Anthropocene 49 (2025) 100462

Contents lists available at ScienceDirect

Anthropocene

journal homepage: www.elsevier.com/locate/ancene

Mining tailings severely impact plant communities in a rainforest watershed

G. Wilson Fernandes [a,b], Letícia Ramos [a], Wénita de Souza Justino [a], Walisson Kenedy-Siqueira [a], João Carlos Gomes Figueiredo [c], Yumi Oki [a], Fernando Figueiredo Goulart [a], Rubens Manoel dos Santos [d], João Herbert Moreira Viana [e], Yule Roberta Ferreira Nunes [f], Ramiro Aguilar [g], Lourens Poorter [h], Masha T. van der Sande [h], Daniel Negreiros [a,b,*]

[a] *Ecologia Evolutiva & Biodiversidade, Departamento de Genética, Ecologia e Evolução/ICB, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais 31270-901, Brazil*
[b] *Knowledge Center for Biodiversity, Belo Horizonte, Minas Gerais 31270-901, Brazil*
[c] *Departamento de Biologia Geral, Centro de Ciências Biológicas e da Saúde, Programa de Pós-Graduação em Biotecnologia - PPGB, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais 39401-089, Brazil*
[d] *Departamento de Ciências Florestais, Universidade Federal de Lavras, CP 3037, Lavras, Minas Gerais 37200-000, Brazil*
[e] *Embrapa Milho e Sorgo, Empresa Brasileira de Pesquisa Agropecuária (Embrapa), Rod. MG-424, Km 45, Sete Lagoas, Minas Gerais 35701-970, Brazil*
[f] *Programa de Pós-Graduação em Botânica Aplicada, Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais 39401-089, Brazil*
[g] *Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba – CONICET CC 495, (5000), Córdoba, Argentina*
[h] *Forest Ecology and Forest Management Group, Wageningen University, Wageningen, the Netherlands*

A R T I C L E I N F O

Keywords:
Ecological restoration
Mining tailings
Reference ecosystems
Rio Doce watershed
Samarco dam breach
Soil-vegetation relationship

A B S T R A C T

The collapse of a mining tailings dam in 2015 drastically affected a large area of an already threatened Atlantic Forest along the Rio Doce in Brazil. We evaluated the interactions between edaphic and floristic factors in impacted and reference sites to understand how the impact of the tailings affected the riparian plant communities along the river. The species richness of the adult and sapling strata was, respectively, 46.4 % and 61.5 % lower in the impacted sites relative to the reference sites. A similar pattern was observed for both species and phylogenetic diversity. We also recorded large changes in species composition in the adult and sapling strata in impacted sites relative to the reference sites along the river. These negative changes in the plant community were correlated with drastic increases in soil iron and phosphorus concentration, and fine sand proportion, and decreases in the proportion of carbon and coarse sand in the sites impacted by the mining tailings. We observed a close relationship between plant composition in both the adult and sapling strata with edaphic factors. The alterations in species composition triggered by the deposition of mining tailings may induce significant shifts in ecosystems, potentially prompting numerous tipping points throughout the river basin, as indicated by the different sapling species, some of which are invasive species of highly difficult eradication. These altered forests might suffer from impoverishment, dominated by a limited species set, some of which could expand its distribution upon neighboring, already threatened, regions. Such expansion could exacerbate the degradation of the Rio Doce watershed to a point of no return to the previous condition.

1. Introduction

Nine years have passed since Brazil's worst ecological disaster, the collapse of the Samarco mine tailings dam, where dozens of millions cubic meters of iron tailings were released into the Rio Doce basin (Fernandes et al., 2016a; Segura et al., 2016). The tsunami of tailings caused the immediate loss of approximately 1469 ha of rain forest vegetation, deeply affecting the riverine ecosystems and their ecological

* Corresponding author at: Ecologia Evolutiva & Biodiversidade, Departamento de Genética, Ecologia e Evolução/ICB, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais 31270-901, Brazil.
E-mail address: negreiros.eco@gmail.com (D. Negreiros).

https://doi.org/10.1016/j.ancene.2025.100462
Received 5 October 2024; Received in revised form 2 January 2025; Accepted 16 January 2025
Available online 22 January 2025

interactions, besides directly killing 19 people (Fernandes et al., 2016a).

Mining tailings in the Iron Quadrangle contain high levels of iron (primarily hematite) and manganese (Schaefer et al., 2015; Guerra et al., 2017). The deposition of these metals compacted the soil along the Rio Doce, creating a physical barrier that waterproofs the surface, hinders root growth, and disrupts both agricultural use and natural regeneration (Schaefer et al., 2015; Guerra et al., 2017; Hatje et al., 2017). This degradation hinders seed and propagule penetration, directly impacting the system's regenerative capacity and ecological functions (Mesquita et al., 2001; Fernandes et al., 2016a). Consequently, bold ecological restoration measures are urgently required for the watershed.

Ecological restoration aims to recover ecosystem functionality by restoring biodiversity, habitat connectivity, and ecosystem services (Rodrigues et al., 2009; Fernandes et al., 2016b; Rosenfield et al., 2022). To achieve this, it is essential that restoration be based on the selection and use of reference areas, from which information is obtained from the best available native ecosystems in the region (Gann et al., 2019; Rosenfield et al., 2022; Toma et al. 2023, 2024). Thus, a set of reference ecosystems is necessary to guide restoration efforts in environments such as the Rio Doce basin (Ramos et al., 2024).

Tropical forests are among the richest and most complex terrestrial ecosystems, supporting a vast array of life forms and possessing a remarkable intrinsic capacity for self-maintenance (Wilson, 1988; Baboo et al., 2017). However, this capacity has been increasingly compromised by excessive pressures caused by climate change and anthropogenic disturbances linked to pollution, deforestation, species invasion, among others (Htun et al., 2011; Bargali et al., 2019; Negi et al., 2024). The success of restoration projects in these forests depends largely on the recovery and reestablishment of soil properties, which create microhabitats that shape the composition and structure of the forest, influencing the establishment of species (van der Sande et al., 2023; Fernandes et al., 2016a; Coelho et al., 2018; Ramos et al., 2024). The loss of plant diversity is a major challenge faced by ecosystems in maintaining the stability and functional sustainability (Hua et al., 2022; Bisht et al., 2023). Understanding the synergistic interactions between soil factors and reference vegetation is essential for comparing communities, assessing functional attributes, and measuring the progress and effectiveness of restoration efforts.

Assessing the relationships between soil properties and vegetation composition is the first step towards understanding the factors and conditions that promote the recovery of biodiversity in degraded ecosystems. This study provides a solid baseline of the plant community along the Rio Doce, comparing the plant community in the adult and sapling layers of the best-preserved remnants of riparian forests available in the region and the impacted riparian forests to guide restoration and aid in the mitigation of the effects of the collapse of Samarco's Fundão dam. This knowledge should result in better restoration planning leading to greater ecosystem connectivity and in positive net gain in biodiversity. Our main objective is to assess the state of natural regeneration of the impacted sites along the Rio Doce seven years after the dam collapse through comparisons with reference sites, thus providing a sound scientific basis for ecological restoration. We evaluated the relationship between the floristic composition of adult and sapling strata and soil quality in both impacted and reference sites. Additionally, we analyzed how landscape properties influenced vegetation composition. We hypothesized that i) Sites affected by the deposition of tailings have different soil characteristics from the reference sites. We expect to find higher concentration of heavy metals and lower concentration of organic matter in the sites impacted by tailings; ii) Tailings deposition severely decreased the richness and diversity of species and phylogenetic diversity of the adult and sapling species strata in relation to reference sites; iii) The deposition of tailings will benefit some species while harming others, directly influencing species composition in the affected sites; iv) There is a strong turnover of plant species in the adult and sapling strata along the river in both the impacted and reference sites; v) Floristic diversity in the impacted sites are more affected by edaphic parameters than by the land use conversion of the surrounding landscape (i.e. forest cover).

2. Material and methods

2.1. Study area

The study was carried out in five riparian forest regions located along the Rio Doce watershed, Minas Gerais, southeastern Brazil (Fig. 1). The five regions were selected in this study because of the availability of preserved riparian forests along the river basin. The dominant vegetation type in the study regions is Atlantic Rain Forest. Mariana (dam breached region), Rio Casca, and Ipatinga regions are located in the upper sector of the basin, while Conselheiro Pena, and Aimorés regions are located in the middle sector of the basin (Table S1). In each region, three unaffected sites and three impacted sites were selected for the study; hence totaling six studied sites per region (Fig. 1; Table S1). The riparian forests in good state of conservation (i.e., late secondary, and old growth forests) were separated at least 2 km from each other, and these forest patches were heretofore called Reference sites (see Ramos et al., 2024). The three impacted sites selected in each region suffered the deposition of tailings from the Samarco dam collapse (see Fernandes et al., 2016a) (Fig. S1).

In this study, regions were defined as spatially proximate sets comprising three impacted sites and three reference sites. These regions were selected exclusively within the state of Minas Gerais, extending from the site of the dam collapse to the towns near Aimorés, the last municipality of Rio Doce watershed in the state. In spite the fact that the mining sludge impacted the entire Rio Doce basin (e.g., Fernandes et al., 2016a), extending all the way to its mouth in the state of Espírito Santo, our evaluation of the impact of the mining tailings deposition on plant communities was done until the municipality of Aimorés at the border of the states of Minas Gerais and Espirito Santo. To select the impacted and reference sites, the most preserved stretches of riparian forest were chosen, ensuring that the forest composition was as similar as possible, with the primary distinction being the deposition of tailings. Furthermore, the selection of impacted sites was done based on visible deposition of mining tailings on the soils of the site. These sites also had to meet other attributes such the maximum proximity to the reference sites, and similar forest structure before the tailings deposition. A total of 20 field campaigns, each lasting more than 15 days, were conducted over two years.

The data on the reference sites used in this study came from a series of studies carried out by our research group. For details on the Mariana region consult Figueiredo et al. (2022, 2024); for Rio Casca see Justino et al., (unpublished manuscript); for Ipatinga see Ramos et al. (2023); for Conselheiro Pena see Souza et al. (2024), and for Aimorés see Sousa et al. (2024). A summary for the trends in the vegetation structure of the reference sites along the entire Rio Doce watershed can be found in Ramos et al. (2024).

2.2. Vegetation and soil sampling

We used the sampling method of fixed area plots (Mueller-Dombois and Ellenberg, 1974) for the phytosociological surveys carried out in 2021–2022, seven years after the disaster. For the phytosociological surveys of the adult stratum in each region, we deployed 90 plots of 10×10 m (100 m^2), 45 plots in the reference sites (distributed over 3 sites with 15 plots each) and 45 plots in impacted sites, totaling 9000 m^2 per region. This totaled 450 plots (45,000 m^2) for the study. For sampling the sapling stratum, we allocated one 5×5 m (25 m2) sub-plot in the lower left corner (watercourse direction) of each 10×10 m plot (for details on each sampled site see the references mentioned above).

The parameters analyzed for the plant community included absolute and relative values of density (the number of individuals per species), dominance (based on the sum of basal area per species), frequency (the

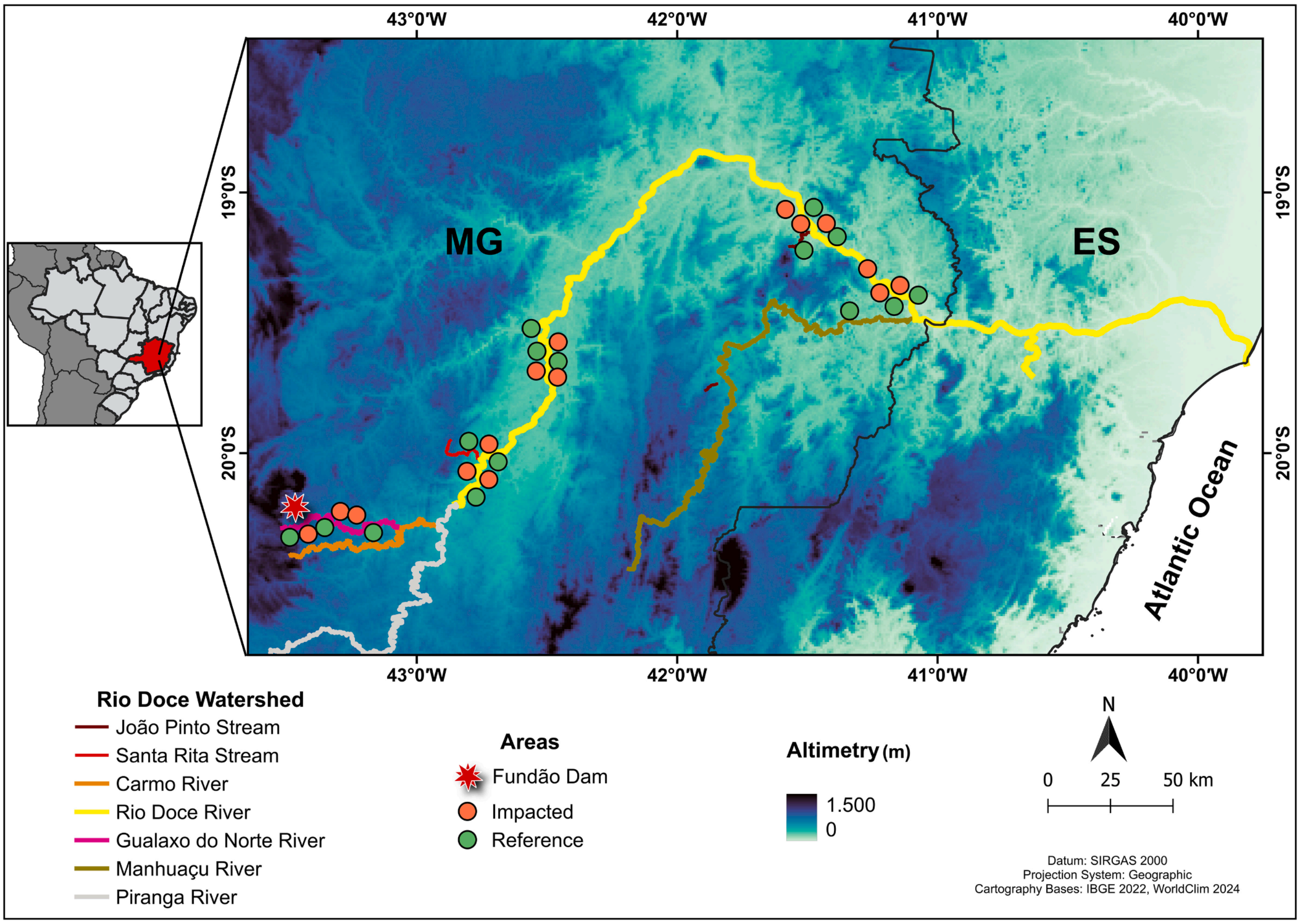

Fig. 1. Map showing the location of the 5 sampling regions (green circles = Reference; orange circles = Impacted) along the Doce River basin, southeastern Brazil.

number of occurrence plots per species), and the importance value (IV) (Mueller-Dombois and Ellenberg, 1974). These parameters were compared to data obtained from phytosociological studies conducted in reference sites during field studies (see Figueiredo et al., 2022, 2024; Ramos et al., 2023; Justino et al., unpublished manuscript; Sousa et al., 2024; Sousa et al., 2024). In each of the 450 sampled plots, we also collected five soil samples of approximately 100 g each (one at each point and one in the middle) from 0 to 20 cm deep; then these five samples were homogenized *in situ* and transformed into a composite sample per plot.

2.3. Land conversion

To classify forest cover at each sampling site, we mapped land cover using Landsat8 satellite images from the entire base year 2022. We created 300 m and 1 km buffers around the sampling sites and overlaid them with 30 × 30 m resolution vegetation maps developed by MapBiomas (https://mapbiomas.org/). The selection of 300 m and 1 km buffers aimed to assess the influence of the surrounding landscape at two distinct spatial scales: a local scale (300 m) to capture immediate environmental characteristics, and a broader scale (1 km) to evaluate larger landscape-level effects on studied sites.

2.4. Statistical analysis

We made all analyses in the R environment (R Core Team, 2023). We conducted all analyses separately for communities of the adult and sapling strata (in both impacted and reference sites). To test hypothesis (i), that tailings deposition alters soil characteristics, and hypothesis (ii), which posits a decrease in species richness, diversity and phylogenetic diversity in impacted sites, Generalised Linear Mixed Models (GLMM) were built to explore the differences between reference and impacted sites in terms of plant richness, plant diversity, forest cover and soil attributes. In these models, we treated sites and regions as random effects, with sites nested within regions in each model. We determined the significance of the models by means of analysis of variance (ANOVA) using the 'lme4' package (Bates et al., (2015). To highlight the distinction between plant species richness between impacted and reference sites, we also used rarefaction curves made using the 'iNEXT' package (Hsieh et al., (2016). To compare phylogenetic diversity between impacted and reference sites, we generated phylogenies for both plant strata using the 'V.PhyloMaker2' package (Jin and Qian, 2022).

To address hypothesis (iii), that tailings deposition favors certain species and disadvantages others, affecting species composition, we constructed Euler diagrams for the adult and seedling strata using the 'eulerr' package (Larsson, 2022). To explore the similarity of the floristic composition between the impacted and reference sites (N = 15 sites per condition), we converted the floristic surveys into matrices with species incidence (presence/absence) per site. Subsequently, to order the sampled communities, we calculated the Sorensen distance using the 'vegdist' function from the 'vegan' package (Oksanen and others, 2022), which operates with presence/absence values. We then carried out a principal coordinates analysis (PCoA) to determine the two main axes of variation in the floristic composition matrix. To visualize the impacted and reference groups, we created a factor map using the 's.class' function of the 'ade4' package (Dray and Dufour, 2007). To test for significant differences between the impacted and reference sites in terms of floristic composition, we used a similarity analysis (ANOSIM) using Sorensen's distance, following the approach described by Quinn and Keough (2002), with the 'with' function from the 'base' package.

For hypothesis (iv), which suggests a significant turnover of species along the river in both strata, we calculated the partitioning of diversity between sites, species composition using total beta diversity by means of Sorensen's dissimilarity index (Baselga, 2010). In addition to total beta diversity (βSor), we calculated turnover using Simpson's dissimilarity index (βSim) to assess species change and calculated nesting as the difference between βSor and βSim. Furthermore, to examine variation in composition between sites, we calculated beta diversity in pairs using the 'betapart' package (Baselga and Orme, 2012).

Finally, to test hypothesis (v) that floristic diversity at impacted sites is more influenced by soil parameters than by the characteristics of the surrounding landscape (e.g. forest cover) we performed a co-inertia analysis (COIA). This analysis measures the agreement between two sets of multivariate datasets, also known as co-structure (Dray et al., 2003). Furthermore, we used Pearson's correlation to assess the association between each soil parameter and COIA axis 1, while we used species coordinates on axis 1 to determine the association between species and COIA axis 1. We made the COIA using the 'ade4' package (Dray and Dufour, 2007).

3. Results

3.1. Soil differences between impacted and reference sites

The physicochemical parameters of the soils in the impacted and reference sites differed significantly. The concentration of iron found in the impacted sites (average concentration = 144.9 mg dm^{-3}) was twofold higher compared to the reference sites (average concentration = 77.7 mg dm^{-3}) ($F = 6.52$; $p = 0.010$; Fig. S2A). Phosphorus levels in the soil of impacted sites (average concentration= 6.6 mg dm^{-3}) were also twice higher in reference sites (average concentration = 3.3 mg dm^{-3}) ($F = 8.36$; $p < 0.001$; Fig S2B). Potential acidity (H+Al) in the impacted sites was significantly lower (average concentration = 2.2 $cmol_c$ dm^{-3}) than in the reference sites (average concentration = 3.9 $cmol_c$ dm^{-3}) ($F = 6.26$; $p = 0.010$; Fig. S3A). Organic carbon concentration in the soil was also lower in the impacted sites (average proportion = 1.2 %) than in reference ones (average proportion = 1.7 %) ($F = 4.43$; $p = 0.040$; Fig. S3B). Regarding soil texture, we found that the proportion of fine sand was 52 % higher in the impacted sites (average proportion = 38.5 %) compared to the reference sites (average proportion = 25.4 %) ($F = 5.77$; $p = 0.020$; Fig. S4A). Finally, the concentration of coarse sand was almost 59 % lower in impacted sites (average proportion = 17.7 %) than in reference sites (average proportion = 30.2 %) ($F = 6.22$; $p = 0.010$; Fig. S4B). For a complete data on average soil parameters for each studied site, see Table S2.

3.2. General plant community in impacted sites

We recorded 1225 individuals from the adult stratum and 723 individuals from the sapling stratum, totaling 1948 individuals sampled in the impacted sites. These specimens belonged to 242 plant species of 45 different plant families. These included 143 species from the adult stratum (Table S3) and 117 species from the sapling stratum (Table S4). In all impacted sites, 36 plant families in the adult stratum were sampled, with the most well represented ones being Fabaceae, with 34 species, followed by Lauraceae and Myrtaceae, both with 9 species each. In the adult stratum, the species with the highest average importance value (IV) was *Guarea macrophylla* (IV: 18.6 %), followed by *Astronium urundeuva* (IV: 5.4 %), and *Plathymenia reticulata* (IV: 3.6 %). For the sapling stratum, 35 families were recorded, with the Fabaceae family accounting for 28 species, followed by Myrtaceae with 12 species, and Sapindaceae with 6 species. In this stratum, the species with the highest average IV was *E. florida* (IV: 10.6 %), followed by *A. urundeuva* (IV: 8.1 %), and *Cupania vernalis* (IV: 4.5 %).

3.3. Community richness, species and phylogenetic diversity trends

We recorded a sharp difference between plant species richness in impacted and reference sites in both adult (Fig. 2A) and sapling (Fig. 2B) strata. Overall, the species richness of the adult stratum was 46.4 % lower in the impacted site (average per plot = 3.2 species) relative to the reference sites (average per plot = 6.1 species) ($\chi^2 = 13.92$; $p < 0.0001$; Fig. 3A). Similarly, the species richness of the sapling stratum was 61.5 % lower in the impacted sites (average per plot = 2.2 species) relative to the reference sites (average per plot = 5.8 species) ($\chi^2 = 24.85$; $p < 0.0001$; Fig. 3B). In general, we recorded greater species diversity in the reference sites along the watershed. In the Mariana region the species richness of the adult stratum in the impacted sites was 42.4 % lower than that in the reference sites (Impacted average = 1.9 species; Reference average = 3.3 species; Fig. 3A). The sapling stratum also varied in a similar way, with the impacted sites being 86.4 % lower in relation to reference sites (Impacted: 1.4; Reference: 10.3; Fig. 3B). In the Rio Casca region, the species richness of the adult stratum of the impacted sites was 4.4 % lower than that of the reference sites (Impacted: 4.3; Reference: 4.5; Fig. 3A). The sapling stratum also varied in a similar way, with the impacted sites being 10.9 % lower (Impacted: 4.1; Reference: 4.6; Fig. 3B). In the Ipatinga region, the species richness of the adult stratum of the impacted sites was 27.6 % lower than the reference sites (Impacted: 4.2; Reference: 5.8; Fig. 3A). For the sapling stratum we observed a richness 73.4 % lower in the impacted sites compared to reference sites (Impacted: 1.7; Reference: 6.4; Fig. 3B). In the Conselheiro Pena region, in contrast to the other evaluated sites, the species richness of the adult stratum was 90.9 % higher in the impacted sites compared to reference sites (Impacted: 4.2; Reference: 2.2; Fig. 3A). For the sapling stratum we observed a richness 40.0 % lower in the impacted sites compared to reference sites (Impacted: 1.2; Reference: 2.0; Fig. 3B). In the Aimorés region the species richness of the adult stratum of the impacted sites was 51.6 % lower compared to reference sites (Impacted: 3.1; Reference: 6.4; Fig. 3A). For the sapling stratum we also observed a richness 61.1 % lower in the impacted sites compared to reference sites (Impacted: 2.1; Reference: 5.4; Fig. 3B).

The Shannon diversity index also highlighted statistical differences between the impacted and reference sites, with the adult stratum diversity 45.5 % lower in the impacted sites (average per plot = 0.58) relative to the reference sites (average per plot = 1.07) ($F = 14.53$; $p < 0.0001$; Fig. 4A). Similarly, the Shannon diversity index of the sapling stratum was 63.9 % lower in the impacted sites (average per plot = 0.42) relative to the reference sites (average per plot = 1.18) ($F = 24.15$; $p < 0.0001$; Fig. 4B).

Trends in taxonomic diversity were also observed when we analyzed the phylogenetic diversity. In the adult stratum the phylogenetic diversity was 6.2 % lower in impacted sites (average per plot = 1.10) compared to reference sites (average per plot = 1.18) ($F = 17.31$; $p < 0.0001$; Fig. S5A). In the sapling stratum phylogenetic diversity followed the same trend, being 33.5 % lower in impacted sites (average per plot = 1.45) compared to reference sites (average per plot = 2.18) ($F = 16.08$; $p < 0.0001$; Fig. S5B).

3.4. Beta diversity and composition along the river

The variation in adult species composition through total beta diversity was very high in both the impacted (Fig. 5A) and reference sites (Fig. 5B). In the adult stratum, the beta diversity observed for the impacted sites was 89 %, while in the reference sites it was 93 %. This high variation observed in species composition was mainly due to turnover both at impacted sites (89 %) and at references (90 %), while the nesting component accounted only to 3 % in both impacted and reference sites (Fig. 5). On the other hand, we found a similar pattern of

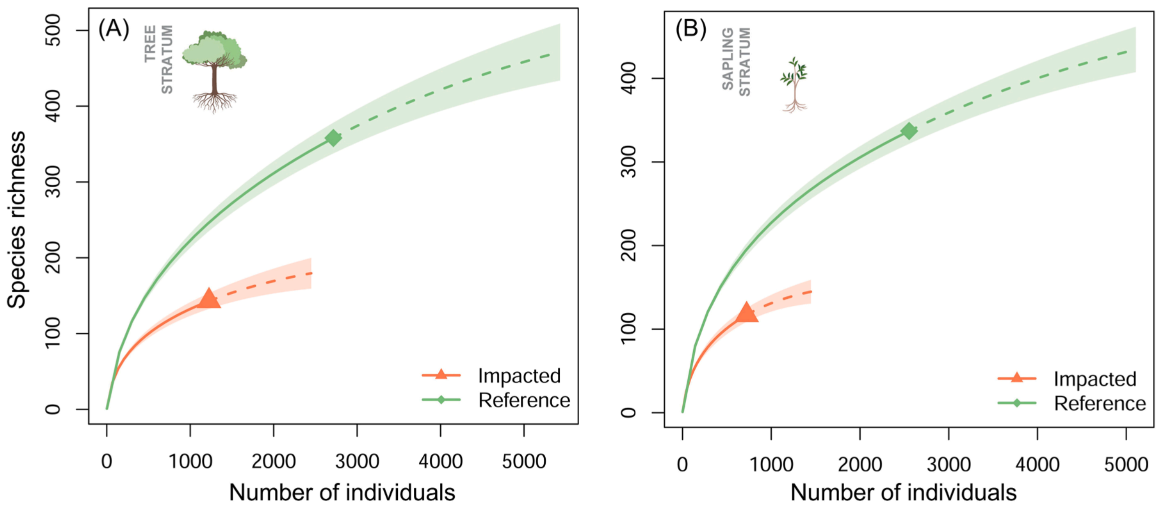

Fig. 2. Rarefaction curves showing estimated species richness for impacted (orange) and reference (green) sites at the adult (A) and sapling (B) strata along the Rio Doce watershed in Minas Gerais, Brazil. Dashed line denotes the extrapolation of the curve that represents the double of sampled number of individuals. It is shown the confidence intervals in light color.

very high beta diversity in the sapling stratum, where the impacted sites showed 93 % (Fig. 6A) while reference sites showed a beta diversity of 93 % (Fig. 6B). Similar to the adult stratum, the high variation in species composition observed in the sapling communities was mainly due to turnover in both impacted (88 %) and reference sites (89 %), while the nesting component was negligible in both impacted (4 %) and reference sites (3 %; Fig. 6).

Regarding the distance based in species composition, we found a clear distinction between impacted and reference sites (Fig. 7). The first two axes of the PCoA analysis of the adult stratum explained, respectively, 12.5 % and 9 % of the total variation in floristic composition of all studied sites (Fig. 7A), while in the sapling stratum these axes explained respectively 12.6 % and 9.2 % of total compositional variation (Fig. 7B). The floristic composition differed significantly between the impacted and reference sites in both the adult stratum (ANOSIM: $r = 0.174$; $p = 0.003$; Fig. 7A) and the sapling stratum (ANOSIM: $r = 0.206$; $p < 0.001$; Fig. 7B). There was a low overlap between impacted and reference sites, and the directional change in species composition can be inferred by the distance between the centroids of the impacted and the reference sites, caused by the mining tailings that may have favored some species and impaired others. Since the occurrence of species determines the position of each site in the multivariate space, such low overlap between groups indicates a clear effect of mine tailing deposition on the floristic composition of the studied riparian forests (Fig. 7).

3.5. Species sharing between impacted and reference sites

In the adult stratum, species richness in impacted sites varied widely across regions (Fig. 8). In Mariana, only 25 adult species were recorded in impacted sites, representing 14.6 % of the species found in reference sites. In Rio Casca, 50 adult species were identified, equivalent to 61.7 % of the richness recorded in reference sites, while in Ipatinga, 52 species were found, corresponding to 65.8 % of the richness recorded in reference sites. Conselheiro Pena showed a contrasting pattern, with 37 species recorded in impacted sites, exceeding the richness recorded in reference sites by 132.1 %. In Aimorés, 32 adult species were sampled, equivalent to 31.4 % of the species richness recorded in reference sites.

For the sapling stratum, a total of 59 species were recorded across both conditions, representing 50.4 % of the richness in impacted sites and 17.5 % in reference sites (Fig. 8). Regionally, in Mariana, only 19 sapling species were recorded in impacted sites, corresponding to 10.3 % of the richness recorded in reference sites. In Rio Casca, 52 sapling species were identified, representing 65.8 % of the richness recorded in reference sites. Ipatinga showed 28 sapling species in impacted sites, corresponding to 32.2 % of the richness recorded in reference sites, while in Conselheiro Pena, 15 sapling species were sampled, equivalent to 55.6 % of the richness recorded in reference sites. Finally, in Aimorés, 31 sapling species were recorded, corresponding to 36.5 % of the richness recorded in reference sites.

3.6. Relationships between soil variables and plant species

The co-inertia analysis (COIA) showed a clear edaphic-floristic gradient in both the adult and sapling strata considering impacted and reference sites. The overall association between adult stratum and edaphic factors was highly significant ($RV = 0.291$; $p < 0.001$) according to the COIA. We found an association of 29.1 % between the edaphic and adult stratum matrices. The percentage of covariance explained by axis 1 was 45.4 % and axis 2 explained 34.2 %, and for this reason we only explore axis 1 in the adult-COIA. The positive side of adult-COIA axis 1 showed plots with less acidic and more fertile soils, with higher base saturation, manganese, fine sand, calcium, zinc, and phosphorus (Fig. 9A). The adult species most strongly associated with the positive side of this axis were *G. macrophylla*, *E. florida*, *G. guidonia*, *Tabernaemontana hystrix*, and *G. integrifolia* (Fig. 9A). On the other hand, the negative side of the adult-COIA axis 1 showed plots with less fertile and more acidic soils, with higher aluminum saturation, potential acidity, suphur, and organic carbon (Fig. 9A). The adult species most strongly associated with the negative side of this axis were *Dalbergia villosa*, *A. colubrina, S. guianensis*, *A. floribunda*, and *E. pelleterianum* (Fig. 9A).

The overall association between sapling stratum and edaphic factors was highly significant ($RV = 0.257$; $p < 0.001$) according to the sapling-COIA. We found a relevant association of 25.7 % between edaphic and sapling stratum matrices. The percentage of covariance explained by axis 1 was 52.0 % and axis 2 explained 24.9 %, and for this reason we will only explore axis 1 in the sapling-COIA. In a similar way to the adult COIA, the positive side of the sapling-COIA axis 1 showed plots with less acidic and more fertile soils, with higher base saturation, calcium, magnesium, zinc, manganese, and phosphorus (Fig. 9B). The sapling stratum species most strongly associated with the positive side of this axis were *G. marginata, E. florida*, *A. urundeuva*, *Pterocarpus zehntneri*, and *S. dictyocarpa* (Fig. 9B). On the other hand, the negative side of the sapling-COIA axis 1 showed plots with less fertile, acidic soils, with higher aluminum saturation, potential acidity, suphur, and organic

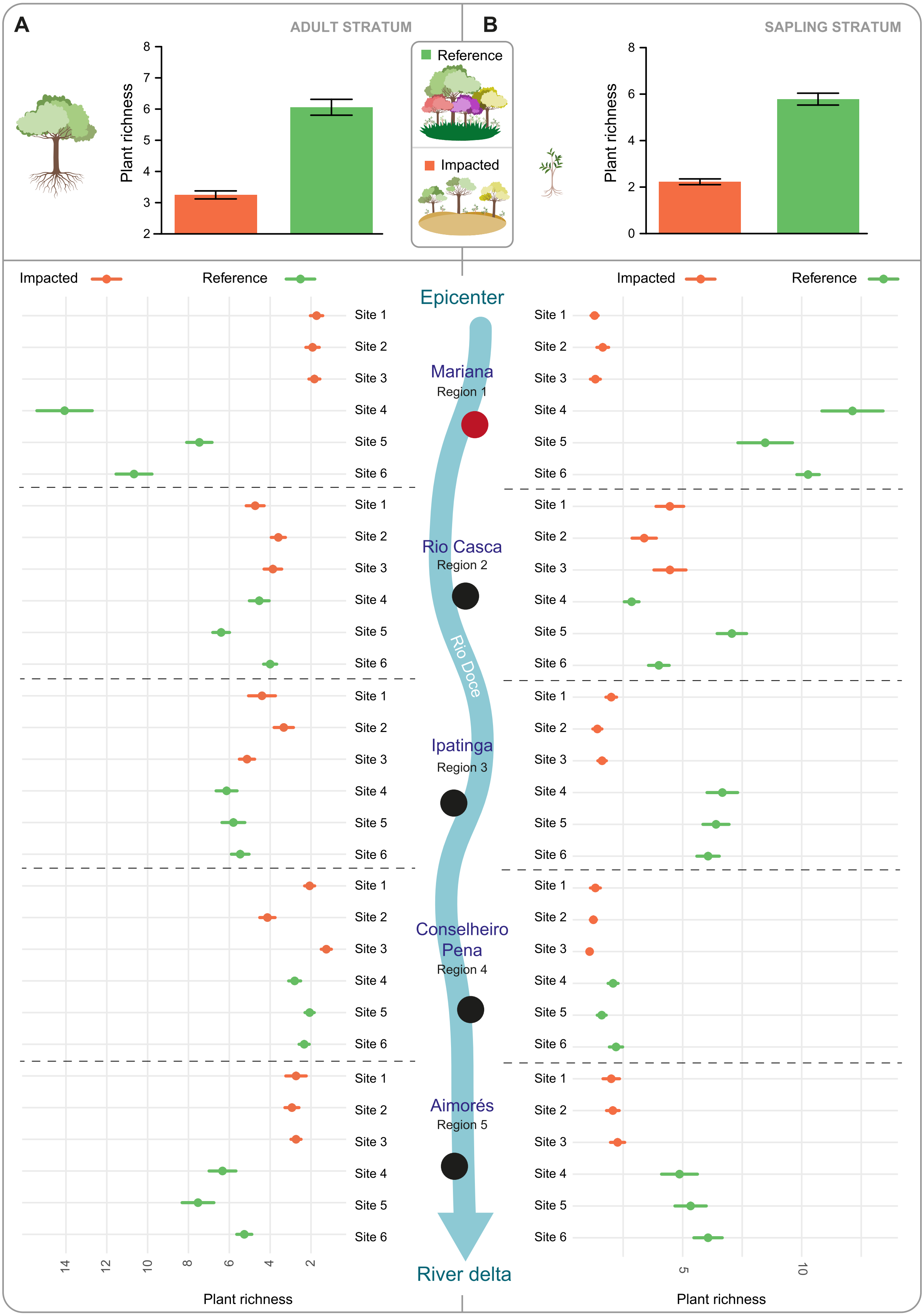

Fig. 3. Richness of species sampled in the impacted and reference sites in adult (A) and sapling (B) strata. Bars represent the mean value and vertical line denote the standard error (N = 15 sites per treatment). Lower pannel shows the mean value (filled circle) and standard error (horizontal line) for each site (N = 15 plots per site).

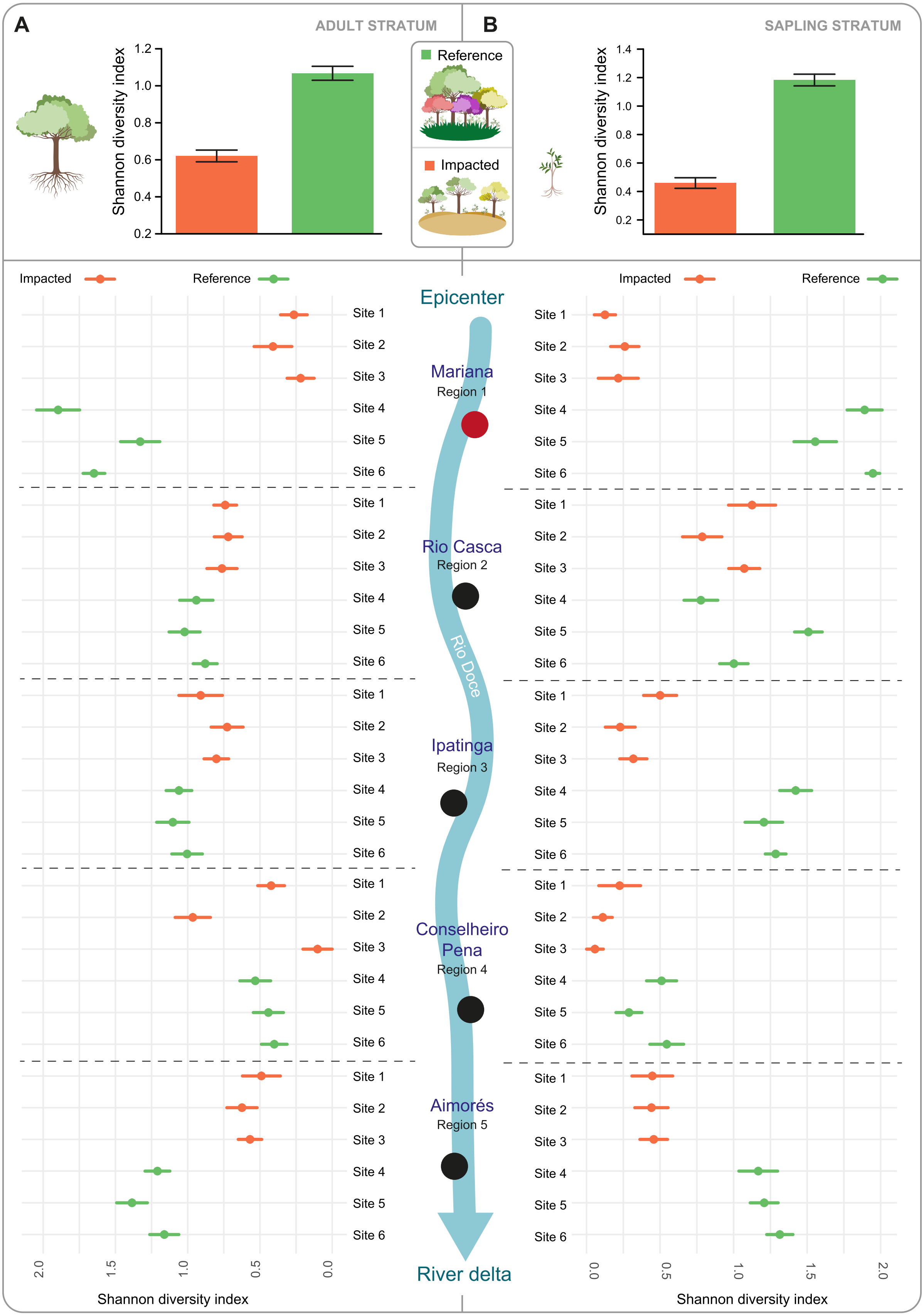

Fig. 4. Shannon diversity index of the species sampled in the impacted and reference sites in adult (A) and sapling (B) strata. Bars represent the mean value and vertical line denote the standard error (N = 15 sites per treatment). Lower pannel shows the mean value (filled circle) and standard error (horizontal line) for each site (N = 15 plots per site).

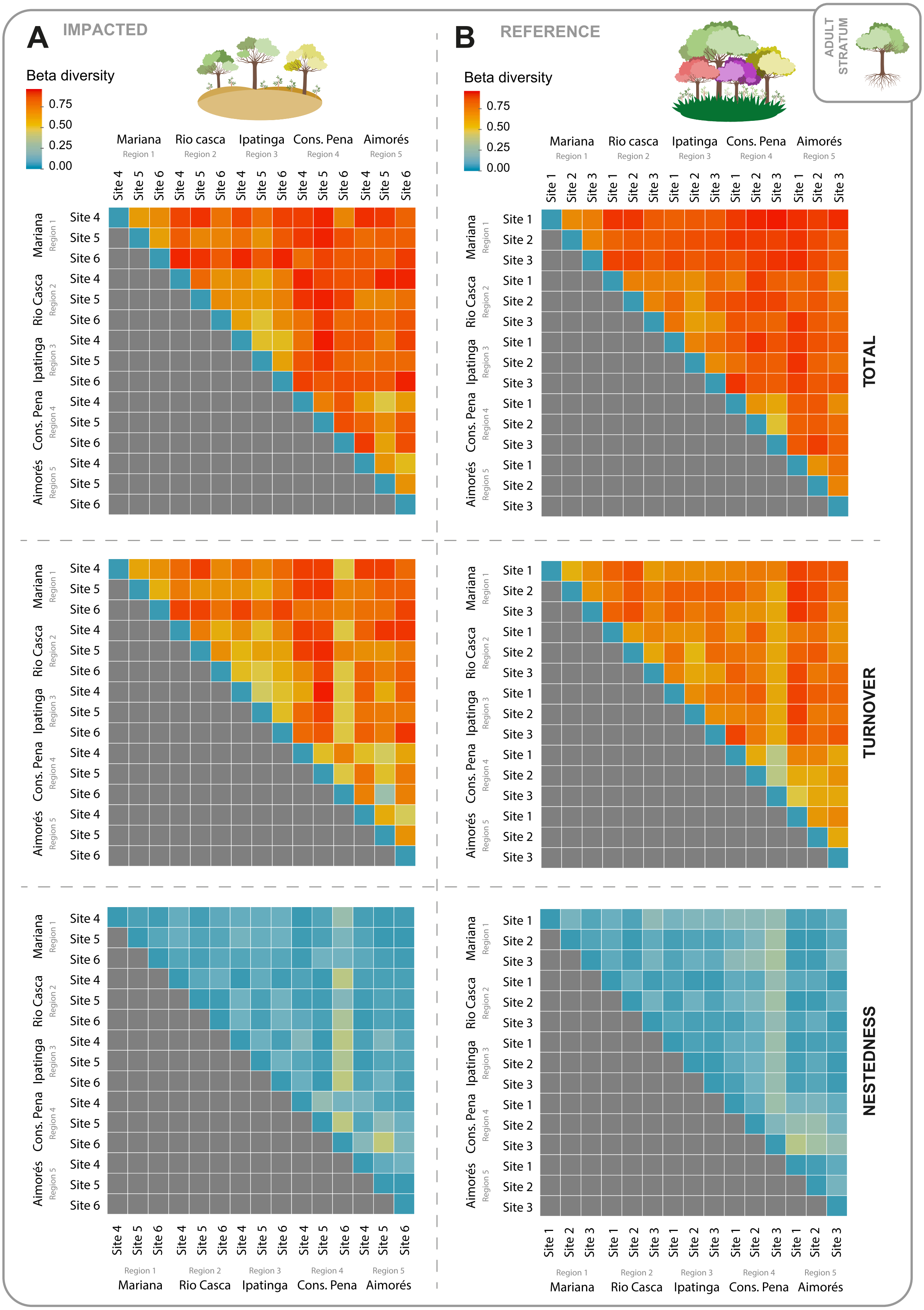

Fig. 5. Pairwise variation in composition of reference (A) and impacted (B) adult stratum according to total diversity (total), change (turnover), and loss (nestedness) of species between sites along the Rio Doce watershed, southeast Brazil.

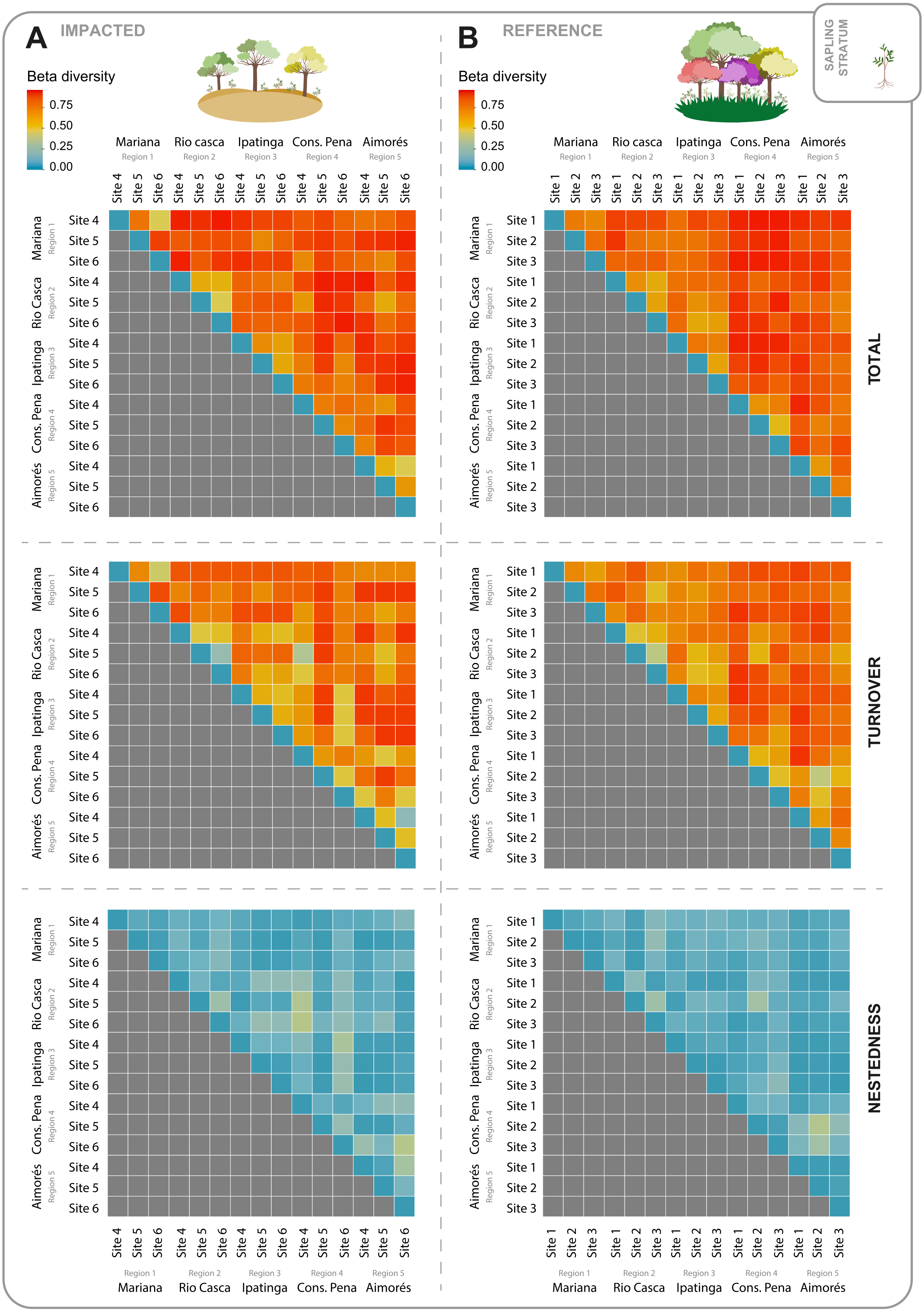

Fig. 6. Pairwise variation in composition of reference (A) and impacted (B) sapling stratum according to total diversity (total), change (turnover), and loss (nestedness) of species between sites along the Rio Doce watershed, southeast Brazil.

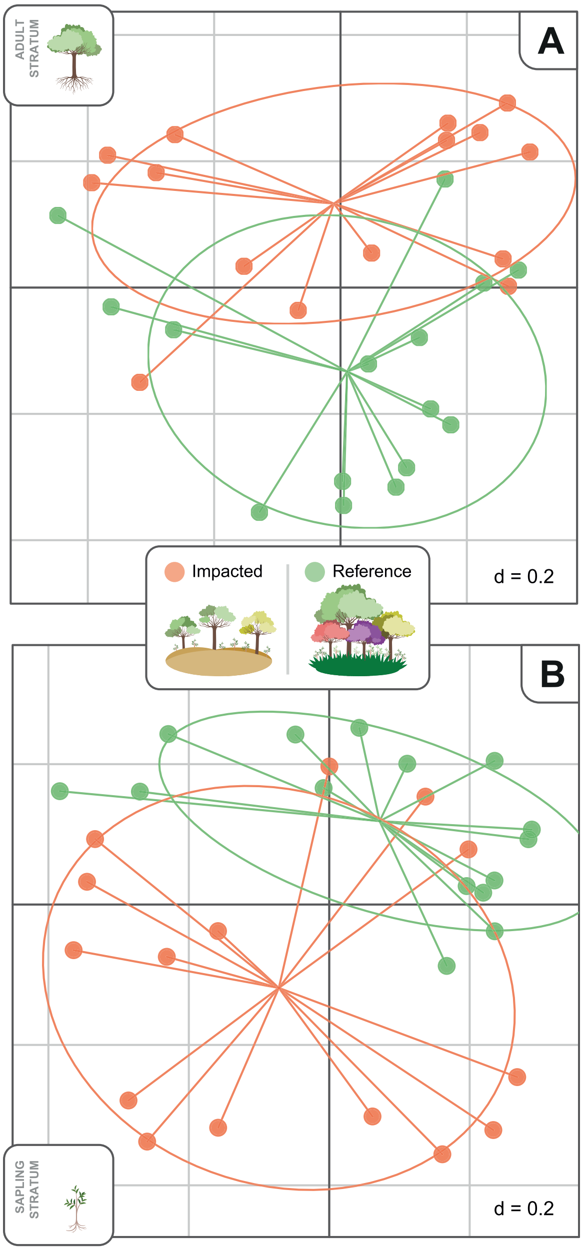

Fig. 7. Factorial plot showing the two main axes of a principal coordinates analysis (PCoA) applied to the matrix of presence and absence of adult (A) and sapling (B) strata along the Rio Doce watershed, southeast Brazil. The vertical and horizontal grid lines are separated by 0.2 units (d) on the scale of each axis.

carbon (Fig. 9B). The sapling species most strongly associated with the negative side of this axis were *S. reginae*, *E. citrifolium*, *P. vellosiana*, *C. emarginata*, and *Amaioua intermedia* (Fig. 9B).

3.7. Land-use change affecting species diversity

Although landscape changes associated with land use can directly affect floristic composition and species diversity, we found no difference in native forest cover between the impacted and reference sites. Both impacted and reference sites were immersed in landscapes with the same levels of conversion. Thus, we did not observe any significant influence at the larger scale, using a 1 km radius buffer around each site ($F = 3.67$; $p = 0.060$; Fig. S6A), or at the more localized scale of 300 m ($F = 0.15$; $p = 0.700$; Fig. S6B).

4. Discussion

We recorded a distinct and clear impact of the mine tailings of the Samarco's dam breach on both the soil and plant community throughout the affected Rio Doce watershed. These findings reveal a significant reduction in plant richness and diversity of plant species, accompanied by drastic alterations in floristic composition. Additionally, we identified deep changes in edaphic parameters attributed to the deposition of the mine tailings following the dam breach. Our study aligns with previous research demonstrating the adverse effects of the mine tailings on various other organisms, including invertebrates (Ribeiro et al., 2023; Soares et al., 2024), vertebrates (Merçon et al., 2021), and marine communities (Oliveira-Filho et al., 2023). Moreover, this study represents the first to directly assess the impact of the mine tailings on the diversity of plant communities in riparian forests along the Rio Doce, in spite of the disaster taking place nine years ago.

4.1. Edaphic variation in impacted sites

The direct effects of the Samarco dam collapse on the plant community are linked to the drastic changes in the soil properties. The collapse of the dam led to the release of ca. dozens of millions cubic meters of a substrate poor in organic matter, rich in iron, high pH values and some heavy metals, such as As, Cr, Cd, Hg and Pb (Fernandes et al., 2016a; Gomes et al., 2017). Throughout the studied regions of the Rio Doce basin (Mariana, Rio Casca, Ipatinga, Conselheiro Pena, and Aimorés), the impacted sites stood out for having soil chemically composed of higher concentration of iron, phosphorus, but lower concentration of carbon and potential acidity. The textures of the impacted soils in these locations showed higher proportion of fine sand and lower proportion of coarse sand than in the reference sites. Similar results were reported by Silva et al. (2021) and da Silva et al. (2022) working on 15 sampling points in the stretch of the Gualaxo do Norte river, Mariana, and by Guerra et al. (2017) that studied 17 sampling points in the sites before the Risoleta Neves Power Station, near Mariana. Due to the magnitude of the disaster, most published studies have been concentrated closer to the source of the accident (e.g., Vieira et al., 2020; Ribeiro et al., 2023; Alves et al., 2024). Therefore, our study highlights that mining sludge equally impacted the entire soil of the riverbanks along the Rio Doce. Changes in texture, nutrient and heavy metal concentration act as strong selection filters for many locally adapted plant species while may favor opportunistic and often invasive species (Smith et al., 2012; van der Putten et al., 2016; Araújo et al., 2024). These changes often have strong and potentially irreversible consequences to the diversity and functioning of riparian ecosystems.

Physico-chemical properties of forest soils vary in space and time because of variation in topography, climate, weathering processes, vegetation cover and microbial activities (Paudel and Sah, 2003) and several other biotic and abiotic factors (Pandey et al., 2024). Soil properties therefore vary within short distances according to parent rocks, vegetation cover and land use. In the highly dissected landscapes, bioclimatic conditions change rapidly with the altitude and may vary within short distances resulting in a pronounced heterogeneity of soil types (Awasthi et al., 2022) hence influence the distribution of vegetation (Manral et al., 2022).

4.2. Variation in plant communities

The Atlantic Forest is known for its high species diversity (Lins-e-Silva et al., 2021) and this study also highlights high species diversity in both the tree and sapling strata in the reference sites. However, in the sites impacted by the mining tailings, there was a clear decline in richness and diversity, as well as significant changes in the composition of species in both the tree and sapling strata, corroborating our first hypothesis. In the two strata studied in the impacted sites, the Fabaceae family showed the highest species richness, followed by the

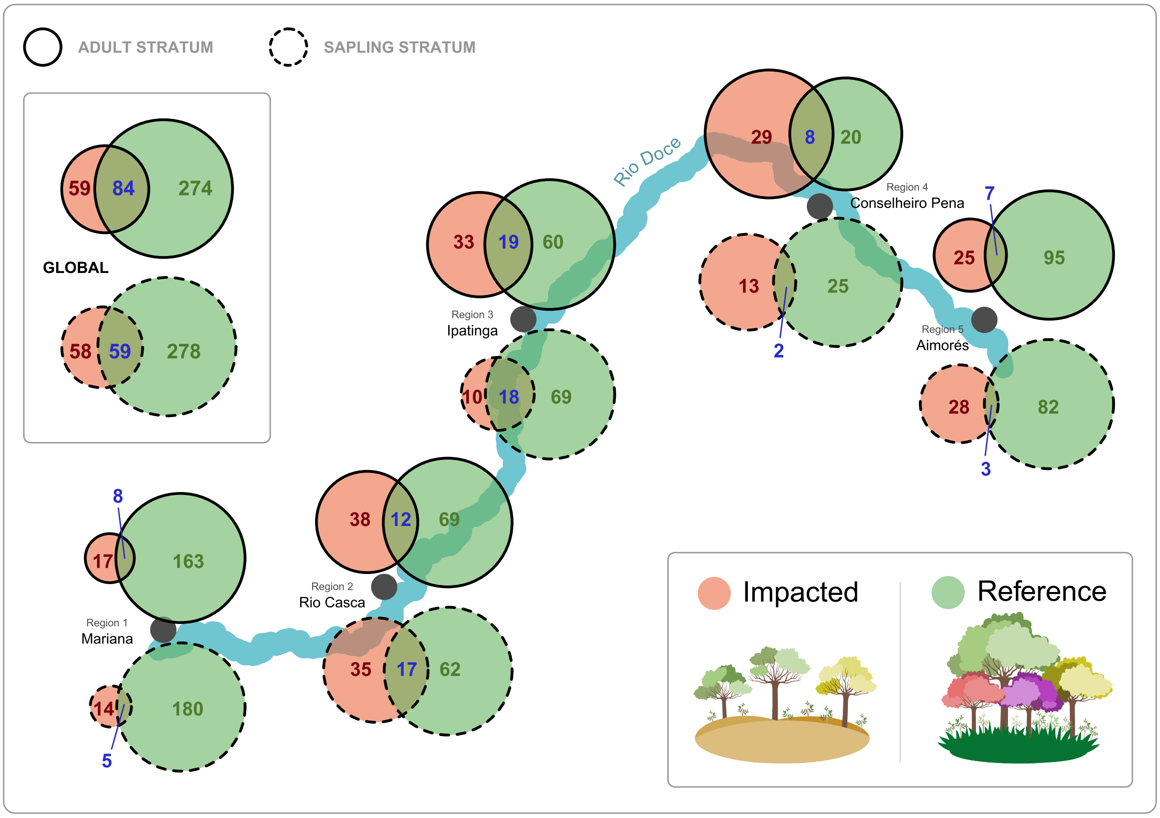

Fig. 8. Euler diagram illustrating the number of exclusive and shared species between impacted and reference sites from five regions of the Rio Doce watershed.

Myrtaceae. These findings are in line with other studies carried out in the Rio Doce watershed (Figueiredo et al., 2022, 2024; Ramos et al., 2023; Justino et al., unpublished manuscript; Sousa et al., 2024; Souza et al., 2024). Fabaceae is one of the most abundant and richest families in tropical forests (Carvalho et al., 2006; Gei et al., 2018). In addition to its high diversity, this family is of major relevance in early succession processes (Gei et al., 2018; Balestrin et al., 2019). The Fabaceae have many fast-growing species adapted to poor soils, providing rapid soil cover and preventing erosion and the development of invasive plants, which are one of the main problems in the restoration processes of Atlantic rain forests (Rodrigues et al., 2009; Brancalion et al., 2014). In addition to high richness of species, the Myrtaceae is known to attract pollinators and dispersers, acting to restore the structure and function of forests (Rodrigues et al., 2009; United Nations, 2019).

4.3. Variation in plant communities between impacted and reference sites

The plant communities in the impacted sites presented lower plant diversity compared to reference sites. Edaphic characteristics modulate the diversity and composition of plant communities (Hulshof and Spasojevic, 2020) and in this work we show that the profound soil changes were accompanied by a significant divergence of impacted and reference sites according to plant species composition (Coelho et al., 2018; Figueiredo et al., 2022, 2024; Ramos et al., 2023). These changes are of enormous concern for conservation of the already threatened Atlantic riparian forests, with a clear and worrying effect on biodiversity and the provision of ecosystem services. In addition, these deep changes in soil properties may represent new potential sites for the establishment of a new ecosystem composed of different species.

4.4. Species composition along the Rio Doce

The knowledge on forest community structure and composition of each region is essential for achieving the highest possible gains in ecological restoration. In general, *Guarea macrophylla* was the most abundant species in the tree stratum, while *Eugenia florida* the most abundant in the sapling stratum. *Guarea macrophylla* has been commonly recommended for riparian restoration in the Atlantic Forest (e.g., Carvalho et al., 2006). This species is reported as being pollinated by insects and its seeds dispersed by birds (Prado, 2013), what might increase the functional diversity of the environment. Similarly, *Eugenia florida* plays an important role in restoring ecosystem functions; its flowers are an important resource for bees while its fruit are dispersed by bats, birds, and monkeys (Gressler et al., 2006). We also recorded a high importance value for *Astronium urundeuva*. Otherwise, this should be viewed with extreme caution, as this species is hyperdominant and widespread in the middle Rio Doce (Souza et al., 2024). Hence, in spite of the high frequency, this species is not recommended in any restoration project. Despite being a native species, it shows strong invasive behavior in this basin, that deep alters colonization by other native species (Fernandes and Negreiros, 2006).

4.5. Sharing species between impacted and reference sites

The impacted sites were floristically and ecologically distant from the reference sites, as they had lower diversity for both strata. In addition, within region impacted and reference sites showed marked changes in community composition with many abundant species not found in the impacted sites. This implies that a marked change in the plant community occurred after the dam collapse. These changes often include the loss of key species and increase in opportunistic species, which tend to dominate in disturbed sites (Smith et al., 2012; van der Putten et al., 2016). These changes can alter ecological interactions, cause biotic homogenization, reduce functional diversity and ecosystem services such as nutrient cycling, seed dispersal and carbon storage (Daru et al., 2021). This indicates that riverine forests may evolve into significantly

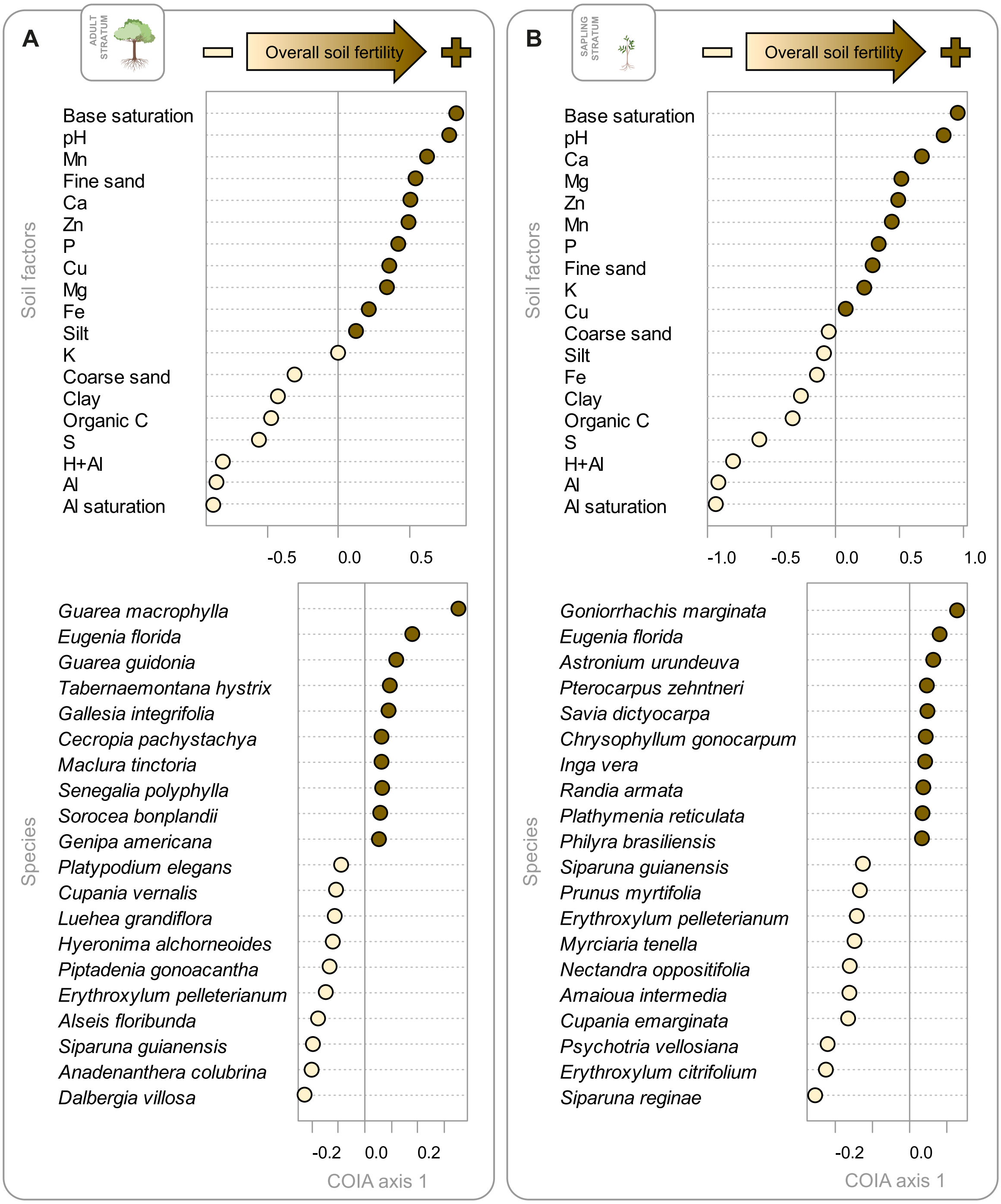

Fig. 9. Co-structure between edaphic factors and community of adult (A) and sapling (B) strata sampled along the Rio Doce watershed, southeast Brazil. The upper dotcharts show the Pearson correlation between edaphic factors and the coordinates of the sites in axis 1 of the co-inertia analysis (COIA). The bottom dotcharts show the coordinates of the species with the highest association with the positive and negative sides of COIA axis 1. The light brown and dark brown circles represent, respectively, the negative and positive correlation values with COIA axis 1 (upper graphs) or coordinates of COIA axis 1 (bottom graphs).

different forests from current ones, with potential long-term consequences for biodiversity and ecological functions.

According to the total beta diversity, the variation in paired beta diversity shows that the changes in species composition were due to the turnover of species at each site in both strata. In other words, we recorded a targeted substitution of species between the impacted and reference sites, i.e. some species were favored by the deposition of tailings while others were harmed. In this new environment created by the deposition of mining tailings from the collapse of the Samarco dam, the vegetation, soil, biodiversity and ecosystem functions were drastically impacted, reduced and/or even eliminated, as proposed by Fernandes et al. (2016a) (see also Knopff et al., 2020; Ribeiro et al., 2023). The study presented here shows that even nine years after the disaster that led to the loss of 1469 ha of the natural vegetation (Fernandes et al., 2016a) the impacted sites still present low richness, abundance and diversity of plant species. In addition, we noticed different species composition between the impacted and reference sites in all regions sampled, i.e., from Mariana (epicenter of the dam breach) to Aimorés, at the way of river delta. These unprecedented results provide further information showing that the impact of the mine tailings along the Rio Doce was extensive. This happened in spite the fact that a large part of the mining tailings (10 million cubic meters) was retained by the Candonga dam of the Risoleta Neves hydroelectric power plant, near Mariana, between the municipalities of Rio Doce and Santa Cruz do Escalvado (Amaral et al., 2021). Urgent studies must investigate the impact of river proximity to the disaster site on community composition by integrating hydrological and geomorphological variables. This approach could facilitate a more nuanced understanding of the spatial distribution of impacts and inform the development of ecological restoration strategies tailored to specific river sections. Indeed, Ramos and others (2024) reported multiple riparian forests along the river, so that assisted restoration would be mandatory for proper biodiversity gain and habitat connectivity.

4.6. Edaphic-floristic gradient and variation in land use

The COIA analysis also indicated a strong connection between soil and floristic composition, where the soil conditions the vegetation. The mining tailings altered the properties of the soil, which had a direct impact on the vegetation of the tree and sapling strata. Soil conditions play a crucial role in Atlantic rainforest species composition (Coelho et al., 2018). In the reference sites there is a gradient of increasing fertility from Mariana to near the estuary, in Linhares, shaping the multiple forests in this ecosystem (Ramos et al., 2024). As observed in the COIA analysis, we observed soils of impacted sites with higher base saturation, higher concentrations of Ca, Mg, and P, that differed from less fertile sites with more acidic soils and higher aluminum saturation. More importantly, there are several species in the tree and sapling strata that are strongly associated with these edaphic extremes. For example, the species *A. urundeuva* is strongly associated with more fertile soils in the sapling stratum. However, *A. urundeuva* is a hyperdominant generalist species in several stretches of the middle Rio Doce watershed, as well as having invasive behavior and competing with the native flora (Fernandes and Negreiros, 2006). At the other edaphic extreme, with more acidic and poorer soils, species of the genus *Siparuna* in both strata, which have animal dispersal and rapid growth in the early stages of succession (Nunes et al., 2023), could help to restore the functions of this degraded environment. On the other hand, we did not observe any effect of the land use pattern and conservation of the forests around the sampled sites, i.e. the landscape parameters were not correlated with the changes in floristic composition observed in this study.

4.7. Could the impacted riparian forest remnants become future tipping points?

For more than 500 years the Atlantic rain forests of Brazil have been under intense land conversion, with stronger deforestation and fragmentation taking place along the coast and rivers. But despite increasing awareness and policies (see, Metzger et al., 2019), forest fragments continue to shrink due to continuous land-use conversion, and consequently in diminished resilience and capacity to natural recover in this speciose biome (Romanelli et al., 2022; Vancine et al., 2024). Notwithstanding the continuous reports of other tropical rain forests areas reaching tipping points (e.g., Flores et al., 2024), we are unaware of studies indicating the incapacity of the complex systems that comprise the Atlantic Rain Forests reaching critical thresholds to points of irreversible consequences. Thus, there is increasing concern that the Samarco mining company's dam breach may have further isolated already fragmented and deforested areas, potentially triggering multiple tipping points along the Rio Doce.

The strong degradation along the Rio Doce is leading the riparian forest remnants to tipping points, where the current forest community is giving way to narrower and poorer forest ecosystems. The waves of resuspension of mining tailings in the Rio Doce river channel after heavy rains represents a relentless source of stress for the river and its riparian forests, from the epicenter of the dam breach all the way to the Atlantic Ocean. This wave of stresses may now constitute a continuous phenomenon. This rewinding will force the surviving organisms to either adapt and tolerate the conditions, face local extinction, or even disappear entirely. To the best of our knowledge, the environmental recovery from this disaster is expected to take hundreds to thousands of years. As a result, the resilience of many native species and the full restoration of the original vegetation and associated communities are highly unlikely to succeed, hence calling for adaptive and assisted ecological restoration. This is strongly supported by the data gathered on the sapling stratum, which largely differs from that recorded in the reference sites.

Misleading policies that favor the use of inappropriate species for ecological restoration would exacerbate the problem rather than solving it. Therefore, the combination of lack of proper governance and the magnitude of the disaster could deliver a final blow to the riparian sites along the Rio Doce, facilitating biotic homogenization throughout the basin. Urgent studies on species ecophysiology, on propagation of the most adequate species for ecological restoration of the rehabilitated sites, and sound long term monitoring of habitat recovery, biodiversity and ecosystem functioning must be implemented to increase habitat resilience and effectively restore the riparian sites of the Rio Doce.

4.8. Conclusion

Restoration projects for the sites impacted by the Samarco's dam breach along the Rio Doce watershed should be guided by lists of species from optimal reference sites closest to the sites to be restored. The decision to restore with a unique selected set of species, based on the urgency to cover the impacted area, on the prompt availability of seeds and saplings and easiness to find them in the market may result in additional damage to the environment, promote biological invasions as well as biotic homogenization and creation of new ecosystems along the Rio Doce watershed. To effectively promote biodiversity and ecosystem connectivity, ecological restoration must adopt reference sites (see Fernandes et al., 2016b; Toma et al., 2023). However, the restoration of Atlantic Forest environments has been done mostly with a small and similar set of species, with serious ecosystem consequences (Almeida et al., 2024; Toma et al., 2024). Examples of misguided restoration leading to biotic homogenization are now being recorded around the planet (Holl et al., 2022). Our results underline that using a single set of species throughout the Rio Doce watershed is a flawed restoration decision, since there are many species that occurred exclusively in each region (see also Ramos et al., 2024). The restoration of riparian forests in the Doce River watershed is urgent, as these forests act in water regulation and guarantee water and food security for millions of people. In addition, the restoration actions are in line with Sustainable Development Goals 3 (health and well-being), 6 (drinking water and sanitation), 13 (action on global climate change), 14 (life in water) and 15 (life on land). This situation is more worrying when it comes to restoration resulting from legal obligations following a disaster such as the collapse of the Samarco dam, so that its mitigation cannot, under any circumstances, generate new negative consequences over time.

CRediT authorship contribution statement

Fernandes G. Wilson: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Ramos Letícia:** Writing – review & editing, Writing – original draft. **Justino Wénita de Souza:** Writing – review & editing, Data curation. **Kenedy-Siqueira Walisson:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Figueiredo João Carlos Gomes:** Writing – review & editing, Writing – original draft, Data curation. **Oki Yumi:** Writing – review & editing, Methodology, Conceptualization. **Goulart Fernando Figueiredo:** Writing – review & editing, Methodology. **dos Santos Rubens Manoel:** Writing – review & editing, Methodology. **Viana João Herbert Moreira:** Writing – review & editing, Methodology. **Nunes Yule Roberta Ferreira Nunes:** Writing – review &

editing, Methodology. **Aguilar Ramiro:** Writing – review & editing. **Poorter Lourens:** Writing – review & editing. **van der Sande Masha T.:** Writing – review & editing. **Negreiros Daniel:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank two anonymous reviewers for their contributions to an earlier version of this manuscript. We also thank Aldemiro Ribeiro, Aline Almeida, Alysson Pereira, Andressa Luna, Barbara Ferreira, Bruna Ribeiro, Carla Rago, Carla Rebeca Vieira, Cristina Veloso, Dario Paiva, Débora Sousa, Glaucia Tolentino, Guilherme Costa Dias, Guilherme Pereira Dias, Gustavo Brant, Jane de Oliveira, João Vitor Cardinali, Jonathan Silveira, José Gustavo Neves, Juliana Aquino, Júlio Lopes, Leda Naiara, Lucas Sousa, Luis Veloso, Marly Ávila, Michel Jacoby, Odirlei Oliveira, Pedro Henrique Melo, Ricardo Fernandes, Samuel Novais, Suely Adriano, Thamires Freitas Vanessa Gomes, and Vitor Flores for their support in fieldwork. We thank Messrs, Alírio, Sérgio, Ivaldil, Vicente, Miguel, and the companies CENIBRA and Eliezer Batista Hydroelectric Power Plant - Alliance Consortium for permission access to the studied sites, and also for the help of the boatmen Jhonatam, Jandersom, Antônio and Cláudio. Logistical support provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Câmara Técnica de Conservação e Biodiversidade (CTBio), and Instituto Estadual de Florestas (IEF) is also appreciated. This research was supported by Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG; APQ-03622-17, APQ-00031-19), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and Knowledge Center for Biodiversity (INCT/CNPq: 406757/2022-4). DN and LR thank the scholarships from CNPq (153706/2024-4, 150126/2024-7). This work is dedicated to those who has suffered the endless environmental consequences of the major environmental disaster of the mining sector in Brazil.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ancene.2025.100462.

Data availability

Data will be made available on request.

References

Almeida, C., Reid, J.L., de Lima, R.A.F., Pinto, L.F.G., Viani, R.A.G., 2024. Restoration plantings in the Atlantic Forest use a small, biased, and homogeneous set of tree species. For. Ecol. Manag. 553, 121628. https://doi.org/10.1016/j.foreco.2023.121628.

Alves, A.V., Mendes, L.A., Teixeira, J.B., dos Santos, V.M.R., de Guarda, V.L.M., Andrade, Â.L., 2024. Evaluating the water quality of springs in Paracatu de Baixo after the Fundão dam collapse. Rev. Virtual Quim. 16, 187–194. https://doi.org/10.21577/1984-6835.20230062.

Amaral, I.B.C., Cavalcante, L.C.D., Fabris, J.D., Prat, B.V., Reis, A.B., 2021. Use of mining tailings or their sedimentation and flotation fractions in a mixture with soil to produce structural ceramics. Sustainability 13, 911. https://doi.org/10.3390/su13020911.

Araújo, B.D., Maia, R.A., Barbosa, M., Silva, T.F., Modolo, L.V., Negreiros, D., Fernandes, G.W., 2024. Mining tailings effects on soil quality and performance of two native species of atlantic forest: implications for restoration. Water Air Soil Poll. 235, 687. https://doi.org/10.1007/s11270-024-07472-z.

Awasthi, P., Bargali, K., Bargali, S.S., Khatri, K., 2022. Nutrient return through decomposing *Coriaria nepalensis* litter in degraded hills of Kumaun Himalaya, India. Front. For. Glob. Change 5, 1008939. https://doi.org/10.3389/ffgc.2022.1008939.

Baboo, B., Sagar, R., Bargali, S.S., Verma, H., 2017. Tree species composition, regeneration and diversity within the protected area of Indian dry tropical forest. Trop. Ecol. 58, 409–423.

Balestrin, D., Cruz, R., Silveira, G., Martins, S.V., 2019. Hydric and edaphic influence on floristic composition in an altered riparian area. Floresta e Ambient 26, e20171002. https://doi.org/10.1590/2179-8087.100217.

Bargali, S.S., Padalia, K., Bargali, K., 2019. Effects of tree fostering on soil health and microbial biomass under different land use systems in central Himalaya. Land Degrad. Dev. 30, 984–1998. https://doi.org/10.1002/ldr.3394.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/JSS.V067.I01.

Bisht, S., Bargali, S.S., Bargali, K., Rawat, Y.S., Rawat, G.S., 2023. Dry matter dynamics and carbon flux along riverine forests of Gori valley, Western Himalaya. Front. For. Glob. Change 6, 1206677. https://doi.org/10.3389/ffgc.2023.1206677.

Brancalion, P.H.S., Cardozo, I.V., Camatta, A., Aronson, J., Rodrigues, R.R., 2014. Cultural ecosystem services and popular perceptions of the benefits of an ecological restoration project in the Brazilian Atlantic Forest. Restor. Ecol. 22, 65–71. https://doi.org/10.1111/rec.12025.

Carvalho, F.A., Nascimento, M.T., Braga, J.M.A., 2006. Composição e riqueza florística do componente arbóreo da Floresta Atlântica submontana na região de Imbaú, Município de Silva Jardim, RJ. Acta Bot. Bras. 20, 727–740. https://doi.org/10.1590/S0102-33062006000300022.

Coelho, M.S., Carlos, P.P., Pinto, V.D., Meireles, A., Negreiros, D., Morellato, L.P.C., Fernandes, G.W., 2018. Connection between tree functional traits and environmental parameters in an archipelago of montane forests surrounded by rupestrian grasslands. Flora 238, 51–59. https://doi.org/10.1016/j.flora.2017.04.003.

da Silva, A.P.V., Silva, A.O., Lima, F.R.D., Benedet, L., Franco, A.D.J., Souza, J.K.D., Ribeiro Júnior, A.C., Batista, É .R., Inda, A.V., Curi, N., Guilherme, L.R.G., Carneiro, M.A.C., 2022. Potentially toxic elements in iron mine tailings: effects of reducing soil pH on available concentrations of toxic elements. Environ. Res. 215, 114321. https://doi.org/10.1016/j.envres.2022.114321.

Daru, B.H., Davies, T.J., Willis, C.G., Meineke, E.K., Ronk, A., Zobel, M., Pärtel, M., Antonelli, A., Davis, C.C., 2021. Widespread homogenization of plant communities in the Anthropocene. Nat. Commun. 12, 6983. https://doi.org/10.1038/s41467-021-27186-8.

Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological data tables. Ecology 84, 3078–3089. https://doi.org/10.1890/03-0178.

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20. https://doi.org/10.18637/jss.v022.i04.

Fernandes, G.W., Goulart, F.F., Ranieri, B.D., Coelho, M.S., Dales, K., Boesche, N., Bustamante, M., Carvalho, F.A., Carvalho, D.C., Dirzo, R., Fernandes, S., Galetti, P.M., Millan, V.E.G., Mielke, C., Ramirez, J.L., Neves, A., Rogass, C., Ribeiro, S.P., Scariot, A., Soares-Filho, B., 2016a. Deep into the mud: ecological and socio-economic impacts of the dam breach in Mariana, Brazil. Nat. Conserv. ção 14, 35–45. https://doi.org/10.1016/j.ncon.2016.10.003.

Fernandes, G.W., Negreiros, D., 2006. A comunidade de insetos galhadores da RPPN fazenda bulcão, Aimorés, Minas Gerais, Brasil. Lundiana 7, 111–120.

Fernandes, G.W., Toma, T.S.P., Angrisano, P., Overbeck, G., 2016b. Challenges in the restoration of quartzitic and ironstone rupestrian grasslands. In: Fernandes, G.W. (Ed.), Ecology and conservation of mountaintop grasslands in Brazil. Springer, Switzerland, pp. 449–477. https://doi.org/10.1007/978-3-319-29808-5_19.

Figueiredo, J.C.G., de Avila, M.A., Souza, C.S., Neves, J.G.S., Tolentino, G.S., Oki, Y., Azevedo, I.F.P., Negreiros, D., Viana, J.H.M., dos Santos, R.M., Fonseca, R.S., Fernandes, G.W., Nunes, Y.R.F., 2022. Relationship of woody species composition with edaphic characteristics in threatened riparian Atlantic Forest remnants in the upper Rio Doce basin, Brazil. Nord. J. Bot. 2022, e03679. https://doi.org/10.1111/njb.03679.

Figueiredo, J.C.G., Negreiros, D., Ramos, L., Paiva, D.C., Oki, Y., Justino, W.S., dos, Santos, R.M., Aguilar, R., Nunes, Y.R.F., Fernandes, G.W., 2024. Reference sites of threatened riverine Atlantic Forest in upper Rio Doce watershed. Nat. Conserv. Res. 9, 58–71. https://doi.org/10.24189/ncr.2024.006.

Flores, B.M., Montoya, E., Sakschewski, B., Nascimento, N., Staal, A., Betts, R.A., Levis, C., Lapola, D.M., Esquível-Muelbert, A., Jakovac, C., Nobre, C.A., Oliveira, R.S., Borma, L.S., Nian, D., Boers, N., Hecht, S.B., Steege, H., Arieira, J., Lucas, I.L., Berenguer, E., Marengo, J.A., Gatti, L.V., Mattos, C.R.C., Hirota, M., 2024. Critical transitions in the Amazon forest system. Nature 626, 555–564. https://doi.org/10.1038/s41586-023-06970-0.

Gann, G.D., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J., Hallett, J.G., Eisenberg, C., Guariguata, M.R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration: second edition. Restor. Ecol. 27, S1–S46. https://doi.org/10.1111/rec.13035.

Gei, M., Rozendaal, D.M.A., Poorter, L., Bongers, F., Sprent, J.I., Garner, M.D., et al., 2018. Legume abundance along successional and rainfall gradients in Neotropical forests. Nat. Ecol. Evol. 2, 1104–1111. https://doi.org/10.1038/s41559-018-0559-6.

Gomes, L.E.O., Correa, L.B., Sá, F., Rodrigues Neto, R., Bernardino, A.F., 2017. The impacts of the samarco mine tailing spill on the Rio Doce Estuary, Eastern Brazil. Mar. Pollut. Bull. 120, 28–36. https://doi.org/10.1016/j.marpolbul.2017.04.056.

Gressler, E., Pizo, M.A., Morellato, L.P.C., 2006. Polinização e dispersão de sementes em Myrtaceae do Brasil. Rev. Bras. Bot. 29, 509–530. https://doi.org/10.1590/S0100-84042006000400002.

Guerra, M.B.B., Teaney, B.T., Mount, B.J., Asunskis, D.J., Jordan, B.T., Barker, R.J., Santos, E.E., Schaefer, C.E.G.R., 2017. Post-catastrophe analysis of the Fundão tailings dam failure in the Doce River system, Southeast Brazil: potentially toxic elements in affected soils. Water Air Soil Pollut. 228, 252. https://doi.org/10.1007/s11270-017-3430-5.

Hatje, V., Pedreira, R.M.A., de Rezende, C.E., Schettini, C.A.F., de Souza, G.C., Marin, D. C., Hackspacher, P.C., 2017. The environmental impacts of one of the largest tailing dam failures worldwide. Sci. Rep. 7, 10706. https://doi.org/10.1038/s41598-017-11143-x.

Holl, K.D., Luong, J.C., Brancalion, P.H.S., 2022. Overcoming biotic homogenization in ecological restoration. Trends Ecol. Evol. 9, 777–778. https://doi.org/10.1016/j.tree.2022.05.002.

Hsieh, T.C., Ma, K., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Meth. Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613.

Htun, N.Z., Mizoue, N., Yoshida, S., 2011. Tree species composition and diversity at different levels of disturbance in Popa Mountain Park, Myanmar. Biotropica 43, 597–603. https://doi.org/10.1111/j.1744-7429.2011.00753.x.

Hua, F., Bruijnzeel, L.A., Meli, P., Martin, P.A., Zhang, J., Nakagawa, S., et al., 2022. The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. Science 376, 839–844. https://doi.org/10.1126/science.abl4649.

Hulshof, C.M., Spasojevic, M.J., 2020. The edaphic control of plant diversity. Glob. Ecol. Biogeogr. 29, 1634–1650. https://doi.org/10.1111/geb.13151.

Jin, Y., Qian, H., 2022. V. PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Divers 44, 335–339. https://doi.org/10.1016/j.pld.2022.05.005.

Justino W.S., Negreiros D., Ramos L., Figueiredo J.C.G., Paiva D.C., Oki Y., dos Santos R. M., Ashworth L., Nunes Y.R.F., Fernandes G.W. (unpublished manuscript). Floristic and edaphic inventory of Atlantic riparian forests: references for restoration projects. Nat. Conserv. Res. (in review).

Knopff, K., Bede, L.C., Arruda, L., Alves, T., Simons, B., 2020. Methods for postdisaster impact assessment: a case study of the impacts of the Fundão dam failure on terrestrial species threatened with extinction. Integr. Environ. Assess. Manag. 16, 676–680. https://doi.org/10.1002/ieam.4265.

Larsson J. 2022. eulerr: Area-Proportional Euler and Venn Diagrams with Ellipses. R package version 7.0.0. ⟨https://CRAN.R-project.org/package=eulerr⟩. (Accessed 6 December 2023).

Lins-e-Silva, A.C.B., Ferreira, P.S.M., Rodal, M.J.N., 2021. The North-Eastern Atlantic Forest: biogeographical, historical, and current aspects in the sugarcane zone. In: Marques, M.C.M., Grelle, C.E.V. (Eds.), The Atlantic Forest. History, Biodiversity, Threats and Opportunities of the Mega-diverse Forest. Springer International Publishing, Cham, pp. 45–61. https://doi.org/10.1007/978-3-030-55322-7_3.

Manral, V., Bargali, K., Bargali, S.S., Jhariya, M.K., Padalia, K., 2022. Relationships between soil and microbial biomass properties and annual flux of nutrients in Central Himalayan forests, India. Land Degrad. Dev. 33, 2014–2025. https://doi.org/10.1002/ldr.4283.

Merçon, J., Cabral, D.S., Teixeira, B.C., Pereira, T.M., Bona, A.M., Armini, C.V.L., Agostinho, S.G.N., Gomes, L.C., 2021. Evidence of reproductive disturbance in *Astyanax lacustris* (Teleostei: Characiformes) from the Doce River after the collapse of the Fundão Dam in Mariana, Brazil. Environ. Sci. Pollut. Res. 28, 66643–66655. https://doi.org/10.1007/s11356-021-15238-x.

Mesquita, R.C.G., Ickes, K., Ganade, G., Williamson, G.B., 2001. Alternative successional pathways in the Amazon Basin. J. Ecol. 89, 528–537. https://doi.org/10.1046/j.1365-2745.2001.00583.x.

Metzger, J.P., Bustamante, M.M., Ferreira, J., Fernandes, G.W., Librán-Embid, F., Pillar, V.D., Prist, V.R., Rodrigues, R.R., Vieria, I.C.G., Overbeck, G.E., 2019. Why Brazil needs its legal reserves. Perspect. Ecol. Conserv. 17, 91–103. https://doi.org/10.1016/j.pecon.2019.07.002.

Mueller-Dombois, D., Ellenberg, D., 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

Negi, B., Khatri, K., Bargali, S.S., Bargali, K., 2024. Factors determining the invasion pattern of Ageratina adenophora Spreng. in Kumaun Himalaya India. Environ. Exp. Bot. 228, 106027. https://doi.org/10.1016/j.envexpbot.2024.106027.

Nunes, M.H., Vaz, M.C., Camargo, J.L.C., Laurance, W.F., Andrade, A., Vicentini, A., Laurance, S., Raumonen, P., Jackson, T., Zuquim, G., Wu, J., Peñuelas, J., Chave, J., Maeda, E.E., 2023. Edge effects on tree architecture exacerbate biomass loss of fragmented Amazonian forests. Nat. Commun. 14, 8129. https://doi.org/10.1038/s41467-023-44004-5.

Oksanen J., Simpson G.L., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R. B., Solymos P., Stevens M.H.H., Szoecs E., Wagner H., Barbour M., Bedward M., Bolker B., Borcard D., Carvalho G., Chirico M., De Caceres M., Durand S., Evangelista H.B.A., FitzJohn R., Friendly M., Furneaux B., Hannigan G., O. Hill M, Lahti L., McGlinn D., Ouellette M.-H., Cunha E.R., Smith T., Stier A., Ter Braak C.J.F., Weedon J. 2022. The vegan package. Community ecology package. R package version 2.6-4. ⟨https://cran.r-project.org/web/packages/vegan/index.html⟩ (Accessed 15 December 2023).

Oliveira-Filho, R.R., Musiello-Fernandes, J., Pichler, H.A., Antunes, M., Vilar, C.C., Mantelatto, F.L., Anker, A., Cattani, A.P., Chiquieri, J., Joyeux, J.C., Hostim-Silva, M., 2023. Marine and estuarine crustacean diversity and assemblage structure in eastern Brazil three years after the Fundão mining dam failure. Reg. Stud. Mar. Sci. 65, 103068.

Pandey, R., Bargali, S.S., Bargali, K., Karki, H., Chaturvedi, R.K., 2024. Dynamics of nitrogen mineralization and fine root decomposition in sub-tropical *Shorea robusta* Gaertner f. forests of Central Himalaya, India. Sci. Total Environ. 921, 170896. https://doi.org/10.1016/j.scitotenv.2024.170896.

Paudel, S., Sah, J.P., 2003. Physico chemical characters of soil in tropical soil (*Shorea robusta* Gaertn.) forests in eastern Nepal. Himal. J. Sci. 1, 107–110. https://doi.org/10.3126/hjs.v1i2.207.

Prado, F., 2013. Feeding behavior, bird visitation, and seed dispersal in *Guarea macrophylla* and *Trichilia quadrijuga* (Meliaceae). Ornitol. Neotrop. 24, 459–468.

Quinn, G., Keough, M., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria.

Ramos, L., Negreiros, D., Ferreira, B.S.S., Figueiredo, J.C.G., Paiva, D.C., Oki, Y., Justino, W.S., dos, Santos, R.M., Aguilar, R., Nunes, Y.R.F., Fernandes, G.W., 2023. Strong relationships between soil and vegetation in reference ecosystems of a riparian Atlantic rainforest in the upper Doce River watershed, southeastern Brazil. iForest 16, 226–233. https://doi.org/10.3832/ifor4313-016.

Ramos, L., Negreiros, D., Goulart, F.F., Figueiredo, J.C.G., Kenedy-Siqueira, W., Toma, T. S.P., Justino, W.S., Maia, R.A., Oliveira, J.T., Oki, Y., Barbosa, M., Aguilar, R., dos Santos, R.M., Dias, H.M., Nunes, Y.R.F., Fernandes, G.W., 2024. Dissimilar forests along Rio Doce watershed calls for multiple restoration references to avoid biotic homogenization. Sci. Tot. Environ. 930, 172720. https://doi.org/10.1016/j.scitotenv.2024.172720.

Ribeiro, L.G., Silva, A.O., Vaz, K.A., dos Santos, J.V., Nunes, C.A., Carneiro, M.A.C., 2023. Soil arthropod community responses to restoration in areas impacted by iron mining tailings deposition after Fundão dam failure. Environ. Monit. Assess. 195, 1299. https://doi.org/10.1007/s10661-023-11843-0.

Rodrigues, R.R., Lima, R.A.F., Gandolfi, S., Nave, A.G., 2009. On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. Biol. Conserv. 142, 1242–1251. https://doi.org/10.1016/j.biocon.2008.12.008.

Romanelli, J.P., Meli, P., Santos, J.P.B., Jacob, I.N., Souza, L.R., Rodrigues, A.V., Rodrigues, R.R., 2022. Biodiversity responses to restoration across the Brazilian Atlantic Forest. Sci. Tot. Environ. 821, 153403. https://doi.org/10.1016/j.scitotenv.2022.153403.

Rosenfield, M.F., Jakovac, C.C., Vieira, D.L.M., Poorter, L., Brancalion, P.H.S., Vieira, I.C. G., de Almeida, D.R.A., Massoca, P., Schietti, J., Albernaz, A.L.M., Ferreira, M.J., Mesquita, R.C.G., 2022. Ecological integrity of tropical secondary forests: concepts and indicators. Biol. Rev. 98, 662–676. https://doi.org/10.1111/brv.12924.

Schaefer, C.E.G.R., Santos, E.E., Souza, C.M., Neto, J.D., Fernandes Filho, E.I., Delpupo, C., 2015. Cenário histórico, quadro físiográfico e estratégias para recuperação ambiental de Tecnossolos nas áreas afetadas pelo rompimento da barragem do Fundão, Mariana, MG. Arq. Mus. Hist. Nat. Jard. Bot. UFMG 24, 104–135.

Segura, F.R., Nunes, E.A., Paniz, F.P., Paulelli, A.C.C., Rodrigues, G.B., Braga, G.Ú.L., Pedreira Filho, W.R., Barbosa, F., Cerchiaro, G., Silva, F.F., Batista, B.L., 2016. Potential risks of the residue from Samarco's mine dam burst (Bento Rodrigues, Brazil). Environ. Pollut. 218, 813–825. https://doi.org/10.1016/j.envpol.2016.08.005.

Silva, A.O., Guimarães, A.A., Lopez, B.D.O., Zanchi, C.S., Veja, C.F.P., Batista, É .R., Moreira, F.M.S., Souza, F.R.C., Pinto, F.A., dos Santos, J.V., Carneiro, J.J., Siqueira, J.O., Kemmelmeier, K., Guilherme, L.R.G., Rufini, M., Dias Junior, M.S., Aragão, O.O.S., Borges, P.H.C., de Oliveira-Longatti, S.M., Carneiro, M.A.C., 2021. Chemical, physical, and biological attributes in soils affected by deposition of iron ore tailings from the Fundão Dam failure. Environ. Monit. Assess. 193, 462. https://doi.org/10.1007/s10661-021-09234-4.

Smith, D.S., Schweitzer, J.A., Turk, P., Bailey, J.K., Hart, S.C., Shuster, S.M., Whitham, T. G., 2012. Soil-mediated local adaptation alters seedling survival and performance. Plant Soil 352, 243–251. https://doi.org/10.1007/s11104-011-0992-7.

Soares, H.M.A., Rocha, I.C., Paprocki, H., Fernandes, G.W., 2024. Mining tailings alter insects: revealing fluctuating asymmetry in the caddisfly *Smicridea coronata*. Environ. Monit. Assess. 196, 531. https://doi.org/10.1007/s10661-024-12715-x.

Sousa, D.O., Negreiros, D., Ramos, L., Figueiredo, J.C.G., Paiva, D.C., Oki, Y., Justino, W. S., dos Santos, R.M., Ashworth, L., Nunes, Y.R.F., Fernandes, G.W., 2024. Strong soil-vegetation relationship in riparian forests of the middle Doce river watershed, southeastern Brazil. South. For. 86, 231–241. https://doi.org/10.2989/20702620.2024.2347498.

Souza, C., Ramos, L., Negreiros, D., Figueiredo, J.C.G., Justino, W.S., Oki, Y., dos Santos, R.M., Nunes, Y.R.F., Fernandes, G.W., 2024. The fate of some reference forests in the Rio Doce: *Astronium urundeuva* hyperdominance. Floresta e Ambient 31, e20230046. https://doi.org/10.1590/2179-8087-FLORAM-2023-0046.

Toma, T.S.P., Oliveira, H.F., Overbeck, G.E., Grelle, C.E., Roque, F.O., Negreiros, D., Rodrigues, D.J., Guimaraes, A.F., Streit, H., Dechoum, M.S., Fonsêca, N.C., Rocha, T. C., Pereira, C.C., Garda, A.A., Bergallo, H.G., Domingos, F.M.C.B., Fernandes, G.W., 2024. Aim for heterogeneous biodiversity restoration, 376 Science 383, 376. https://doi.org/10.1126/science.adn3767.

Toma, T.S.P., Overbeck, G.E., Mendonça, M.D.S., Fernandes, G.W., 2023. Optimal references for ecological restoration: the need to protect references in the tropics. Perspect. Ecol. Conserv. 21, 25–32. https://doi.org/10.1016/j.pecon.2023.01.003.

United Nations. 2019. United Nations Environment Agency Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021–2030). http://documents-dds-ny.un.org/doc/UNDOC/GEN/N19/060/16/PDF/N1906016.pdf Accessed on 19 Oct 2022.

van der Putten, W.H., Bradford, M.A., Brinkman, E.P., van de Voorde, T.F., Veen, G.F., 2016. Where, when and how plant–soil feedback matters in a changing world. Funct. Ecol. 30, 1109–1121. https://doi.org/10.1111/1365-2435.12657.

van der Sande, M.T., Powers, J.S., Kuyper, T.W., Norden, N., Salgado-Negret, B., Almeida, J.S., Bongers, F., Delgado, D., Dent, D.H., Derroire, G., Espírito-Santo, M. M., Dupuy, J.M., Fernandes, G.W., Finegan, B., Gavito, M.E., Hernández-Stefanoni, J.L., Jakovac, C.C., Jones, I.L., Veloso, M.D.M., Meave, J.A., Mora, F., Muñoz, R., Pérez-Cárdenas, N., Piotto, D., Álvarez-Dávila, E., Caceres-Siani, Y., Dalban-Pilon, C., Dourdain, A., Du, D.V., Villalobos, D.G., Nunes, Y.R.F., Sanchez-Azofeifa, A., Poorter, L., 2023. Soil resistance and recovery during neotropical forest succession. Philos. Trans. R. Soc. B Biol. Sci. 378, 20210074. https://doi.org/10.1098/rstb.2021.0074.

Vancine, M.H., Muylaert, R.L., Niebuhr, B.B., Oshima, J.E.F., Tonetti, V., Bernardo, R., de Angelo, C., Rosa, M.R., Grohmann, C.H., Ribeiro, M.C., 2024. The Atlantic Forest of South America: spatiotemporal dynamics of the vegetation and implications for conservation. Biol. Conserv. 291, 110499. https://doi.org/10.1016/j.biocon.2024.110499.

Vieira, K.I.C., Werneck, H.A., Santos Júnior, J.E., Flores, D.S.S., Serrão, J.E., Campos, L. A.O., Resende, H.C., 2020. Bees and the environmental impact of the rupture of the Fundão dam. Integr. Environ. Assess. Manag. 16, 631–635. https://doi.org/10.1002/ieam.4288.

Wilson, E.O., 1988. In: The current state of biological diversity. Biodiversity. National Academy Press, Washington, DC, pp. 3–18.