REFERENCE SITES OF THREATENED RIVERINE ATLANTIC FOREST IN UPPER RIO DOCE WATERSHED

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The most important condition of ecological restoration is the identification of reference ecosystems, which function as a guide for assertive practice with which biological integrity and ecosystem structure and function can be compared. For restoration and conservation projects to be effective in the current scenario of biodiversity and ecosystem services decay worldwide, it is fundamental to understand the soil-plant interactions in each environment. In this study, we evaluated the structure and composition of the flora in 45 plots, equally distributed in three preserved areas (reference ecosystems) of Atlantic Forest in the upper Rio Doce watershed, Southeast Brazil. We also tested whether differences in species composition were influenced by edaphic factors, both in the adult tree and sapling strata. In both tree and sapling strata, Fabaceae was the species-richest family, followed by Myrtaceae, and Lauraceae. The Fabaceae family also showed the highest importance value for both strata. The soils of the riparian forests were highly heterogeneous among the studied sites. Co-inertia analyses indicated a clear edaphic-floristic gradient in both tree (RV = 0.467; p < 0.001) and sapling (RV = 0.478; p < 0.001) strata, with a connection of 46.7% and 47.8% between the edaphic and floristic matrices for trees and saplings, respectively. We identified the groups of tree and sapling strata species that were strongly associated with either nutritionally richer or poorer soils on each studied site. Understanding how ecological and life-history traits of plant species relate with edaphic factors is an important step to provide scientific-based knowledge to support policies for ecosystem recovery and restoration in the stretches of the Rio Doce watershed.

Key words: phytosociology, preserved forest, taxon-environment relationships, tree stratum, sapling stratum, vegetation structure

Introduction

Restoration is the process of recovering of an ecosystem that has been degraded, damaged, or destroyed (SER, 2004). This process initiates and/or accelerates the recovery of degraded areas, which premise is to re-arrange the complexity of biological assemblages, encompassing species composition and structure, and sustaining the biota of a given ecosystem over time (Suding et al., 2015; Rosenfield & Müller, 2017; Temperton et al., 2019). Given the current degradation of ecosystems all over the world, restoration actions are urgently needed and should focus on restoring ecosystem functionality and properties (e.g. Fernandes et al., 2016b; Kollmann et al., 2016; Gann et al., 2019).

The initiation of the restoration process must encompass the dissimilarities between current and expected future conditions in terms of composition, structure, and functions of the ecosystem (Laughlin, 2014). In this sense, one of the most important conditions of ecological restoration is the identification of reference ecosystems (Goebel et al., 2005; Toma et al., 2023). Reference ecosystems are defined as one or more existing, pre-existing, or hypothetical ecosystems that will serve as a reference template for restoration or mitigation projects (Hobbs & Harris, 2001; Miller & Hobbs, 2007; Miller et al., 2012; Toma et al., 2023). Reference ecosystems act as a guide for assertive practices and goals (Nestler et al., 2010; Temperton et al., 2019), from which biological integrity and ecosystem structure and function can be compared (Miller et al., 2012; Balaguer et al., 2014). The structure and composition of the plant community is the main factor

responsible for creating and maintaining ecosystem functions and providing the basis for the development of other biotic communities (Whitham et al., 2006; De Deyn et al., 2008). Therefore, the evidence provided by reference ecosystems gives us the baselines to elucidate possible future trajectories and to measure the initiatives of ecological restoration success (Keenleyside et al., 2012; Higgs et al., 2014; Toma et al., 2023).

The characterisation of soil-plant interactions on reference ecosystems is of central importance for restoration and the effectiveness of conservation projects (e.g. Suding et al., 2015; Bauer et al., 2017). Soils play an important role in the diversity and functioning of tropical forests (Rodrigues et al., 2020; Bañares-de-Dios et al., 2022; Figueiredo et al., 2022; van der Sande et al., 2023), and a complex integrative system exists between soil formation and forest taxonomic composition, modulating patterns of niche differentiation on a global scale (Fujii et al., 2018). Soil nutrient availability shapes the distribution of tropical tree species, confirming the role of soils in plant community assembly as a mechanism for structuring these communities (John et al., 2007; Chadwick & Asner, 2018; Rodrigues et al., 2019; Lourenço et al., 2021; Figueiredo et al., 2022).

Understanding how soil factors modulate the structure of plant species composition and the underlying ecosystem processes is far from trivial. This is especially true for tropical forests that host more than half of the world's biodiversity and provide important ecosystem services for human survival (Lewis et al., 2015). The Brazilian Atlantic Forest is considered the 5th global biodiversity hotspot (Murray-Smith et al., 2009) with a high capacity of storing carbon (Magnago et al., 2015). However, it is one of the most threatened tropical forests in the world, mainly due to deforestation, which has generated an intense fragmentation process of this important ecosystem (Ribeiro et al., 2011a; Marques & Grelle, 2021). Additionally, we highlight the environmental disaster in the Rio Doce watershed, which caused the collapse of the Fundão dam in the municipality of Mariana (MG), southeast Brazil, in 2015. A tsunami of tailings caused the loss of approximately 14.69 km² of vegetation and 90% of the riparian vegetation of the River Fundão, River Gualaxo do Norte, and River Carmelo (Fernandes et al., 2016a; Bottino et al., 2017). The riparian habitats are considered Permanent

Protected Areas under the Brazilian legislation (Metzger et al., 2019). This disaster caused numerous problems, affecting ecosystems and ecological interactions in this region (e.g. do Carmo et al., 2017; Sánchez et al., 2018). The wave of tailings released by the dam breach affected riparian habitats of the Atlantic Forest, leading to the loss of much of their regenerative capacity (Fernandes et al., 2016a). Therefore, it is of urgent importance to describe the interaction between edaphic factors and plant communities in reference ecosystems on the Rio Doce watershed in order to guide further restoration projects.

Our aim was to evaluate the structure and composition of the adult and sapling strata and its relationship with edaphic properties in the preserved areas (reference ecosystems) of the upper Rio Doce watershed. Our hypothesis was that small-scale edaphic heterogeneity plays an important role in shaping the species composition of adult and sapling strata. We expect this study to provide subsidies for the delimitation of a reference ecosystem that can be used in the planning of ecological restoration programmes in riparian forests, especially in the areas intensely affected after the environmental disaster of the collapse of the Fundão dam in Mariana municipality, in the upper Rio Doce watershed.

Material and Methods
Study site
To achieve our aims we sampled vegetation and soil in three old-growth riparian forests, located in the upper Rio Doce watershed, in Mariana municipality, Minas Gerais, southeastern Brazil (Fig. 1). The sampled sites are situated in three districts of the municipality of Mariana. Site 1: Santa Rita Durão district (20.276111° S, 43.430556° W) (Fig. S1a); Site 2: Monsenhor Horta district (20.304722° S, 43.219833° W) (Fig. S1b); Site 3: Camargos district (20.285361° S, 43.396806° W) (Fig. S1c). We selected reference sites for the study based on their state of conservation, prioritising sampling on accessible fragments that were in later stages of succession, and where the predominant physiognomy was an ombrophilous forest. According to the Köppen climate classification, the municipality of Mariana has a mesothermal climate (Cwa), with rainy summers and dry winters, average annual precipitation of 1571 mm and temperature ranging at 16.0–22.0°C, with an average value of 19.5°C (Alvares et al., 2013).
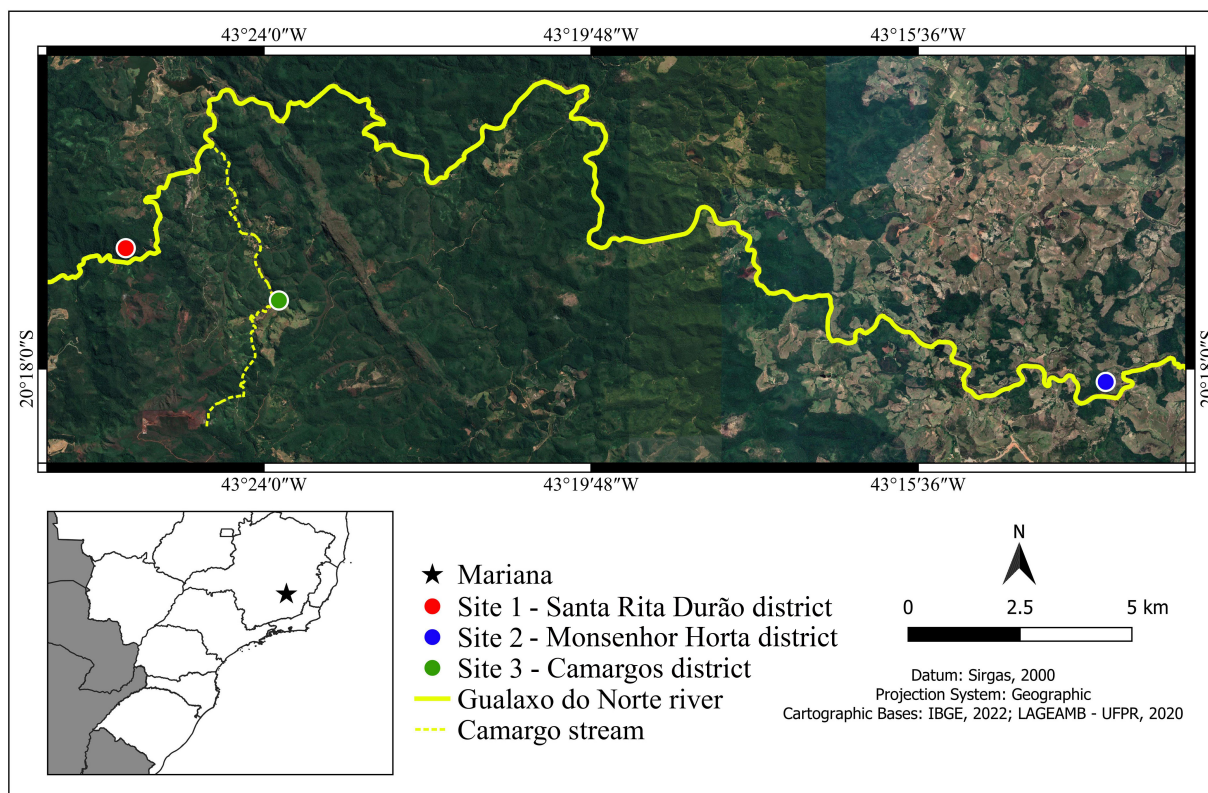
Fig. 1. Map showing the location of the three sampling sites in riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Site 1 – Santa Rita Durão district; Site 2 – Monsenhor Horta district; Site 3 – Camargos district.

Vegetation sampling

We used the plot method to sample and characterise the reference ecosystem sites (Mueller-Dombois & Ellenberg, 1974). The phytosociological survey was conducted in 15 plots of 100 m² (10 × 10 m) at least 10 m apart from each other, totalling 45 plots (4500 m²). We marked the plots with the aid of a level compass. To sample the tree stratum, we inventoried all tree individuals in each plot with DBH (diameter at breast height at 1.3 m from the ground) ≥ 5 cm. We marked all trees with aluminium plates in the trunk attached by nails and measured the circumference at breast height (CBH) using a tape measure (in cm). Samples of each plant individual were collected, identified with numbered adhesive tapes, and pressed to be later identified to the lowest possible taxonomic level. Because many individuals were not flowering at the sampling time, several further trips had to be made to the sites to collect fertile material for proper species identification.

Regarding the sampling of the sapling stratum, we allocated a 5 × 5 m sub-plot in the lower left corner (watercourse direction) within each 10 × 10 m plot. Within each sub-plot, with the aid of a digital caliper, we inventoried all herbaceous and shrubby individuals with DGH (diameter at ground height) between ≥ 1 and ≤ 5 cm. We marked all individuals within the sampling criteria with numbered aluminium plates, tied with nylon thread, and measured the height of each individual with the aid of a wooden tape measure (Menino et al., 2009, 2012).

We collected plant material (vegetative or reproductive) for identification with specialised literature and existing material, and to make exsiccates. After this step, we deposited all identified specimens in the Montes Claros Herbarium (MCMG) at the State University of Montes Claros (Unimontes). The family names followed the Angiosperm Phylogeny Group (APG IV, 2016). Synonymy verification, nomenclature and species authors were obtained through the «WorldFlora» package (Kindt, 2020) in the R environment (R Core Team, 2018), standardised according to World Flora Online (https://www.worldfloraonline.org/). We made additional checks with the Flora e Funga do Brasil (2022) for species, which were not found in World Flora Online. The parameters calculated for the vegetation phytosociology were the absolute and relative values of density, dominance, frequency, and importance value (IV) (Mueller-Dombois & Ellenberg, 1974).

Soil sampling

We collected about 100 g of simple soil samples at 20 cm depth at the four corners of each plot and at its centre. These were mixed *in situ* and transformed into a composite sample per plot, totaling 45 soil samples for the study. Each composite sample represented a valid estimate of the mean edaphic parameters for the plot (Binkley & Vitousek, 1989). We collected the soil samples according to the procedures described in Dick et al. (1996), where each sample was dried in the shade, kept at room temperature, crushed, completely homogenised, and identified, and then sent for chemical and granulometric analysis by the Soil Department of the Federal University of Viçosa (UFV). All soil granulometric analyses (coarse sand, fine sand, silt, and clay fractions) followed the protocol proposed by Donagemma et al. (2017). The measurement of pH in water used 1.0 : 2.5 (v/v) soil : solution ratios. The exchangeable Ca^{2+}, Mg^{2+}, and Al^{3+} cations were extracted by 1 mol/L KCl solution, and the Ca^{2+} and Mg^{2+} contents were determined in the extract by titration with EDTA 0.01 mol/L and the Al^{3+} contents by titration with NaOH 0.025 mol/L, according to Silva et al. (1999). The elements P and K were extracted by Mehlich 1 solution, and the levels of these elements in the extracts were determined by spectrophotometry, according to Silva et al. (1999). Potential acidity (H + Al) was extracted by 0.5 mol/L calcium acetate solution at pH 7.0 and determined by alkalimetric titration of the extract (Silva et al., 1999). The base saturation and aluminium saturation were calculated, respectively as follows (see Alvarez Venegas et al., 1999):

$$\text{Base saturation} = 100 \times \frac{K + Ca^{2+} + Mg^{2+}}{K + Ca^{2+} + Mg^{2+} + H + Al}$$

$$\text{Aluminium saturation} = 100 \times \frac{Al}{K + Ca^{2+} + Mg^{2+} + Al^{3+}}$$

Data analyses

To access the sufficiency of the sampling efforts, we constructed rarefaction curves for species diversity using the function «rare_Rao» from package «adiv» (Pavoine, 2020) in the R environment (R Core Team, 2018) following Ricotta et al. (2012), in which expected species diversity for each sampling site was computed as a function of the cumulative number of plots. We used the resampling approach with 10 000 iterations. We evaluated the pattern of exclusive and shared species among the three studied sites through Venn diagrams constructed for both tree and sapling stratum using the package «VennDiagram» (Chen & Boutros, 2011) in the R environment (R Core Team, 2018).

To compare the mean values of each edaphic factor between sites, we used ANOVA followed by post-hoc pairwise Tuckey tests. We tested the normality of ANOVA residuals using the Shapiro-Wilk test, and when the residuals were non-normal, we used the Kruskal-Wallis followed by post-hoc pairwise Mann-Whitney tests (Quinn & Keough, 2002). To determine the relationships between the edaphic variables and the plant species community, we used the co-inertia analysis. This analysis is a general and flexible method that measures the concordance (also called co-structure) between two multivariate data sets (Dolédec & Chessel, 1994; Dray et al., 2003). We applied the co-inertia analysis to quantify and test the association between two matrices simultaneously. We defined the edaphic matrix as the mean values of 13 edaphic factors across the 45 plots, while the floristic matrix consisted of the incidence (presence and absence) of 174 tree species and 189 sapling species across the 45 plots. The co-inertia analysis results in a value called «RV», which measures the strength of association between the two matrices. The RV value is limited to 0 (i.e. no association) and 1 (i.e. maximum association). We accessed the significance of the co-inertia (p-value) by Monte Carlo permutation, performed with 10 000 randomisations. To implement the co-inertia, we used a standardised and **centred PCA (mean = 0; standard deviation = 1)** for the edaphic matrix, and a centred PCA (mean = 0) for the floristic matrix, according to Dray et al. (2003). To achieve the assumptions of normality in the edaphic data, we used the square root transformation for magnesium (Mg), aluminium (Al), base saturation, and fine sand content. In addition, we used logarithmic transformation for phosphorus (P), calcium (Ca), and clay contents. We performed the co-inertia analysis in the R environment (R Core Team, 2018) using the package «ade4» (Dray & Dufour, 2007). To evaluate the association between each edaphic variable and the co-ordinates of the plots on axis 1 of co-inertia, we used Pearson's correlation, while we defined the association between species and axis 1 of co-inertia by the co-ordinates of the species on this axis (Pavoine et al., 2011).

Results

In this study, we recorded 291 plant species belonging to 49 families, of which 174 species of 45 families at the tree stratum (Table S1), and 189 species of 40 families at the sapling stratum (Table S2). The rarefaction curves shown in Fig. 2 indicate a sufficient sampling of species diversity for the three sites of both tree (Fig. 2a,b,c) and sapling stratum (Fig. 2d,e,f) since the expected species diversity showed a trend for stabilisation.

At the tree stratum, the richest families were Fabaceae (26 species), followed by Myrtaceae (18 species), Lauraceae (12 species), and Melastomataceae (8 species). Twenty families were represented by only one species (Table S1). Regarding the importance value (IV), Fabaceae accounted for 21.3% of IV, followed by Lauraceae (9.2%), Myrtaceae (8.9%), and Sapindaceae (7.4%) (Table S1). The most important tree species was *Hieronyma alchorneoides* Allemão (Phyllanthaceae; IV = 5.8%), followed by *Nectandra megapotamica* (Spreng.) Mez (Lauraceae; IV = 4.0%), *Siparuna guianensis* Aubl. (Siparunaceae; IV = 4.0%), and *Cupania vernalis* Cambess. (Sapindaceae; IV = 3.2%) (Table S1). At the tree stratum 19 taxa could not be identified and these unidentified species accounted for 5.2% of IV.

At the sapling stratum, the richest families were Fabaceae (23 species), followed by Myrtaceae (21 species), Lauraceae (12 species), and Rubiaceae (11 species). Fifteen families were represented by only one species (Table S2). Regarding the IV, the family Fabaceae accounted for 18.2% of IV, followed by Siparunaceae (IV = 11.6%), Rubiaceae (IV = 9.8%), and Myrtaceae (IV = 9.5%) (Table S2). The most important sapling species was *Dalbergia nigra* (Vell.) Allemão ex Benth. (Fabaceae; IV = 11.4%), followed by *Siparuna guianensis* (IV = 7.0%), *S. reginae* (Tul.) A.DC. (Siparunaceae; IV = 4.5%), and *Psychotria vellosiana* Benth. (Rubiaceae; IV = 3.8%) (Table S2). At the sapling stratum, 21 taxa were not identified and these unidentified species accounted for 4.5% of IV.

Ten species from the tree stratum occurred on all three studied sites, namely *Aniba firmula* Mez (Lauraceae), *Annona sylvatica* A.St.-Hil. (Annonaceae), *Dalbergia nigra*, *Guatteria villosissima* A.St.-Hil. (Annonaceae), *Machaerium hirtum* (Vell.) Stellfeld (Fabaceae), *Nectandra oppositifolia* Nees & Mart. (Lauraceae), *Platypodium elegans* Vogel (Fabaceae), *Senna mul-*

tijuga (Rich.) H.S.Irwin & Barneby (Fabaceae), *Siparuna guianensis*, and *Xylopia sericea* A.St.-Hil. (Annonaceae) (Fig. 3a). Among these species, only *Platypodium elegans* stands among the ten most important species from the tree stratum. Most species occurred exclusively on just one site. The number of exclusive tree species on site 1, 2, and 3 were, respectively, 73 (74%), 29 (58%), and 43 (67%) (Fig. 3a). Regarding the sapling stratum, six species occurred on all three studied sites, *Cestrum axillare* Vell. (Solanaceae), *Dalbergia nigra*, *Guatteria villosissima*, *Nectandra oppositifolia*, *Siparuna reginae*, and *Xylopia sericea* (Fig. 3b). With the exception of *Guatteria villosissima* and *Xylopia sericea*, these species stand among the ten most important species of the sapling stratum (Table S2). Similar to the tree stratum, the majority of sapling species were exclusive for one site. The number of exclusive sapling species on site 1, 2, and 3 were, respectively, 64 (67%), 51 (72%), and 39 (62%) (Fig. 3b).
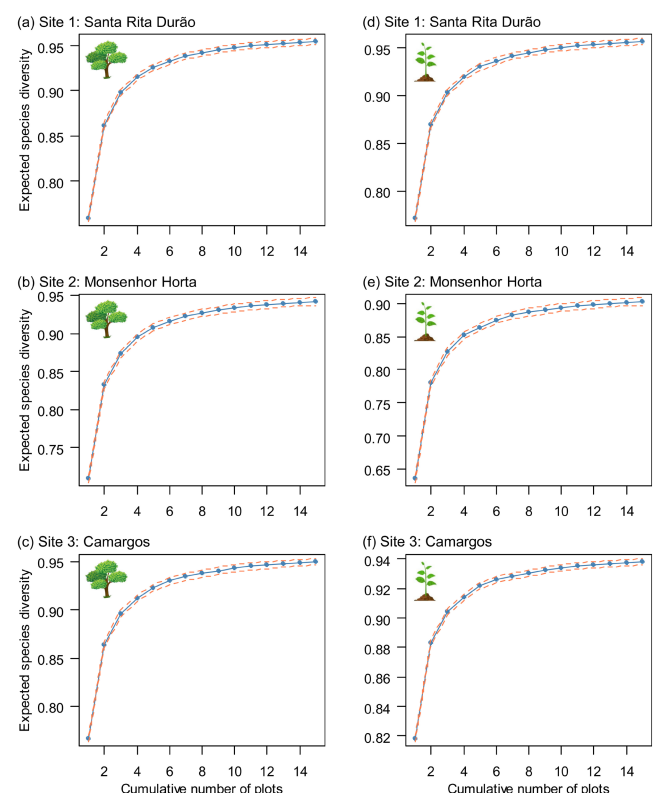

Fig. 2. Rarefaction curves for species diversity (Gini-Simpson index) as a function of sampling effort (cumulative number of plots) on three sampling sites of riparian forests in the upper Rio Doce watershed, Mariana, Minas Gerais, southeastern Brazil. Designations: a, b, c – tree stratum on sites 1, 2, 3, respectively; d, e, f – sapling stratum on sites 1, 2, 3, respectively. Blue dots and continuous line indicate the expected species diversity; red dashed line indicates the 95% confidence interval. The districts of each site are indicated.
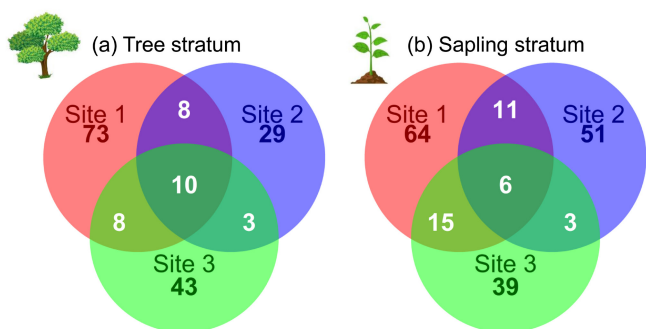
Fig. 3. Venn diagram illustrating the exclusive and shared species among three studied sites from tree (a) and sapling (b) strata of riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Designations: Site 1 – Santa Rita Durão district; Site 2 – Monsenhor Horta district; Site 3 – Camargos district.

The soils of the studied riparian forests showed a considerable variation that indicates a high heterogeneity among the sites (Table 1). According to the soil chemical properties, the pH ranged from highly acidic (3.6) to mildly acidic (6.1), while the aluminium saturation ranged from 0.0% to 90.1%. The base saturation ranged from 1.7% to 67.1%, the content of calcium ranged from 0.0 $cmol_c/dm^3$ to 4.0 $cmol_c/dm^3$, and the content of phosphorus ranged from 0.9 mg/dm^3 to 7.6 mg/dm^3. Regarding the soil texture, there was also a wide variation among the sampling plots (Table 1). The proportion of fine sand ranged from 5.7% to 69.0%, while the proportion of clay ranged from 7.0% to 54.5%. The comparison among sites indicated that there were significant differences among sites for all edaphic factors analysed (Table 1). The soil from site 3 (Camargos district) was significantly more acidic, and less fertile, with a higher aluminium concentration, while the soil from site 1 (Santa Rita Durão district) showed the op-

posite pattern, with less acidic, more fertile, and had a lower aluminium concentration (Table 1).

The co-inertia analysis (COIA) evidenced a clear edaphic-floristic gradient at both tree and sapling strata. The overall association between tree species and edaphic parameters was highly significant (RV = 0.467; p < 0.001) according to the COIA (Monte Carlo with 10 000 permutations). We found a connection of 46.7% between the edaphic and tree floristic matrices. The percentage of covariance explained by the tree stratum COIA axis 1 was 83.7%, while axis 2 explained 10.0% of the covariance. Thus, we further explored only the COIA axis 1. The positive side of the COIA axis 1 showed plots with nutritionally rich and less acidic soils, a higher content of calcium and magnesium, and a higher proportion of fine sand (Fig. 4a). Tree species more strongly associated with the positive side of this axis were *Nectandra megapotamica*, *Schinus terebinthifolia* Raddi (Anacardiaceae), *Guarea guidonia* (L.) Sleumer (Meliaceae), *Eugenia florida* DC. (Myrtaceae), *Syzygium jambos* (L.) Alston (Myrtaceae), and *Dendropanax cuneatus* Decne. & Planch. (Araliaceae) (Fig. 4b). On the other hand, the negative side of COIA axis 1 showed plots with acidic and nutritionally poor soils, with a higher aluminium saturation, a higher content of aluminium, potential acidity (H + Al), phosphorus, and a higher proportion of clay and coarse sand (Fig. 4a). Tree species more strongly associated with the negative side of this axis were *Erythroxylum pelleterianum* A.St.-Hil. (Erythroxylaceae), *Cupania vernalis*, *Piptadenia gonoacantha* (Mart.) J.F.Macbr. (Fabaceae), *Moquiniastrum paniculatum* (Less.) G.Sancho (Asteraceae), *Myrcia guianensis* DC., *M. retorta* Cambess. (Myrtaceae), and *Nectandra oppositifolia* (Fig. 4b).

Table 1. Soil parameters for each sampling site (N = 15 plots per site) in riparian forests in the upper Rio Doce whatershed, Mariana, Minas Gerais, southeastern Brazil

Site	Site 1 Santa Rita Durão M ± SE	Site 2 Monsenhor Horta M ± SE	Site 3 Camargos M ± SE	Statistics (p-value)
pH (H$_2$O)	5.23 ± 0.12[a]	4.61 ± 0.07[b]	3.88 ± 0.05[c]	F = 66.12 (p < 0.001)
P (mg/dm^3)	2.36 ± 0.19[a]	2.41 ± 0.22[a]	4.19 ± 0.42[b]	F = 9.52 (p < 0.001)
K (mg/dm^3)	51.19 ± 3.39[a]	29.72 ± 3.26[b]	54.40 ± 2.03[a]	F = 20.64 (p < 0.001)
Ca (cmol$_c$/dm^3)	1.99 ± 0.24[a]	0.89 ± 0.07[b]	0.33 ± 0.19[c]	H = 27.76 (p < 0.001)
Mg (cmol$_c$/dm^3)	0.87 ± 0.07[a]	0.38 ± 0.03[b]	0.28 ± 0.07[c]	H = 25.10 (p < 0.001)
Al (cmol$_c$/dm^3)	0.12 ± 0.04[a]	0.59 ± 0.06[b]	1.85 ± 0.09[c]	F = 167.80 (p < 0.001)
H+Al (cmol$_c$/dm^3)	4.34 ± 0.55[a]	5.00 ± 0.67[a]	11.55 ± 0.32[b]	H = 26.97 (p < 0.001)
Base saturation (%)	42.79 ± 4.31[a]	24.13 ± 2.88[b]	5.74 ± 1.70[c]	F = 48.58 (p < 0.001)
Al saturation (%)	5.64 ± 2.56[a]	31.00 ± 2.93[b]	75.95 ± 5.15[c]	H = 33.93 (p < 0.001)
Coarse sand (%)	10.27 ± 1.56[a]	14.11 ± 1.95[ab]	19.97 ± 1.91[b]	F = 7.27 (p < 0.01)
Fine sand (%)	38.33 ± 3.12[a]	41.48 ± 3.22[a]	17.37 ± 1.53[b]	H = 28.80 (p < 0.001)
Silt (%)	33.80 ± 2.24[a]	25.95 ± 2.87[a]	17.08 ± 2.06[b]	F = 12.02 (p < 0.001)
Clay (%)	17.60 ± 1.32[a]	18.48 ± 1.68[a]	45.58 ± 1.39[b]	H = 29.42 (p < 0.001)

Note: M – mean value, SE – standard error. Districts of each site are indicated. Lowercase letters denote significant differences (p < 0.05) according to ANOVA (F) followed by the post-hoc Tuckey pairwise test, or Kruskal-Wallis (H) followed by the Mann-Whitney pairwise test when residuals of ANOVA were not normal.
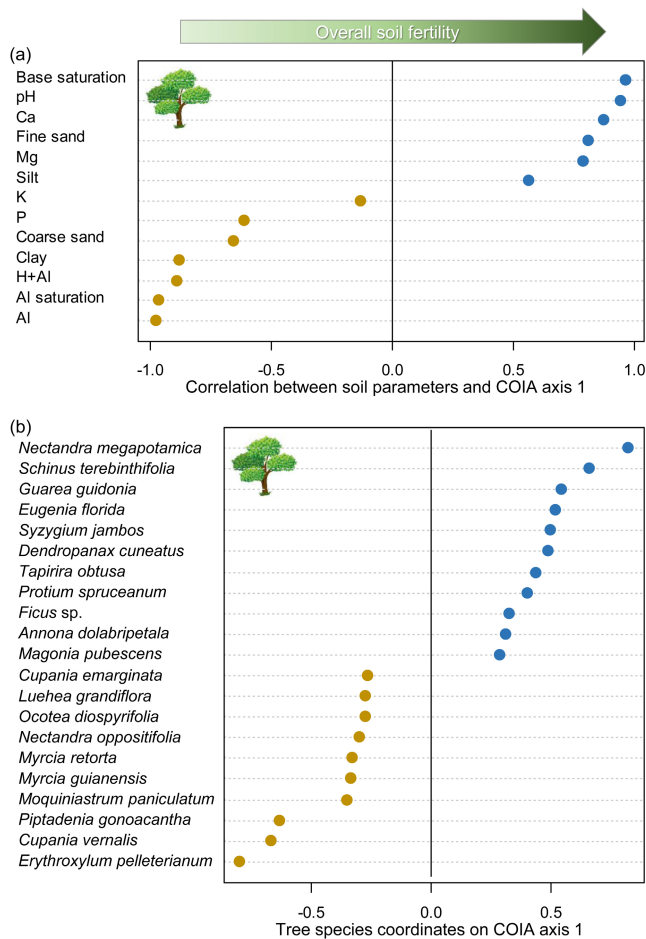
Fig. 4. Co-structure between edaphic parameters and tree species community sampled on three sites from riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Designations: (a) – Pearson's correlation between edaphic factors and plot co-ordinates on co-inertia analysis (COIA) axis 1; (b) – co-ordinates of tree species with highest association with positive and negative side of COIA axis 1. The green arrow at the top indicates the overall direction of the soil fertility gradient. Orange and blue circles represent, respectively, negative and positive values of correlation (a) or co-ordinates (b) on COIA axis 1.

Fig. 5. Co-structure between edaphic parameters and sapling species community sampled on three sites from riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Designations: (a) – Pearson's correlation between edaphic factors and plot co-ordinates on co-inertia analysis (COIA) axis 1; (b) – co-ordinates of sapling species with the highest association with positive and negative side of COIA axis 1. The green arrow at the top indicates the overall direction of the soil fertility gradient. Orange and blue circles represent, respectively, negative and positive values of correlation (a) or co-ordinates (b) on COIA axis 1.

Regarding the sapling stratum, the overall association between sapling species and edaphic parameters was also highly significant (RV = 0.478; p < 0.001) according to the COIA (Monte Carlo with 10 000 permutations). We found a connection of 47.8% between the edaphic and sapling floristic matrices. The percentage of covariance explained by COIA axis 1 was 82.4%, while axis 2 explained 10.7% of the covariance. Thus, similar to the COIA based on the tree stratum, we further explored only the COIA axis 1 for the sapling stratum. The positive side of the sapling-based COIA axis 1 evidenced a very similar pattern to the tree-based COIA, showing plots with nutritionally rich and less acidic soils, with a higher content of calcium and magnesium and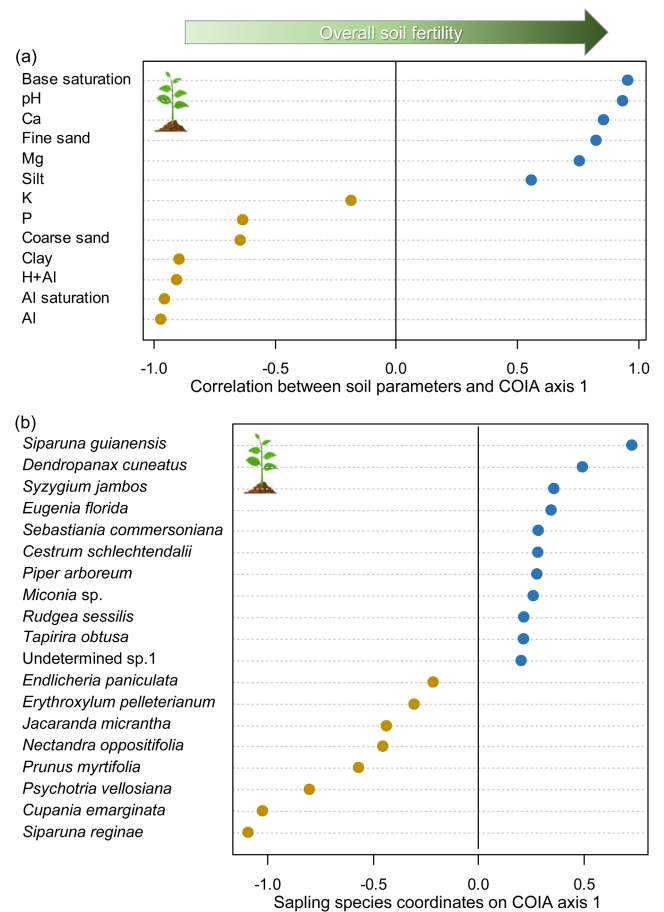 a higher proportion of fine sand (Fig. 5a). Sapling species more strongly associated with the positive side of this axis were: *Siparuna guianensis*, *Dendropanax cuneatus*, *Syzygium jambos*, *Eugenia florida*, *Sebastiania commersoniana* (Baill.) L.B.Sm. & Downs (Euphorbiaceae), and *Cestrum schlechtendalii* G.Don (Solanaceae) (Fig. 5b). On the other hand, likewise the tree stratum COIA, the negative side of sapling-based COIA axis 1 showed plots with acidic and nutritionally poor soils, a higher aluminium saturation, a higher content of aluminium, phosphorus, and a higher proportion of clay and coarse sand (Fig. 5a). Sapling species more strongly associated with the negative side of this axis were: *Siparuna reginae*, *Cupania emarginata* Cambess. (Sapindaceae), *Psychotria vellosiana*, *Prunus myrtifolia* (L.) Urb. (Rosaceae), *Nectan-*

dra oppositifolia, and *Jacaranda micrantha* Cham. (Bignoniaceae) (Fig. 5b).

Discussion

Understanding the processes that drive biodiversity in natural environments is essential for creating effective policies that ensure the success of restoration projects. Phytosociological studies integrated with edaphic factors surveys stand out for their high importance, as they allow the comparison across various sites with varied situations of the same ecosystem. As a result, we may be able to identify the agents or factors that boost the recovery of the environment and assist in the definition of mitigating measures (Balestrin et al., 2019). Furthermore, these studies are indispensable in the process of establishing reference ecosystems, a crucial step in the restoration process, because this information allows us to set goals and to monitor the success of the restoration (Turchetto et al., 2017; Durbecq et al., 2020; Toma et al., 2023). In the present case, scientific knowledge about the reference ecosystem for the proper restoration of the riverine forests in the Rio Doce watershed is fundamental and urgent because many initiatives are being implemented, unfortunately without understanding the native vegetation of the riparian ecosystems.

Our phytosociological data showed a high floristic diversity, in which 820 individuals of in total 291 species were sampled in the tree stratum, and 899 individuals belonging to 189 species were sampled in the sapling stratum. The number of species reflects the high floristic diversity found in the Atlantic Forest, shaped by local environmental conditions, such as variation in soil quality (Fagundes et al., 2019; Figueiredo et al., 2022) and successional stages (Forzza et al., 2012). Here, we found a predominance of species from the Fabaceae and Myrtaceae families, corroborating previous floristic surveys conducted at various regions of the Atlantic Forest (Oliveira et al., 2011; Miranda et al., 2019; Dias et al., 2021). These families are important indicators of community development (Tabarelli et al., 1994; Gei et al., 2018). Some species from the Myrtaceae family are indicators of the forest quality, where degraded habitats tend to have lower species richness of this family (Amorim et al., 2009; Rigueira et al., 2013). The Fabaceae family is widely distributed in the Neotropical forests and many species are nitrogen-fixing, contributing to a greater availability of this nutrient in the ecosystem (Gei et al., 2018).

Among all species sampled in the sapling stratum, *Dalbergia nigra* stood out by presenting the highest importance value. This species has a distribution restricted to the Atlantic Forest (Silva Júnior et al., 2022), and is known for its economic and ecological potential (Carvalho, 1994). Due to the overexploitation of *Dalbergia nigra* populations and anthropic impacts on its natural habitat (Ribeiro et al., 2011b), this species is classified as Vulnerable in relation to the risk of extinction (Varty, 1998). This pioneer species is classified as evergreen to semideciduous and occurs on well-drained slopes, as well as inside dense primary forests and in secondary formations (Lorenzi, 1992). *Dalbergia nigra* produces a high abundance of seeds, allowing it to colonise a wide variety of environments. These ecological traits make *Dalbergia nigra* a species with great potential for mitigation projects or in the recovery of degraded environment, besides influencing the nutritional factors of the soil due to its nitrogen-fixing capability (Silva Júnior et al., 2020).

The species with the highest IV for both tree and sapling stratum are predominantly composed of species with zoochoric dispersal. For example, in the sapling stratum, *Siparuna guianensis* and *S. reginae* are respectively the second and third most important species in the studied riparian forests. *Siparuna guianensis* has fruits dispersed mainly by ants, birds, and mammals (Oliveira & Paula, 2001; Magalhães et al., 2018), and *Siparuna reginae* has also a zoochoric dispersal (Armando et al., 2011). The association of these species with animals helps to promote the recovery of ecosystem services and favours the structuring of these environments. The recurrence of species with zoochoric dispersal is a pattern commonly found in other studies in the Atlantic Forest (Oliveira et al., 2011; Suganuma et al., 2013; Franco et al., 2014). Plant species dispersed by animals can accelerate the successional process, facilitating the recovery of ecosystems (Sansevero et al., 2011). The local fauna is an important driver of the spatial distribution of vegetation in forest ecosystems (Negrini et al., 2012; Franco et al., 2014) increasing the genetic variability of species (Almeida et al., 2008). Limiting factors that affect dispersal simplify species composition, where closer communities tend to have similar composition, even without taking into account ecological similarity (Beaudrot et al., 2013).

Our data support the importance of soil characteristics in modulating the structure of plant

species composition in tropical forests (e.g. Veloso et al., 2014; Coelho et al., 2018; Fagundes et al., 2019; Figueiredo et al., 2022; van der Sande et al., 2023). We found congeneric species associated with opposite conditions of the edaphic gradient, both in the tree and sapling stratum. In the sapling stratum *Siparuna guianensis* was associated with less acidic, nutritionally richer soils with a higher proportion of fine sand. On the other hand, *Siparuna reginae* was associated with more acid soils, nutritionally poor, and a higher proportion of clay. Therefore, we emphasise that the results found here should not be extrapolated to other taxonomically close species, because in many cases species of the same genus may respond in contrasting ways to the characteristics of each location, as shown here. Similarly, the congeneric pair of the tree stratum, *Nectandra megapotamica* and *N. oppositifolia*, were associated with opposite edaphic gradient conditions. *Nectandra megapotamica* was associated with less acidic and nutritionally richer soils. This species is classified as late secondary, shade tolerant, and strongly associated with moist soils (Lorenzi, 1998). On the other hand, *Nectandra oppositifolia* was associated with more acidic soils, nutritionally poor, and with a higher proportion of clay. *Nectandra oppositifolia* has a rapid growth in both the early and secondary stage, and its fruits are dispersed by birds (Gandolfi et al., 1995). Pioneer species that dominate early succession stages are fundamental in facilitating processes, helping plant community re-composition (Kong et al., 2023). Thus, *Nectandra oppositifolia* potentially plays an important role in the recruitment of species in areas with relatively more restrictive edaphic characteristics.

Conclusions

Understanding how ecological and life-history traits of plant species, such as dispersal mechanisms and growth relate to edaphic factors is an important step to providing scientific-based knowledge to support policies for ecosystem recovery and restoration (Garnier et al., 2004; Kattge et al., 2011). We emphasise that studies of this nature must be conducted in various regions of the Atlantic Forest to broaden our knowledge about the association patterns between plant species and soil characteristics of this mega-diverse ecosystem. These patterns of association are extremely important because of modifying patterns of richness and act on species composition, showing that each type of habitat needs specific conservation plans for the ecosystem. Our results provide a solid attempt to generate information for reference ecosystems in the Rio Doce watershed, southeast Brazil, a region subjected to large-scale human disturbances that need urgent restoration practice.

Supporting Information

Additional data for the paper of Figueiredo et al. (2024) may be found in the **Supporting Information**.

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ЭТАЛОННЫЕ УЧАСТКИ ПРИБРЕЖНЫХ АТЛАНТИЧЕСКИХ ЛЕСОВ, НАХОДЯЩИЕСЯ ПОД УГРОЗОЙ ИСЧЕЗНОВЕНИЯ В ВЕРХНЕЙ ЧАСТИ ВОДОРАЗДЕЛА РИУ-ДОСИ

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Наиболее важной особенностью экологического восстановления является выявление эталонных экосистем, которые могут служить для сравнения биологической целостности, структуры и функций экосистем. Чтобы проекты по восстановлению и сохранению экосистем были эффективными в современном сценарии снижения биоразнообразия и экосистемных услуг во всем мире, крайне важно понимать взаимодействие почвы и растений в каждой среде обитания. В этом исследовании мы оценили структуру и состав флоры на 45 участках, равномерно распределенных на трех охраняемых территориях (эталонных экосистемах) Атлантического леса в верхней части водораздела Риу-Доси на юго-востоке Бразилии. Мы также проверили, влияют ли на различия в видовом составе эдафические факторы в ярусе деревьев и ярусе подроста. В обоих ярусах наибольшим числом видов были представлены семейства Fabaceae, Myrtaceae и Lauraceae. Также для семейства Fabaceae было отмечено наивысшее значение значимости в обоих ярусах. Почвы прибрежных лесов на исследованных участках отличались высокой неоднородностью. Анализ коинерции показал явный эдафически-флористический градиент как для яруса деревьев (RV = 0.467; p < 0.001), так и для яруса подроста (RV = 0.478; p < 0.001) со связью 46.7% и 47.8% между эдафической и флористической матрицами для деревьев и подроста соответственно. На каждом исследуемом участке мы определили группы видов деревьев и подроста, которые были тесно связаны с почвами либо более богатыми, либо более бедными питательными веществами. Понимание того, как особенности экологии и жизненного цикла растений связаны с эдафическими факторами, является важным шагом на пути получения научно обоснованных знаний для поддержки политики восстановления экосистем на участках водораздела Риу-Доси.

Ключевые слова: взаимоотношения таксон – окружающая среда, охраняемый лес, структура растительности, фитоценология, ярус деревьев, ярус подроста