Original Articles

Comparison between Anderson nuclei and mixed planting: how spacing influences growth performance and functional groups of native species in the restoration of Araucaria forests in southern Brazil

Raimundo Gomes da Silva Junior [a]*, Alessandro Camargo Ângelo [b], Nelson Luiz Cosmo [b], Roman Carlos Rios [b], Alexandre Dal Forno Mastella [c], Chaiane Rodrigues Schneider [d], Karen Koch Fernandes de Souza [e], Ingo Isernhagen [f], Elivane Salete Capellesso [b], Emi Silva Oliveira [g]

[a] Federal University of Paraná, Department of Forest Sciences, Curitiba, Brazil.
[b] Department of Forest Sciences at the Federal University of Paraná, Curitiba, Brazil.
[c] Water and Land Institute, IAT, Paraná, Brazil.
[d] State University of Pará, Uepa, Campus VIII Maraba, Pará, Brazil.
[e] Newton Freire Maia State Center for Professional Education, Paraná, Brazil.
[f] Embrapa Forests, Colombo, Paraná, Brazil.
[g] Federal Institute of Education, Science and Technology of Rondônia, School of Forestry Engineering, Ji-Paraná, Rondônia, Brazil.

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Corresponding author: raimundo.junior@ifro.edu.br

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Abstract

Active restoration strategies are crucial for accelerating forest recovery in highly degraded landscapes within the Araucaria Forest. This study evaluated the effects of two different spatial arrangements: Anderson nuclei and mixed planting on the dendrometric performance of three representative native species (*Mimosa scabrella*, *Araucaria angustifolia*, and *Solanum diploconos*). Data were collected 45 and 57 months after planting and analyzed using multivariate tests (MANOVA) and univariate comparisons. The results showed significant effects of treatments, species, and their interactions on height, diameter at ground level, and canopy projection. *Mimosa scabrella*, a fast-growing pioneer species, maintained structural dominance across all treatments and years. *Araucaria angustifolia*, a mid- to late-succession species, showed modest growth in 2023 but responded significantly in 2024, particularly in the Anderson nuclei. *Solanum diploconos* showed consistently lower values, but with gradual increases, compatible with its shade-tolerant understory niche. Comparisons between the arrangements indicated that the Anderson cores promoted more pronounced facilitation effects, favoring the growth performance of mid- and late-successional species and accelerating canopy closure. At the same time, mixed planting resulted in more homogeneous but less expressive growth patterns. The Anderson's core technique is an ecologically sound alternative to mixed plantings, as it combines the rapid growth of pioneer species with the creation of a facilitative environment, accelerating the succession process and helping achieve restoration objectives more efficiently.

Keywords: spatial arrangement, applied nucleation, tree spacing, Anderson core, Atlantic forest restoration.

Introduction

Large-scale ecological restoration has become an urgent priority in tropical regions due to the accelerated loss of biodiversity and ecosystem services. In Brazil, the Atlantic Forest is one of the most degraded biomes, with less than 12% of it original cover remaining, mainly in fragmented and disturbed areas (Brancalion et al., 2015). The Brazilian Forest Code (Law 12.651/2012) defines the rules for the restoration of permanent preservation areas and legal reserves, presenting both opportunities and challenges for efficient restoration (Meli et al., 2017). In this context, active restoration practices have gained prominence, as they help recover areas more quickly than passive approaches, especially in significantly degraded areas where natural regeneration is difficult (Assis et al., 2013; Campoe et al., 2010).

The Araucaria Forest, a type of Atlantic Forest, is critically endangered. Recently, it was estimated that only about 4.3% of it original range remains. Furthermore, only 13.5% of these areas are protected (Zorek et al., 2024). The remaining populations of Araucaria angustifolia are increasingly isolated, poorly protected, and disconnected from each other, primarily due to climate change and land use (Tagliari et al., 2021). Restoring this ecosystem is challenging, mainly due to the exotic grasses that dominate the area, soil degradation, and the complexity of the restoration process, which involves several phases of plant growth (Almeida, 1998; Pozzan et al., 2020). A common strategy is the planting of native trees, but the success of this effort depends not only on the choice of species but also on how and where they are planted, considering the spacing between them (Corbin & Holl 2012; Leles et al., 2011). The spatial arrangement of seedlings affects the amount of light reaching the plants, competition for resources, and also helps facilitate the growth of different types of species, from pioneers to those that appear in the final stages of succession (Ganade et al., 2011; McCallum et al., 2017).

Although there have been advances in forest restoration, few studies have directly compared how different forms of spatial arrangement of plants affect the growth of native species in recovering Araucaria forests. Specifically, very different arrangements, such as dense clumps of trees, known as Anderson cores, and plantations with wider mixed spacing, have not yet been systematically tested under the same conditions. This lack of information is important because the way plants are arranged in space can alter the balance between facilitating or competing with each other, influencing growth and survivorship over time and the natural stages of forest renewal.

Given this gap, this study seeks to answer the following question: how do different spatial arrangements influence the dendrometric characteristics (height, diameter at ground level, and canopy projection) of native species of the Mixed Ombrophilous Forest in areas undergoing ecological restoration? To this end, two contrasting spatial arrangements were compared: dense plantings in Anderson cores (0.5 × 0.5 m) and mixed plantings with wide spacing (3 × 2 m). The performance of three key species (Mimosa scabrella, Solanum diploconos, and Araucaria angustifolia) was evaluated at 45 and 57 months after established each of the treatments.

We aimed to evaluate the effect of spacing and planting arrangement on the dendrometric performance of native species during the initial stages of ecological restoration.

Materials and methods

Study area. The experiment was carried out at the Experimental Station Fazenda Canguiri, belonging to the Federal University of Paraná (UFPR), located in the municipality of Pinhais, Paraná State, southern Brazil (25°23′38.31″S, 49°07′37.56″W), at an average altitude of 900 m above sea level (Figure 1). The site is situated within the catchment basin of the Iraí Reservoir, a strategic water supply source for the metropolitan region of Curitiba.

According to Köppen's classification, the regional climate is Cfb, humid subtropical mesothermal, with rainfall evenly distributed throughout the year and no defined dry season (Alvares et al., 2013), (Aparecido et al., 2016). The mean annual temperature ranges from 15 to 17 °C, with the warmest month not exceeding a mean of 22 °C. Annual precipitation varies between 1,100 and 1,920 mm, and frosts are frequent, occurring between 10 and 25 days per year, especially in higher altitudes (Aparecido et al., 2016).

The local relief is predominantly flat, and its soils are composed mostly of Cambisols, which occupy approximately 57% of the area, in addition to a significant presence of Latosols, which cover approximately 25% of the area (Jocelito et al., 2019). Prior to the establishment of the experiment, the area was subjected to intensive agricultural practices. During winter, the land was cultivated with *Raphanus sativus* L. (forage radish) and used for grazing with *Avena strigosa* Schreb. (black oat), while in summer it was predominantly cultivated with *Zea mays* L. (maize). This historical alternation between crop rotation and grazing reflects a typical pattern of degradation in agricultural landscapes of southern Brazil, making the site representative for ecological restoration experiments.

Implementation of the experiment: The experiment was established in December 2019 in a 1.45 ha area, using a randomized block design (B1, B2, B3, and B4). Each experimental plot measured 432 m² (24 ×

18 m), with four replicates per treatment. Two restoration strategies were evaluated: (i) T1 – Anderson nuclei planting and (ii) T2 – mixed planting with native species (Figure 2).

In treatment T1, six Anderson nuclei were established per block, each measuring 3 × 3 m, with seedlings planted at 0.5 × 0.5 m spacing. Each nucleus comprised nine native species of the Mixed Ombrophilous Forest (MOF), selected based on functional traits and complementary successional strategies. The composition included two individuals of *Solanum diploconos* (Mart.) Bohs, two of *Mimosa scabrella* Benth., and one of each: *Araucaria angustifolia* (Bertol.) Kuntze, *Eugenia conceptionis* (Kuntze) K. Schum., *Rollinia umbellata* (Mart.) Mez, *Myrsine ferruginea* Spreng., and *Psidium cattleyanum* Sabine, totaling 54 seedlings per block (Figure 2A).

Treatment T2 consisted of mixed planting at 3 × 2 m spacing (row × plant), totaling 72 individuals per plot. Eight native tree species were included, with six individuals of each: *Casearia decandra* Jacq., *Cassia leptophylla* Vogel, *Luehea divaricata* Mart. and Zucc., *Vitex megapotamica* (Spreng.) Moldenke, *Inga sessilis* (Vell.) Mart., and

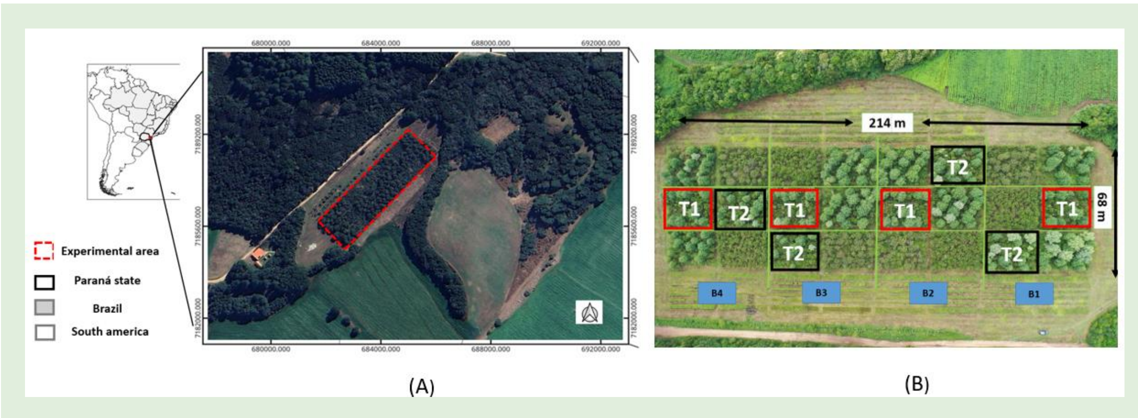

Figure 1. Location and experimental design at the Canguiri Experimental Farm, Federal University of Paraná (UFPR), in Pinhais, PR, Brazil. (A) Location of the experimental área. (B) Diagram of the experimental design showing the spatial distribution of treatments in the study area.

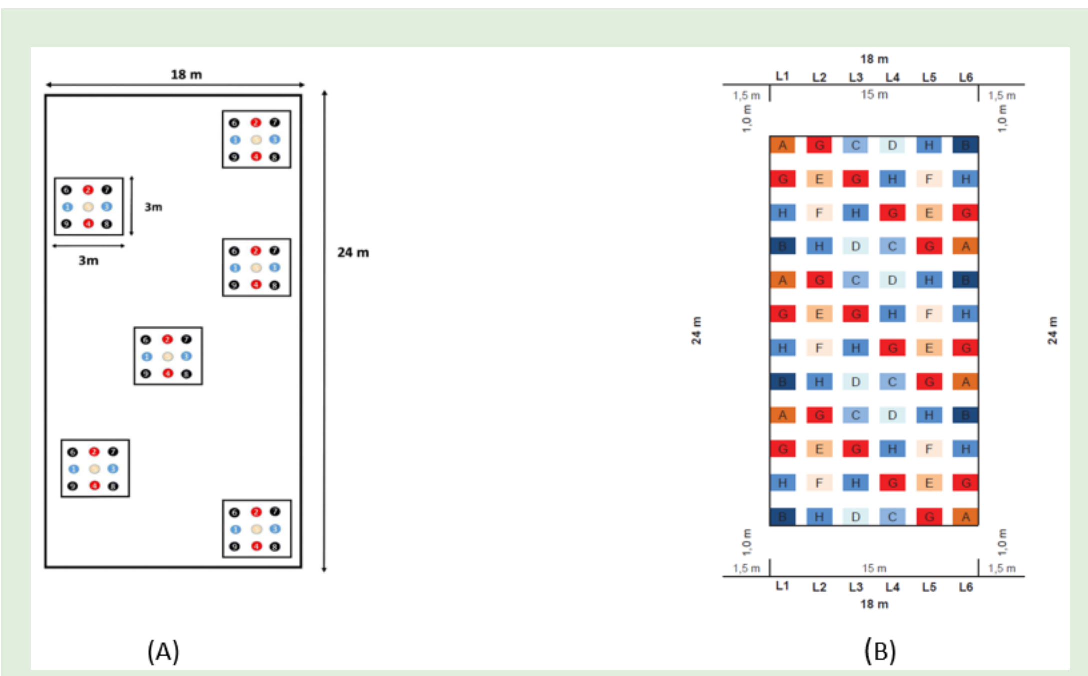

Figure 2. Spatial arrangement of the restoration treatments. (A) Anderson nuclei (3 × 3 m) in treatment T1, with seedlings planted at 0.5 × 0.5 m spacing. Numbers indicate different species. (B) Mixed planting in treatment T2, with 3 × 2 m spacing (row × plant).

A. angustifolia (Bertol.) Kuntze. In addition, each plot received 18 seedlings of *M. scabrella* and 18 of *S. diploconos* (Figure 2B).

Data collection. The experiment was conducted in a degraded pasture area, using a randomized block design with two contrasting restoration treatments: T1 – Anderson cores (0.5 x 0.5 m) and T2 – mixed planting (3 x 2 m). Treatment T1 included nine native tree species, while T2 included eight species.

The difference in floristic composition reflects practical limitations arising from the availability of seedlings at the time of planting; however, the functional groups (Table 1) present in both treatments were similar, ensuring ecological comparability. It should be noted that the objective of this study was not to evaluate the entire plant community but rather the performance of three target species that were consistently present across all treatments.

The selection of these three species was based on their successional roles and functional relevance for Araucaria forest restoration. *M. scabrella* (Benth) was chosen as the pioneer species due to its rapid growth, nitrogen fixation capacity, and potential to promote microclimate improvements. *A. angustifolia* (Bertol.) Kuntze was included as a mid- to late-successional conifer of high ecological and cultural importance, but sensitive to competition and dependent on facilitating processes during initial establishment. *S. diploconos* (Mart.) Bohs was selected as a shade-tolerant understory species, representing the late-successional guild and adapted to more stable shaded environments. These species constitute a functional gradient that allows us to assess the influence of spacing and spatial arrangement on pioneer dominance, the facilitation of intermediate species, and the establishment of shade-tolerant taxa. In T1, sampling included 12 individuals of *M. scabrella*, 12 of *S. diploconos*, and 6 of *A. angustifolia* per block (B1, B2, B3, and B4). In T2, 18 individuals of *M. scabrella*, 18 of S. diploconos, and 6 of *A. angustifolia* were measured per block.

The variables evaluated were total height, diameter at ground height (DAS), and crown projection. Total height was determined using a clinometer and a three-meter graduated ruler positioned near the stem, recording the distance from the base of the plant to the highest branch tip. DAS was measured with a caliper. Crown projection was assessed with a tape measure, taking two perpendicular measurements per individual to calculate the projected crown area.

Data analysis: To assess differences between treatments and species for each performance parameter (height, ground-level diameter, and crown projection), a multivariate analysis of variance (MANOVA) was conducted using the manova function, followed by summary. aov to evaluate univariate effects, both from the stats package (R Core Team, 2025). In this model, Treatment, Species, and Year were included as fixed factors, along with their interactions (Treatment × Species and Species × Year), allowing simultaneous testing of spatial arrangement and temporal variation effects on species performance. Differences among groups for each parameter were subsequently examined using general linear hypotheses (post hoc) with the glht function from the multcomp package (Hothorn et al., 2025).

All variables were log-transformed, and assumptions of normality and homogeneity of variances were assessed using Shapiro–Wilk and Levene's tests, respectively, with both assumptions being met. Figures were generated using the ggplot2 (Wickham, 2025) and patchwork (Pedersen, 2025) packages. All analyses were performed in the R statistical environment (R Core Team, 2024)

Table 1. The ecological characteristics and main functional attributes of native tree species (*Mimosa scabrella* Benth, *Solanum diploconos* (Mart.) Bohs and *Araucaria angustifolia* (Bertol.) Kuntze) evaluated in treatments T1 and T2.

Species	Successional group	Shade tolerance	Dispersal syndrome	Main functional attributes relevant to restoration
Mimosa scabrella Benth.	Pioneer	Shade-intolerant (heliophilous)	Autochory and zoochory	Fast-growing nitrogen-fixing legume that improves soil fertility and facilitates natural succession (Gerber et al., 2021; Reis et al., 2010; Citadini-Zanette et al., 2017).
Solanum diploconos (Mart.) Bohs	Late-successional / understory	Shade-tolerant	Zoochory	Understory species with fleshy fruits attractive to birds, enhancing natural regeneration and biodiversity (Jacomassa, 2016; Gagetti et al., 2016; Suganuma and Durigan, 2021).
Araucaria angustifolia (Bertol.) Kuntze	Mid- to late-successional	Moderately shade-tolerant (especially in early stages)	Zoochory	Long-lived emergent tree, benefits from initial shading and animal dispersal; key species for forest structure and biodiversity (Duarte et al., 2002; Sasso et al., 2020; Marcon et al., 2021).

Results

Multivariate analysis (MANOVA) showed statistically significant effects on the dendrometric variables evaluated: height, diameter at ground level, and canopy projection. The treatment factor was significant (F = 9.647; df = 3; P < 0.001), as was the species factor (F = 23.378; df = 6; P < 0.001). Furthermore, the Treatment × Species (F = 3.205; df = 6; P < 0.010) and Species × Year (F = 11.531; df = 6; P < 0.001) interactions also demonstrated statistical significance.

Regarding height (Figure 3A), *M. scabrella* demonstrated consistently higher values in both arrangements and years, demonstrating its structural dominance. *Araucaria angustifolia* showed moderate growth in 2023, with a significant increase in 2024, especially under the Anderson centers. *Solanum diploconos* showed the lowest height values throughout the period, although with gradual increases over the years. Differences between species were statistically significant (*P* < 0.001), as were variations between treatments in 2024, when the Anderson centers promoted greater growth (P < 0.050).

For diameter at ground level (Figure 3B), *M. scabrella* again presented superior values throughout the study. *Araucaria angustifolia* showed pronounced increments in 2024, especially in the nuclear system, while *S. diploconos* also increased but at lower magnitudes. Statistical effects were significant for species (P < 0.001) and for treatment in 2024, when Anderson nuclei favored the development of *A. angustifolia.*

Regarding canopy projection (Figure 3C), *M. scabrella* remained structurally dominant, with marked expansions between years. *Araucaria angustifolia* showed significant gains in 2024, while *S. diploconos* showed smaller but steady increases. Differences were significant between species (P < 0.001) and between years (P < 0.050). In 2024, a clear treatment effect was observed, with Anderson cores associated with larger canopy projections for both *M. scabrella* and *A. angustifolia*.

Discussion

The results reveal distinct variations in dendrometric performance among the three species, reflecting their successional strategies and the influence of spatial arrangements. Regarding height (Figure 3A), *M. scabrella* showed stability in structural dominance throughout the experimental period and under different treatments, confirming its role as a fast-growing pioneer species, capable of tolerating adverse conditions and modifying the environment through shading, increasing soil organic matter, and establishing associations with rhizobia and arbuscular mycorrhizal fungi (Lammel et al., 2015; Ferreira et al., 2019; Gerber et al., 2021). These characteristics may explain its superior performance and its potential to act as a facilitator species in ecological restoration processes.

A. angustifolia showed restricted initial development but demonstrated a positive response in 2024, especially in Anderson's nuclei (Figure 3A, B). This behavior is consistent with its classification as a mid- to late-successional species, which benefits from the microclimatic conditions established by the canopy of pioneer species. The shading and moderate competition promoted by *M. scabrella* likely favored *A. angustifolia* by reducing abiotic stress and increasing light availability under intermediate conditions (Duarte et al., 2002; Olguin et al., 2019; Dobner et al., 2019; Stepka et al., 2021; Olguin et al., 2023; Olmedo et al., 2024).

Solanum diploconos consistently presented lower height, diameter, and crown projection values (Figure 3A-C), a pattern consistent with its classification as a shade-tolerant understory species (Ávalos, 2019). Although growth increases were modest, the observed continuous development indicates that facilitation by pioneer species may provide indirect benefits to more demanding species by promoting the formation of shaded and stable microhabitats. Canopy projection patterns (Figure 3C) corroborated the functional dominance of *M. scabrella*, characterized by the rapid expansion of its canopy structure and modulation of understory conditions, in line with studies reporting its ability to form monospecific stands and drive successional trajectories (Steenbock et al., 2011; Gerber et al., 2021). The ability of *M. scabrella* to modify competitive dynamics highlights its importance as a facilitator species in ecological restoration strategies.

When comparing the arrangements, the treatment effects were most evident in 2024. Anderson's cores especially favored *A. angustifolia* (Figure 3B–C), suggesting that the higher density intensified not only competition but also facilitation, generating microenvironments suitable for mid- and late-successional species. On the other hand, the mixed arrangement presented more uniform but less striking results, suggesting that greater spacing may decrease the potential to facilitate plant growth (Caramori et al., 1996; Ganade et al., 2011). McCallum et al. (2017) suggest that spatial planning is essential to the outcomes of ecological restoration, as it influences the dynamics of competition and facilitation among species.

The results indicate that attributes associated with functional groups of the species, succession, and spatial arrangement of plants exert a combined influence on tree growth in restoration areas (Connell and Slatyer, 1977; Aerts et al., 2011; Manohan et al., 2023). The combination of pioneer and late-succession species in cluster-based (nucleation) planting systems, such as Anderson cores, constitutes an effective strategy for accelerating the succession process in highly degraded areas (Aerts et al., 2011; Zahawi et al., 2013; Toledo-Aceves et al., 2021).

Our results, although derived from a controlled experimental environment, offer useful insights for planning large-scale restoration projects. Clustered arrangements, such as Anderson's cores, are logistically simple, require fewer seedlings per hectare compared to homogeneous plantings, and favor rapid canopy closure, contributing to reduced maintenance costs. These attributes are particularly relevant in large-scale programs, such as those established by the Brazilian Forest Code or aligned with global initiatives, such as the UN Decade on Ecosystem Restoration.

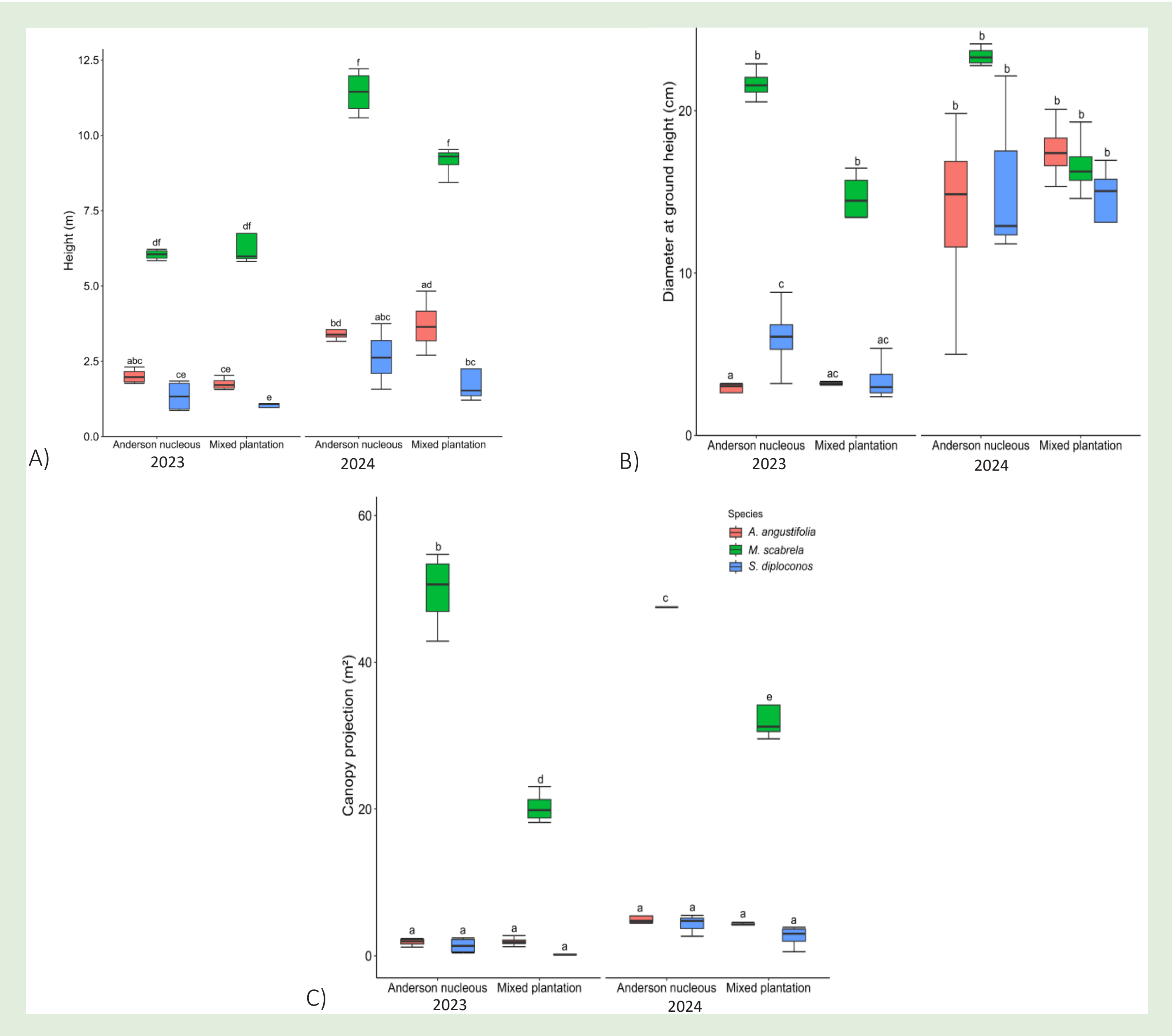

Figure 3. Mean (± SE) of (3A) height, (3B) diameter at ground level and (3C) crown projection of *Mimosa scabrella*, *Solanum diploconos* and *Araucaria angustifolia* in Anderson nuclei and in mixed planting, at 45 and 57 months after planting. Different letters indicate statistically significant differences (P < 0.05).

The patterns observed in this study, especially the facilitation of mid- and late-successional species, indicate that spatial planning can be a determining factor in scaling up restoration efforts in degraded Araucaria forests.

Therefore, future research should focus on three main areas. First, long-term monitoring to investigate how different spatial arrangements evolve over decades and to assess their effects on succession dynamics and final forest structure. Second, ecosystem services, to analyze how planting strategies influence the attraction of seed-dispersing fauna, nutrient cycling, and the recovery of functional biodiversity over time. Third, conduct cost–benefit analyses comparing the economic efficiency of Anderson cores with other restoration methods, particularly across different landscape scales.

Conclusion

This study demonstrates that functional species groups and successional characteristics, along with spatial arrangements, influence dendrometric performance in restoration plantations in the Araucaria Forest, particularly in terms of height growth, stem diameter, and canopy development.

M. scabrella confirmed its role as a fast-growing pioneer and functional facilitator, while *A. angustifolia* and *S. diploconos* showed responses consistent with their successional positions, benefiting from the microenvironments created by the pioneer species' canopy.

Treatments in Anderson nuclei indicated greater facilitation effects, particularly for *A. angustifolia*. In contrast, mixed plantations produced more homogeneous but less expressive growth patterns.

In practical terms, these results indicate that the Anderson core-plot strategy is an efficient and sustainable approach for restoring severely degraded areas, as it promotes rapid canopy closure and the formation of microhabitats that favor the establishment of intermediate- and late-successional species over time.

By relating structural performance to careful spatial planning, this study contributes to the understanding of how active restoration strategies can accelerate forest recovery and increase the resilience of mixed tropical forest ecosystems.

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Author contribution

R.J.: Conceptualization, Data analysis, Methodology, Writing-original draft, Writing-review, editing, and investigation; A.A.: Conceptualization, Methodology, Data curation, Supervision, review; N.L.: Supervision, Writing; R.C.: Supervision and writing Alexandre Mastella: Methodology; C.S.: Methodology; K.S.: Methodology; I.I.: Conceptualization, Methodology, Data curation, Supervision; E.S.C.: Conceptualization, Methodology, Data curation, Supervision writing; E.S.O.I.: Supervision writing.

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