

Vertical stratification reveals early community reorganization in regenerating Atlantic Forest vegetation

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Research Article

Keywords: enrichment planting, recruitment dynamics, floristic turnover, understory filtering, species dominance, vertical stratification

Posted Date: July 1st, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9999196/v1>

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Additional Declarations: No competing interests reported.

Abstract

Understanding how regenerating plant communities are structurally organized is a central challenge in tropical forest ecology. Vertical differentiation and recruitment dynamics can provide early signs of community formation before detectable floristic change occurs. We evaluated whether natural regeneration developing under an established stand of *Mimosa scabrella*, enriched by 10 native species, shows signs of community reorganization in a degraded area of the Atlantic Forest in southern Brazil. Establishment of the facilitator species began in 2012, followed by planting of native tree species in 2017. Naturally recruited individuals were sampled in 2023 and 2024 in three vertical compartments representing the lower, intermediate, and upper vegetation strata. Species richness, diversity, evenness, abundance, and Importance Value Index were calculated, and floristic composition was assessed using Bray-Curtis dissimilarity, Principal Coordinate Analysis, and PERMANOVA. The regenerating community showed clear vertical differentiation in both years. The lower compartment showed the strongest short-term response, with significant increases in richness, diversity, and abundance between 2023 and 2024, while the intermediate and upper compartments remained comparatively stable. Floristic composition differed significantly between compartments but did not show temporal changes over the one-year interval. Dominance patterns revealed structural continuity of woody taxa in the intermediate and upper compartments, while the lower compartment exhibited greater turnover and a higher representation of opportunistic species. These results indicate that structural and demographic changes preceded detectable floristic replacement, suggesting that the initial community reorganization was driven primarily by recruitment dynamics and vertical differentiation, rather than compositional turnover. Our findings corroborate the view that structural organization emerges before broader compositional changes during ecological succession and demonstrate that vertical stratification can serve as a sensitive indicator of initial community formation in regenerating tropical forests.

1. Introduction

Community assembly in tropical forests is driven by the interaction between recruitment processes, environmental filtering, species-specific responses to local conditions, and stochastic events, producing temporal changes in vegetation structure, species dominance, and floristic composition (Chazdon 2008; Lebrija-Trejos et al. 2010; Weiher et al. 2011; Fukami 2015). During succession, plant communities become progressively organized through the establishment, persistence, and replacement of species, generating increasing structural complexity and ecological differentiation among vegetation compartments (Connell and Slatyer 1977; Walker et al. 2010; Fukami 2015). Understanding how these organizational patterns emerge remains a central challenge in tropical forest ecology because structural and compositional responses often occur at different temporal scales.

In degraded tropical landscapes, community assembly is frequently constrained by strong abiotic and biotic filters that limit recruitment and delay vegetation development. Soil compaction, invasive grasses, reduced propagule availability, and harsh microclimatic conditions can restrict species establishment and persistence, thereby slowing successional dynamics and reducing opportunities for natural

regeneration (Shoo and Catterall 2013; Elgar et al. 2014; Buisson et al. 2018). These constraints are particularly severe in the Atlantic Forest, where long-term fragmentation and land-use change have altered vegetation dynamics and reduced the resilience of regenerating plant communities (Ferreira et al. 2019; Roder et al. 2022; Broggio et al. 2024).

As succession progresses and environmental constraints become less restrictive, recruitment dynamics and species establishment contribute to the gradual reorganization of vegetation structure. Structural differentiation may emerge before substantial changes in floristic composition become detectable, particularly in regenerating forests where community development is still in its early stages (Chazdon et al. 2007; Van Breugel et al. 2007; Lebrija-Trejos et al. 2010; Wills et al. 2020). Accordingly, short-term variation in richness, diversity, abundance, and species dominance may provide evidence of ongoing community assembly processes even when floristic turnover remains limited (Sun et al. 2017; Chazdon et al. 2022; Li et al. 2022).

Within this framework, vertical vegetation strata can be interpreted as functional compartments of community organization. Forest vertical structure reflects the outcome of recruitment, competition, growth, and mortality processes operating through time and constitutes a fundamental dimension of plant community organization (Richards 1996; Whitmore 1998). Beyond representing the structural consequences of succession, vertical stratification is also associated with gradients of light availability, microclimatic conditions, and competitive interactions that influence species establishment, persistence, and performance within regenerating forests (Xing et al. 2023; Laurans et al. 2014). As a result, different vegetation layers may function as ecological filters that influence species distribution and contribute to ecological differentiation during community assembly (Elkins and Spiegelman 2021; Cornwell and Ackerly 2009). Different strata often represent distinct stages of plant establishment and development, reflecting variation in recruitment, growth, competition, and persistence throughout succession (Chang and Turner 2019; Li et al. 2022). The lower compartment is typically associated with the arrival and establishment of new individuals, the intermediate compartment with the consolidation of woody vegetation, and the upper compartment with the development of a more persistent structural framework. Examining how ecological attributes are distributed across these compartments may therefore provide a mechanistic understanding of how community assembly unfolds during forest regeneration and how structural organization emerges as plant communities become progressively differentiated through time.

Although restoration studies frequently emphasize vegetation cover, planted-tree performance, or total species richness, such metrics may not fully capture the processes underlying community organization (Crouzeilles et al. 2017; Holl et al. 2017; Martins et al. 2020). Analyses based on vertical stratification offer an alternative perspective because they allow evaluation of how recruitment, dominance, and vegetation structure are distributed within regenerating communities. Structural differentiation among strata may thus represent an early signal of community reorganization before broader compositional changes become evident.

We investigated whether naturally regenerating vegetation developing beneath an established restoration stand exhibits measurable signs of early community reorganization. Specifically, we evaluated how species richness, diversity, abundance, floristic composition, and species dominance were distributed across lower, intermediate, and upper vegetation compartments, and whether these patterns changed between October 2023 and October 2024. By examining vertical stratification as a component of vegetation organization, we aimed to determine whether structural differentiation could reveal early stages of community assembly before detectable floristic turnover occurs.

We hypothesized that the regenerating community would exhibit increasing structural differentiation among vertical compartments, reflecting ongoing community assembly. We expected the lower compartment to show the strongest short-term responses in richness, diversity, and abundance because it represents the principal zone of recruitment, whereas the intermediate and upper compartments would display greater structural stability. We further expected floristic composition to remain comparatively stable over the monitoring interval, reflecting the commonly observed pattern that demographic and structural changes precede broader compositional turnover during succession and community assembly (Van Breugel et al. 2007; Chazdon et al. 2007; Rozendaal et al. 2019; Li et al. 2022).

2. Material and methods

2.1 Study area

The study was conducted at the Canguiri Experimental Farm of the Federal University of Paraná (UFPR), in Pinhais, Paraná, southern Brazil (25°23'38.31"S, 49°07'37.56"W; 900 m a.s.l.) (Fig. 1). The site lies within the Atlantic Forest biome. According to the Köppen classification, the regional climate is humid subtropical (Cfb), with mean annual temperatures ranging from 15 to 17°C and annual precipitation between 1,100 and 1,920 mm, distributed throughout the year (Alvares et al., 2013; Aparecido et al., 2016). These environmental conditions provide the regional context within which the site's edaphic characteristics and degradation history influenced forest recovery.

The soil is classified as a typical dystrophic Haplic Cambisol according to the Brazilian Soil Classification System (Santos et al., 2018). Before restoration, the area had been subjected to intensive agricultural use and repeated heavy-machinery traffic, which resulted in severe soil compaction and the complete removal of the original forest structure. These disturbances created a highly degraded site with strong physical barriers to spontaneous forest recovery, requiring active restoration interventions

2.2 Implementation of the experiment

The ecological restoration actions are part of the Arboretum Project, an initiative established to meet the demand of local producers for technical guidance on the forestry component of their properties. Prior to the implementation of the experiment, the area presented a critical diagnosis: a high degree of soil compaction and degradation of the surface layers. This degradation scenario resulted from the history of agricultural activities and, above all, the intense traffic of heavy machinery used in driver training.

These conditions required a series of interventions to restore the physical suitability of the site for forest establishment.

The soil preparation protocol began with the strategic sowing of *Raphanus sativus* L. (forage turnip), aiming at the biological decompaction of the area. Following this, mechanized mowing and harrowing were carried out across the entire area to incorporate plant residues into the soil. The subsequent step consisted of subsoiling to a depth of 40 cm, performed concurrently with the opening of the planting rows, followed by the application of dolomitic limestone and phosphate. Finally, the digging of the planting holes was completed using a semi-mechanized method, reaching a depth of 30 cm (Souza, 2015). Once site preparation was completed, restoration planting was initiated.

Restoration began in 2012 with the establishment of a facilitator planting of *M. scabrella*. A total of 72 seedlings were planted in six rows (12 individuals per row), with 4 m spacing between plants within the rows and 3 m between rows, covering an area of 1,080 m² (48 × 18 m).

In September 2017, an enrichment planting was carried out with 10 native tree species between the already established rows of *M. scabrella*. One hundred individuals were introduced, distributed in five rows (20 individuals per row), with 2 m spacing between plants within the row and positioned 1.5 m from the adjacent rows of *M. scabrella*. Each species was represented by two individuals in each enrichment row.

The enriched planting included the following tree species from the Atlantic Forest: *Inga* sp., *Ocotea puberula* (Rich.) Nees, *Luehea divaricata* Mart. & Zucc., *Cabralea canjerana* (Vell.) Mart., *Campomanesia guaviroba* (DC.) Kiaersk., *Eugenia uniflora* L., *Myrcia multiflora* (Lam.) DC., *Podocarpus lambertii* Klotzsch ex Endl., *Allophylus edulis* (A.St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl., and *Matayba elaeagnoides* Radlk.

The experiment was delimited by *Pinus* plantations in the northern, southern, and western portions, while the eastern portion was bordered by a road. Figure 2 presents a schematic representation of the spatial arrangement of the facilitating plants and environmental enrichment.

Post-planting management included mechanical mowing between rows, manual vegetation control around seedlings, and mulching with *Pinus* sp. needles to retain moisture and reduce weed cover. No soil amendment, liming, fertilization, or mechanical decompaction was applied. Management was therefore restricted to seedling establishment and vegetation control.

2.3 Experiment data collection

Field surveys were conducted in October 2023 and October 2024 to quantify stratified natural regeneration within the restored site. Sampling followed a concentric nested-plot design (Mueller-Dombois and Ellenberg, 1974) combined with stratified natural regeneration criteria (Finol, 1971). A total of 30 sampling units were systematically distributed across the study area (Fig. 3). The structure of each sampling unit was designed to represent different vertical components of the regenerating vegetation.

Each sampling unit comprised three nested plots corresponding to vertical strata, with DBH thresholds selected to represent distinct ecological life stages within the regenerating community: the lower stratum (1 × 1 m, DBH < 1 cm) captures recent recruitment and seedling establishment; the intermediate stratum (4 × 4 m, 1 cm ≤ DBH ≤ 4 cm) represents established saplings transitioning to the sub-canopy and consolidating woody structure; and the upper stratum (6 × 4 m, DBH > 4 cm) identifies dominant individuals forming the vertical forest architecture.

For individuals taller than 1.30 m, diameter was measured at breast height (1.30 m). For individuals shorter than 1.30 m, stem diameter was measured at ground level. To focus on natural regeneration under the facilitator-based restoration system, only naturally recruited individuals were included in the survey. All seedlings introduced during the 2017 enrichment planting, as well as the trees of the *M. scabrella* facilitator stand, were excluded from the analysis. Plant identification followed APG IV (Angiosperm Phylogeny Group, 2016).

2.4. Data analysis

Community diversity was described using species richness, Shannon's diversity index (H'), and Pielou's evenness index (J') (Magurran, 2013). Structural importance was assessed using the Importance Value Index (IVI), calculated based on standard phytosociological parameters (Moro and Martins, 2011). These metrics provided the basis for subsequent statistical comparisons between years and vegetation strata.

Data normality was evaluated using the Shapiro–Wilk test. Because the assumptions of normality were not met, differences in richness, diversity, evenness, and abundance among years (2023 and 2024) and among strata were tested using the Kruskal–Wallis test ($p < 0.05$). When significant differences among strata were detected, pairwise comparisons were performed using Dunn's post hoc test.

Floristic composition was analyzed using Principal Coordinates Analysis (PCoA) based on Bray–Curtis dissimilarity. The effects of stratum, year, and their interaction on community composition were tested using Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations, implemented with the `adonis2` function. Multivariate analyses were used to evaluate patterns of floristic differentiation within the regenerating community. All analyses were conducted in R version 4.3.2 (R Core Team, 2023) using the packages `vegan` (Oksanen et al., 2022) and `dunn.test` (Dinno, 2024). Because the study did not include an unenriched control stand, inference is restricted to patterns of internal organization and short-term change within the monitored restoration stand.

3. Results

To assess whether natural regeneration under the *M. scabrella* facilitator stand shows signs of initial community reorganization, we analyzed variation in species richness, diversity, abundance, floristic composition, and species dominance across vertical strata between 2023 and 2024.

3.1 Community Structure and Diversity Patterns

Species richness, Shannon diversity, Pielou's evenness, and individual abundance differed significantly among vertical strata in both monitoring years, indicating clear structural differentiation within the regenerating stand (Table 1; Table S3).

In 2023, significant differences among strata were detected for species richness ($H = 19.88$, $p < 0.001$), Shannon diversity ($H = 18.03$, $p < 0.001$), Pielou's evenness ($H = 18.89$, $p < 0.001$), and abundance ($H = 23.68$, $p < 0.001$) (Table S3). This vertical pattern was maintained in 2024, with significant differences in richness ($H = 19.07$, $p < 0.001$), Shannon diversity ($H = 18.57$, $p < 0.001$), evenness ($H = 9.76$, $p = 0.008$), and abundance ($H = 23.25$, $p < 0.001$) (Table S3).

The significant differences among strata were accompanied by consistent differences in the distribution of diversity and abundance across the vertical profile. Across both years, the upper stratum consistently showed the lowest richness, abundance, and diversity. In contrast, the intermediate stratum concentrated the highest richness and abundance, whereas the lower stratum showed intermediate values and greater short-term variation than the other layers (Table 1).

3.2. Temporal Dynamics and Recruitment

The lower stratum showed the strongest temporal response between 2023 and 2024 (Table 1; Table S2). In this layer, mean species richness increased from 5.00 ± 1.33 to 7.50 ± 1.78 , Shannon diversity increased from 1.55 ± 0.25 to 1.96 ± 0.23 , and abundance increased from 5.60 ± 1.43 to 8.80 ± 2.66 .

These increases were supported by significant temporal differences in the lower stratum for species richness ($H = 8.73$, $p = 0.003$), Shannon diversity ($H = 8.32$, $p = 0.004$), and abundance ($H = 8.46$, $p = 0.004$) (Table S2). No significant temporal differences were detected in the intermediate or upper strata ($p > 0.05$), indicating that short-term change was concentrated in the lowest vegetation layer.

3.3 Floristic Composition and Multivariate Ordination

Principal Coordinates Analysis (PCoA) revealed clear floristic differentiation among strata (Fig. 4). The first two axes explained 15.53% and 8.71% of the total variation, respectively. PERMANOVA confirmed significant compositional differences among strata ($F = 7.90$, $p < 0.001$, $R^2 = 23.18\%$).

However, no significant differences were detected between years ($F = 0.44$, $p = 0.968$, $R^2 = 0.65\%$) or for the year $\times$ stratum interaction ($F = 0.45$, $p = 0.990$, $R^2 = 1.34\%$). Collectively, the multivariate analyses showed that community organization was more strongly associated with vertical stratification than with short-term temporal variation.

3.4 Phytosociological Structure and Species Dominance

The Importance Value Index (IVI) revealed distinct dominance patterns across the vertical profile (Tables 2 and 3; Table S1). In the upper stratum, the community was dominated by established woody taxa, especially *Myrsine coriacea*, *Schinus terebinthifolia*, *Jacaranda puberula*, *Solanum diploconos*, and *Morus nigra*. This pattern remained relatively stable between years.

The intermediate stratum also showed strong compositional continuity. In 2023, *M. coriacea*, *J. puberula*, and *C. decandra* had the highest IVI values. In 2024, *M. coriacea* remained dominant, followed by *C. decandra*, *Allophylus edulis*, and *J. puberula*.

In contrast, the lower stratum showed greater turnover and stronger representation of opportunistic taxa. In 2023, the most important species were *A. edulis* and *Synedrella nodiflora*, whereas in 2024 the lower layer was dominated by *Pseudechinolaena polystachya*, *S. nodiflora*, *Christella dentata*, and *Mikania micrantha*. Together, these patterns reveal increasing dominance continuity in the intermediate and upper strata, whereas species turnover remained concentrated in the lower compartment of the regenerating community.

4. Discussion

The regenerating plant community exhibited clear vertical stratification and evidence of early community reorganization. As expected, vegetation organization was more strongly associated with vertical differentiation than with short-term temporal variation, with the intermediate compartment representing the principal zone of woody structural consolidation and the lower compartment concentrating the strongest recruitment responses. The observed patterns demonstrate that vegetation was not randomly distributed along the vertical profile and are consistent with a process of community assembly characterized by increasing structural differentiation within the developing community.

The observed vertical differentiation and concentration of recruitment in the lower compartment provide further evidence that community reorganization was occurring through distinct structural pathways within the regenerating vegetation. Such patterns align with theoretical expectations of community assembly in regenerating forests, where recruitment, establishment, and demographic processes contribute to increasing structural organization as succession progresses (Connell and Slatyer 1977; Lebrija-Trejos et al. 2010; Fukami 2015). As environmental constraints become progressively relaxed, regenerating communities tend to develop increasing internal differentiation, reflecting the combined effects of species establishment, growth, competition, and persistence. Because this study focused on patterns of vegetation organization within a single regenerating stand, the results should be interpreted as evidence of internal community dynamics rather than as a comparative assessment of restoration strategies.

The absence of significant temporal changes in floristic composition over the one-year interval indicates that the monitoring period was likely insufficient to detect broader species replacement. However, this result does not imply ecological stagnation. Rather, the observed stability supports the interpretation that structural and demographic responses may become detectable before major compositional turnover occurs, a pattern frequently observed in regenerating tropical forests where stand architecture develops more rapidly than species replacement (Van Breugel et al. 2007; Lebrija-Trejos et al. 2010; Rozendaal et al. 2019). In the present study, the community appears to be undergoing a phase of structural consolidation in which recruitment and vegetation organization are actively changing while

floristic composition remains comparatively stable. The absence of detectable compositional change over the one-year interval therefore suggests that community reorganization was primarily expressed through demographic and structural processes that typically precede broader floristic turnover during succession.

4.1 Vertical Structure and Community Assembly

The increase in richness, diversity, and abundance observed in the lower compartment between 2023 and 2024 reinforces the ecological importance of this layer as the principal zone of recruitment and short-term renewal within the community. In regenerating communities subjected to strong environmental constraints, such responses may indicate that establishment barriers are being progressively relaxed (Shoo and Catterall 2013; Elgar et al. 2014; Buisson et al. 2018), even when broader compositional changes remain undetectable over short time scales (Crouzeilles et al. 2017; Wills et al. 2020). This pattern agrees with theoretical expectations that early community-level responses should emerge first in the compartment where new individuals enter the system, before being reflected in the overall floristic structure.

The vertical stratification observed here indicates that community organization within the stand was structured rather than random (Chazdon et al. 2007; Walker et al. 2010). Significant differences among strata, together with the concentration of short-term gains in the lower compartment, suggest that regeneration was already organized into distinct structural compartments. Within this organization, the intermediate compartment appears to represent the principal zone of woody structural consolidation, whereas the lower compartment functions as the main zone of ongoing recruitment and turnover. Floristic differentiation among strata further indicates that species were not distributed uniformly throughout the vertical profile, but rather in association with different ecological conditions and establishment opportunities within the developing community (Van Breugel et al. 2007; Fukami 2015).

The observed differentiation indicates that vertical structure contributes to environmental heterogeneity in regenerating forests by promoting variations in light availability, microclimatic conditions, and competitive environments among different vegetation layers (Laurans et al. 2014; Oliveira and Scheffers 2019). Consequently, the different strata can act as ecological filters that shape the chances of recruitment and persistence of species, contributing to ecological differentiation and the gradual organization of plant communities throughout succession (Mason et al. 2013; Lohbeck et al. 2014).

The dominance of woody taxa such as *Myrsine coriacea*, *Jacaranda puberula*, and *Casearia decandra* in the intermediate and upper compartments indicates the development of a persistent woody framework within the community. The dominance of these woody taxa indicates that a relatively stable structural architecture has begun to emerge, providing the basis upon which subsequent successional processes may unfold. At the same time, the strong representation of opportunistic and invasive species in the lower compartment indicates that environmental conditions remain sufficiently permissive to support species associated with disturbance and higher resource availability (Elgar et al. 2014; Prach et al. 2020;

Hobbs and Norton 2004). Thus, although community assembly progressed structurally, the regenerating vegetation still exhibits characteristics typically associated with early successional stages. The persistence of species such as *Eriobotrya japonica* and *Morus nigra* further suggests that competitive exclusion of disturbance-associated taxa has not yet become a dominant process within the understory.

The increased representation of zoochorous species in 2024 is consistent with, although not direct evidence of, a possible contribution of biotic dispersal processes to community development. The greater representation of zoochorous species may reflect increasing use of the regenerating stand by seed-dispersing fauna, potentially facilitating the arrival of additional native species. However, because dispersal processes were not directly measured, this interpretation remains speculative and should be evaluated through future studies incorporating seed rain, seed bank dynamics, or direct observations of animal-mediated dispersal.

4.2 Ecological Implications

From a community ecology perspective, the results suggest that vertical stratification represents a useful dimension for detecting early stages of community assembly. Beyond its role as an indicator of vegetation development, vertical stratification can be interpreted as a fundamental organizational dimension through which ecological processes operate during succession. By establishing and reflecting environmental heterogeneity within regenerating stands, vertical structure influences recruitment dynamics, species persistence, and ecological differentiation among vegetation layers, thereby contributing to the progressive assembly of plant communities. Because structural differentiation may emerge before substantial floristic turnover occurs, analyses based on vegetation compartments can reveal ecological changes that remain undetected when only species composition is considered. This highlights the value of incorporating vertical structure into studies of regenerating forests seeking to understand how plant communities become organized through time.

The differentiation observed among vertical compartments demonstrates that community organization can become increasingly structured even when floristic composition remains relatively stable. Consequently, vertical stratification may provide a sensitive ecological indicator of early community reorganization, particularly during the initial phases of succession when demographic and structural processes dominate vegetation dynamics. Rather than representing merely a descriptive characteristic of vegetation, vertical structure appears to capture important dimensions of how recruitment, dominance, and species persistence contribute to the progressive organization of regenerating plant communities (Hobbs and Norton 2004; Lamb et al. 2005).

5. Conclusion

This study investigated whether vertical stratification could show signs of early community reorganization in a regenerating, degraded Atlantic Forest. The results demonstrated clear differentiation between vegetation compartments, with the intermediate compartment functioning as the main zone of structural consolidation of woody vegetation and the lower compartment concentrating the most

intense short-term recruitment responses. Although the floristic composition remained stable during the monitoring period, community formation actively progressed through increased structural differentiation.

These findings support the view that structural and demographic responses can precede detectable floristic turnover during succession. By demonstrating that vertical stratification captured ecological changes that were not reflected in species composition, the study highlights the value of vegetation structure as an indicator of early community assembly and community reorganization in regenerating tropical forests.

The study was restricted to a single regenerating stand and a one-year monitoring interval, which limits inference regarding long-term floristic dynamics and precludes direct evaluation of the mechanisms underlying the observed patterns. In addition, environmental filtering, dispersal processes, and species interactions were not directly measured.

Future studies should combine longer monitoring periods with direct measurements of biotic and abiotic drivers to determine how recruitment dynamics, structural differentiation, and floristic turnover interact during community assembly. Such approaches will improve our understanding of the mechanisms governing vegetation organization throughout tropical forest succession.

Declarations

Author's contribution

Raimundo Junior: Conceptualization, Data analysis, Methodology, Writing-original draft, Writing-review, editing, and investigation. Alessandro Angelo: Conceptualization, Methodology, Data curation, Supervision; Nelson Luiz: Supervision; Roman Carlos: Supervision; Alexandre Mastella: Methodology; Chaiane Schneider: Methodology; Karen Souza: Methodology; Jaqueline Gomes: Supervision; Elivane Salete Capellesso: Conceptualization, Methodology, Data curation; Emi Silva Oliveira: Supervision; Lorena Bressiani: Methodology; Rodrigo Dall'Agnol: Methodology

Acknowledgments

The authors thank the Federal University of Paraná and the Federal Institute of Education, Science and Technology of Rondônia.

Ethics Statement Data/Material Availability

The datasets generated during this study are available from the corresponding author upon reasonable request and within the framework of cooperation agreements and scientific research projects.

Conflict of interest

The authors declare no conflict of interest.

Financing

The study received no external or internal funding.

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Tables

Tables are available in the Supplementary Files section.

Figures

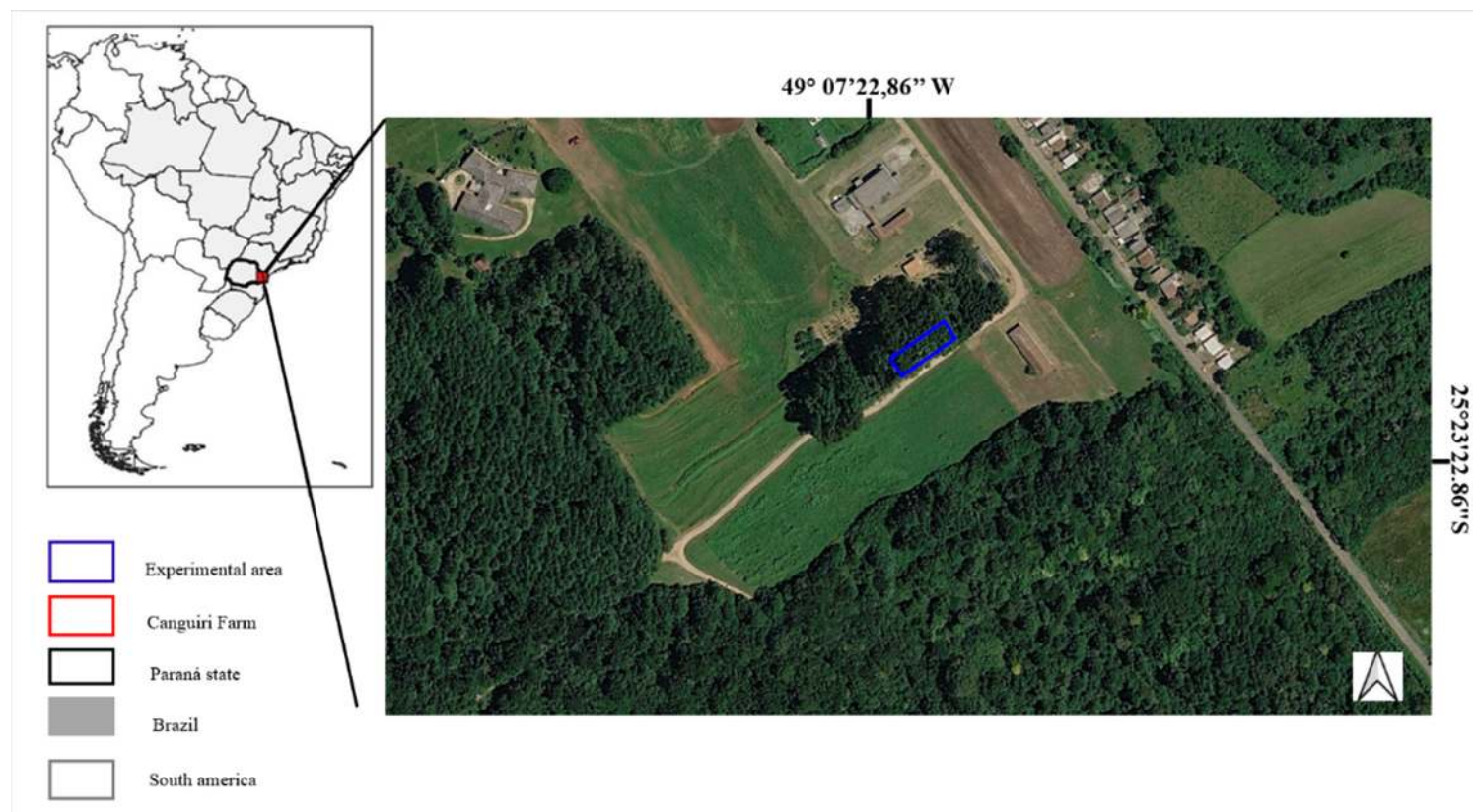


Figure 1

Location of the experimental restoration site at Fazenda Canguiri, Federal University of Paraná (UFPR), Pinhais, Paraná State, southern Brazil. The blue rectangle indicates the experimental area

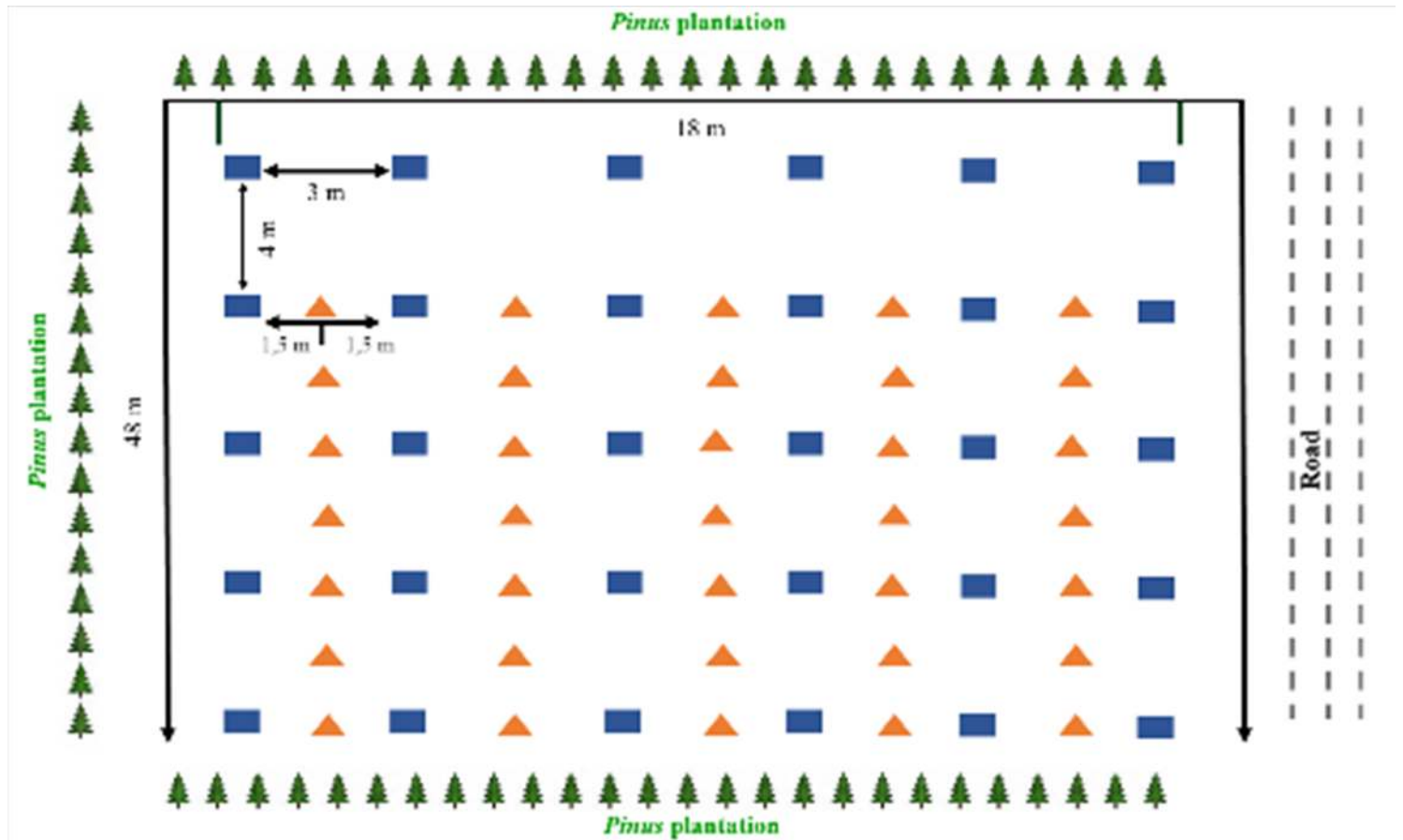


Figure 2

Schematic layout of the restoration experiment (48 × 18 m) at Fazenda Canguiri, Brazil. Squares represent *Mimosa scabrella* individuals and triangles represent enrichment plantings of 10 native tree species. Numbers indicate planting distances (m). The experimental area was bordered by *Pinus* plantations on the northern, southern, and western sides and by a road on the eastern side

Pinus plantation

48 m

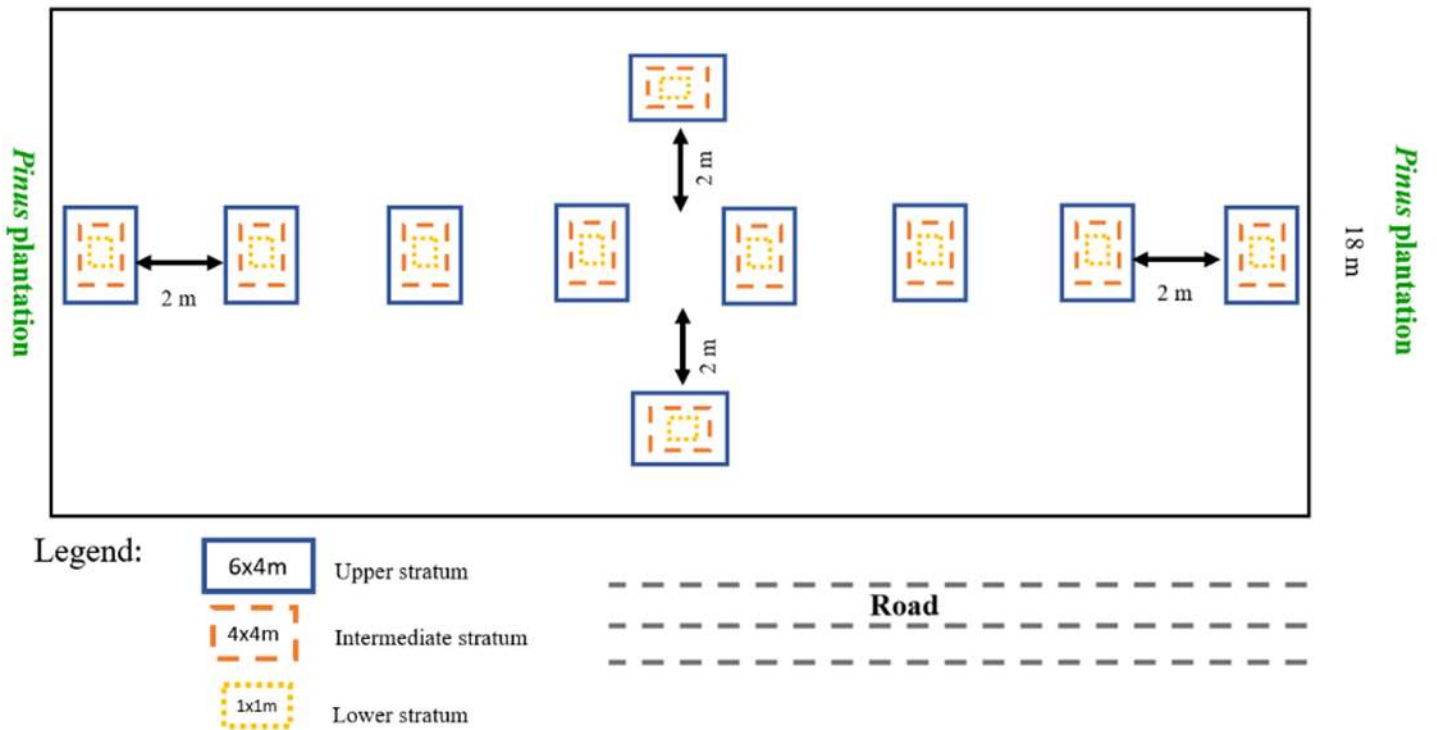


Figure 3

Systematic arrangement of nested sampling plots used to assess vertical stratification of natural regeneration. The upper stratum was sampled in 6 × 4 m plots, the intermediate stratum in 4 × 4 m plots, and the lower stratum in 1 × 1 m subplots nested within the larger sampling units

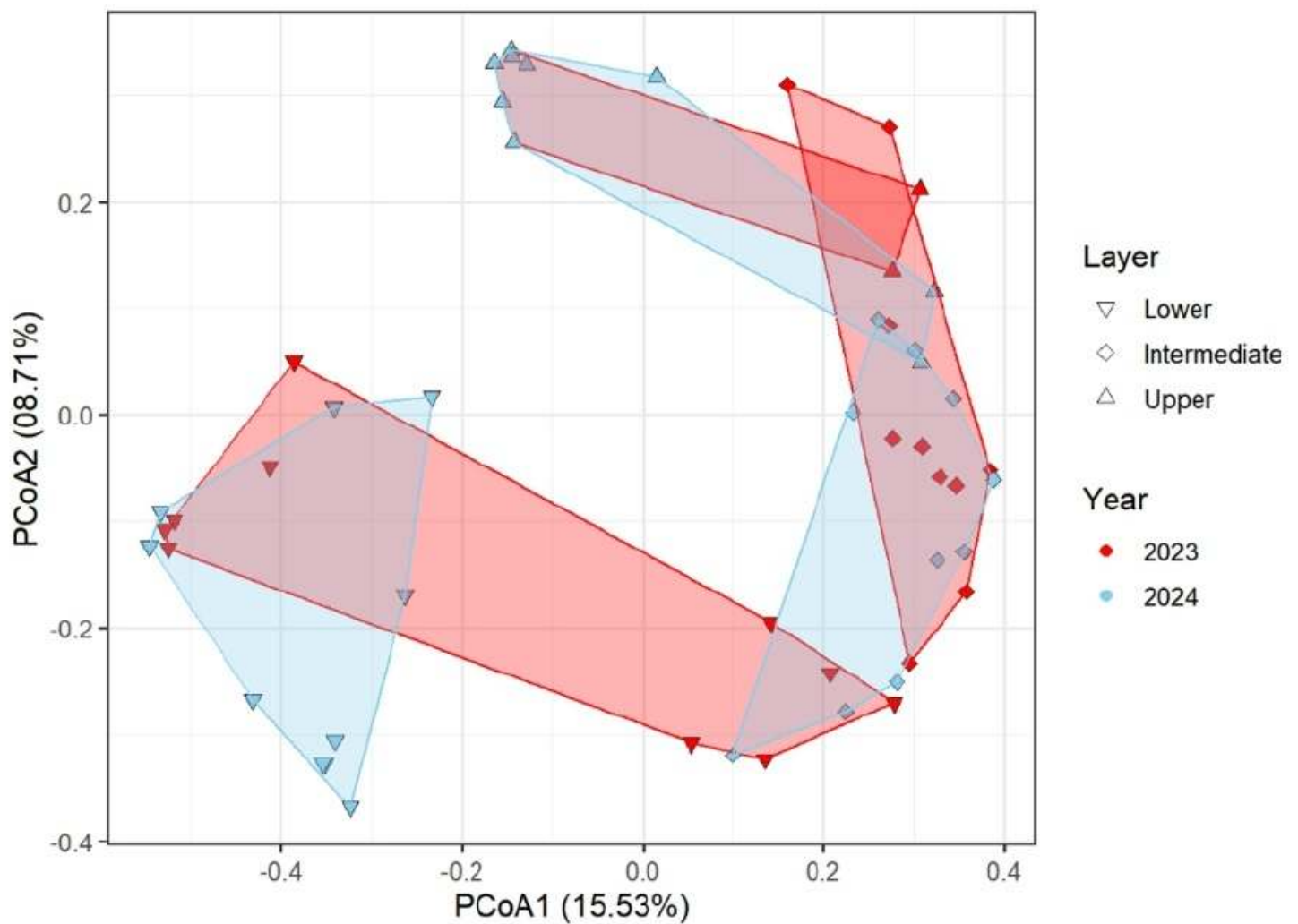


Figure 4

Principal Coordinates Analysis (PCoA) showing variation in species abundance patterns and regeneration structure between 2023 (red) and 2024 (blue) across the lower, intermediate, and upper strata. Symbols represent sampling units and polygons represent the multivariate dispersion of samples within each year

Supplementary Files

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