

The Fate of *Astronium urundeuva* Monodominance in Reference Ecosystems Within Riparian Forests of the Rio Doce

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Abstract

The Brazilian Atlantic Forest has suffered from historical degradation and this work assessed the vegetation structure and soil quality by examining 45 plots divided in three sites in reference ecosystems from Conselheiro Pena-MG, Brazil. We recorded 28 species from 14 families in the tree stratum and 26 species from 13 families in the sapling stratum. We found a clear edaphic-floristic gradient suggesting a strong association between some particular taxa to contrasting edaphic conditions. The tree *Astronium urundeuva* behaved as a monodominant species, with the highest importance value (IV) in both strata (62.0% in tree, and 31.5% in the sapling strata). In the tree stratum, this species was present in 97.8% of the plots (44 out of 45). This scenario is worrying because this species occurs in a monodominant form in the middle section of the Rio Doce watershed behaving as an invasive species, preventing the colonization of other native species.

Keywords: Atlantic rainforest, phytosociology, reference ecosystem, Fundão dam breach, vegetation structure.

1. INTRODUCTION

We are currently in the Decade of Ecosystem Restoration (2021-2030), as designated by the United Nations. This initiative seeks to prevent, halt, and reverse the degradation of various ecosystems, with a particular focus on tropical forests (Bustamante et al. 2019). Ecological restoration represents an important tool to preserve the remaining biodiversity and to maintain ecosystem services (e.g., Bustamante et al. 2019, Toma et al. 2023). Through ecological restoration, a functional recovery of the environment can occur at a fast pace, creating habitats, increasing biological diversity and integrity, and restoring ecosystem services (Clewell et al. 2004, Fernandes et al. 2016b, Buisson et al. 2021). However, restoration efforts

are frequently hindered by inefficiencies, often due to the absence of reference ecosystems that can guide the restoration process and ensure gains in biodiversity.

The first step towards an efficient restoration strategy is to identify a reference ecosystem, which serves as a guide for planning and to obtain a measure of success (Clewell et al. 2004, Toma et al. 2023). Ideally, reference models are based on data obtained directly from native ecosystems that are spatially close to the ecosystems to be restored. The restored ecosystem should reflect the species composition of the previously established reference area so that the established communities create environmental conditions conducive to the establishment of other species (Clewell et al. 2004, Toma et al. 2023). In addition to the recovery of a similar set of functional

species, the success of restoration projects is strongly linked to the recovery and restoration of soil properties, as they shape the ecological succession and accelerate the recovery of tropical forests (Poorter et al. 2016, Rozendaal et al. 2019, Bañares-de-Dios et al. 2022, van der Sande et al. 2022). Soil plays an important role in creating essential microhabitats for the diversity and taxonomic composition of the forest (e.g., Bañares-de-Dios et al. 2022). It is therefore important to understand how edaphic factors act on a small scale to shape community composition and species distributions at geographically closer target sites (e.g., Coelho et al. 2018, Fagundes et al. 2019, Figueiredo et al. 2022, Nunes et al. 2022). In addition to creating guidelines for adequate conservation and restoration policies (Fernandes et al. 2016b, Turchetto et al. 2017, Metzger et al. 2019), studies of soil-vegetation relationships help to better define reference ecosystems (Gomes et al. 2021, Figueiredo et al. 2022).

The Atlantic Forest is recognized as one of the world's main biodiversity hotspots (Myers et al. 2000), but this biome has suffered a continuous history of degradation, with only 11-16% of its natural forest remaining (Ribeiro et al. 2009). Despite this intense degradation, the remaining forest fragments still support an impressive diversity of plant species (Figueiredo et al. 2024, Ramos et al. 2023). However, in environments that have suffered severe degradation and changes in soil quality, some highly invasive species can become monodominant (Fernandes and Negreiros 2006, Siqueira and Carmo 2021). This monodominance can lead to a significant loss of diversity by preventing the emergence and establishment of other native species. Therefore, it is crucial to understand the specific characteristics of these environments and how edaphic properties shape species composition to develop effective restoration and monitoring strategies.

In 2015, the collapse of the Fundão dam in Mariana, Brazil, caused severe damage to approximately 1,469 hectares of Atlantic riparian forest. The diverse ecosystems and ecological interactions in these areas were heavily impacted by mining tailings (e.g., Fernandes et al. 2016a, Omachi et al. 2018, Sánchez et al. 2018). Bold ecological restoration efforts are essential for these affected environments. In this context, understanding the relationship between edaphic properties and vegetation composition in nearby, unaffected reference areas is a crucial step towards grasping the species-specific factors that contribute to the high diversity of the Atlantic Forest (Fernandes et al. 2016a). This knowledge will aid in promoting effective restoration strategies that support the recovery of biodiversity in areas impacted by mining tailings. Our objective was to examine how the floristic composition

of tree and sapling strata relates to small-scale edaphic variation in the Atlantic Forest and to determine whether soil heterogeneity can explain the structure and composition of vegetation in these strata. We hypothesize that small-scale edaphic heterogeneity significantly influences the structure of tree and sapling communities in Atlantic Forest remnants within the Doce River watershed, southeastern Brazil.

2. MATERIAL AND METHODS

2.1. Study sites and data sampling

We selected three sites of Atlantic riparian forest along the Rio Doce river and tributaries, in the Municipality of Conselheiro Pena, in Minas Gerais for the vegetation sampling (Fig. 1, Fig. S1, Supplementary Material). The criteria of choice of the three sites was the good state of conservation of the riparian forest. We gave priority to sample accessible fragments that were old growth in later stages of succession and presented a sapling stratum. The regional climate of the region is mesothermal (Cwa in the Köppen classification), with rainy summers and dry winters, average annual precipitation of 1571 mm and average temperature ranging between 16.0 and 22.0 °C (Alvares et al. 2013, reference municipality: Conselheiro Pena). Were delimited in each sample site as follow: Site 1 (19° 06' 51.4" S and 41° 28' 33.3" W) with 15 plots; Site 2 (19° 10' 10.6" S and 41° 26' 32.8" W), with 15 plots; and Site 3 (19° 11' 17.6" S and 41° 29' 35.1" W).

The plot method was used (Mueller-Dombois and Ellenberg 1974) for vegetation characterization and sampling. For the study of the tree stratum, 15 plots of 10 × 10 m (100 m²), totaling 4500 m². In each site, the plots were located 10 m apart from each other. All individuals within the plots with DBH ≥ 5 cm (diameter at breast height – measured 1.30 m above ground level) had their height estimated, were identified, and marked with numbered aluminum plates. The choice of this protocol follows standards already defined in phytosociological sampling in the Atlantic Forest (Turchetto et al. 2017, Figueiredo et al. 2022, Ramos et al. 2023). In addition, it allows a delimitation in the sampling of individuals already well established within the plots. For the sapling stratum, one sub-plot of 5 × 5 m was allocated in the lower left corner (riverbank towards the interior of the forest remnant) of each 100 m² plot. Within each sub-plot, with the aid of a digital caliper, all juvenile tree individuals with DAS (diameter at ground height) ≥ 1 cm and ≤ 5 cm were inventoried. In addition, these individuals were marked with nylon thread and their height was estimated.

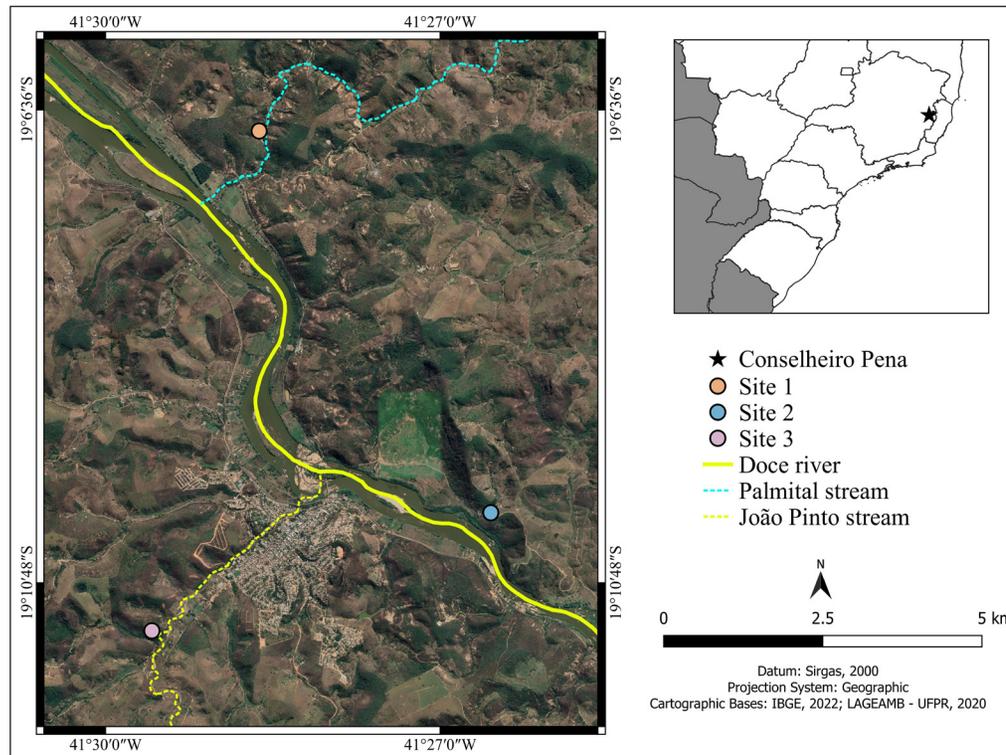


Figure 1. Map showing the location of three sampling sites of riparian forests in the middle Rio Doce watershed, Municipality of Conselheiro Pena, MG, southeast Brazil.

The plant individual's identification was carried out in the field, given prior species knowledge. Plant material was collected (vegetative or reproductive) for identification through specialized literature and existing material, and if not identified to the species level, were sent to specialists. Vouchers for all plant species were collected, identified, and deposited in the Montes Claros (MCMG) Herbarium, from Unimontes, and Norte Mineiro (ICA-UFMG) Herbarium. The family names followed the Angiosperm Phylogeny Group (APG IV 2016), and species names were confirmed in the Flora e Funga do Brasil (2022) (<http://floradobrasil.jbrj.gov.br/>) and updated/corrected whenever necessary. Synonymy verification, nomenclature, and species authors were obtained through the 'WorldFlora' package (Kindt 2020) in the R environment (R Core Team 2018), standardized according to World Flora Online (WFO; <http://www.worldfloraonline.org/>). We calculated the following phytosociological parameters: absolute and relative values of density, dominance, frequency, and importance value (IV) (see Mueller-Dombois and Ellenberg 1974).

In each plot, five simple soil samples were collected between 10 and 20 cm in depth, which were transformed into a composite sample per plot. Therefore, it was assumed

that each composite sample represented a valid estimate of the mean edaphic parameters of the five simple samples (according to Binkley and Vitousek 1989). Composite sampling was performed according to procedures described in Dick et al. (1996), with each composite sample dried in the shade at room temperature, carefully crushed, completely mixed, homogenized, sub-sampled and promptly sent for analysis by the Department of Soils of the Federal University of Viçosa. The granulometric analysis of the soils (coarse sand, fine sand, silt and clay fractions) was carried out according to Donagemma et al. (2017). The pH in water was measured using 1:2.5 (v/v) soil:solution ratios. The organic carbon content was determined by the Walkley-Black method. The exchangeable Ca^{2+} , Mg^{2+} and Al^{3+} cations were extracted by 1 mol L^{-1} KCl solution and the Ca^{2+} and Mg^{2+} contents were determined in the extract by titration with EDTA 0.01 mol L^{-1} . The Al^{3+} contents were determined by titration with 0.025 NaOH 0,025 mol L^{-1} , according to Silva et al. (1999). The elements P, K, Zn, Fe, Mn, Cu were extracted by Mehlich 1 solution, the sulfate (S) by monocalcium phosphate solution in acetic acid, and the contents of these elements in the extracts determined by spectrophotometry, according to Silva et al. (1999). Potential acidity (H+Al) was extracted by

0.5 mol L⁻¹ calcium acetate solution at pH 7.0 and determined by alkalimetric titration of the extract (Silva et al. 1999). The base saturation and aluminum saturation were calculated, respectively as follows: Base saturation = $100 \cdot (K + Ca^{2+} + Mg^{2+}) / (K + Ca^{2+} + Mg^{2+} + H + Al)$; Aluminum saturation = $100 \cdot Al^{3+} / (K + Ca^{2+} + Mg^{2+} + Al^{3+})$ (Alvarez Venegas et al. 1999).

2.2. Data analysis

Data analysis was performed for each sampled site and tree and sapling strata. We estimated the sampling completeness for each sampled site by computing the Chao 1 species richness estimator (Chao 1984, Colwell and Coddington 1994) using the iNEXT package (Hsieh et al. 2014) in R (R Core Team 2021). With the same package, we also plotted rarefaction and extrapolation curves (Hsieh et al. 2014). Classic quantitative phytosociological parameters (Mueller-Dombois and Ellenberg 1974) were used: relative density, dominance and frequency, and importance value (IV) index. To test the association between the monodominant species *Astronium urundeuva* and species richness we used linear regression analyses, with *A. urundeuva* abundance in tree stratum as independent variable and species richness of the tree stratum as dependent variable. To assess the differences in species composition, Cluster analysis (using the frequency matrix) was performed using the UPGMA linkage method and the Bray-Curtis dissimilarity matrix results.

To determine the relationship between soil factors and the plant species community, we performed a co-inertia analysis (COIA). This robust and flexible analysis measures the agreement between two multivariate data sets, also called co-structure (Dolédec and Chessel 1994, Dray et al. 2003). We performed the COIA for the tree and sapling strata separately. The edaphic matrix was defined as the values of 17 soil factors in the 45 plots (15 per site), while the floristic matrix was defined as the incidence (presence and absence) of 28 tree species or 26 sapling species in the 45 plots.

The COIA outputs a value called RV coefficient, which measures the strength of the association between the two matrices (i.e., floristic and edaphic). The RV coefficient is bounded to 0 (i.e., no association) and 1 (i.e., maximum association). The significance (p-value) of the RV coefficient was defined by Monte Carlo permutation, performed with 10.000 randomizations. To perform the COIA, a Principal Components Analysis (PCA; mean = 0; standard deviation = 1) was used for the soil matrix, and a centered PCA (mean = 0) was used for each floristic matrix, according to Dray et al. (2003). To attain the assumptions of normality in the soil data, we performed square root transformation for potassium (K), iron (Fe), and organic carbon (C),

and logarithmic transformation for sulphur (S), copper (Cu), silt, and clay. To access the association between each soil factor and COIA axis 1, we performed a Pearson's correlation between soil values and plot coordinates on COIA axis 1. The association between species and the COIA axis 1 was defined by the species coordinates on this axis. The COIA was performed using the 'ade4' package (Dray and Dufour 2007). All analyses were performed in the R environment (R Core Team 2021).

3. RESULTS

In the tree stratum 509 adult individuals from 28 species belonging to 14 plant families were recorded (Table S1, Supplementary Material). The samples of the sapling stratum recorded 173 individuals from 26 species belonging to 13 families (Table S2, Supplementary Material). Seven species could not be identified because fertile material was not obtained from these individuals to allow their taxonomic identification, even after several visits to the study site.

The rarefaction curves indicated that the sampling of species richness for the three sites at both tree (Fig. 2a), and sapling strata (Fig. 2b) were sound since the expected species richness showed a trend for stabilization. Among the tree stratum, the family Fabaceae was the most representative (7 species), followed by Anacardiaceae, Bignoniaceae, Euphorbiaceae, Moraceae, Phyllanthaceae, and Salicaceae, with 2 species each. The species with the highest importance value (IV) in the tree stratum were: *Astronium urundeuva* (M.Allemão) Engl. (Anacardiaceae) (IV: 62.0%), *Ficus gomelleira* Hort.Monac. ex Kunth & C.D.Bouché (Moraceae) (IV: 5.4%), *Peltophorum dubium* (Spreng.) Taub. (Fabaceae) (IV: 5.0%), and *Savia dictyocarpa* Müll.Arg. (Phyllanthaceae) (IV: 3.8%) (Fig. 2c). In this stratum, *A. urundeuva* behaved as an invasive monodominant species, occurring in 97.8% of plots (44 out of 45 plots), with 79.1% of the tree individuals (402 out of 508 species), and 66.1% of the basal area (7.1 out of 10.8 m²). Another worrying pattern featured in our dataset shows a significant negative relationship between *A. urundeuva* relative density and plot species richness, given that *A. urundeuva* abundance alone can explain 38.2% of the variation in species richness (Fig. S2).

Fabaceae was also the richest family in the sapling stratum, with seven species, followed by Anacardiaceae, Euphorbiaceae, Myrtaceae, and Rubiaceae, also with two species each. The species with the highest IV in the sapling stratum were: *A. urundeuva* (IV: 31.5%), *Randia armata* (Sw.) DC. (Rubiaceae) (IV: 12.2%); *S. dictyocarpa* (IV: 10.2%), and *Lonchocarpus sericeus* (Poir.) Kunth ex DC. (Fabaceae) (IV: 8.6%) (Fig. 2d).

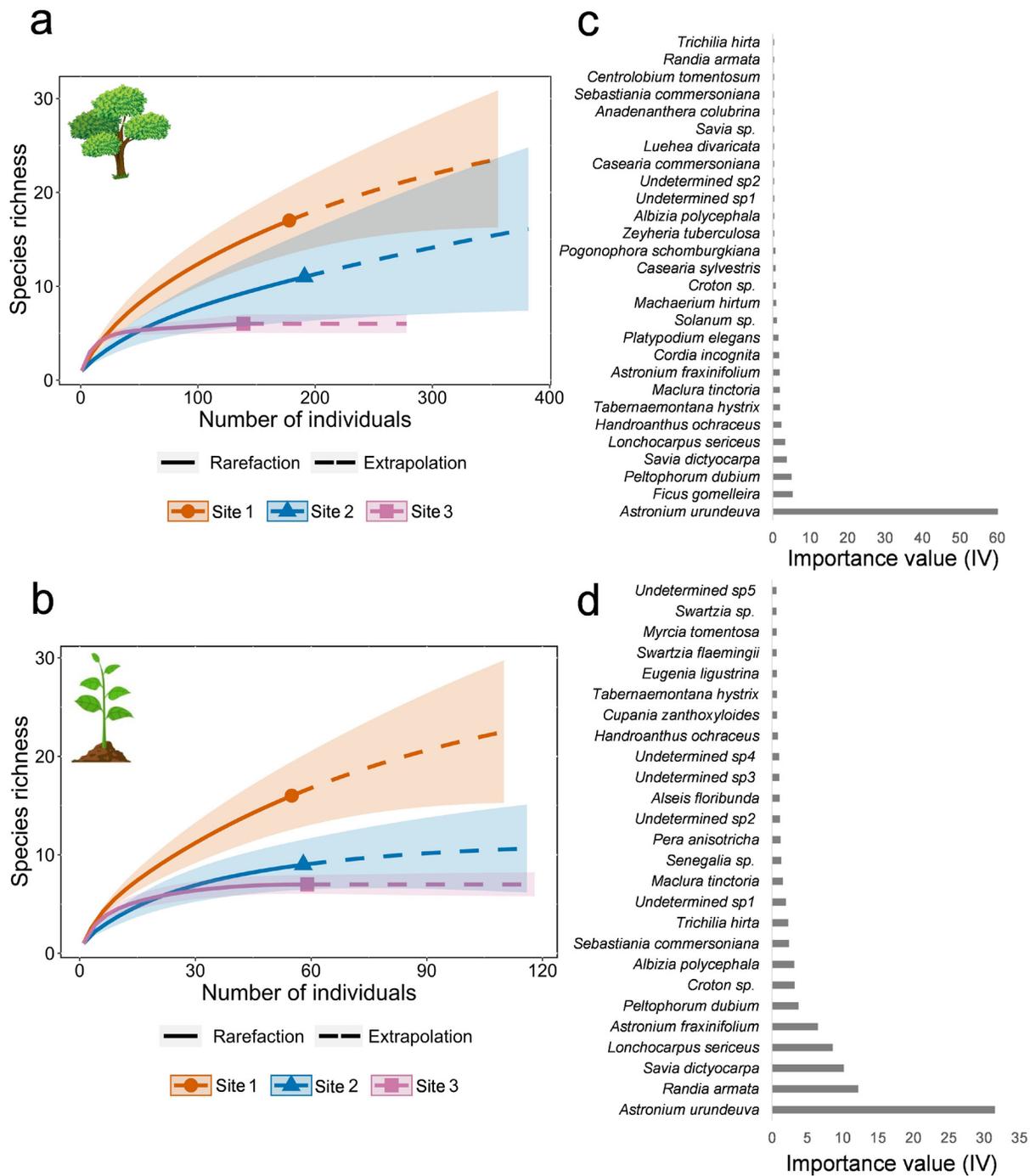


Figure 2. Rarefaction and extrapolation curve using the Chao 1 estimator of species richness and sampling effort calculated as the ratio of observed and estimated species richness for the sampled sites for the tree (a) and sapling (b) strata. Species sampled and IV (importance value) for the tree (c) and sapling (d) strata.

Three tree species were found in all sample sites (*A. urundeuva*, *L. sericeus*, and *P. dubium*), while site 1 presented the higher number of species recorded (14) (Fig. 2c). As for the sapling stratum, the three sampled sites shared only two species (*A. urundeuva*, and *R. armata*). Thus, the cluster

analysis showed an unclear division for the plots sampled in the tree stratum. For the sapling stratum, 12 out of 15 plots from site 3 formed a cluster, with a greater similarity between them. However, in general, the plots showed a high uniformity in their species composition (Fig. 3).

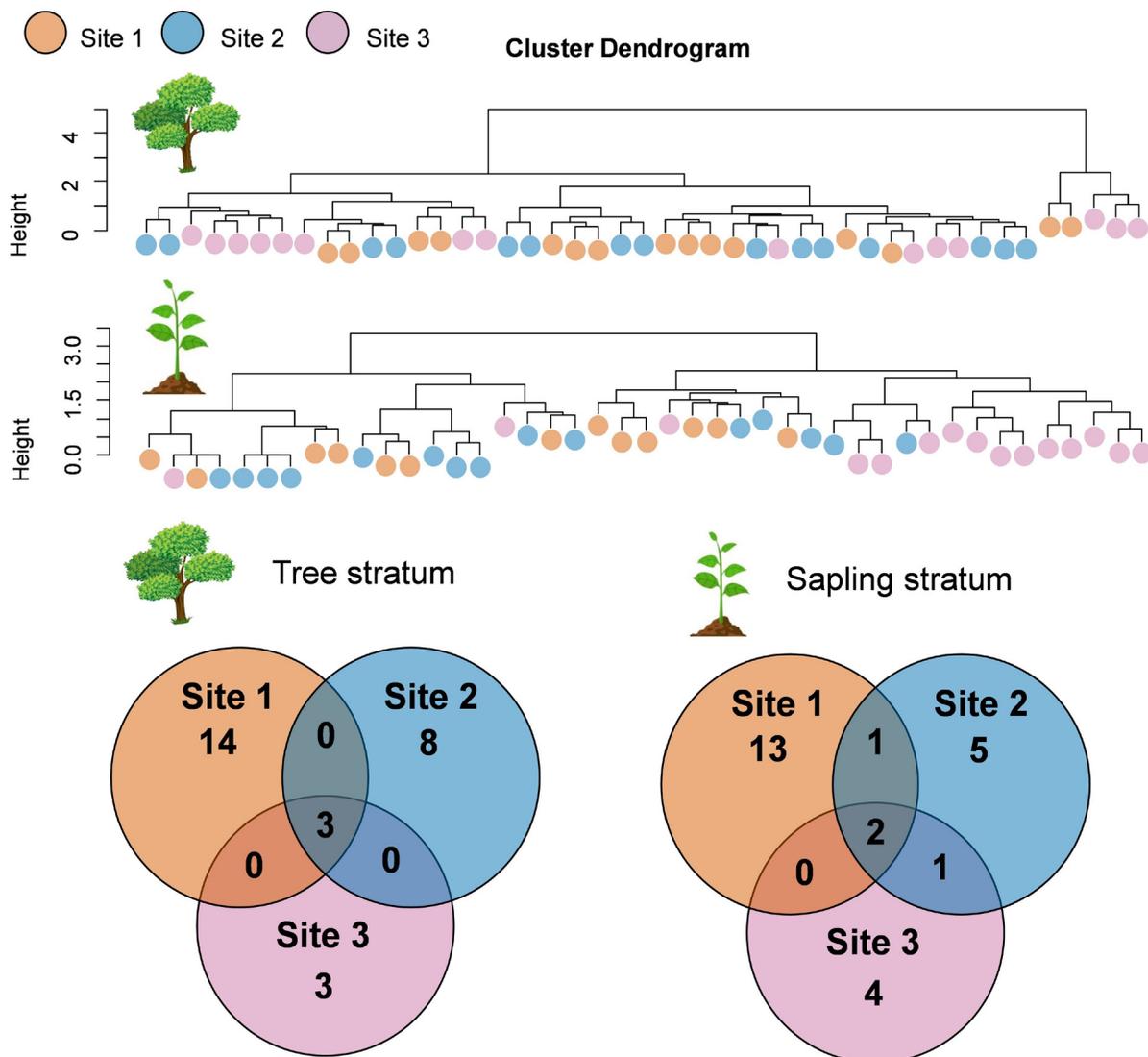


Figure 3. Composition of tree and sapling strata in relation to the sampled areas. Above are shown the cluster dendrogram for the tree and sapling strata and below the Veen diagram for the species composition of each sampled stratum.

The COIA showed a significant association ($p < 0.001$) between the edaphic parameters and the floristic composition in the sampled sites for both tree ($RV = 0.37$; 36.9% concordance) and sapling stratum ($RV = 0.38$; 37.7% of concordance). The percentage of covariance explained by the tree-based COIA axis 1 was 64.4%, while axis 2 explained 13.7% of the covariation. The percentage of covariance explained by sapling-based COIA axis 1 was 76.5%, while axis 2 explained 11.1% of the covariation. Thus, we further explored only the COIA axis 1 for both strata. The positive side of tree-based COIA axis 1 shows plots with soils that are richer in nutrients, less acidic and with higher levels of calcium, organic carbon, manganese and magnesium (Fig. 4a). The tree species most strongly associated with the positive

side of this axis were *S. dictyocarpa*, *P. dubium* and *Maclura tinctoria* (L.) D.Don ex Steud. (Moraceae) (Fig. 4a). On the other hand, the negative side of the tree-based COIA axis 1 showed plots with soils that were nutrient poorer, more acidic and with higher levels of sulphur, aluminium (both in absolute and relative terms), copper and with a higher proportion of fine and coarse sand (Fig. 4a). Tree species more strongly associated with the negative side of this axis were *Handroanthus ochraceus* (Cham.) Mattos (Bignoniaceae), *Astronium fraxinifolium* Schott (Anacardiaceae), and *Casearia sylvestris* Sw. (Salicaceae) (Fig. 4a). Since the monodominant *A. urundeuva* was present in almost all sampled plots, it did not show any association with the edaphic-floristic gradient indicated by the tree-based COIA axis 1.

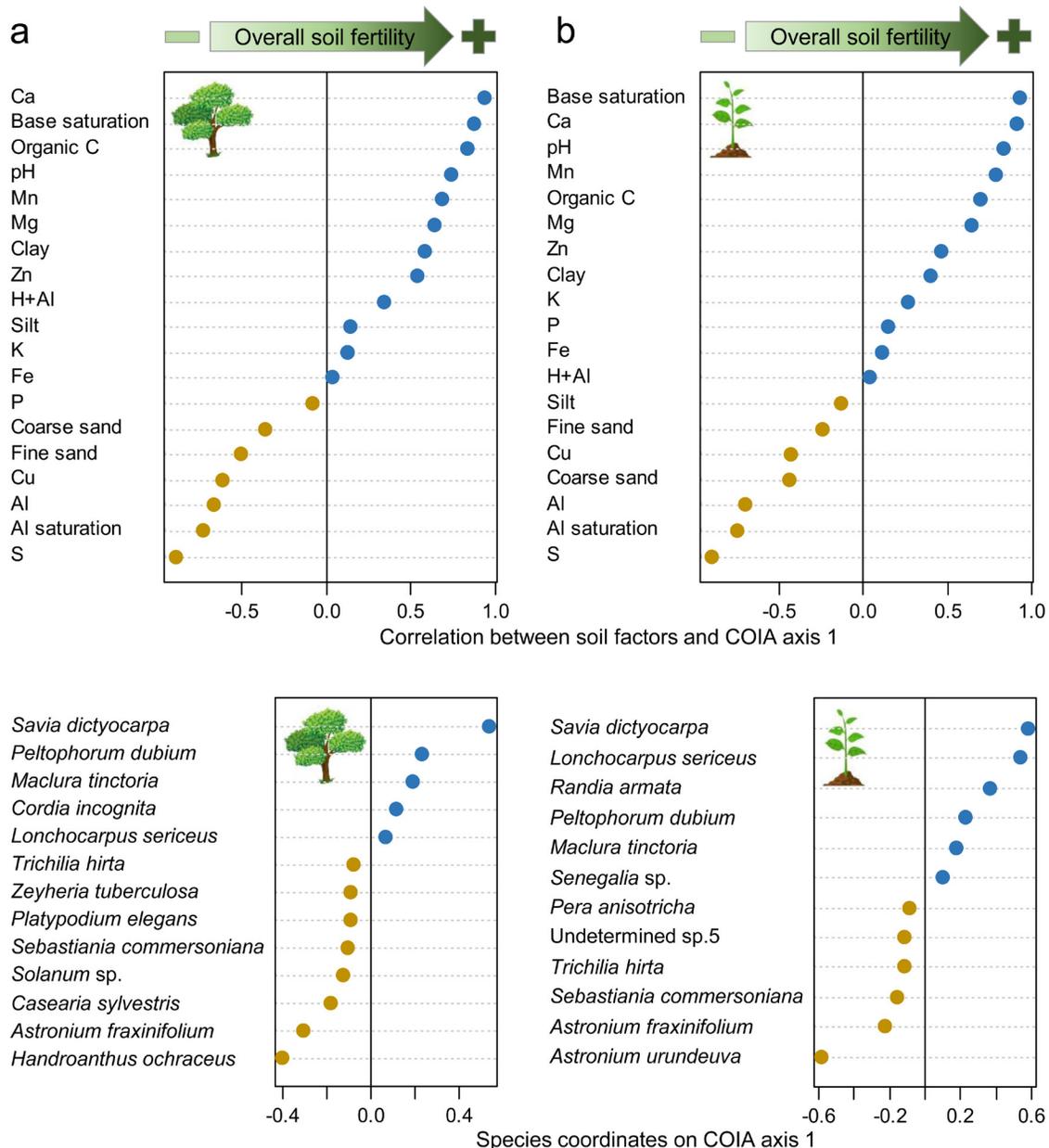


Figure 4. Co-structure between edaphic parameters and plant community sampled in the riparian forests in the middle Rio Doce watershed, in the Municipality of Conselheiro Pena, MG. Pearson correlation between edaphic factors and plot coordinates on axis 1 of co-inertia (upper panels) and coordinates of the most important plant species on axis 1 of co-inertia (lower panels). (a) Tree stratum; (b) Sapling stratum.

The positive side of the sapling-based COIA axis 1 indicated a very similar pattern to the tree-based COIA, showing plots with soils that are richer in nutrients, less acidic and with higher levels of calcium, manganese, organic carbon, and magnesium (Fig. 4b). The sapling species most strongly associated with the positive side of this axis were also similar to tree stratum, being mainly *S. dictyocarpa*, *L. sericeus*, and *R. armata*, among others (Fig. 4b). Similarly, the negative side of sapling-based COIA axis 1 showed plots with soils that were poorer in nutrients, more acidic, with higher levels of sulphur, aluminium and copper and with higher proportion of coarse sand (Fig 4b).

The sapling strata species most strongly associated with the negative side of this axis were *A. urundeuva*, *A. fraxinifolium*, and *Sebastiania commersoniana* (Baill.) L.B.Sm. & Downs (Euphorbiaceae) (Fig. 4b).

4. DISCUSSION

Ecological restoration aims to recover the natural ecological processes of degraded ecosystems based on reference ecosystems (DeLuca et al. 2010, Rosenfield et al. 2022, Toma et al. 2023). In fragmented regions, such as the Atlantic rain forest,

reference ecosystems can be based on plots of forest patches that are in the process of natural recovery (Gann et al. 2019, Toma et al. 2023, Ramos et al. 2023). This is the case of the Doce river watershed, an environment with a long history of degradation (Rodrigues et al. 2009) that was further deepened by the Fundão dam breach (see Fernandes et al. 2016a). Therefore, selecting multiple reference ecosystems near the restoration areas is crucial to account for the biotic and abiotic factors necessary for speeding up the recovery of plant communities (Ramos et al. 2023, Toma et al. 2023).

The low number of species shared between sample sites along this stretch of the Rio Doce basin may stem from the high floristic diversity characteristic of the Atlantic Forest, which is influenced by local environmental factors such as variations in soil quality and different successional stages (Azevedo et al. 2014, Forzza et al. 2012, Veloso et al. 2014, Fagundes et al. 2019). However, in this study we observed a low species richness compared to other studies carried out in the Doce River watershed, suggesting an intense history of degradation in these forests. In a study conducted by Figueiredo et al. (2022), 227 species were sampled from the adult stratum, while Ramos et al. (2023) sampled 90 species from the adult stratum, both studies being conducted in the Rio Doce watershed. Important to note is that the selected sites represented the best-preserved riparian forests along the Doce river in the region. The low species richness of this particular region, may also be related to the monodominance of one or few particular species (see below).

Soil quality is an important factor relevant to the restoration processes. In this work, nutrient-poor soils with high concentration of aluminium and sand favored highly abundant species such as *Astronium urundeuva* (in the sapling stratum) and *Astronium fraxinifolium* (in both strata). Both species are classified as early and late secondary (Lorenzi 2002). *Astronium fraxinifolium* presents the ability to release secondary compounds that inhibit other plants and favor its establishment (Reigosa et al. 2012) and rapid growth of populations, especially in disturbed environments. Native fast-growing species adapted to poor soils play an important role in quickly restoring the original structure of the forest, allowing for rapid ground cover, and preventing the emergence of invasive species (Rodrigues et al. 2009, Brancalion et al. 2014). On the other hand, the monodominance of *A. urundeuva* observed in this study should be viewed with concern. This species, although native to the Atlantic Forest (Silva-Luz et al. 2024), tends to occur in a monodominant form in the middle section of the Doce river, showing incredible invasive behavior to the detriment of the native flora (see, Fernandes and Negreiros 2006, Siqueira and Carmo 2021). Although dominating the tree stratum,

this species was favored in the acidic and nutritionally poorer soils at the sapling stratum. Future management programs must consider the populational control of this opportunistic species. Furthermore, we argue that any regional restoration initiative involving revegetation of degraded sites should avoid the inclusion of this species that, in spite of being native, behave as an invasive species in this region. A successful restoration initiative in this stretch of the Rio Doce must not only avoid the inclusion of *A. urundeuva*, but also make usual plant pest control to prevent recruitment of some it in the restored plots as well as other exotic and invasive species, as also observed by Xavier et al. (2023).

In a study conducted by Oliveira (2015), a monodominance of *A. urundeuva* was observed in a forest fragment in the Rio Doce watershed. This author also pointed out that its monodominance was related to soil degradation processes, which affects the agroecosystems of the region and causes damage to farmers and ranchers. The presence of allelopathic compounds in *A. urundeuva* have been shown to reduce the germination of other species (da Silva 2015). Despite its wide distribution in South America and its monodominance in several places, *A. urundeuva* stood until recently on the list of endangered species of the Brazilian flora (Mendonça and Lins 2000). It was only in December 2014 that the species was removed from the list of threatened species (MMA Ordinance No. 443, of December 17, 2014). However, there are still inconsistencies with MMA Normative Instruction No. 6 (December 2006), IBAMA Regulation No. 83 (September 1991) and Article 28 of Law 11.428 (December 2006). We stress the urgent need for further research to assess the impact of this species on the structure and composition of plant communities, as well as its invasive potential, to provide a current understanding of its population size and better assess the risks posed by a growing *A. urundeuva* population to native flora. Additionally, experimental studies on the colonization and performance of this species in the region are crucial to understanding its potential to continue driving soil degradation and biotic homogenization.

5. CONCLUSION

We observed a low number of species shared between sampled sites in the tree and sapling strata, indicating high heterogeneity in species composition across sites. This variation in species composition aligned with differences in edaphic factors at the study site, revealing a clear edaphic-floristic gradient. We also highlight the link between edaphic factors and the presence of species with the potential to become monodominant, such as *A. urundeuva* (particularly in the sapling stratum). Edaphic factors influence species

performance and community organization over time and space. Notably, *A. urundeuva* already dominates the adult stratum across diverse soil qualities, while it tends to thrive in less fertile soils in the sapling stratum. Our study advances the identification of reference sites for restoring anthropized Atlantic Forest. We emphasize the need to map and understand the unique characteristics of different sites along the Rio Doce watershed due to the pronounced heterogeneity in species composition and edaphic factors. Such studies are crucial for understanding biodiversity dynamics in natural environments and for developing effective policies to ensure the success of restoration projects.

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SUPPLEMENTARY MATERIAL

The following online material is available for this article:

Figure S1. Sampling sites in riparian forests of the middle Rio Doce watershed, Conselheiro Pena-MG, southeast Brazil.

(a): Site 1; (b) Site 2; (c): Site 3. Photos by J.C.G. Figueiredo.

Figure S2. Relationship between the relative density (percentage of number of *Astronium urundeuva* individuals) in tree stratum and species richness in plots of tree stratum riverine forests along Rio Doce watershed, southeast Brazil.

Table S1. Phytosociological parameters of species from the tree stratum sampled in three sites at riparian forests from Rio Doce watershed, Conselheiro Pena-MG, southeast Brazil.

Table S2. Phytosociological parameters of species from the sapling stratum sampled in three sites at riparian forests from Rio Doce watershed, Conselheiro Pena-MG, southeast Brazil.

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