secondary forests, influencing successional trajectories and long-term ecosystem functioning (Chazdon et al. 2007; Zahawi et al. 2015). The ecological imprint of past land use may persist for decades after forest regeneration, creating long-lasting legacy effects that continue to influence species establishment, community dominance, and ecosystem functioning through processes collectively referred to as ecological memory (Foster et al. 2003; Johnstone et al. 2016). Moreover, different management practices, such as agroforestry systems and selective logging, can alter dispersal processes, regeneration dynamics, and species interactions, thereby generating persistent effects on tree community composition and structure (Holmes & Matlack 2017; Garcia-Florez et al. 2017; Villa et al. 2018). In urban forest remnants, where historical management is often followed by prolonged periods of natural regeneration, these silvicultural legacies may remain embedded in community structure long after direct human interventions have ceased, interacting with environmental heterogeneity to shape contemporary biodiversity patterns (Kowarik 2018; Aronson et al. 2017).

The intensity and duration of past land use can generate divergent community assembly trajectories, ranging from increased dominance by a few species to higher compositional heterogeneity, depending on the interaction between disturbance regimes, environmental conditions, and successional dynamics (Chazdon et al. 2007; Holmes & Matlack 2017; Garcia-Florez et al. 2017). These historical contingencies may influence not only which species persist within communities but also how abundances are distributed among them, potentially leaving contrasting signatures across different dimensions of biodiversity. In some cases, land-use legacy effects may be stronger predictors of biodiversity patterns than contemporary environmental variables, particularly in fragmented landscapes where dispersal limitation and isolation further constrain community assembly (Coelho et al. 2022). This is especially relevant in urban landscapes, where fragmentation, environmental heterogeneity, and historical management interact across relatively small spatial scales to generate highly heterogeneous regeneration pathways (Kowarik 2018; Aronson et al. 2017; Livesley et al. 2016). Despite significant advances in restoration ecology, relatively few studies have explicitly integrated environmental gradients and historical land-use legacies to explain variation across multiple dimensions of biodiversity in tropical secondary forests (Chazdon et al. 2016). Furthermore, these interactions remain poorly understood in urban forest remnants, despite their increasing importance as reservoirs of native biodiversity and priority targets for ecological restoration and adaptive management (Aronson et al. 2017; Kowarik 2018). Consequently, it remains unclear whether environmental filtering and historical land-use legacies act synergistically or independently to shape species richness, community dominance, and biodiversity patterns during forest regeneration.

Biodiversity is inherently multidimensional, encompassing not only species richness but also patterns of relative abundance and dominance within communities (McGill et al. 2007; Chase et al. 2018). The Hill numbers framework provides a unified and ecologically meaningful approach to quantify these different dimensions of diversity by integrating species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$) within a single analytical framework (Chao et al. 2014). Importantly, these metrics differentially weight rare and common species, allowing the disentanglement of ecological processes operating across abundance gradients (McGill et al. 2007; Chase et al. 2018). Environmental filtering, driven by soil physicochemical properties and topographic heterogeneity, is expected to primarily constrain species establishment and thus exert stronger effects on richness ($q = 0$), which is more sensitive to rare taxa (Kraft et al. 2015; John et al. 2007). In contrast, abundance-weighted metrics ($q = 1$ and $q = 2$) are more likely to reflect processes related to competitive interactions, resource dominance, and historical land-use legacies, which shape the relative abundance structure of communities (Chase and Leibold 2003; Chazdon et al. 2007). Despite this conceptual framework, how environmental filtering, topographic heterogeneity, and land-use legacies interact to influence different dimensions of diversity remains poorly understood in tropical secondary forests (Chase et al. 2018; Kraft et al. 2015). Specifically, it is unclear whether rare species are predominantly structured by abiotic constraints, while dominant species respond more strongly to biotic interactions and historical processes, highlighting a critical gap in our understanding of community assembly in regenerating secondary forest (Chase and Leibold 2003; Chazdon et al. 2007).

Here, we investigate how multiple dimensions of taxonomic diversity respond to environmental gradients and contrasting silvicultural legacies within a secondary Atlantic Forest. Taking advantage of a historical silvicultural mosaic embedded within the Botanical Garden of the Universidade Federal de Juiz de Fora, located in one of the largest urban Atlantic Forest fragment of the Zona da Mata region of southeastern Brazil, we evaluate whether communities sharing a common land-use origin but differing in post-abandonment management history exhibit persistent differences in diversity patterns and community composition. Specifically, we assessed how different dimensions of taxonomic diversity, species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$) vary along gradients of soil physicochemical properties, topographic heterogeneity, and contrasting management histories. We hypothesize that these dimensions of taxonomic diversity respond asymmetrically to environmental filtering and land-use legacies. We predict that species richness, which is more sensitive to rare species, will be primarily constrained by abiotic conditions associated with soil properties, reflecting the role of environmental filtering along environmental gradients. In contrast, abundance-weighted diversity metrics ($q = 1$ and $q = 2$) are expected to respond more strongly to topographic variation and management history, reflecting shifts in dominance patterns and compositional structure driven by competitive interactions and legacy effects. Furthermore, we anticipate that beta diversity will vary along environmental gradients and among management types, reflecting the combined influence of environmental heterogeneity and land-use history on species turnover and dominance structure. Thus, integrating environmental gradients and management history across multiple dimensions of taxonomic

diversity, this study provides a mechanistic understanding of biodiversity patterns in regenerating Atlantic Forest ecosystems.

2 Methods

2.1 Study area and land-use history

The study was conducted at the Botanical Garden of the Federal University of Juiz de Fora (JB-UFJF; Fig. 1), considering three Atlantic Forest tree communities with distinct land-use histories. The JB-UFJF is in the central region of the municipality of Juiz de Fora (21° 41' 20" S, 43° 20' 40" W), Minas Gerais, Brazil, near the Paraibuna River. It covers approximately 80 hectares and connects to the 292-hectare Mata do Krambeck State Park, forming one of the largest urban forest fragments in the Zona da Mata region of Minas Gerais. The predominant soils in the region are Dystrophic Red-Yellow Latosols (FEAM 2011), and the forest vegetation is classified as Montane Semideciduous Seasonal Forest (IBGE 2012). The climate is classified as subtropical in altitude (Cwa) according to Koppen (Alvares et al. 2014), characterized by a dry season with lower temperatures between May and September and a hot season with higher precipitation from October to April, with average temperatures around 19°C and mean annual precipitation around 1500 mm (Costemalle et al. 2023).

Based on their different historical land use and management practices, the studied communities were designated as Second growth forest after silvicultural system with management (SGAM), Second growth forest after enriched silvicultural system (SGAE), and Second growth forest after silvicultural system (SGA). SGAM was previously used for coffee and fruit tree cultivation under a shaded system with secondary forest cover, with more intense management based on selective logging and understory suppression until these practices were abandoned approximately 20 years ago. SGAE was previously used for coffee cultivation within a secondary forest enriched with *juçara* palm (*Euterpe edulis*) trees, with no evidence of selective logging. Lastly, SGA was formerly cultivated with coffee under a secondary forest canopy, with minimal anthropogenic disturbance since the crops were abandoned roughly 80 years ago. A major strength of this study is that the three regeneration contexts are embedded within the same forest fragment and share a common land-use origin as abandoned shaded coffee agroforestry systems. Although not originally established as a controlled experiment, this historical silvicultural mosaic represents a rare long-term natural experiment in which contrasting management trajectories unfolded under a common regional species pool, climate, geological substrate, and landscape context. This setting reduces many sources of variation that commonly confound comparisons among secondary forests and provides a unique opportunity to evaluate the long-term legacy of silvicultural practices on contemporary tree diversity patterns.

2.2 Tree community sampling

In each of the three tree communities (SGA, SGAE, and SGAM), 25 permanent 20 x 20 m plots were established, totaling 75 plots and 3 hectares of sampling area, which are appropriate for tropical forest

studies. Within each plot, all tree individuals with a diameter at breast height (DBH) ≥ 5.00 cm were systematically sampled, tagged with numbered aluminum plates, measured, and individually identified at the species level (Felfili 2005; Santana et al. 2018). When field identification was not possible, botanical material was collected using high-reach pruning shears, stored, and transported to the Federal University of Juiz de Fora (UFJF) for comparison with the taxonomic literature and specimens in the Leopoldo Krieger Herbarium (CESJ). The list of species and their abundance in each area is available in the supplementary material (Table S1).

2.3 Taxonomic diversity

Taxonomic diversity of tree communities was quantified using the Hill numbers framework, which provides a unified family of diversity measures parameterized by the order q , allowing the integration of species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$) within a single analytical framework (Hill 1973; Chao et al. 2014; Hsieh et al. 2016). This approach expresses diversity as the effective number of species and enables the assessment of the relative contribution of rare and dominant species to community structure (Jost 2006; Chao et al. 2014). Because empirical diversity estimates are inherently sensitive to sampling effort and completeness, we applied rarefaction and extrapolation methods to standardize comparisons among communities. Specifically, we used the iNEXT framework to generate both sample-size-based and coverage-based rarefaction and extrapolation curves, which allow diversity to be compared either at equivalent numbers of individuals or at equivalent levels of sample completeness (Chao and Jost 2012; Hsieh et al. 2016). Sample-size-based curves describe how diversity accumulates with increasing numbers of individuals, whereas coverage-based curves standardize comparisons by accounting for sample completeness, providing a more robust basis for comparing assemblages with unequal sampling effort (Chao and Jost 2012; Chao et al. 2014). Confidence intervals for diversity estimates were obtained via bootstrap resampling, enabling statistical comparisons among communities (Hsieh et al. 2016).

To further investigate the partitioning of diversity across spatial scales, we applied the iNEXT.beta3D framework to decompose diversity into its alpha (within-community), beta (among-community), and gamma (regional) components under a unified Hill numbers approach (Chao et al. 2023). In this framework, beta diversity is defined as the ratio between gamma and alpha diversity and quantifies the extent of compositional differentiation among communities, with richness-based beta diversity ($q = 0$) reflecting species turnover and abundance-based beta diversity ($q > 0$) incorporating shifts in species dominance (Jost 2007; Chao et al. 2023). Coverage-based standardization was used to remove the dependence of beta diversity on sampling effort and species pool size, ensuring that observed differences reflect true ecological variation rather than sampling artifacts (Chao et al. 2023).

2.4 Soil sampling and analysis

In each plot, three random soil subsamples were collected from the topsoil layer (0–20 cm) using a soil auger and then homogenized to form a composite sample representative of the plot (Estrada-Villegas et al. 2020). A total of 75 composite samples were obtained (25 per community), stored in labeled plastic

bags, and transported to the Multi-user Laboratory at UFJF. Following standard EMBRAPA protocols (Teixeira et al. 2017), the samples were air-dried, subsampled, and sent to a specialized external laboratory to determine the following parameters: organic matter (OM, dag/dm³), pH (H₂O), phosphorus (P, mg/dm³), potassium (K, mg/dm³), calcium (Ca, cmol_c/dm³), magnesium (Mg, cmol_c/dm³), aluminium (Al, cmol_c/dm³), exchangeable acidity potencial (H + Al, cmol_c/dm³), total exchangeable bases (SB, cmol_c/dm³), effective cation exchange capacity (ECEC, cmol_c/dm³), base saturation (BS, percentual), and the sand, silt and clay contents.

2.5 Litter sampling and analysis

Litter samples were collected from 1 m² subplots positioned at the center of each permanent plot in which all accumulated material was harvested, including non-decomposed leaves, seeds, branches, fruits, and flowers (Silva et al. 2018). This approach is appropriate for tropical forest studies, as it allows assessment of litter accumulation under high spatial variability. The collected material was stored in labeled plastic bags and transported to the Multi-user Laboratory at UFJF. Samples were air-dried for two weeks, transferred to paper bags, and oven-dried at 70°C for 72 hours (or until a constant weight was reached). Subsequently, an analytical precision balance was used to determine the litter dry mass (g/m²), and the result was converted to megagrams per hectare (Mg/ha; Villa et al. 2022). To determine chemical properties, a composite subsample was obtained for each plot by pooling five random aliquots of the total content. These subsamples were sent to a specialized external laboratory to analyze organic carbon (Litter OC, g/kg; muffle furnace method), nitrogen content (Litter N, g/kg; sulfur digestion method), and determine the carbon-to-nitrogen ratio (Litter C:N ratio).

2.6 Elevation assessment

Geographic coordinates were recorded at a representative point within each plot using a Garmin handheld GPS receiver (Ahmed and Lemessa 2024). Elevation values were subsequently derived from the Copernicus Global Digital Surface Model (DSM), which provides a 30-meter spatial resolution (European Space Agency 2022). Data extraction was performed in QGIS (QGIS Development Team 2026) by intersecting the plot coordinates with the digital elevation model. This approach ensured a standardized topographic variable across all plots, effectively minimizing vertical uncertainties and local atmospheric interference often associated with direct field altimetric measurements. The elevation value obtained for each plot was assigned to all individuals (stems) within that plot.

2.7 Statistical analysis

As the areas under different management intensities showed substantial variation in stem density, we standardized the sampling effort by number of individuals (Poorter et al. 2015; Rozendaal et al. 2019). Consequently, each analytical unit consisted of a fixed number of individuals (25 stems), resulting in 68 analytical units in SGA, 23 in SGAM, and 59 in SGAE. This approach allows for more robust comparisons of community composition, diversity, and relative structure across areas by minimizing the effects of unequal sampling effort and density differences associated with management history (Chiu 2023;

Colwell et al. 2012). The soil, litter, and elevation characteristics obtained for each plot were assigned to all individuals (stems) within that plot. Subsequently, the environmental attributes for each sampling unit (each set of 25 stems) were calculated as the weighted average of the properties assigned to the constituent individuals, ensuring that the environmental data directly corresponded to the specific group of trees analyzed and allowing for a robust evaluation of environmental gradients.

To synthesize the main environmental gradients across the sampled plots and reduce the dimensionality of the environmental dataset, we performed a Principal Component Analysis (PCA) based on the correlation matrix, which is appropriate for variables measured at different scales. Prior to the analysis, all environmental variables were centered and standardized to ensure equal contribution to the ordination axes. The set of variables included elevation as a topographic attribute, soil texture fractions (sand, silt, and clay), soil chemical properties, such as organic matter (OM), exchangeable aluminum (Al), pH, total exchangeable bases (SB), and effective cation exchange capacity (ECEC), as well as litter attributes (C:N ratio and litter dry mass). Variable selection was preceded by collinearity assessment, retaining only predictors with low redundancy to ensure robust interpretation of the PCA axes (Supplementary material, Figure S1; Villa et al. 2022). Principal Component Analysis (PCA) was performed using the FactoMineR package (Husson et al. 2017), and graphical visualization of the ordination results was conducted using the factoextra package (Kassambara and Mundt 2020) in combination with ggplot2 (Wickham 2016). The first two principal components were retained for interpretation as they explained the largest proportion of environmental variance and were interpreted as integrated environmental gradients. To identify the contribution of each variable to the ordination, correlations between the original variables and PCA axes were examined. Additionally, taxonomic diversity metrics based on Hill numbers ($q = 0$, $q = 1$, and $q = 2$) were projected as supplementary variables onto the ordination space, allowing the evaluation of how different dimensions of diversity are distributed along environmental gradients. Patterns of species composition were explored using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity, a robust ordination technique widely used to represent ecological distances among communities in reduced-dimensional space (Legendre and Legendre 2012). The Bray–Curtis index was selected due to its sensitivity to species abundances and its suitability for ecological community data, as it emphasizes differences in both species composition and relative abundance among assemblages. The analysis was conducted using the metaMDS function in the vegan package (Oksanen et al. 2024), which performs iterative optimization with multiple random starts to achieve a stable ordination solution and minimize stress. Stress values were used to assess the goodness of fit of the ordination, with lower values indicating a better representation of the data's multivariate structure (Supplementary material, Figure S2). This approach allowed us to visualize patterns of compositional similarity among communities and to identify potential clustering or gradients associated with environmental variation and land-use history. Finally, to statistically test differences in species composition among groups, we performed a permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity, implemented using the adonis2 function in the *vegan* package (Oksanen et al. 2024).

The effects of environmental factors on different dimensions of taxonomic alpha diversity (Hill numbers, $q = 0$, $q = 1$, and $q = 2$) were evaluated using Generalized Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs) via the lme4 package (Bates et al. 2015). We considered attributes previously selected based on their ecological relevance and low collinearity, as indicated by the Principal Component Analysis (PCA). The selected fixed predictors represented distinct environmental dimensions, including topographic attributes (elevation), soil texture (sand, silt, and clay content), soil fertility (pH, total exchangeable bases, effective cation exchange capacity, organic matter, and exchangeable aluminum), and litter characteristics (dry weight and C:N ratio). To investigate environmental effects on species richness ($q = 0$), GLMMs were fitted with a Poisson distribution and a log link function, which are appropriate for discrete data (species counts). For abundance-weighted diversity ($q = 1$ and $q = 2$), LMMs were used with a Gaussian distribution and an identity link function, suitable for continuous variables. In all models, a random intercept (1 | GROUP) was included to represent the different tree communities and reflect distinct management legacies, accounting for the hierarchical structure and non-independence of the sampling units. The effects of environmental variables were initially assessed using univariate mixed models to investigate their isolated effects on each diversity dimension. Subsequently, multiple predictor models were fitted by combining non-collinear environmental variables, based on the prior assessment of predictor redundancy (Supplementary material, Table S2). Specifically, elevation was included as a key variable, alongside various edaphic and litter attributes, to evaluate the joint effects of these variables across environmental gradients. Certain continuous predictor variables were standardized using the scale function in R to improve numerical stability of the models, particularly where scaling issues were identified during model fitting. The elevation variable was standardized across all models to maintain consistency in the interpretation of effects. The presence of overdispersion in the Poisson models was evaluated by the ratio between the Pearson chi-square and the residual degrees of freedom, but no overdispersion was detected in the fitted models. Model adequacy was evaluated through graphical inspection of residuals (residual vs. fitted values plots and Q-Q plots), with no relevant deviations from the assumptions of normality and homogeneity observed.

To synthesize and compare the magnitude of the effects of the selected predictors, effect size plots were constructed from the estimated model coefficients using the plot_summs function from the jtools package (Long 2024). These plots display standardized coefficients and their respective confidence intervals, allowing direct comparison of predictors across different models.

To ensure comparability, coefficients were presented on a standardized scale when applicable, and confidence intervals were set at 90%. The relative importance of the predictors was estimated by partitioning the marginal coefficient of determination (R^2 marginal), which represents the variance explained solely by the fixed effects of the mixed models. For this purpose, the partR2 package (Stoffel et al. 2021) was used, which allows the decomposition of R^2 into independent contributions from each predictor variable while maintaining the hierarchical structure of the data by including the random factor. Initially, a global model including all selected environmental predictors (soil texture, fertility, litter attributes, and elevation) was fitted, and subsequently, the partR2 function was applied to each predictor across 100 bootstrap resamples to obtain robust estimates of its unique contribution. The independent

contributions were then normalized to percentages, allowing for relative comparison among variables. For visualization purposes, the results were organized and presented as horizontal bar charts using the ggplot2 package (Wickham 2016), with predictors ordered by relative importance. This procedure was applied consistently across the diversity metrics, enabling comparison between different dimensions of taxonomic diversity. All analyses were conducted in R via the RStudio interface (Posit Team 2024).

3 Results

3.1 Environmental gradients

Principal Component Analysis (PCA; Fig. 2) revealed that the first two axes accounted for 62.72% of the total variability in the data, indicating two primary environmental gradients. The first axis (PCA1; 41.65% of the variance) primarily represented a gradient of soil fertility and texture, showing positive correlations with aluminum (Al; $R = 0.88$, $p < 0.05$), sand content ($R = 0.81$, $p < 0.05$), and litter C:N ratio ($R = 0.75$, $p < 0.05$). Furthermore, PCA1 was positively associated with the diversity indices q_0 ($R = 0.53$, $p < 0.05$), q_1 ($R = 0.68$, $p < 0.05$), and q_2 ($R = 0.72$, $p < 0.05$), which are characteristics predominantly linked to SGA. Conversely, PCA1 exhibited negative correlations with the sum of bases (SB; $R = -0.79$, $p < 0.05$), clay content ($R = -0.79$, $p < 0.05$), and pH ($R = -0.76$, $p < 0.05$), reflecting a separation of the more fertile and clay-rich soils associated with SGAE. The second axis (PCA2; 21.07% of the variance) primarily captured variation associated with elevation and soil organic matter properties and was inversely related to SGAM. This axis was positively correlated with effective cation exchange capacity (ECEC; $R = 0.75$, $p < 0.05$), elevation ($R = 0.61$, $p < 0.05$), organic matter (OM; $R = 0.60$, $p < 0.05$), and silt content ($R = 0.56$, $p < 0.05$). Additionally, diversity indices q_0 ($R = 0.64$, $p < 0.05$), q_1 ($R = 0.55$, $p < 0.05$), and q_2 ($R = 0.44$, $p < 0.05$) also showed positive associations with this axis.

3.2 Community composition

The study areas exhibited pronounced differences in species composition among the tree communities (stress = 0.25; PERMANOVA, Bray-Curtis; $F(2,147) = 49.63$, $R^2 = 0.40$, $p = 0.001$). Axis 1 from the non-metric multidimensional scaling (NMDS; Fig. 3) primarily separated SGA from the other groups, whereas Axis 2 distinguished SGAM from SGAE. Within-group dispersion also varied across the sites, with SGAM displaying the highest degree of floristic heterogeneity.

3.3 Taxonomic diversity

Based on the results of rarefaction and extrapolation of taxonomic alpha diversity (Fig. 4), species richness was highest in SGAE and SGA and lowest in SGAM; these differences remained consistent even at equivalent levels of sample coverage. The overlapping confidence intervals for SGAE and SGA indicate that there is no statistically significant difference in species richness between these two areas. Regarding evenness and dominance, SGA exhibited higher values, indicating a more homogeneous distribution of abundances among species and a lower concentration of individuals in a few dominant

species. In contrast, SGAE and SGAM showed a stronger influence of dominant species, as reflected in lower Shannon and Simpson diversity values ($q = 1$ and $q = 2$).

The sample-size-based curves for species richness did not reach an asymptote in any area, suggesting the presence of rare species that remain unsampled. Conversely, metrics accounting for species abundance ($q = 1$ and $q = 2$) stabilized, indicating that a set of more abundant species characterizes the communities. These observed patterns suggest that differences among the areas are primarily driven by the richness of rare species, whereas the composition of dominant species remains relatively similar (Fig. 4).

In the decomposition of taxonomic alpha, beta, and gamma diversity, coverage-based rarefaction and extrapolation curves revealed consistent patterns across the three diversity orders ($q = 0, 1$, and 2). We observed a trend toward higher gamma diversity in SGAE and SGA, with no statistically robust differences between them, and lower gamma diversity in SGAM (Fig. 5). For Shannon and Simpson diversity, the differences were less pronounced, suggesting that the areas share similar sets of common and dominant species at the regional scale.

Alpha diversity derived from the gamma–beta partitioning was highest in SGA across all q orders and significantly different from the other communities, indicating a locally richer community with greater evenness. In contrast, SGAE and SGAM exhibited lower local diversity values, particularly for abundance-weighted metrics ($q = 1$ and $q = 2$), suggesting a stronger influence of dominant species. Beta diversity based on richness ($q = 0$) and common species ($q = 1$) showed overlapping confidence intervals among the areas, indicating no robust differences in the turnover of rare and common species. On the other hand, for Simpson diversity, the confidence intervals for SGAE did not overlap with the other groups, with SGAE showing lower beta diversity values. This pattern indicates greater homogeneity in the composition of dominant species in SGAE, whereas SGA and SGAM exhibit higher variation in dominance among sampling units (Fig. 5).

3.4 Relationships between environmental gradients and taxonomic diversity

The models (Fig. 6) indicate that elevation (Estimate = 0.063, $z = 2.093$, $p = 0.036$) has a significant positive effect on species richness, whereas management type has a minimal effect (ICC = 0.004). Effective cation exchange capacity (ECEC) also had a significant positive effect on richness (Estimate = 0.097, $z = 1.956$, $p = 0.050$), with management history again showing low influence (ICC = 0.010). Elevation maintains a significant positive effect on richness (Estimate = 0.088, $z = 3.702$, $p < 0.001$) when analyzed in conjunction with sand content (Estimate = 0.004, $z = 2.139$, $p = 0.032$), also without management influence (ICC = 0.000). Conversely, clay content has a significant negative effect on richness (Estimate = -0.005 , $z = -2.389$, $p = 0.017$); however, elevation continues to exert a significant positive effect (Estimate = 0.079, $z = 3.301$, $p = 0.001$), again with no management effect (ICC = 0.000). Finally, in models that include the litter carbon-to-nitrogen (C:N) ratio (Estimate = 0.023, $z = 3.264$, $p =$

0.001) and elevation (Estimate = 0.082, $z = 3.429$, $p = 0.001$), both variables significantly and positively influence richness, with no contribution from management type (ICC = 0.000).

For the abundance-weighted diversity indices—evenness, the exponential of Shannon diversity ($q = 1$), and the inverse of Simpson diversity ($q = 2$)—the tested models (Fig. 6) indicate a greater influence of management, with ICC values ranging from 0.125 to 0.439. The litter carbon-to-nitrogen (C:N) ratio (Estimate = 0.786, $t = 2.750$, $p = 0.007$) and elevation (Estimate = 0.708, $t = 2.515$, $p = 0.014$) exhibited significant positive effects on Shannon diversity. Together with management type (ICC = 0.137), these variables accounted for 24.3% of the total variation in diversity.

Similarly, Simpson diversity increased significantly with the litter C:N ratio (Estimate = 0.602, $t = 2.267$, $p = 0.025$), but no significant effect of elevation was observed (Estimate = 0.404, $t = 1.533$, $p = 0.128$). In this case, the effect of management type explained approximately 25% of the total variation (ICC = 0.248). Elevation (Estimate = 0.677, $t = 2.241$, $p = 0.027$) also exerted a positive effect on Shannon diversity when considered alongside litter weight (Estimate = 0.036, $t = 0.287$, $p = 0.774$), which in turn showed a non-significant positive effect. This model also revealed substantial effects of management type (ICC = 0.265, total $R^2 = 0.296$).

The relative importance of the selected predictors (Fig. 7) varied substantially across Hill number orders, highlighting contrasting responses of different dimensions of taxonomic diversity to environmental gradients. Species richness ($q = 0$) was strongly explained by elevation (80.3%), which accounted for most of the independent effects, whereas edaphic variables contributed little individually ($< 10\%$). For Shannon diversity ($q = 1$), the importance of predictors was more widely distributed, with significant contributions from elevation (46.2%), the litter C:N ratio (37.0%), and effective cation exchange capacity (ECEC; 15.4%). For Simpson diversity ($q = 2$), a more balanced distribution of effects was again observed, with litter quality (C:N ratio; 36.5%) showing the highest importance, followed by elevation (29.8%) and ECEC (27.2%).

4 Discussion

Understanding how environmental filtering and historical forest management jointly shape community assembly remains a central challenge in community ecology, particularly in human-modified tropical forests where multiple ecological processes operate simultaneously. Using a unique silvicultural mosaic preserved within a regenerating Atlantic Forest remnant, we demonstrate that environmental conditions and land-use legacy leave distinct and complementary signatures across multiple dimensions of tree taxonomic diversity. Within the UFJF Botanical Garden, tree communities sharing a common origin as abandoned shaded coffee agroforestry systems and drawing from the same regional species pool diverged in species richness, evenness, and dominance according to both contemporary environmental gradients and historical silvicultural interventions. Consistent with our hypotheses, environmental filtering was more strongly associated with variation in species richness, whereas management legacy was primarily reflected in abundance-weighted diversity and community dominance. These contrasting

responses demonstrate that different dimensions of biodiversity capture complementary ecological processes, revealing patterns of community assembly that would remain partially hidden if evaluated through species richness alone. More broadly, our findings provide empirical evidence that silvicultural practices can generate long-lasting ecological legacies that persist for decades after agricultural abandonment, reinforcing the importance of integrating historical land use with contemporary environmental heterogeneity when interpreting biodiversity patterns in secondary forests. This perspective has direct implications for the conservation, restoration, and adaptive management of urban forest remnants, where historical contingencies continue to shape present-day biodiversity.

Elevation played a central role in structuring the tree communities evaluated here, influencing both local richness and evenness. Although the study area spans a short altitudinal gradient (Supplementary material, Figure S5), subtle topographic variation appears sufficient to generate fine-scale environmental heterogeneity capable of altering the spatial distribution of resources and acting as a biological filter. When considered together with soil and litter characteristics, topography helped explain variation in diversity, but its predictive power decreased across Hill numbers as the order of q increased and the contribution of rare species became less important. This pattern diverged from our initial expectation that abundance-weighted metrics would respond more strongly to topographic variation. Instead, species richness ($q = 0$) showed the clearest response to environmental gradients, highlighting the sensitivity of this metric to rare species within the community. Because richness does not account for relative abundance, it is strongly influenced by the occurrence of low-density species which, due to their narrower niche breadth, tend to be more susceptible to environmental heterogeneity than generalist species (Brown et al. 1996; Slatyer et al. 2013; Vincent et al. 2020). Spatial patterns of richness therefore reflect a niche-based filtering process in which micro-scale topographic variation, together with soil and litter quality, determines the presence of the species set that characterizes these secondary Atlantic Forest communities.

Litter C:N ratio also showed positive and highly significant effects across all diversity orders ($q = 0$, $q = 1$, and $q = 2$). Variables associated with litter quality reflect the autogenic feedback between colonizing trees and the ecosystem, and our results indicate that environments with more conservative nutrient cycling, reflected in higher C:N ratios, tend to constrain the rapid expansion of a few highly competitive species (Long et al. 2012; Russo et al. 2005). Rather than favoring dominance, this surface-level nutritional restriction appears to reduce competitive exclusion and promote a more even community structure (Tilman 1985; Gastauer and Meira-Neto 2014). This interpretation is strengthened by the multivariate patterns observed in the PCA, in which better litter nutritional quality was associated with the area of more fertile soil, whereas poorer litter nutritional quality was associated with the less fertile soil area, and the litter C:N ratio was also correlated in the correlation matrix (Supplementary material, S1) with variables linked to more fertile soils. Together, these relationships suggest that litter quality operates as an integrated gradient that is strongly associated with soil nutritional status, rather than as an isolated surface attribute. A similar interpretation helps explain the patterns observed in SGA, where higher evenness and greater abundance-weighted diversity were associated with more restrictive soil and litter conditions identified by the PCA. Under less fertile conditions or lower resource availability,

fewer species are able to monopolize available resources, allowing a larger number of species to maintain relatively balanced abundances (Huston 1999; Campos et al. 2021). As a result, the less intensively managed area appears to sustain a more even and internally homogeneous community. Although these interpretations are consistent with the patterns observed here, future studies directly testing the mechanisms underlying these relationships would be valuable for drawing firmer conclusions.

Our models further showed that richness and abundance structure did not respond in the same way to the environmental factors examined, and that silvicultural legacy, expressed through different management histories, primarily affected abundance structure across the three communities. This asymmetric response indicates that different components of taxonomic diversity register distinct aspects of the ecological history of the system, with silvicultural legacy remaining the main driver of evenness and dominance even decades after agricultural abandonment (Chase et al. 2018, Jakovac et al. 2016). While the less intensively managed area (SGA) was the most diverse in terms of evenness, the high abundance of the palm species used for enrichment in SGAE appears to have altered the relative distribution of abundances, reducing evenness and increasing dominance without changing species richness. This provides a clear example of how historical interventions can reshape community structure without necessarily reducing the number of species, but still promote biodiversity loss in terms of evenness when the internal balance between dominance and rarity is profoundly altered. Selective cutting in SGAM also appears to have reduced diversity, as this area showed the lowest richness, the lowest number of individuals, and intermediate evenness among the three communities.

The analysis of spatial beta-diversity patterns indicated that floristic heterogeneity among plots within the same area varied according to the diversity component considered. When only incidence was considered ($q = 0$), beta-diversity curves did not differ among areas, indicating that the turnover of less abundant species among internal plots remained similar regardless of the community. In contrast, abundance-weighted beta diversity ($q = 2$) revealed lower internal spatial variation in the area with a history of silvicultural enrichment (SGAE). The lower magnitude of this curve indicates that plots within this community came to share very similar sets of dominant species. Although direct causal relationships between management and spatial variation were not tested through predictive models, the observed structural pattern suggests a possible process of monodominance associated with land-use legacies. This interpretation is consistent with our initial hypothesis that biodiversity dimensions respond asymmetrically during community assembly: while the spatial turnover of species continues to reflect microhabitat heterogeneity, variation in dominance appears to retain the marks of past disturbance (Longworth et al. 2014; Jakovac et al. 2016). Together, these results show that secondary forests can maintain spatial variability in the base of the community while simultaneously exhibiting homogenization among their most abundant populations, reinforcing the importance of multidimensional metrics for revealing features of forest organization that would remain hidden in assessments based exclusively on taxonomic richness.

From a conservation perspective, understanding management as a long-term ecological driver rather than a discrete disturbance event is essential because high dominance inherited from past interventions can fundamentally reshape community assembly trajectories and compromise long-term forest integrity, a phenomenon evidenced by the severe multidimensional erosion of biodiversity driven by açai palm intensification in Amazonian estuarine forests (Freitas et al. 2021; Freitas et al. 2025). If left unchecked, this monodominance by native species may eventually lead to the competitive exclusion of rare species that persist in the system through dominance-induced rarity (Freitas et al. 2015). Consequently, traditional conservation and restoration assessments based exclusively on species richness are insufficient because they can mask chronic degradation in community structure and the monopolization of resources by a few dominant populations (McGill et al. 2007; Chase et al. 2018). By simultaneously incorporating richness, evenness, and dominance, multidimensional indicators such as the Hill numbers framework are therefore indispensable for revealing these imbalances, providing a more mechanistic understanding of how ecological communities respond to environmental filtering and historical management. This integrative perspective allows restoration strategies to move beyond maximizing species richness towards maintaining balanced community structure and ecological resilience, guiding targeted successional practices such as selectively reducing hyper-dominant populations when necessary to foster structurally even, functionally resilient, and compositionally stable secondary Atlantic Forest communities.

5 Conclusions

Our study demonstrates that the taxonomic diversity of secondary Atlantic Forest communities responds asymmetrically to fine-scale environmental gradients and historical land-use legacies. Environmental filtering, primarily driven by topographic variation and soil resource limitations, acts as the fundamental mechanism sustaining species richness and maintaining the spatial turnover of rare taxa. Conversely, past silvicultural interventions exert a long-lasting and predominant influence on the abundance distribution of the forest canopy, substantially altering species evenness and promoting dominance across the landscape. These contrasting responses highlight that historical human disturbances can profoundly restructure community assembly processes, competitive interactions, and community integrity without necessarily driving local species extinctions. Consequently, traditional restoration assessments relying exclusively on species richness may obscure biodiversity losses and structural degradation. Our findings further demonstrate that species richness, evenness, and dominance capture complementary ecological responses to environmental filtering and historical management, providing a more comprehensive understanding of biodiversity dynamics during forest regeneration. Ultimately, integrating multidimensional biodiversity metrics with knowledge of environmental heterogeneity and land-use history offers a more robust framework for assessing forest recovery, identifying hidden degradation, and guiding conservation, restoration, and adaptive management of secondary urban Atlantic Forests.

Declarations

Declaration of Competing Interest

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.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Funding Declaration

This work was supported by Probiodiversa Brasil. Author M.C.M.F. has received research support from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – Brasil through a scholarship.

Acknowledgements

We thank Probiodiversa Brasil for providing the resources necessary to complete this work, CNPq for the scholarship, and the Botanic Garden of UFJF for allowing and supporting this research.

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Figures

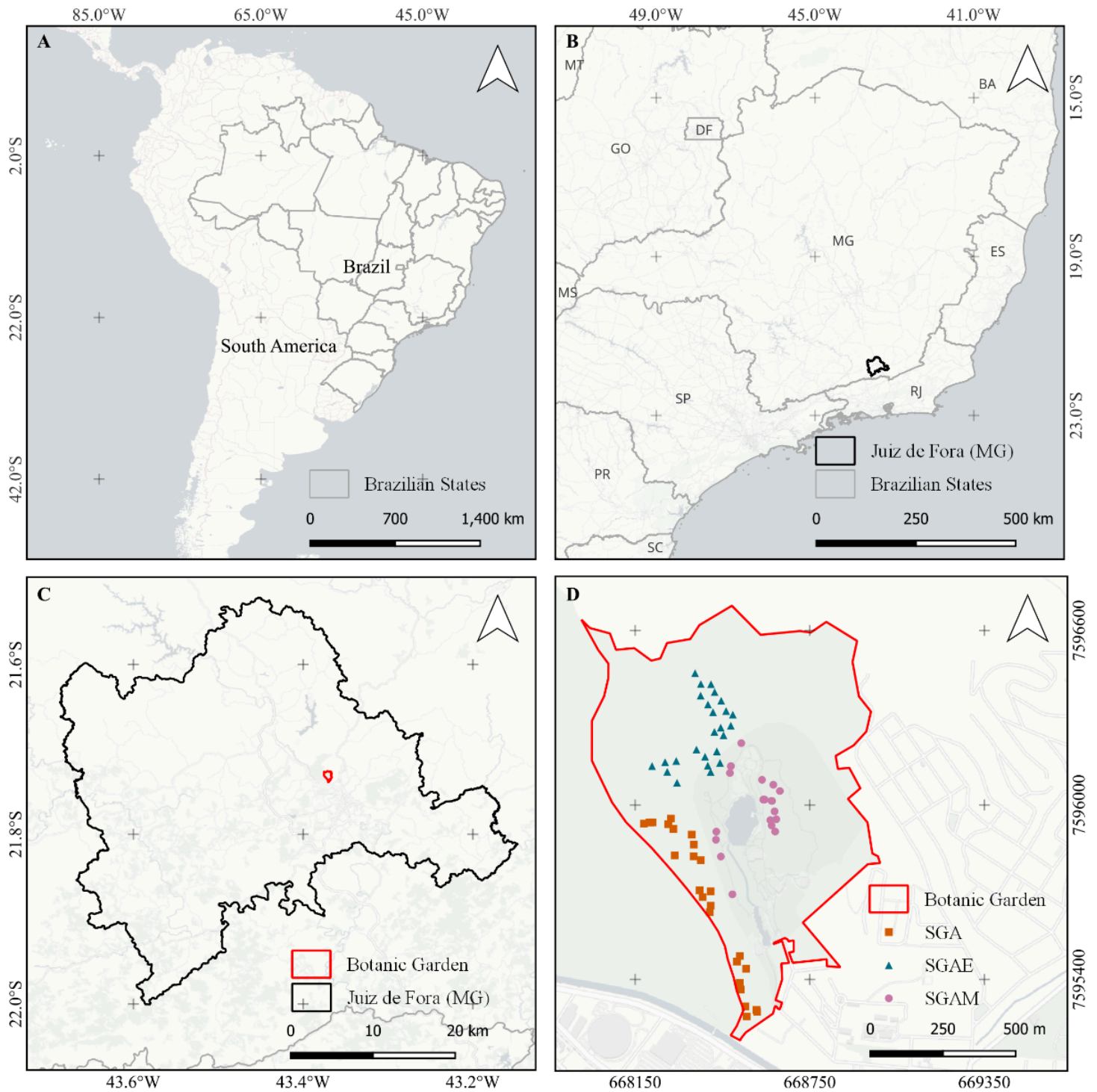


Figure 1

Location of the study area and sampling plots concerning South America (A), Brazil (A), Minas Gerais State (B), Juiz de Fora (B and C), and the Botanic Garden (C and D) showing the distribution of second-growth forest patches sampled (symbols): second growth forest after silvicultural system with management (SGAM), second growth forest after enriched silvicultural system (SGAE) and second growth forest after silvicultural system (SGA).

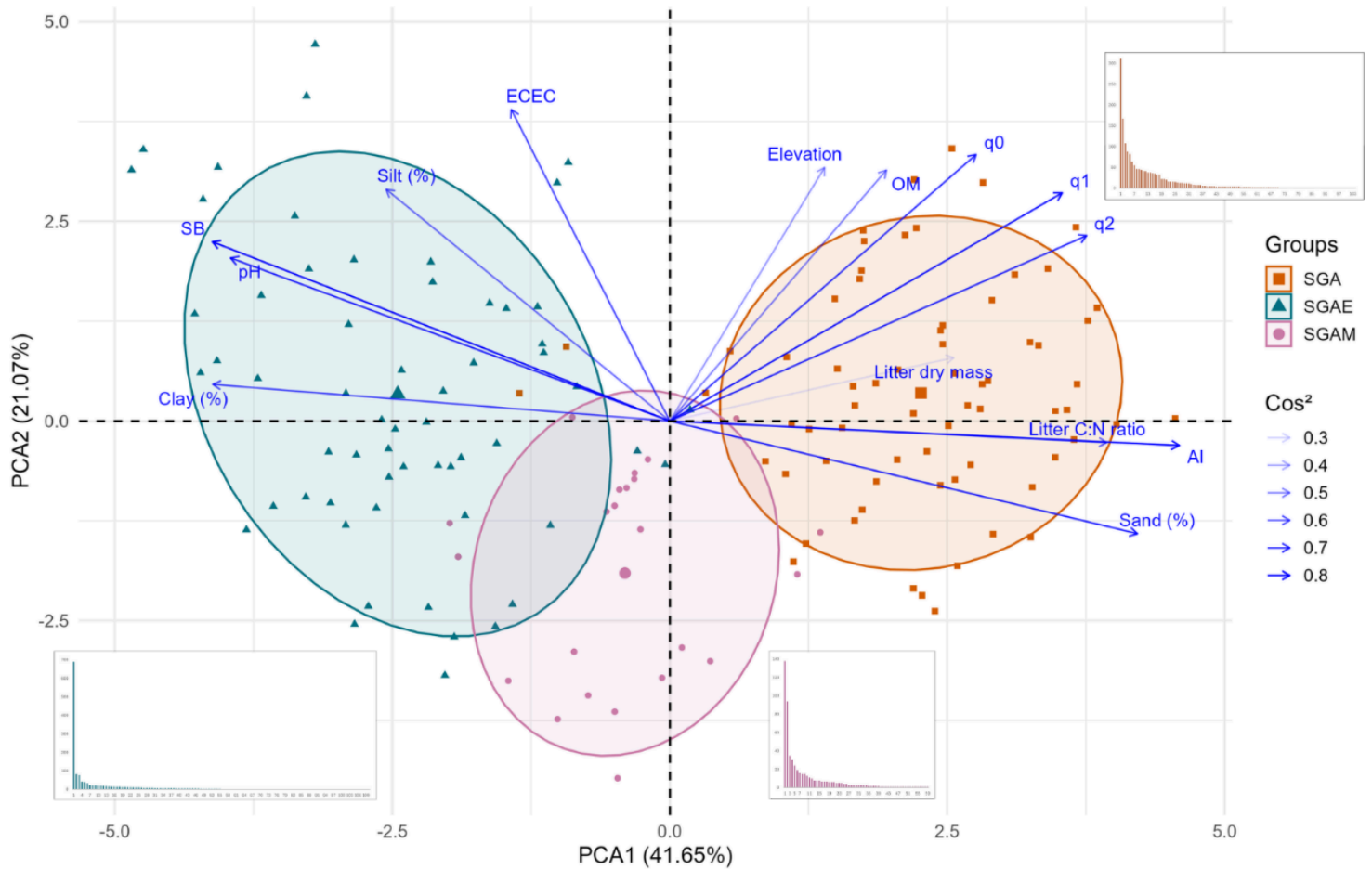


Figure 2

Principal Component Analysis (PCA) with PCA1 on the X-axis and PCA2 on the Y-axis. Soil texture is represented by percentages of sand, silt, and clay. Soil chemical variables include: organic matter (OM), aluminum (Al), pH, sum of bases (SB), and effective cation exchange capacity (ECEC). Litter variables include: litter carbon-to-nitrogen ratio (Litter C:N ratio) and litter dry mass. Diversity variables based on the Hill numbers approach include: species richness (q0), the exponential of Shannon’s diversity index (q1), and the inverse of Simpson’s concentration index (q2). Bar charts represent the distribution of richness across each community, with species on the X-axis and the number of individuals on the Y-axis (Supplementary material, Figures S3, S4, S5). The secondary growth forest types are indicated as follows: second-growth forest after silvicultural system with management (SGAM), second-growth forest after enriched silvicultural system (SGAE), and second-growth forest after silvicultural system (SGA).

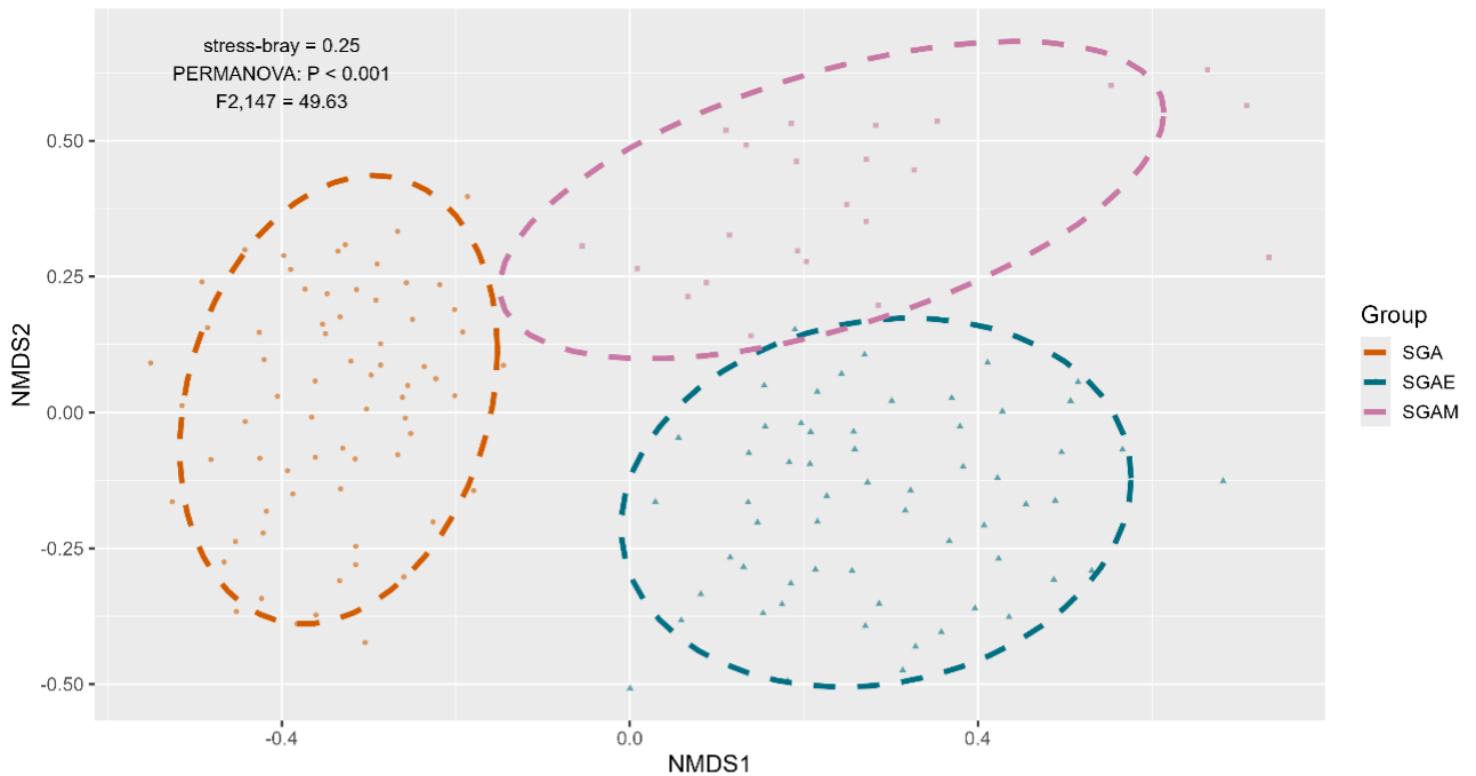


Figure 3

Non-metric multidimensional scaling (NMDS) based on the species composition of the sampled forest plots. The ordination illustrates the relationships in tree species composition among forest communities with distinct management histories. The following forest types are indicated: second-growth forest after silvicultural system with management (SGAM), second-growth forest after enriched silvicultural system (SGAE), and second-growth forest after silvicultural system (SGA).

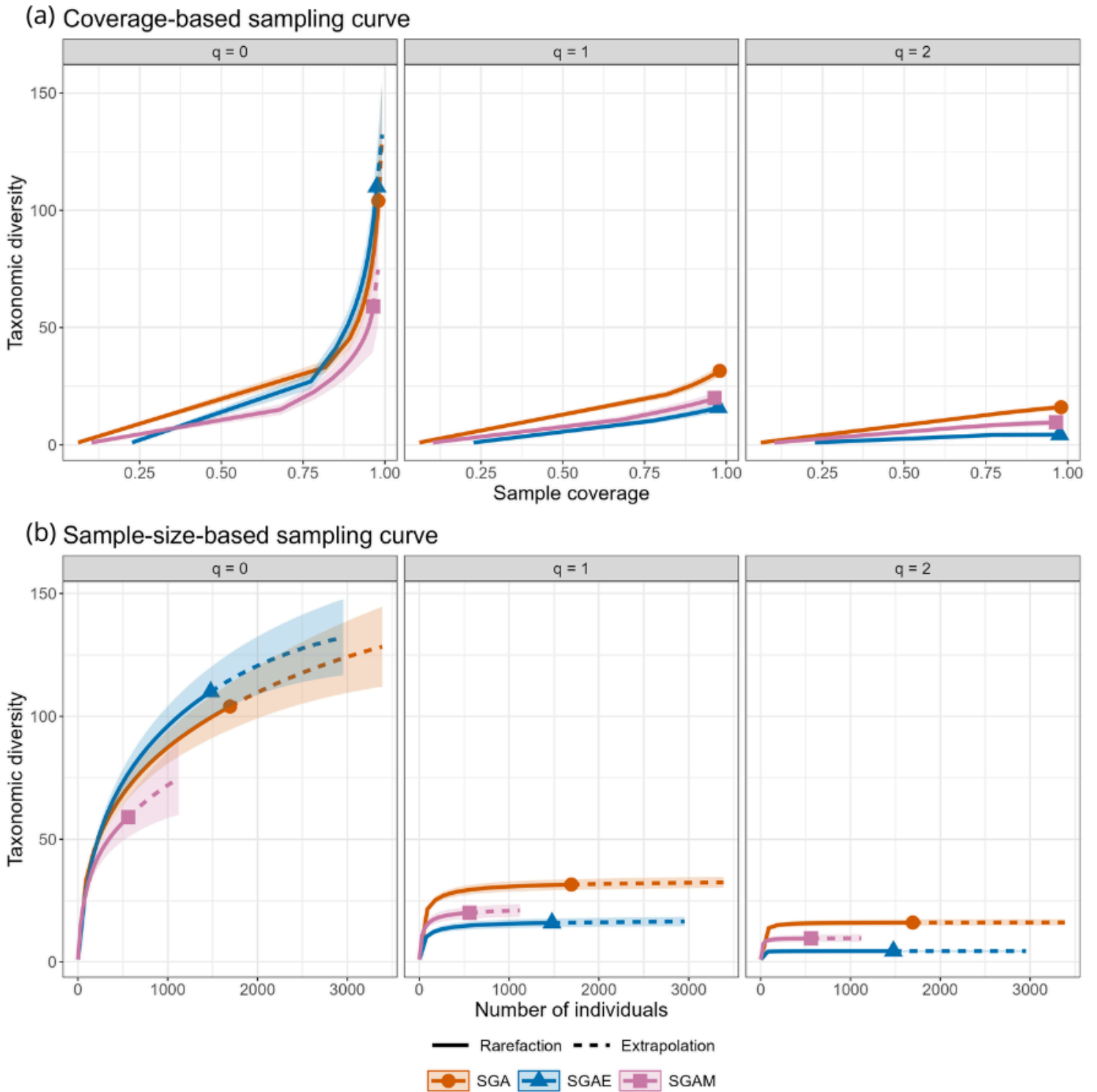


Figure 4

Rarefaction and extrapolation curves for taxonomic diversity (Hill numbers: q_0 , q_1 , and q_2) for second-growth forest after silvicultural system with management (SGAM), second-growth forest after enriched silvicultural system (SGAE), and second-growth forest after silvicultural system (SGA). (a) Coverage-based standardization curves show that SGA exhibits higher effective diversity when compared at equivalent levels of sample completeness. (b) Sample-size-based curves, highlighting differences influenced by the number of individuals. Solid lines represent rarefaction.

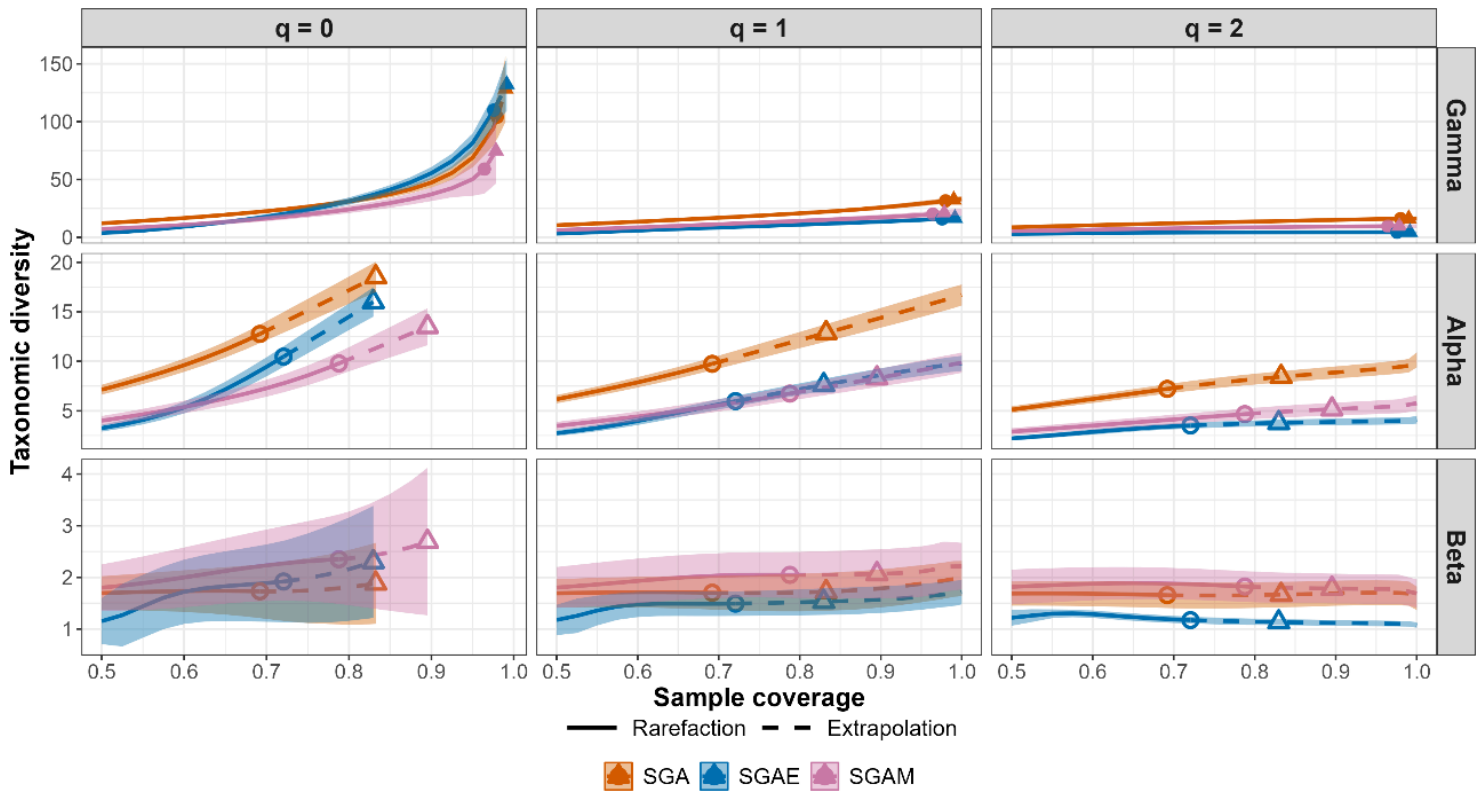


Figure 5

Coverage-based rarefaction and extrapolation curves for taxonomic diversity (Hill numbers: $q = 0, 1, \text{ and } 2$) across the three evaluated communities (second-growth forest after silvicultural system with management (SGAM), second-growth forest after enriched silvicultural system (SGAE), and second-growth forest after silvicultural system (SGA)), showing the gamma, alpha, and beta diversity components. Solid lines represent rarefaction, dashed lines represent extrapolation, and shaded areas indicate 95% confidence intervals.

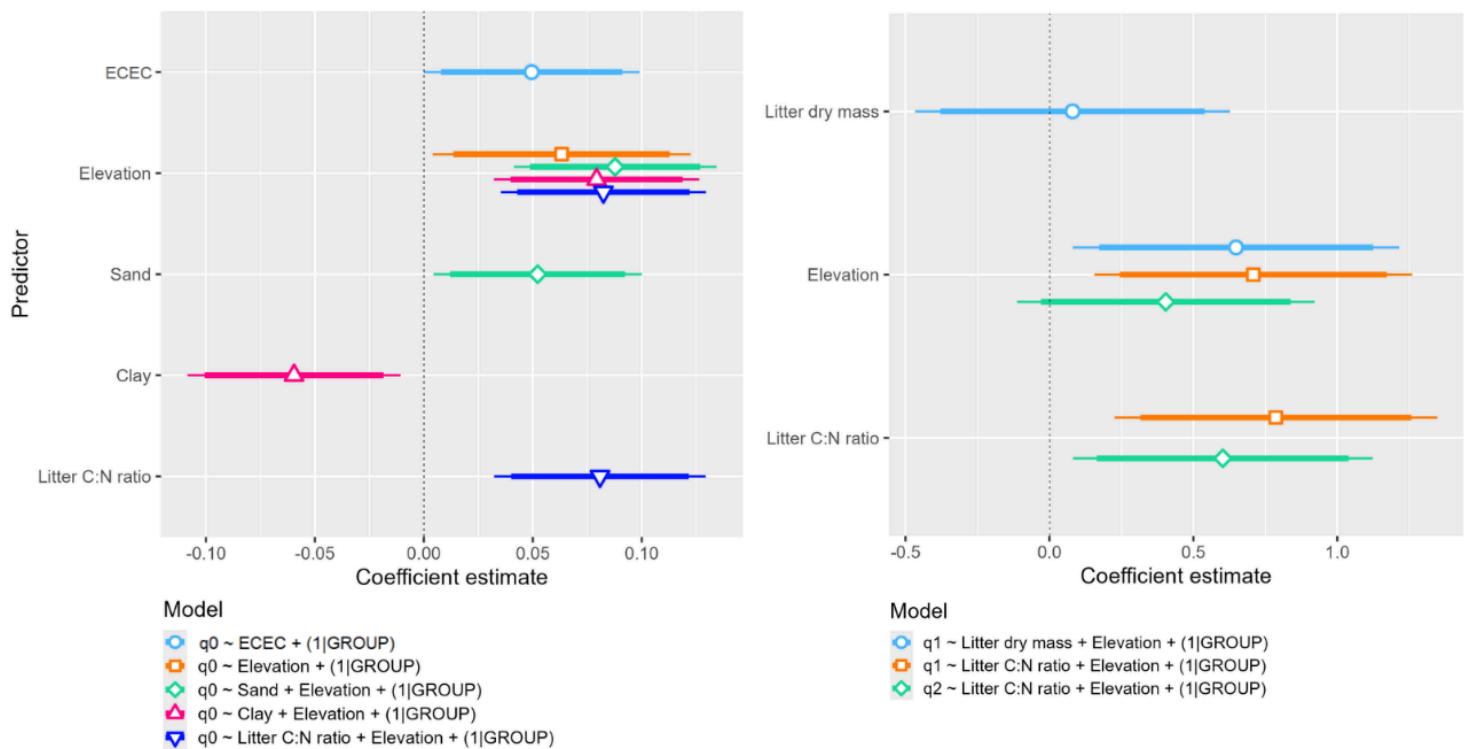


Figure 6

Estimated coefficients from the generalized linear mixed-effects models (GLMMs) fitted to explain taxonomic diversity (Hill numbers: q0, q1, and q2) as a function of selected environmental variables. The left panel presents the models for q0, including the effects of effective cation exchange capacity (ECEC), elevation, sand and clay content, and the litter C:N ratio. The right panel presents the models for q1 and q2, highlighting the effects of litter dry mass, elevation, and the litter C:N ratio. Symbols represent the estimated coefficients, and horizontal bars indicate 95% confidence intervals. Positive values indicate an increase in diversity with the increase of the predictor variable, while negative values indicate inverse effects. All models include a random effect for group (1|GROUP).

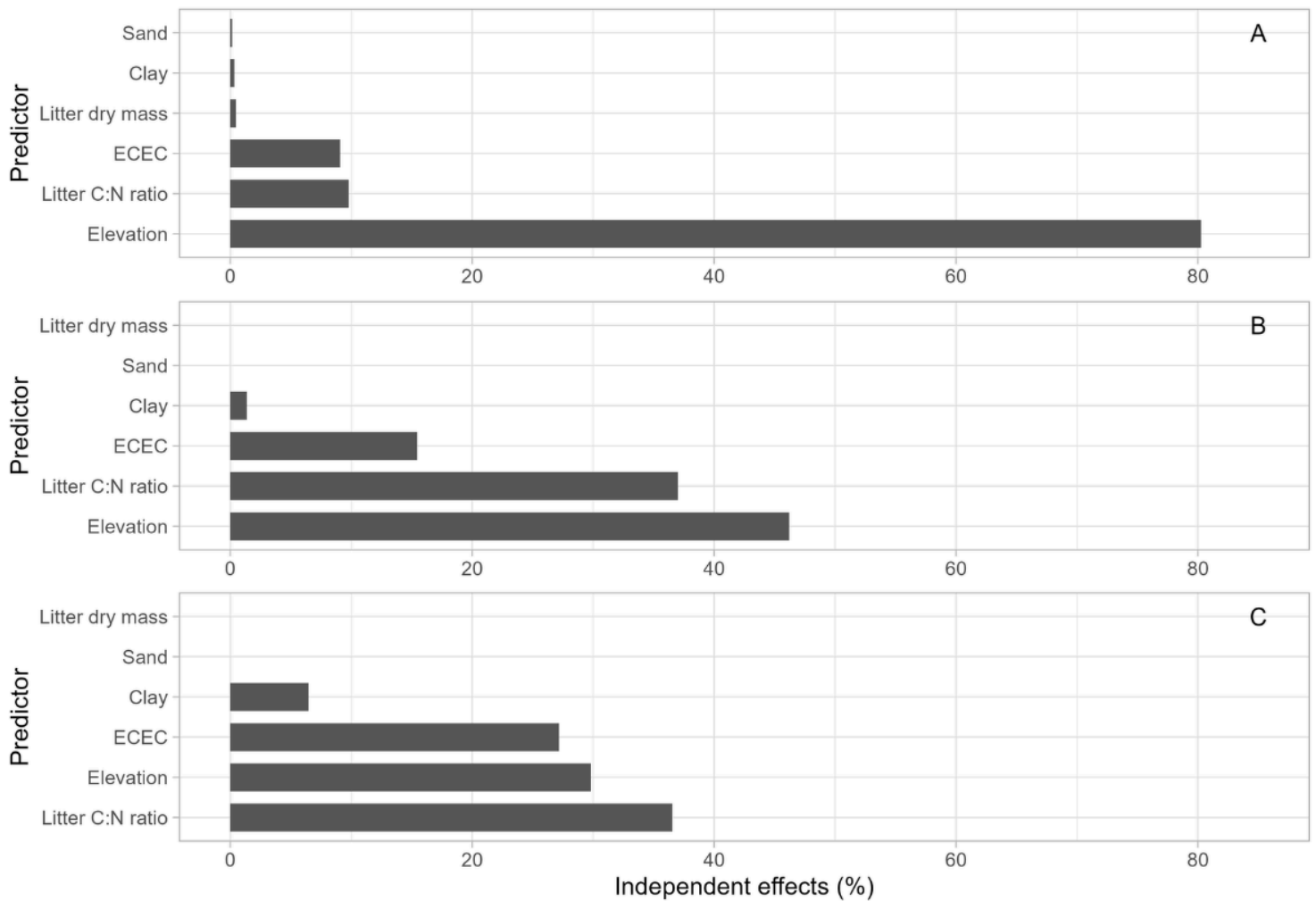


Figure 7

Independent effects of the predictors used to explain taxonomic diversity (Hill numbers: q0, q1, and q2) based on selected environmental variables, with management type included as a random effect in the global model. The panels present the results for species richness (Hill number q0; panel A), Shannon diversity (Hill number q1; panel B), and Simpson diversity (Hill number q2; panel C), including the effects of sand and clay content, effective cation exchange capacity (ECEC), elevation, and the litter C:N ratio, ordered from the predictor with the lowest to the highest effect. The effect values for each predictor are presented as percentages, with the sum totaling 100% for each response variable.

Supplementary Files

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- [SupplementaryMaterial.docx](#)