

Research article

Relationship of woody species composition with edaphic characteristics in threatened riparian Atlantic Forest remnants in the upper Rio Doce basin, Brazil

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Studies on the composition, richness and diversity of plant species in tropical communities are essential for understanding relevant ecological processes and for developing appropriate conservation policies. Considering that areas subject to direct impacts due to dam breach may in the long-term present changes in species composition and in soil parameters, we evaluated the composition of the flora, described the current vegetation profile, and evaluated whether differences in species composition was influenced by soil variables of three areas along the Gualaxo River, in Minas Gerais State, Brazil. In addition, we identified important plant species through occurrence and phytosociological parameters for ecological restoration projects in the affected region, serving as reference areas. We sampled plant species with DBH \geq 5 cm (diameter at breast height – measured 1.30 m above ground level) in 77 plots distributed in three riparian forest areas. We calculated phytosociological parameters and related them to edaphic factors. A total of 1579 individual plants belonging to 53 botanical families and 227 species were sampled in the three areas. The Fabaceae family was the most representative with 46 species. Species composition and diversity among the sampled areas was similar and was associated with edaphic factors. Furthermore, some species (e.g. *Xylopia sericea*, *Cupania emarginata* and *Ocotea pulchalla*) showed an important relation with soil variables. Some species of the genera (e.g. *Byrsonima*, *Xylopia*, *Ocotea* and *Croton*) and families (e.g. Fabaceae and Myrtaceae) found here, can be important species in the restoration process for the local and regional maintenance of floristic identity in the Rio Doce river.

Keywords: dam collapse, Gualaxo do Norte river, plant distribution, restoration ecology



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Introduction

Around the globe, for many reasons ecosystems are losing their vegetation originality (Rezende et al. 2018, Zwiener et al. 2018, Konings et al. 2021), also due to the invasion of alien species (Stinca et al. 2021, Gonçalves-Oliveira et al. 2022). Further studies on the composition, richness and diversity of old growth plant communities are essential for understanding relevant ecological processes and for developing appropriate conservation policies (Fernandes et al. 2016, Metzger et al. 2019). The collapse of the Fundão dam in the district of Bento Rodrigues, municipality of Mariana (MG), Brazil, caused the devastation of approximately 1469 ha of vegetation and 90% of the riverine habitats of the Fundão, Gualaxo do Norte and Carmelo rivers (Fernandes et al. 2016, Bottino et al. 2017). This disaster led to multiple environmental damages and affected countless ecosystems and ecological interactions by the tailing mud discharged into the Doce river (Sánchez et al. 2018). Riparian environments (Atlantic Forest) affected by the tailings flow have lost most of their regenerative capacity due to the loss of 'ecological memory' (Fernandes et al. 2016). This lost memory derives from off-site (e.g. forest patches, ecological corridors) as well as from within the site (e.g. soil organic matter, remnant vegetation) components that represent the species dispersal potential (external memory) or the potential of local regeneration (internal memory) (Chazdon and Guariguata 2016). The remaining species, interactions and structures that are part of this ecological memory ensure the reorganization of the ecosystem (Bengtsson et al. 2003), being a key component of ecological resilience, that is, the system's capacity to absorb disturbances, reorganize and maintain its adaptive capacity (Gunderson 2000).

The Rio Doce River Basin presents 98% of its area within the Atlantic Forest domain (83 400 km²) (Fernandes et al. 2016), with the Seasonal Semi-deciduous Forests being part of the vegetation. Tailings also directly reached 863.7 ha of permanent preservation areas associated with watercourses in protected areas, and 135 fragments of Seasonal Semi-deciduous Forest (Carmo et al. 2017). Over the past 500 years, the size of the Atlantic Forest domain has been reduced to less than 15% due to human activities (Scarano and Ceotto 2015). In addition, what we currently know about this domain is only 0.01% of the 18.5 million of forest hectares remaining (Lima et al. 2015). Recent remote sensing surveys after this ore dam failure estimate an Atlantic Forest loss of 457.6 ha along the watercourses (Omachi et al. 2018). Due to the vegetation loss and changes in edaphic parameters and watercourses after the collapse of the Fundão dam, the restoration of the impacted sites became urgent (Whitham et al. 2006, Omachi et al. 2018). Otherwise, proper restoration of this vanishing ecosystem requires species that provide structural and functional sustainability to the rest of the biotic community (Whitham et al. 2006, De Deyn et al. 2008, Hughes et al. 2008, Gomes et al. 2021), especially those that influence the land–water interface. Species, called basal constitute the foundation of

ecosystems, as they create the habitats occupied by other species and/or contribute an important fraction of energy to the food web (Jones et al. 1994, Ellison et al. 2005, 2010, Davidson and Jeppesen 2013). Due to the influence that basal species exert on other organisms, the phenotypic variability of these plants in response to extrinsic factors – biotic or abiotic – and intrinsic genetic factors, will determine the spatio-temporal heterogeneity, biodiversity and environmental ecosystem services (Whitham et al. 2006). Thus, the conservation of these natural systems and even the restoration environment depend on the persistence and success (eco-efficiency) of these species in the environment (Fernandes et al. 2016, Kollmann et al. 2016, Gomes et al. 2021, Pisani et al. 2021).

Species that promote ecosystem structuring can be known from phytosociological surveys conducted in reference ecosystem areas (Moore et al. 1999, Fletcher et al. 2003, Goebel et al. 2005). The first step is to sample information on species composition, vegetation structure, as well as the interactions between vegetation and edaphic factors (Madeira et al. 2009). In this study, we evaluated the flora composition and described the current vegetation profile of three areas in Gualaxo River. We evaluated the species composition and verified whether the differences in species composition was influenced by soil variables. In addition, we identified potential species to be used in ecological restoration projects in the affected area. We expected that 1) similar species diversity and composition in the sampled areas due to the similar environmental conditions (e.g. similar edaphic variables) of the basin in the area; 2) abundant plant species will be more important for the community structure and these species tend to be more strongly associated with soil variables (infertile and acidic soils).

Material and methods

Study area and data sampling

We selected three areas of riparian forest (Seasonal Semideciduous Forest – Atlantic Forest) along the Gualaxo do Norte River, affluent of the Rio Doce River, in the Municipality of Mariana, MG (Fig. 1) for the vegetation sampling. The choice of these three areas was since they present a good state of conservation, still maintaining the characteristics of riparian forest. The Gualaxo do Norte River was directly affected from the Samarco dam breach, as the ore tailings flow crossed the entire Gualaxo River until getting into the Rio Doce river (Fernandes et al. 2016, Cruz and Domingues 2017). For the selection of the study reference sites, areas of primary riparian forest were chosen. These areas were selected based on the conservation status, giving priority to sampling in accessible fragments that were old growth of in later stages of succession. The regional climate is mesothermal (Cwa in the Köppen-Geiger classification 1961), with rainy summers and dry winters, average annual precipitation of 1571 mm and average temperature ranging between

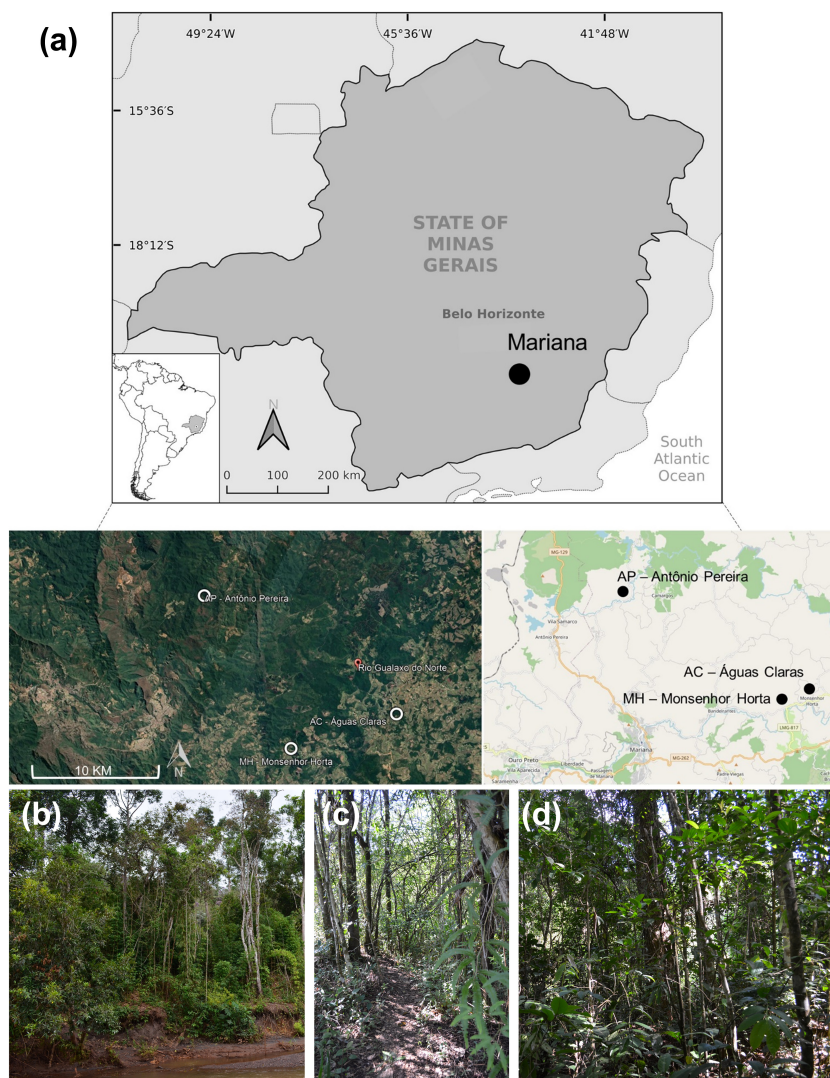


Figure 1. Studied areas. (a) Location of the three sample sites along the Gualaxo do Norte River, Mariana – MG, Brazil; (b) Antônio Pereira – AP (altitude: 720 m a.s.l.); (c) Monsenhor Horta – MH (altitude: 650 m a.s.l.); and (d) Águas Claras – AC (altitude: 650 m a.s.l.).

16.0 and 22.0°C (Alvares et al. 2013; reference municipality: Mariana; Fig. 1).

The plot method was used (Mueller-Dombois and Ellenberg 1974) for vegetation characterization and sampling. The floristic and phytosociological survey of the adult stratum was carried out in 77 plots of 100 m² (10 × 10 m) established in three areas of Gualaxo do Norte River as follow: Águas Claras – AC (20°17'16.5"S, 43°14'59.0"W) with 28 plots, Antônio Pereira – AP (20°16'34.0"S, 43°25'50.0"W), with 24 plots, and Monsenhor Horta – MH (20°20'52.7"S, 43°18'42.7"W) with 25 plots, totalling 7700 m². The distances among the sampling areas were: AC to AP 48 km, AC to MH 35 km and AP to MH 35 km. In each area, the plots were distributed both upstream and downstream of the dam, from the bank, 10 m apart (Fig. 1). The plots were marked with the aid of a compass with levelling, and georeferenced. All individuals within the plots with DBH ≥ 5 cm (diameter at breast height – measured 1.30 m above ground level)

had their height estimated, were identified and marked with numbered aluminium plates. The choice of this protocol follows standards already defined in phytosociological sampling in the Atlantic Forest (Turchetto et al. 2017). In addition, it allows a delimitation in the sampling of individuals already well established within the plots.

The individual's identification was carried out in the field, given prior species knowledge. Plant material was collected (vegetative or reproductive) for identification through specialized literature and existing material, and if not identified to the species level, were sent to specialists. Vouchers for all plant species were collected, identified and deposited in the Montes Claros (MCMG) Herbarium, from Unimontes, and Universidade Federal de Minas Gerais (BHCB) Herbarium. The family names followed the Angiosperm Phylogeny Group (APG IV 2016), and species names were confirmed in the Plant list database (<www.theplantlist.org/>) and updated/corrected whenever necessary.

In each 100-m² plot (all 77 plots), five soil samples from 0 to 20 cm in depth were collected in the corners and center of the plots. Soil collection in this topsoil (0–20 cm) followed the procedures adopted in the studies of phytosociology and plant ecology studies in tropical ecosystems (Barros et al. 2018, Costa et al. 2019, Safar et al. 2019, Cruz et al. 2020). Furthermore, in this soil depth range is where the highest concentration of nutrients recycled by the plant is concentrated (Jobbágy and Jackson 2001). The soil texture and the chemical variables of each composite sample were performed at the Laboratory for Soil Analysis at the Institute of Agricultural Sciences (Universidade Federal de Minas Gerais) according to Teixeira et al. (2017). The pH was measured at a soil/water ratio of 1:2.5 with a pH meter. The exchangeable cations (Ca, Mg and Al) were extracted with a 1 M KCl solution and measured with an ICP-OES. The Mehlich 1 solution was used to extract P, K and micronutrients. The exchangeable acidity (H⁺ + Al³⁺) was extracted with calcium acetate solution (0.5 M).

Data analysis

Data analysis was performed for each sampled area. Classic quantitative phytosociological parameters (Mueller-Dombois and Ellenberg 1974) were used: relative density, dominance and frequency, and importance value (IV) index. For each area and stratum, the Shannon species diversity index (H') was calculated, as well as the Pielou evenness (J') (Krebs 1989). Shannon diversity indices between areas were compared using the Hutcheson t-test (Zar 1996). To assess the differences in species composition, first Cluster analysis (using the frequency matrix) was performed using the UPGMA linkage method and the Bray–Curtis dissimilarity matrix results. Second, nonmetric multidimensional scaling (NMDS) was calculated using the Euclidean distance between species (Legendre and Legendre 1998), where the records contain combinations of numerical data. The distance is always a number between 0 (identical) and 1 (maximally dissimilar) (Legendre and Legendre 1998). The resulting dissimilarity matrix was used for computing the NMDS ordination with the function metaMDSiter in the vegan package in R, which identifies a stable solution using several random starts with smaller stress values (Borcard et al. 2011, Oksanen et al. 2016). In our analysis, we set the number of random starts as 2000, and examined whether solutions with two or three dimensions best described the data. The optimal number of dimensions was two because the stress remained with acceptable value (Borcard et al. 2011).

To determine the relationship between the edaphic variables and the tree species community, the coinertia analysis was used. This analysis constitutes a general and flexible method that measures the concordance (also called co-structure) between two sets of multivariate data (Dolédec and Chessel 1994, Dray et al. 2003). Coinertia was applied to quantify and test the association between two matrices simultaneously. The edaphic matrix was defined as the mean values of 12 edaphic parameters in the 77 plots, while the floristic

matrix consisted of the incidence (presence and absence) of 227 tree species in the 77 plots. The coinertia analysis results in a value called 'RV', which measures the association strength between the two matrices. The RV value is limited to 0 (i.e. no association) and 1 (i.e. maximum association). The significance of c coinertia (p value) is accessed by the Monte Carlo permutation, performed with 100 000 randomizations. To implement the coinertia, a centered and standardized PCA (mean = 0; standard deviation = 1) was performed for the edaphic matrix, and a centred PCA (mean = 0) for the floristic matrix, according to Dray et al. (2003). To achieve the normality assumptions in the edaphic data, the square root transformation was used for the aluminium (Al) content, and the logarithmic transformation for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), manganese (Mn), zinc (Zn) and base saturation (V). The coincidence analysis was performed in the R environment (<www.r-project.org>) using the ade4 package (Dray and Dufour 2007). To assess the association between each edaphic variable and the plots coordinates on axis 1 of coinertia, Pearson's correlation was used, while the association between species and axis 1 of coinertia was defined by the coordinates of the species on this axis (Pavoine et al. 2011).

Results

A total of 1579 adult individuals belonging to 53 plant families and 227 species were sampled (Supporting information). The Fabaceae family was the most representative with 46 species, followed by Myrtaceae (25), Euphorbiaceae and Rubiaceae (12 each). The species with the highest number of adult individuals was *Xylopia sericea* A. St. – Hil. (74 individuals) while 78 species had only one individual each. The five species with the highest importance value (IV) were: *Nectandra oppositifolia* Nees. (Lauraceae) (3.7%), *Piptadenia gonoacantha* (Mart.) J.F.Macbr. (Fabaceae) (3.66%), *Xylopia sericea* (Annonaceae) (3.62%), *Cupania emarginata* Cambess. (Sapindaceae) (2.87%) and *Platypodium elegans* Vogel (Fabaceae) (2.6%) (Table 1). The areas presented, separately, diversity indices for adult vegetation that ranged from 4.11 to 3.92, and evenness indices of 0.86 (Table 2).

The most representative families of the Antônio Pereira – AP area were Fabaceae (18 species) and Myrtaceae (16). The species with the highest number of individuals were *Nectandra oppositifolia* (53), *Lacistema pubescens* Mart. (31) and *Dalbergia nigra* (Vell.) (28), and those with the highest IV were *Nectandra oppositifolia* (5.68%), *Eugenia florida* DC. (4.35%), *Cupania emarginata* (3.38%), *Hieronyma alchorneoides* Allemão (3.33%) and *Guarea* sp. (2.73%). The Fabaceae family also had a high number of species (19) followed by Rubiaceae (8) and Myrtaceae (7), in the Monsenhor Horta – MH area. *Matayba guianensis* Aubl. was the species with most individuals (40), followed by *Luehea candicans* Mart. & Zucc. (26), *Lacistema pubescens* Mart. (24), *Siparuna guianensis* Aubl. (22) and *Dalbergia brasiliensis* Vogel (20). The species with the highest IV were *Piptadenia gonoacantha*

Table 1. List of the 20 adult tree species with the highest IV (importance value) of the riparian vegetation of the Rio Doce river at the Mariana Municipality (MG), Brazil.

Family	Species	IV (%)
Lauraceae	<i>Nectandra oppositifolia</i> Nees	3.699
Fabaceae	<i>Piptadenia gonoacantha</i> (Mart.) J.F.Macbr.	3.662
Annonaceae	<i>Xylopia sericea</i> A.St.-Hil.	3.615
Sapindaceae	<i>Cupania emarginata</i> Cambess.	2.871
Fabaceae	<i>Platypodium elegans</i> Vogel	2.580
Sapindaceae	<i>Matayba guianensis</i> Aubl.	2.262
Fabaceae	<i>Dalbergia nigra</i> (Vell.)	2.218
Lacistemataceae	<i>Lacistema pubescens</i> Mart.	2.214
Erythroxylaceae	<i>Erythroxylum pelleterianum</i> A. St. – Hil.	2.212
Siparunaceae	<i>Siparuna guianensis</i> Aubl.	2.034
Fabaceae	<i>Copaifera langsdorffii</i> Desf.	1.993
Anacardiaceae	<i>Tapirira obtusa</i> (Benth.) J.D.Mitch.	1.951
Malvaceae	<i>Luehea candicans</i> Mart. & Zucc.	1.951
Lauraceae	<i>Ocotea pulchella</i> (Nees & Mart.)	1.893
Myrtaceae	<i>Eugenia florida</i> DC.	1.664
Urticaceae	<i>Cecropia hololeuca</i> Miq.	1.507
Phyllanthaceae	<i>Byrsonima alchorneoides</i> Allemão	1.334
Fabaceae	<i>Caesalpinia echinata</i> Lam.	1.308
Euphorbiaceae	<i>Croton floribundus</i> Spreng.	1.295
Fabaceae	<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	1.253

(8.22%), *Matayba guianensis* (6.59%), *Luehea candicans* (4.69%), *Lacistema pubescens* (3.80%) and *Dalbergia brasiliensis* (3.58%). In the Águas Claras – AC area, Fabaceae family continued with the highest number of species (29), followed by Myrtaceae (9) and Rubiaceae (6). The species with the most individuals were: *Xylopia sericea* (63), *Ocotea pulchella* (Nees & Mart.) (27) and *Cupania emarginata* (25), with *Xylopia sericea* the species with the highest IV (8.28%), followed by *Copaifera langsdorffii* Desf. (4.32%), *Ocotea pulchella* (4.26%), *Cupania emarginata* (4.23%) and *Caesalpinia echinata* Lam. (3.58%).

Regarding species diversity, Águas Claras showed no difference in relation the species diversity from Antônio Peireira ($t = -0.203$, $df = 1033.4$, $p > 0.01$; Table 2) and from Monsenhor Horta ($t = 1.258$, $df = 932.28$, $p > 0.01$). The same result was found for and Antônio Pereira and Monsenhor Horta, where the two areas did not differ in terms of species diversity ($t = 1.578$, $df = 939.14$, $p > 0.01$). The floristic similarity between the studied areas highlighted

Table 2. Number of individuals (No. of individuals), species richness (Richness), Shannon diversity index (H'), Pielou equability index (J') in the riparian vegetation of three areas along the Gualaxo do Norte River, Mariana (MG), Brazil. AC: Águas Claras; AP: Antônio Pereira; MH: Monsenhor Horta.

Area	No. of individuals	Richness	H'	J'
AC – Águas Claras	498	103	4.01	0.86
AP – Antônio Pereira	698	116	4.11	0.86
MH – Monsenhor Horta	438	94	3.92	0.86

the similarity between the three evaluated areas (Fig. 2). The Águas Claras area was the most different in relation to species composition, while the Antônio Pereira and Monsenhor Horta were more similar in species composition. The species common to all areas were *Cecropia hololeuca* Miq., *Copaifera langsdorffii*, *Dalbergia nigra*, *Dalbergia villosa* (Benth.) Benth., *Erythroxylum pelleterianum* A. St. – Hil., *Guapira hirsute* (Choisy) Lundell, *Guatteria villosissima* A. St – Hil., *Himatanthus lancifolius* (Müll. Arg.) Woodson, *Inga vera* Willd., *Lacistema pubescens*, *Luehea candicans*, *Matayba guianensis*, *Nectandra oppositifolia*, *Platypodium elegans*, *Siparuna guianensis* and *Xylopia sericea*.

The coinertia analysis showed a significant association ($p < 0.001$) between the edaphic parameters and the floristic composition in the sampled areas. The RV index found ($RV = 0.260$) indicates 26% of association between the edaphic parameters and the floristic composition in the studied plots. The percentage of variance explained by axis 1 of coinertia was 79.7%, while axis 2 explained 8.0% of the variation. Thus, the interpretation of the results considered only axis 1 of coinertia. On the positive side of axis 1 of the coinertia are the plots with more infertile and acidic soils, with higher contents of Al and Fe, lower base saturation, lower pH and lower contents of Mn, Ca, Mg, Zn, P and Cu (Fig. 3). The main species with the high association with the positive side of axis 1 of coincidence were *Xylopia sericea*, *Cupania emarginata*, *Ocotea pulchella*, *Erythroxylum pelleterianum*, *Aralia excelsa* (Griseb.) J. Wen, *Copaifera langsdorffii*, *Croton floribundus* Spreng., *Apuleia leiocarpa* (Vogel) J.F.Macbr., *Byrsonima pachyphylla* A. Juss., *Caesalpinia echinata*, *Guatteria villosissima*, *Platypodium elegans*, *Dalbergia nigra*, *Cupania vernalis*, *Byrsonima crassa* Nied., *Salacia elliptica* (Mart.) G. Don and *Siparuna reginae* (Tul.) A. DC. In contrast, on the negative side of the coinertia axis 1 presents the plots with higher fertility, lower acidity, higher base saturation, higher pH and higher contents of Mn, Ca, Mg, Zn, P and Cu, and lower contents of Al and Fe. The main species with high association with the negative side of coinertia axis 1 were *Luehea candicans*, *Aniba canelilla* (Kunth) Mez, *Matayba guianensis*, *Plinia grandifolia* (Mattos) Sobral and *Magonia pubescens* A.St.-Hil. The other species had low relation with the coinertia axis 1.

Discussion

Species composition and diversity among the sampled areas was similar and associated with edaphic factors. Furthermore, some species like *Xylopia sericea*, *Cupania emarginata*, *Ocotea pulchella* and *Erythroxylum pelleterianum* showed an important relation with soil variables. In this way, the influence of local factors in a riparian forest (e.g. soil and surrounding vegetation), can originated a specific floristic composition, with common species of riparian forests (Azevedo et al. 2014, Veloso et al. 2014). The evenness index (J) is related to the diversity index (Crepaldi and Peixoto 2013) and showed a similar floristic heterogeneity in the three sampled areas (high

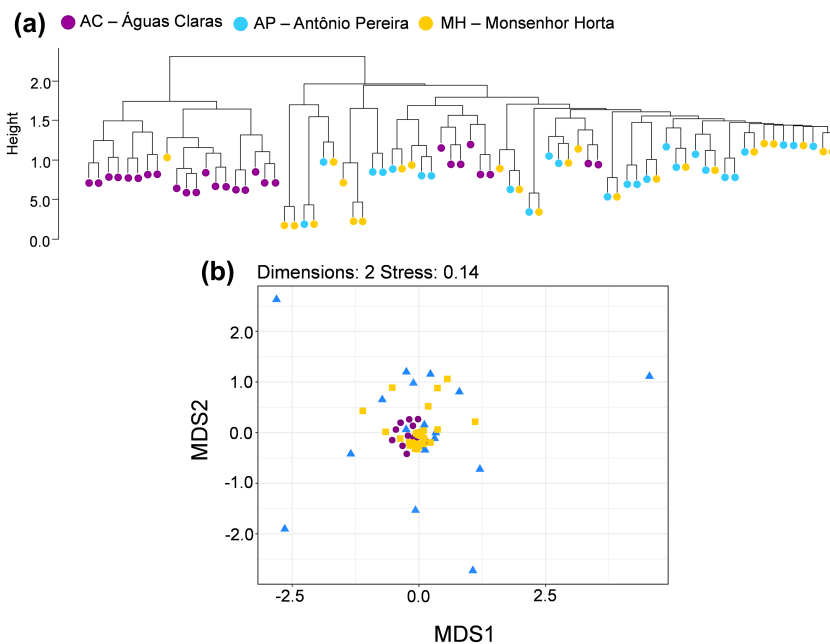


Figure 2. Composition of tree species in relation to the sampled areas. (a) Cluster dendrogram for the sampled plots and areas in the Gualaxo do Norte River, Mariana, MG, Brazil; and (b) NMS2 results for the plots and sampled areas.

number of species). The species belonging to the Fabaceae family were the most representative in this study, with high species richness, being common in all areas. Species of this family are also commonly found in greater proportions in phytosociological studies in fragments of the Atlantic Forest (Lima et al. 2017, Miranda et al. 2019), including *Apuleia leiocarpa* and *Piptadenia gonoacantha*, mainly because they are

generally emergent species (Lopes et al. 2014). The Fabaceae family is considered the third largest family of angiosperms in the world, with about 685 genera and 18 860 described species, distributed in temperate, tropical and subtropical regions, and in Brazil this family has the largest number of plant species (Knothe et al. 2016). Fabaceae species have the characteristic of nitrogen fixation capacity, in addition to

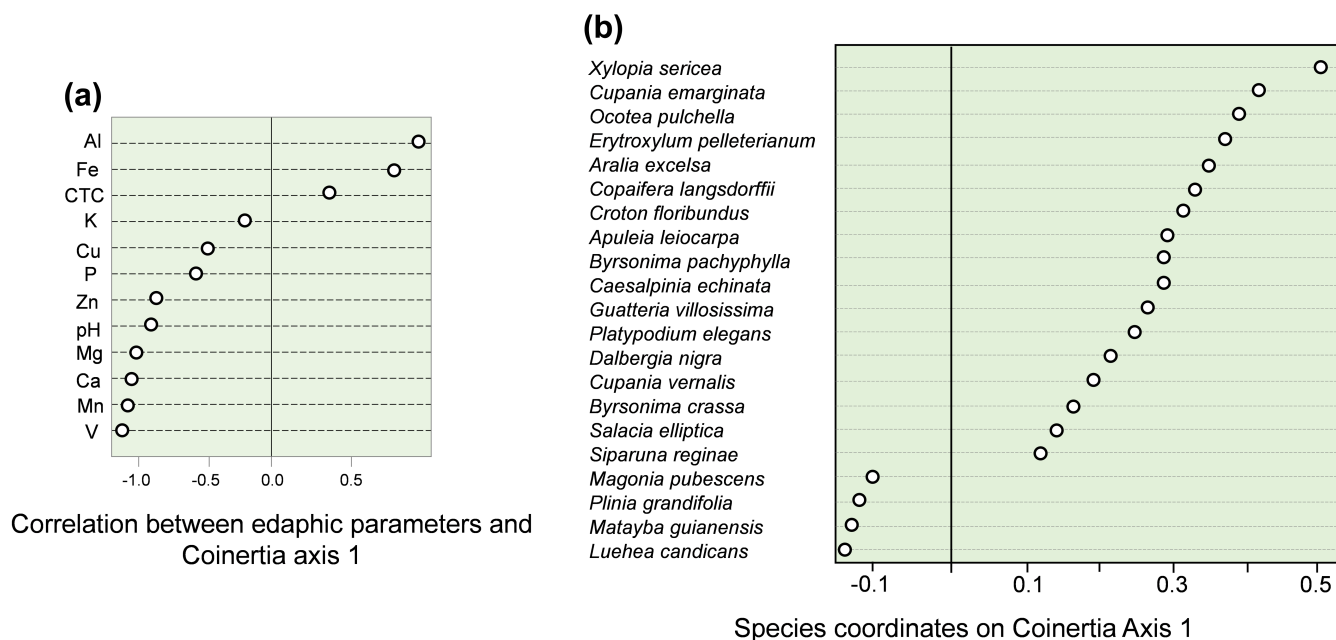


Figure 3. Co-structure between edaphic parameters and tree species community sampled in the riparian forest of the Gualaxo do Norte River, in Mariana, MG, Brazil. (a) Pearson correlation between edaphic parameters and plot coordinates on axis 1 of coinertia; and (b) coordinates of the most important tree species on axis 1 of coinertia. CTC: effective cation exchange capacity; and V: base saturation.

being responsible for ensuring productivity in most terrestrial ecosystems (Lima et al. 2017, Gei et al. 2018). Myrtaceae was the second most diverse plant family representing for the study area the maintenance of diversity and ecological interactions, especially those involving animal-plant interactions (Carim et al. 2007). Species in this family are commonly attractive to dispersal vertebrates, which function as crucial elements for the continuity of the successional processes (Rocha and Silva 2002).

Among species with high importance values (IV), we identified the predominance of zoochoric species, what follows the well-known tropical forest pattern (Howe and Smallwood 1982, Jordano 2000, Sansevero et al. 2011). Likewise, in the present study, the predominance of zoochoric species was evident among the species with greater association with infertile soils. Include zoochoric trees species in restoration projects is considered an important strategy to accelerate ecological succession (Parrotta et al. 1997, Reay and Norton 1999). The species with the highest importance, in relation to all study areas, was *Nectandra oppositifolia*. This species is considered as late secondary or even climax (Gandolfi et al. 1995). The high abundance of individuals of *Nectandra oppositifolia* in the Atlantic Forest has already been observed in other studies (Bechara et al. 2009, Meyer et al. 2013).

Coinertia analysis showed that there is a significant association between the edaphic variables and the floristic composition of the 77 evaluated plots. The species with the high association with the infertile soils and rich in Fe and Al of the principal axis of coinertia was *Xylopia sericea*, a species of the late secondary ecological group (Meira-Junior et al. 2015). Individuals of this species are adapted to dry areas with low fertility, which may explain its strong association with the edaphic variables shown in the coinertia (Lorenzi 2000). Soil rich in organic matter is related to high soil fertility, allowing the passage of water and air, promoting better root penetration, and providing accumulation of nutrients (Dantas and Batalha 2011). Therefore, fertile soils tend to have high richness, as they allow the coexistence of more species and greater basal area, resulting in greater biomass gains (Souza et al. 2007, Dantas and Batalha 2011). Nutrient contents were likely more limiting in the habitats studied here. The higher aluminium content may be due to leaching or even due to the origin of the soil, and tends to cause soil impoverishment, which results in competition for essential minerals and toxicity (Ruggiero et al. 2002), leading to selection of species aluminium tolerant.

Active ecological restoration of degraded areas is the most efficient way to return biodiversity and provision of ecosystem services along the Rio Doce river. This strategy tends to promote faster recovery of affected areas. In the epicenter of the area affected by the Fundão dam breach, restoration needs to be carried out based on knowledge of the local reference areas and monitored over a long period (Kollmann et al. 2016, Metzger et al. 2019). The use of aloctones or even exotic species can favour the development of new ecosystems, representing another problem to be solved for the already impacted Atlantic Forest. The correct use of species in the restoration

of riparian areas is essential to accelerate and guarantee the water and food security of the Rio Doce river, such as water flow regulation and soil fixation (Brancalion et al. 2016, Bustamante et al. 2019, Metzger et al. 2019). However, due to the impacts of tailings on soils along the Rio Doce river, ecological restoration can take decades, or even several centuries (Fernandes et al. 2016). The intentional planting of seedlings allows the forest structure to recover more quickly. But the choice of species is essential because it needs to be carried out with species capable of maintaining the ecosystem's structure, allowing colonization by more species, attracting fauna and thus the return of fundamental processes in the long term (Holl and Aide 2011, Fernandes et al. 2016). Due to the considerable variations that riparian forests present along rivers (Azevedo et al. 2014, Veloso et al. 2014), the species selection needs to be based on studies previously carried out in reference areas. Even in highly degraded environments, such as most grazing areas (Florentine and Westbrooke 2004, Sansevero et al. 2011) or mining areas (Parrotta et al. 1997, Parrotta and Knowles 1999), the planting of native species facilitate the recolonization process, which originate from the regional pool of species (Ruiz-Jaén and Aide 2005, Metzger et al. 2019). In the studied environment and disaster scenario, this may be the most important strategy.

Thus, long-term monitoring and scientific studies on species development are critical to determine whether ecosystems will continue the desired trajectory, particularly in light of accelerated climate change (Kollmann et al. 2016, Holl 2017, Bustamante et al. 2019). The Atlantic Forest remnants studied presents plants genera that already occurred since the glacial and interglacial periods (*Copaifera*, *Luehea*, *Matayba*, *Piper*, *Solanum*, *Zanthoxylum*, among others) (Ledru et al. 2016) as species of current marginal habitats (Joly et al. 2012) that contributed to the increase in the richness of the Atlantic Domain.

Conclusion

The sampled areas had a similar floristic composition with some shared species (e.g. *Cecropia hololeuca*, *Copaifera langsdorffii* and *Dalbergia nigra*). Species composition was related to edaphic factors, with some species such as *Xylopia sericea*, *Cupania emarginata*, *Ocotea pulchella* and *Erythroxylum peltarianum* having a high association with the analysed edaphic factors. The use of species from these genera can be important for the maintenance of local and regional floristic identity, which should be valued and used in restoration projects in the Rio Doce river basin. On the other hand, detailed studies of other functional attributes, in progress, may provide more elements for a safe selection of species that can accelerate the restoration of degraded areas along the Rio Doce river.

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.m37pvmd5g>> (Nunes et al. 2022). In addition, all information on the species and plots sampled is available in the Supporting information of the manuscript.

Supporting information

The Supporting information associated with this article is available with the online version.

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