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Strong relationships between soil and vegetation in reference ecosystems of a riparian Atlantic rainforest in the upper Doce River watershed, southeastern Brazil

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Habitat loss and fragmentation have been impacting ecosystem services essential for human survival. The Brazilian Atlantic rainforest, a biodiversity hotspot, has suffered from historical deforestation and, more recently, from an environmental disaster caused by the Fundão dam collapse that released ore tailings drastically affecting a large territory in the Doce River watershed. This work aims to assess the relationships between soil properties and vegetation in a reference ecosystem to provide guidelines for restoration projects in areas affected by the dam collapse. We conducted phytosociological (vegetation characteristic) and soil quality studies in three distinct natural sites and studied different vegetation strata to better understand plant species composition in reference sites along the impacted Doce River and their potential role in community structuring and functioning. We recorded 140 species, 78 in the tree stratum, and 90 in the sapling stratum. Furthermore, our results highlight the influence of soil on floristic composition in the Atlantic rainforest. Small-scale edaphic variation influenced species composition in both sapling and tree strata. We also identified species of the same genus with strong association with the extremes of the edaphic gradient. Therefore, we highlight that studies in various regions along the Doce River watershed are of utmost importance to evaluate the association between species and soils. The particularities of the species are crucial to the effectiveness of restoration processes since this plant-soil correlation should not be extrapolated even within the same genus. This knowledge is of strategic relevance to provide scientific-based guidance for restoring these environments, aiming at the recovery of biodiversity and ecosystem services.

Keywords: Dam Breach, Fundão Dam Collapse, Reference Ecosystem, Restoration Ecology, Soil-vegetation Relationships

Introduction

The increasing loss and fragmentation of tropical forests have led to the simplification of these environments, substantially affecting key ecosystem services essential for human survival. The simplification of environments comes along with biodiversity loss, which affects healthy soil maintenance and the provision of clean water and air, as well as compromises livelihoods, food security, and general quality of life worldwide (Shimamoto et al. 2018, Gann et al. 2019). Native ecosystems have a high resilience when faced with mild disturbances and reduce the effects of climate change (Gann et al. 2019). However, the degradation of native ecosystems has affected their regenerative capacity and ecological functions. To mitigate these impacts and promote the restoration of degraded areas, the United Nations (UN) has declared the present decade (from 2021 to 2030) as "the decade of restoration" (United Nations 2019).

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Through ecological restoration, it is possible to recover the environment functionally by re-creating habitats, and increasing diversity, biological integrity, and ecosystem services (Clewell et al. 2004, Rosenfield et al. 2022). One of the main steps in restoration is the identification of a reference ecosystem, which serves as a guide for planning and measuring the success of the project, so the recovered environment must resemble what it was before degradation (Clewell et al. 2004, Goebel et al. 2005, Toma et al. 2023). In forest restoration, the goal is to create plant assemblages with similar species composition found in the reference area previously established (Rodrigues et al. 2009, Rosenfield et al. 2022). To be effective, these restored plant assemblages must modulate environmental conditions and ecosystem services, which in turn favor the establishment of other native species (Rosenfield et al. 2022).

The success of restoration projects is strongly tied up to the recovery and re-establishment of soil properties, as they shape ecological succession and accelerate the recovery of tropical forests (Gei et al. 2018, Rozendaal et al. 2019, Jakovac et al. 2022, Van Der Sande et al. 2022), with an important role in creating microhabitats essential for forest diversity and taxonomic composition (Figueiredo et al. 2022). Land use history and disturbance intensity determine the availability of seeds and propagules, as well as the presence of dispersing agents, which guide the regenerative capacity of the system (Mesquita et al. 2001). Thus, the analysis of soil factors concomitant with phytosociological (vegetation characteristic) surveys is an indispensable tool for understanding the differences among communities and their functional attributes (Coelho et al. 2018). Besides creating guidelines for appropriate conservation and restoration policies (Metzger 2009, Fernandes et al. 2016), studies of soil-vegetation relationships help to define properly the reference ecosystems.

Although biodiversity studies have been growing in the last decades, environmental degradation keeps rising at concerning levels (Leclère et al. 2020). Tropical forests have been drastically devastated. For instance, the Brazilian Atlantic rainforest, one of the 25 most biodiverse and threatened ecoregions of the world (Myers et al. 2000, Marques & Grelle 2021), now comprises only fragments corresponding to abount 12% of its original area (Ribeiro et al. 2009), although new estimates point to a larger native cover area (28% – Rezende et al. 2018). Even the riparian forests that are protected by specific environmental legislation have suffered intense degradation and disturbance (Rezende et al. 2018) and this scenario is worsening because of the loosening of the laws (Guidotti et al. 2020). Riparian forests are associated with water courses and have high relevance in the preservation of species and natural resources, ensuring the maintenance of ecosystem integrity (Guidotti et al. 2020). However, stretches of riparian formations associated with the Doce River and its main tributaries have been degraded due to their history of inadequate management (Pires et al. 2017). The environmental disaster caused by the rupture of the Fundão dam in the municipality of Mariana (MG) is another major vector of stress imposed on the vanishing Atlantic rainforest. The dam breach released tailings that drastically affected the entire riparian vegetation of the Doce River (Fernandes et al. 2016, Omachi et al. 2018). The tsunami of iron ore mud affected the "ecological memory" of this site (Fernandes et al. 2016) and the gradual and natural capacity for resiliency (Brancalion et al. 2014), therefore requiring bold ecological restoration actions.

The assessment of the relationships between edaphic properties and vegetation composition in reference areas of threatened ecosystems is a first step towards understanding the particular species and edaphic conditions that promote diversity in these ecosystems, helping to expand the regenerative potential of impacted areas (Fernandes et al. 2016). Our objective was to evaluate the relationship between floristic composition of the tree and shrub strata and small-scale edaphic variation in Atlantic forests, assessing whether soil variation can explain vegetation structure and composition in these two strata. Our hypothesis is that small-scale edaphic heterogeneity plays an important role in tree and sapling communities in riparian Atlantic Forest remnants in the upper Doce River watershed, southeastern Brazil.

Material and methods

Study area

We carried out the study in three sites (Fig. 1) of riparian Brazilian Atlantic rainforest

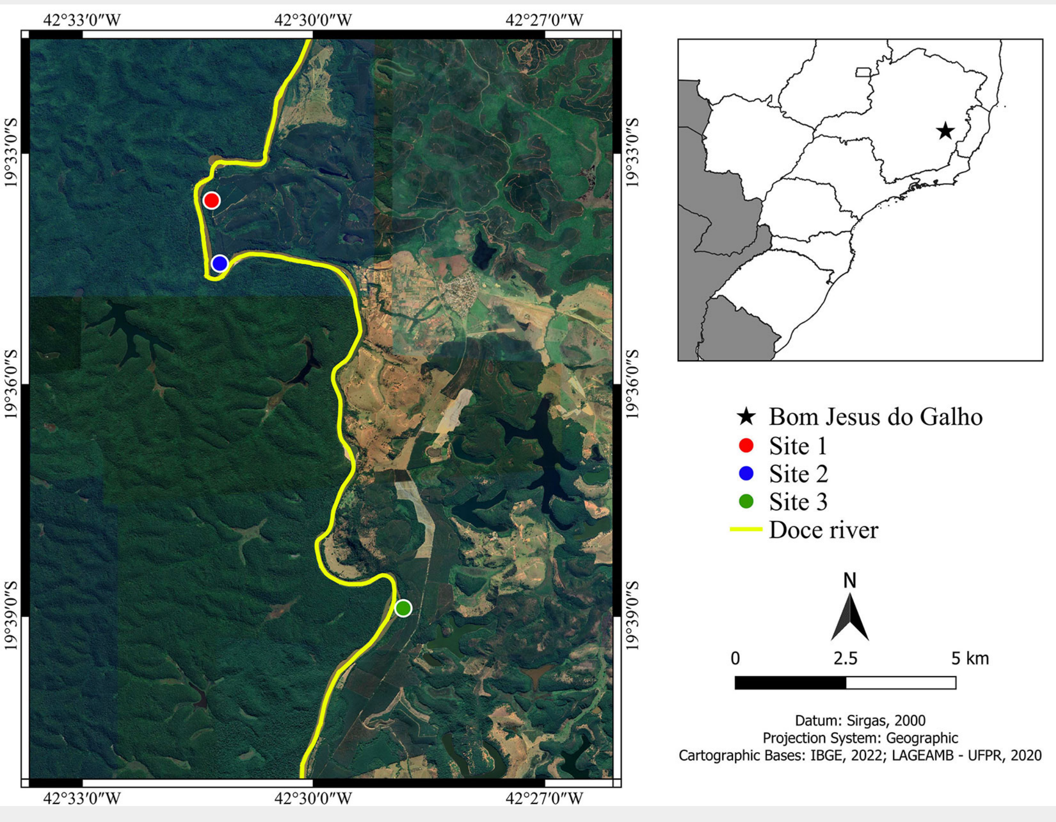

Fig. 1 - Map showing the location of three sampling sites in riparian Atlantic Rain Forest at the upper Doce River watershed, Bom Jesus do Galho-MG, southeastern Brazil.

est (Semideciduous Seasonal Forest) remnants located in the north of the municipality of Bom Jesus do Galho, district of Revés de Belém, state of Minas Gerais, southeastern Brazil (Fig. 1). The location of the three sampling sites were: Site 1: 19° 33′ 30.4″ S, 42° 31′ 25.6″ W; Site 2: 19° 34′ 32.2″ S, 42° 31′ 19.2″ W; Site 3: 20° 38′ 53.8″ S, 42° 28′ 50.0″ W. The study sites are located within the buffer zone of the Doce River State Park. Created in 1944, the park was the first state conservation unit in Minas Gerais. With an area of 36,000 ha, it is one of the largest Atlantic rainforest remnants in the country. According to the Köppen classification, the regional climate is categorised as Cwa, humid subtropical with dry winter (May to October) and hot rainy summer (November to April – Alvares et al. 2013). The historical average annual temperature is 21.4 °C and the annual precipitation is 1325 mm (Alvares et al. 2013). The soil use in Bom Jesus do Galho is predominantly anthropic, being occupied by crops and pasture, along with forest remnants (MapBiomas 2023). This municipality has been losing its native areas considerably. From 1985 to 2021 more than 38% of the native areas were lost, and the areas destined for monocultures and coffee plantations have had an increase of more than 4000 ha (MapBiomas 2023).

Sampling vegetation and edaphic parameters

To characterize the vegetation structure, we used the fixed area plot sampling method proposed by Mueller-Dombois & Ellenberg (1974). We selected three sites with a minimum distance of 2 km between them, with preserved riparian forest remnants. For the study of the tree stratum, we systematically demarcated 15 plots of 10 × 10 m (100 m²) in each sampling site, at least 10 m apart, totaling 45 plots. Within each plot, all woody individuals with DBH (diameter at breast height = 1.30 m above the ground) > 5 cm were inventoried. It is worth mentioning that all individuals of the tree stratum were woody species. We marked the sampled individuals with numbered aluminum plates attached by nails to their trunks. Samples of each plant individual were collected, identified with numbered adhesive tapes, and pressed to be later identified to the lower taxonomic level possible. Since many individuals were not flowering at the sampling time, several trips had to be done to the sites to collect material with reproductive structures for proper species identification.

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. Within each subplot, with the aid of a digital caliper, we inventoried all herbaceous and shrubby individuals with DAS (diameter at ground height) ≥ 1 cm and ≤ 5 cm. We marked the sampled individuals with numbered aluminum plates attached with nylon thread. Subsequently, we collected plant branches ideally with reproductive structures from all individuals for taxonomical identification. Sixteen species did not flower during sampling, which prevented taxonomic identification.

We treated the plant material collected for the tree and sapling strata according to conventional herborization techniques and deposited them in the Herbarium of Norte Mineiro (ICA-UFMG) and the Herbarium of Montes Claros Minas Gerais (Unimontes). The identification of the botanical material collected was done by consulting experts, using specialized literature, and comparing it with the existing *exsiccata* in these herbaria. We used the Angiosperm Phylogeny Group IV (APG IV 2016) system to classify the species into families. Synonymy verification, nomenclature, and species authors were obtained through the "WorldFlora" package (Kindt 2020) in the R environment (R Core Team 2018), standardized according to World Flora Online (WFO – http://www.worldfloraonline.org). For species not found in WFO, we performed additional checks through the Flora e Funga do Brasil (2022). We calculated the following parameters: absolute and relative values of density, dominance, frequency, and value of importance (IV). To calculate the IV, we used the average of the relative density, relative dominance, and relative frequency.

In each plot, at the four corners and the center, we collected 100 grams of soil obtained at 20 cm deep, then we mixed the five samples into one composite sample. Each composite sample represented a valid estimate of the average soil parameters. Each soil sample was shade dried, kept at room temperature, crumbled, completely homogenized, identified, and then sent for chemical and particle size analyses by the Soil Department of the Federal University of Viçosa. All soil granulometric analyses (coarse sand, fine sand, silt, and clay fractions) followed the description found in Donagemma et al. (2017). The pH in water was measured using 1:2.5 (v/v) soil: solution ratios. The organic matter content was determined by the Walkley-Black method. The exchangeable cations Ca^{2+}, Mg^{2+}, and Al^{3+} were extracted using a 1 mol L^{-1} KCl solution. The Ca^{2+} and Mg^{2+} contents were determined in the extract by titration with EDTA 0.01 mol_c L^{-1}, and the Al^{3+} contents by titration with NaOH 0.025 mol_c L^{-1}, according to Silva et al. (1999). The elements P, K, Zn, Fe, Mn, and Cu were extracted by the Mehlich 1 solution, the sulphur (S), by a solution of monocalcium phosphate in acetic acid, and the contents of these elements in the extracts were determined by spectrophotometry, according to Silva et al. (1999). Potential acidity (H+Al) was extracted by a 0.5 mol L^{-1} calcium acetate solution at pH 7.0 and determined by alkalimetric titration of the extract (Silva et al. 1999). The base saturation (S_b) and aluminum saturation (S_{Al}) were calculated, respectively, according to the following expressions (eqn. 1, eqn. 2):

$$S_b = 100\,\frac{K + Ca^{2+} + Mg^{2+}}{K + Ca^{2+} + Mg^{2+} + H + Al} \qquad (1)$$

$$S_{Al} = 100\,\frac{Al^{3+}}{K + Ca^{2+} + Mg^{2+} + Al^{3+}} \qquad (2)$$

Statistical analyses

To assess the adequacy of sampling effort, we constructed rarefaction curves for species diversity in R (R Core Team 2018) using the function "rare_Rao" from package "adiv" (Pavoine 2020), in which expected species diversity for each sampling site was computed as a function of the cumulative number of plots. We used the resampling approach with 10,000 iterations. We evaluated the pattern of exclusive and shared species among the three studied sites through Venn diagrams constructed for both tree and sapling strata using the package "VennDiagram" (Chen & Boutros 2011).

To determine the relationship between soil factors and the plant species community, we made a co-inertia analysis (COIA). This robust and flexible analysis measures the agreement between two multivariate data sets, also called co-structure (Dolédec & Chessel 1994, Dray et al. 2003). We performed the COIA for the tree and sapling strata separately. The edaphic matrix was defined as the values of 17 soil factors in the 45 plots (15 per site), while the floristic matrix was defined as the incidence (presence and absence) of 78 tree species or 90 sapling species in the 45 plots. We removed rare species (species that appear only once in each stratum) from the COIA in order to reduce bias in the detection of relationships between community composition and edaphic factors (McCune & Grace 2002).

An RV coefficient, which measures the strength of the association between the two matrices, was calculated from COIA outputs. The RV coefficient is bounded to 0 (*i.e.*, no association) and 1 (*i.e.*, maximum association). The significance (p-value) of the RV coefficient was obtained through Monte Carlo permutation, performed with 10,000 randomizations. To analyse the COIA, a Principal Components Analysis (PCA – mean = 0; standard deviation = 1) was used for the soil matrix, and a centered PCA (mean = 0) was used for each floristic matrix, according to Dray et al. (2003). To attain the assumptions of normality in the soil data, we performed square root transformation for potassium (K), iron (Fe), and organic carbon (C), and logarithmic transformation for sulphur (S), copper (Cu), silt, and clay. To assess the association between each soil factor and COIA axis 1, we performed a Pearson's correlation between soil values and plot coordinates on COIA axis 1. The association between species and the COIA axis 1 was defined by the species coordinates on this

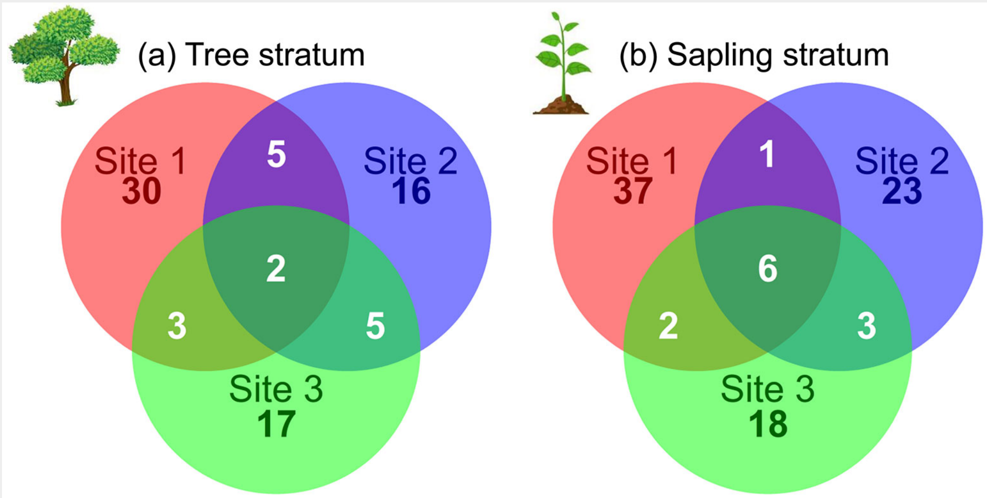

Fig. 2 - Venn diagram illustrating the exclusive and shared species among three studied sites from tree (a) and sapling strata (b) of riparian forests at the upper Doce River watershed, Bom Jesus do Galho-MG, southeastern Brazil.

axis. The COIA was performed using the "ade4" package (Dray & Dufour 2007). All analyses were done in the R environment (R Core Team 2018).

Results

In this study, we found 140 plant species belonging to 28 families. Seventy-eight species belonged to the tree stratum and 90 to the sapling stratum (see Tab. S1 and Tab. S2 in Supplementary material). The rarefaction curves shown in Fig. S2 indicate that the sampling of species diversity for the three sites at both tree (Fig. S2a-c) and sapling strata (Fig. S2d-f) was solid, since the expected species diversity shows a trend for stabilization.

In the tree stratum, the richest families were Fabaceae (10 species), followed by Moraceae (6 species), Meliaceae (5 species), and Myrtaceae (5 species). Eight families were represented by only one single species (Tab. S1 in Supplementary material). Regarding the importance value (IV), Meliaceae accounted for 38.9% of IV, followed by Fabaceae (9.7%), Petiveriaceae (9.1%), and Sapindaceae (8.5% – Tab. S1). The most important tree species was *Guarea macrophylla* Vahl (IV: 22.6%), followed by *Guarea guidonia* (L.) Sleumer (Meliaceae, 11.2%), *Gallesia integrifolia* (Spreng.) Harms (Petiveriaceae, 8.0%), and *Cupania emarginata* Cambess. (Sapindaceae, 3.6%) (Tab. S1). Seventeen species were not identified, and these unidentified species accounted for 7.0% of IV. These species did not flower during sampling, which prevented taxonomic identification.

In the sapling stratum, the richest families were Fabaceae (13 species), followed by Myrtaceae (12 species), Meliaceae (8 species), Sapindaceae (7 species), Lauraceae (6 species), and Moraceae (5 species). Eight families were represented by only one species (Tab. S2 in Supplementary material). Regarding the IV, the family Sapindaceae accounted for 20.0% of the IV, followed by Myrtaceae (18.3%), Lauraceae (12.1%), and Meliaceae (8.3% – Tab. S2). The most important sapling species was *Cupania emarginata* (IV: 11.2%), *Aniba firmula* Mez (Lauraceae, 10.6%), *Eugenia ligustrina* (Sw.) Willd. (Myrtaceae, 5.6%), *Trichilia pallens* C.DC. (5.0%), and *Eugenia umbrosa* O.Berg (Myrtaceae, 4.5% – Tab. S2). Sixteen species were not identified, and these unidentified species accounted for 3.9% of the IV.

Two species of the tree stratum occurred at the three studied sites, *Eugenia florida* DC. (Myrtaceae), and *Maclura tinctoria* (L.) D.Don ex Steud. (Moraceae – Fig. 2a), and these two species stand out among the ten most important species from the tree stratum. However, most species were exclusive of each site. The number of exclusive tree species at sites 1, 2, and 3 was, respectively, 30 (75%), 16 (57%), and 17 (63%) (Fig. 2a). Regarding the sapling stratum, six species occurred at the three studied sites, *A. firmula, Cu. emarginata, E. florida, Ga. integrifolia, Gu. macrophylla*, and *T. pallens* (Fig. 2b), and except for *Gu. macrophylla*, these species stand among the ten most important species from the sapling stratum (Tab. S2). Similar to the tree stratum, the majority of sapling species were exclusive from each site. The number of exclusive sapling species at sites 1, 2, and 3 was, respectively, 37 (80%), 23 (70%), and 18 (62%) (Fig. 2b).

The soils from the riparian Atlantic rainforests at the studied sites showed a considerable variation that indicated a high heterogeneity among the plots (Tab. S3 in Supplementary material). According to the chemical properties, the sampled soils were considered fertile, with the base saturation ranging from 49.3% to 84.6%, and the Al concentration was negligible. The pH was acidic (pH < 5.5) for 49% of plots and neutral for 51% of plots. The concentration of phosphorus ranged from 0.8 to 8.9 mg dm^{-3}, the potassium ranged from 21 to 114 mg dm^{-3}, and the organic carbon ranged from 0.1% to 3.0%. The iron content showed a wide variation, ranging from 10.3 to 438.1 mg dm^{-3}, and the manganese ranged from 44.8 to 196.3 mg dm^{-3}. Regarding the soil texture, there was also a wide variation in the sampling plots (Tab. S3). The proportion of fine sand ranged from 7.1% to 81.9%, while the proportion of clay ranged from 8.7% to 50.5%.

The co-inertia analysis (COIA) indicated a clear edaphic-floristic gradient at both tree and sapling strata. The overall association between tree species and edaphic factors was highly significant (RV = 0.445, $p < 0.001$), according to the COIA. We found a connection of 44.5% between the edaphic and tree floristic matrices. The percentage of covariance explained by the tree-COIA axis 1 was 70.8%, while axis 2 explained 17.5% of the covariance. Thus, we further explored only the tree-COIA axis 1. The positive side of the tree-COIA axis 1 showed plots with acidic soils with higher proportion of clay and silt, and higher concentration of magnesium and organic carbon (Fig. 3a). The tree species more strongly associated with the positive side of this axis were *Gu. macrophylla, Cu. emarginata, T. pallens*, Fabaceae sp.1, *Macl. tinctoria*, and *Machaerium villosum* Vogel (Fabaceae – Fig. 3b). On the other hand, the negative side of tree-COIA axis 1 showed plots with less acidic soils, nutritionally richer, with higher proportion of fine sand, and higher amounts of phosphorus, manganese, and iron (Fig. 3a). The tree species more strongly associated with the negative side of this axis were *Gu. guidonia, Psychotria carthagenensis* Jacq. (Rubiaceae), *A. firmula, Cu. oblongifolia, Clarisia ilicifolia* (Spreng.) Lanj. & Rossberg (Moraceae), and *Seguieria langsdorffii* Moq. (Petiveriaceae – Fig. 3b).

Regarding the sapling stratum, the overall association between sapling species and edaphic factors was also highly significant (RV = 0.357, $p < 0.001$) according to the COIA. We found a connection of 35.7% between the edaphic and sapling floristic matrices. The percentage of covariance explained by COIA axis 1 was 53.2%, while axis 2 explained 29.2% of the covariance. Thus, similar to the tree-COIA, we further explored only the sapling-COIA axis 1 for the sapling stratum. The positive side of the

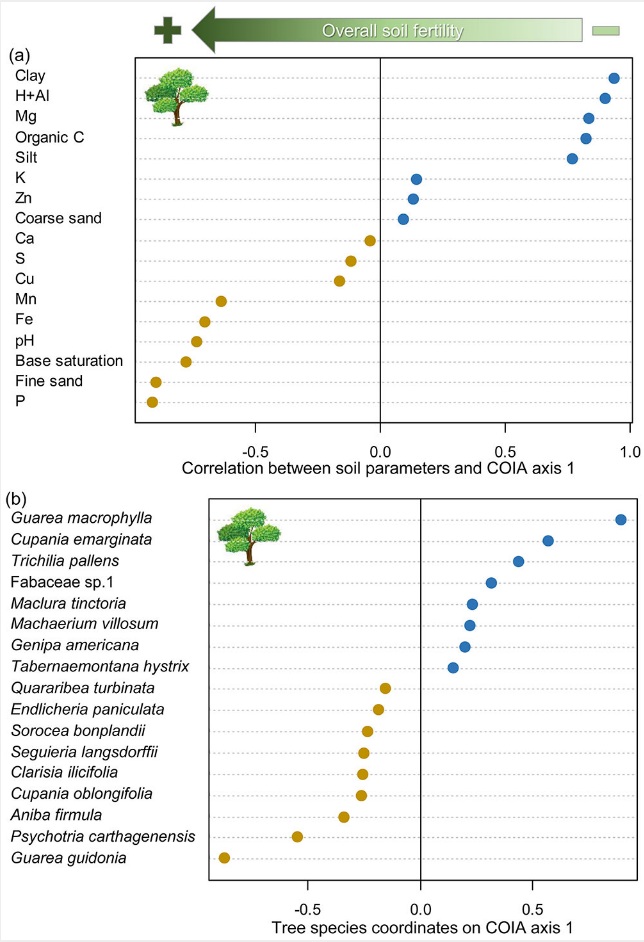

Fig. 3 - Co-structure between edaphic factors and tree species community sampled at three sites from riparian forests at the upper Doce River watershed, Bom Jesus do Galho-MG, southeastern Brazil. (a): Pearson's correlation between edaphic factors and plot coordinates on co-inertia analysis (COIA) axis 1; (b) coordinates of tree species with the highest associations with negative and positive sides of COIA axis 1. Green arrow on the top indicates the overall direction of the soil fertility gradient. Orange and blue circles represent, respectively, negative and positive values of correlation (a) or coordinates (b) on COIA axis 1.

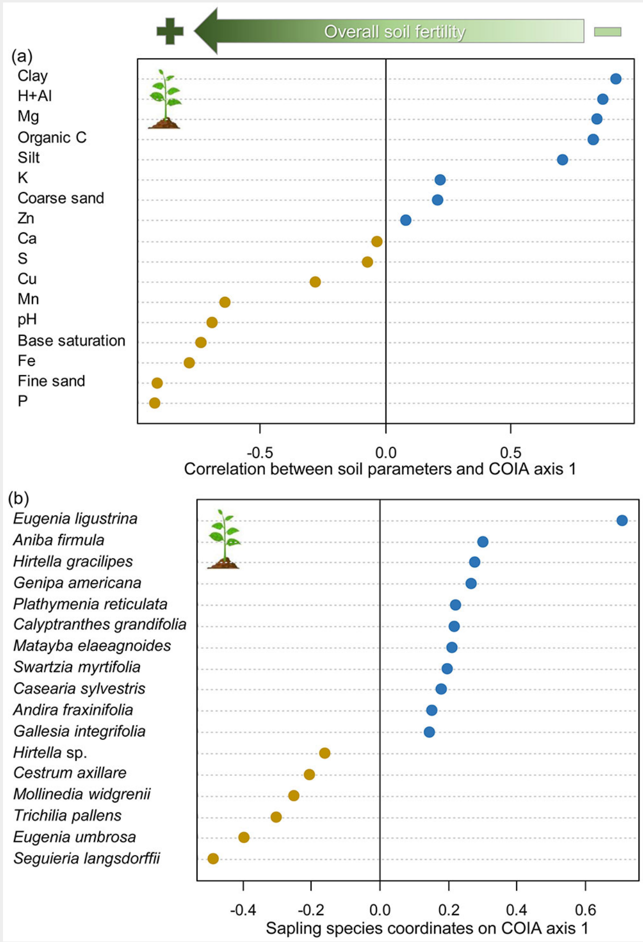

Fig. 4 - Co-structure between edaphic factors and sapling species community sampled at three sites from riparian forests at the upper Doce River watershed, Bom Jesus do Galho-MG, southeastern Brazil. (a): Pearson's correlation between edaphic factors and plot coordinates on co-inertia analysis (COIA) axis 1; (b) coordinates of sapling species with the highest associations with negative and positive sides of COIA axis 1. Green arrow on the top indicates the overall direction of the soil fertility gradient. Orange and blue circles represent, respectively, negative and positive values of correlation (a) or coordinates (b) on COIA axis 1.

sapling-COIA axis 1 indicated a very similar pattern as the tree-COIA, showing plots with acidic soils with a higher proportion of clay and silt, and higher content of magnesium and organic carbon (Fig. 4a). The sapling species more strongly associated with the positive side of this axis were *E. ligustrina, A. firmula, Hirtella gracilipes* (Hook.f.) Prance (Chrysobalanaceae), *Genipa americana* L. (Rubiaceae), *Plathymenia reticulata* Benth. (Fabaceae), and *Calyptranthes grandifolia* O.Berg (Myrtaceae) (Fig. 4b). On the other hand, like the tree-COIA, the negative side of sapling-COIA axis 1 showed plots with less acidic soils, nutritionally richer, with higher proportion of fine sand, and higher amounts of phosphorus, iron, and manganese (Fig. 4a). The sapling species more strongly associated with the negative side of this axis were *S. langsdorffii, E. umbrosa, T. pallens, Mollinedia widgrenii* A.DC. (Monimiaceae), and *Cestrum axillare* Vell. (Solanaceae) (Fig. 4b).

Discussion

The Doce River basin, which has experienced a long historical degradation process (Rodrigues et al. 2009) and more recently the large-scale drastic dam collapse, is still under successive waves of iron ore tailings due to the marked seasonality of the region. These affected riparian forests show no signs of natural regeneration (Fernandes et al. 2016). Thus, it is essential to select multiple reference ecosystems near the sites to be restored, encompassing abiotic factors necessary to accelerate the succession of the plant communities (Durbecq et al. 2020).

Our results highlight the strong influence of soil properties on the floristic composition of well-preserved Atlantic Rainforest sites studied here. Small-scale edaphic variation contributed significantly to explaining sapling and tree species composition. Soil conditions are among the most important factors shaping plant species composition (Coelho et al. 2018, Durbecq et al. 2020, Jakovac et al. 2022, Figueiredo et al. 2022). We observed a soil gradient in which areas with a higher concentration of clay, organic carbon, and silt were distinct from areas with proportionally more phosphorus, fine sand, and less acidic soils. In this sense, the tree species with the highest value of importance were *Guarea macrophylla* followed by *Guarea guidonia*. These were also the species most strongly associated with the extremes of the soil quality gradient, as shown by our co-inertia analysis. *Guarea macrophylla* is a species commonly recommended in restoration processes of riparian Atlantic Rainforests for its dense canopy (Carvalho et al. 2006). We found that *Guarea macrophylla* had a strong association with poorer, more acidic soils with higher clay and silt ratios. Moreover, *Guarea macrophylla* is pollinated mainly by moths and coleoptera (Silva-Junior & Pereira 2009), and its seeds are dispersed by birds (Prado 2013), thus promoting greater functional diversity in these areas. On the other hand, the species *Guarea guidonia* is a species of the secondary stage of succession (De Oliveira et al. 2013), which may explain the strong association with less acidic and richer sandy soils of the edaphic gradient. This species has high crown density, biotic seed dispersal, and is tolerant to seasonal flooding (Carvalho et al. 2006). Similar to the genus *Guarea*, the congeneric species *Cupania oblongifolia* and *Cupania emarginata* from the tree stratum, and the sapling species *Eugenia ligustrina* and *Eugenia umbrosa* were also at opposite ends of the edaphic gradient. This niche differentiation observed in these congeneric species may reflect selective pressures acting on an evolutionary scale, such as competition, which led to the specialization of the species to distinct tolerable environments (Wiegand et al. 2007). Thus, we emphasize that what was observed in our results should not be extrapolated to other representatives of the genus without first understanding each particularity.

Recovery techniques should encompass various plant formations. The exclusive use of tree species may not adequately restore biodiversity in tropical forests (Gentry & Dodson 1987). Life forms from other strata may provide resources in short time intervals for mutualistic and antagonistic animals (Morellato & Haddad 2000) boosting the recovery of ecosystem functions. In this study, we did not find high plant species diversity in the evaluated areas (140 species, of which 78 occur at the tree stratum, and 90 at the sapling stratum), although it is worth noting that most of the sampled species occur uniquely in each site. Therefore, more studies need to be developed along the Doce River watershed, to better understand its plant diversity and community changes along the river. In the area affected by the collapse of the Fundão dam, 166 threatened species were described (Knopff et al. 2020), which is not a surprising number, since this catastrophe affected one of the world's biodiversity hotspots that is extremely endangered. The possibility of high turnover rates of plant species composition along the Doce River from its origin to its end at the Atlantic Ocean represents information of major relevance to the ecological restoration of biodiversity and ecosystem services in the region.

In both vegetation strata studied, the family Fabaceae had higher species richness, which was expected as this family is one of the most abundant and rich in tropical rainforests (Carvalho et al. 2006, Gei et al. 2018, Miranda et al. 2019) as well as in forest remnants in the Doce River watershed (Figueiredo et al. 2022). This group has representative species that are characteristic of the initial restoration processes (Gei et al. 2018). These are fast-growing native species adapted to poor soils, performing the function of quickly restoring the initial structure of the forest, allowing rapid ground cover, and avoiding the appearance of exotic species, which is one of the main problems for the success of forest restoration (Rodrigues et al. 2009, Brancalion et al. 2014). The family Myrtaceae was the second most diverse in the sapling stratum. Species of Myrtaceae are also often found in early succession processes (Carvalho et al. 2006, Balestrin et al. 2019). In addition, species of this family promote the maintenance of the forest structure enabling greater functional diversity in the system, such as attracting pollinators and dispersers (Rodrigues et al. 2009, United Nations 2019). In this study, the species with the highest importance value sampled in both sapling and tree strata are dispersed by animals. Similarly, the species that occurred at the three sites in both strata also show zoochoric dispersal, except for *Gallesia integrifolia*, which is wind-dispersed. Therefore, including species with this type of dispersal should favor the reestablishment of ecological interactions important for the continuity and acceleration of successional processes (Carvalho et al. 2006, Rodrigues et al. 2009) and should be prioritized in the selection of species to be planted.

Conclusion

Our results confirmed that small-scale edaphic variation contributes significantly to explaining sapling and tree species composition. In addition, we identified species from both extremes of the edaphic gradient of the reference areas and highlighted the importance of studies in several regions of the Doce River watershed to evaluate the association among species and soils. The particularities of the species are crucial to the effectiveness of restoration processes since this plant-soil correlation should not be extrapolated even within the same genus. Neglecting that the floristic composition is a mosaic shaped by intrinsic local conditions can create erroneous knowledge to be used in restoration policies, which can be costly and inefficient, besides not restoring biodiversity and ecosystem services.

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References

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JDM, Sparovek G (2013). Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728. - doi: 10.1127/0941-2948/2013/0507

Balestrin D, Cruz R, Silveira G, Martins SV (2019). Hydric and edaphic influence on floristic composition in an altered riparian area. Floresta e Ambiente 26: e20171002. - doi: 10.1590/2179-8087.100217

Brancalion PHS, Cardozo IV, Camatta A, Aronson J, Rodrigues RR (2014). Cultural ecosystem services and popular perceptions of the benefits of an ecological restoration project in the Brazilian Atlantic Forest. Restoration Ecology 22: 65-71. - doi: 10.1111/rec.12025

Carvalho FA, Nascimento MT, Braga JMA (2006). Composição e riqueza florística do componente arbóreo da Floresta Atlântica submontana na região de Imbaú, Município de Silva Jardim, RJ [Composition and floristic richness of the tree component of the submontane Atlantic Forest in the region of Imbaú, Municipality of Silva Jardim, RJ]. Acta Botanica Brasilica 20: 727-740. [in Portuguese] - doi: 10.1590/S0102-33062006000300022

Chen H, Boutros PC (2011). VennDiagram: a package for the generation of highly-customizable Venn and Euler diagrams in R. BMC Bioinformatics 12: 35. - doi: 10.1186/1471-2105-12-35

Clewell A, Aronson J, Winterhalder K (2004). The SER international primer on ecological restoration. Society for Ecological Restoration International Science and Policy Working Group, Tucson, AZ, USA, pp. 13.

Coelho MS, Carlos PP, Pinto VD, Meireles A, Negreiros D, Morellato LPC, Fernandes GW (2018). Connection between tree functional traits and environmental parameters in an archipelago of montane forests surrounded by rupestrian grasslands. Flora 238: 51-59. - doi: 10.1016/j.flora.2017.04.003

De Oliveira RR, Solórzano A, Sales GPS, Beauclair M, Scheel-Ybert R (2013). Ecologia histórica de populações da carrapeta (*Guarea guidonia* (L.) Sleumer) em florestas de encosta do Rio de Janeiro [Historical ecology of carrapeta (*Guarea guidonia* (L.) Sleumer) populations in hillside forests of Rio de Janeiro]. Pesquisas Botnica 64: 323-339. [in Portuguese]

Dolédec S, Chessel D (1994). Co-inertia analysis: an alternative method for studying species-environment relationships. Freshwater Biology 31: 277-294. - doi: 10.1111/j.1365-2427.1994.tb01741.x

Donagemma GK, Viana JHM, Almeida BG, Ruiz HA, Klein VA, Dechen SCF, Fernandes RBA (2017). Análise granulométrica [Particle size analysis]. In: "Manual de Métodos de Análise de Solo (3rd edn)" (Teixeira PC, Donagemma GK, Fontana A, Teixeira WG eds). Embrapa Solos, Brasília, Brazil, pp. 95-116. [in Portuguese]

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

Dray S, Dufour AB (2007). The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22: 1-20. - doi: 10.18637/jss.v022.i04

Durbecq A, Jaunatre R, Buisson E, Cluchier A, Bischoff A (2020). Identifying reference communities in ecological restoration: the use of environmental conditions driving vegetation composition. Restoration Ecology 28: 1445-1453. - doi: 10.1111/rec.13232

Fernandes GW, Goulart FF, Ranieri BD, Coelho MS, Dales K, Boesche N, Bustamante M, Carvalho FA, Carvalho DC, Dirzo R, Fernandes S, Galetti PM, Millan VEG, Mielke C, Ramirez JL, Neves A, Rogass C, Ribeiro SP, Scariot A, Soares-Filho B (2016). Deep into the mud: ecological and socio-economic impacts of the dam breach in Mariana, Brazil. Natureza and Conservação 14: 35-45. - doi: 10.1016/j.ncon.2016.10.003

Figueiredo JCG, De Avila MA, Souza CS, Neves JGS, Tolentino GS, Oki Y, Azevedo IFP, Negreiros D, Viana JHM, Dos Santos RM, Fonseca RS, Fernandes GW, Nunes YRF (2022). Relationship of woody species composition with edaphic characteristics in threatened riparian Atlantic Forest remnants in the upper Rio Doce basin, Brazil. Nordic Journal of Botany 2022: e03679. - doi: 10.1111/njb.03679

Flora e Funga do Brasil (2022). Jardim botânico do Rio de Janeiro [Botanical garden of Rio de Janeiro]. Web site. [in Portuguese] [online] URL: http://floradobrasil.jbrj.gov.br/

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, Hallett JG, Eisenberg C, Guariguata MR, Liu J, Hua F, Echeverría C, Gonzales E, Shaw N, DeCleer K, Dixon KW (2019). International principles and standards for the practice of ecological restoration: summary. Society for Ecological Restoration, Washington, DC, USA. pp. 11. [online] URL: http://espace.curtin.edu.au/handle/20.500.11937/88522

Gei M, Rozendaal DMA, Poorter L, Bongers F, Sprent JI, Garner MD, Aide TM, Andrade JL, Balvanera P, Becknell JM (2018). Legume abundance along successional and rainfall gradients in Neotropical forests. Nature Ecology and Evolution 2: 1104-1111. - doi: 10.1038/s41559-018-0559-6

Gentry AH, Dodson C (1987). Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19: 149-156. - doi: 10.2307/2388737

Goebel PC, Wyse TC, Corace IIIRG (2005). Determining reference ecosystem conditions for disturbed landscapes within the context of contemporary resource management issues. Journal of Forestry 103: 351-356. - doi: 10.1093/jof/103.7.351

Guidotti V, Ferraz SFB, Pinto LFG, Sparovek G, Taniwaki RH, Garcia LG, Brancalion PHS (2020). Changes in Brazil's forest code can erode the potential of riparian buffers to supply watershed services. Land Use Policy 94: 104511. - doi: 10.1016/j.landusepol.2020.104511

Jakovac CC, Meave JA, Bongers F, Letcher SG, Dupuy JM, Piotto D, Rozendaal DM, Peña-Claros M, Craven D, Santos BA, Siminski A, Fantini AC, Rodrigues AC, Hernández-Jaramillo A, Idárraga A, Junqueira AB, Zambrano AM, de Jong BH, Pinho BX, Finegan B, Castellano-Castro C, Zambiazi DC, Dent DH, García DH, Kennard D, Delgado D, Broadbent EN, Ortiz-Malavassi E, Pérez-García EA, Lebrija-Trejos E, Berenguer E, Marín-Spiotta E, Alvarez-Davila E, de Sá Sampaio EV, Melo F, Elias F, França F, Oberleitner F, Mora F, Williamson GB, Colletta GD, Cabral GA, Derroire G, Fernandes GW, van der Wal H, Teixeira HM, Vester HF, García H, Vieira IC, Jiménez-Montoya J, de Almeida-Cortez JS, Hall JS, Chave J, Zimmerman JK, Nieto JE, Ferreira J, Rodríguez-Velázquez J, Ruíz J, Barlow J, Aguilar-Cano J, Hernández-Stefanoni JL, Engel J, Becknell JM, Zanini K, Lohbeck M, Tabarelli M, Romero-Romero MA, Uriarte M, Veloso MD, Espírito-Santo MM, van der Sande MT, van Breugel M, Martínez-Ramos M, Schwartz NB, Norden N, Pérez-Cárdenas N, González-Valdivia N, Petronelli P, Balvanera P, Massoca P, Brancalion PH, Villa PM, Hietz P, Ostertag R, López-Camacho R, César RG, Mesquita R, Chazdon RL, Muñoz R, Dewalt SJ, Müller SC, Durán SM, Martins SV, Ochoa-Gaona S, Rodríguez-Buritica S, Aide TM, Bentos TV, de S. Moreno V, Granda V, Thomas W, Silver WL, Nunes YR, Poorter L (2022). Strong floristic distinctiveness across Neotropical successional forests. Science Advances 8 (26): 589. - doi: 10.1126/sciadv.abn1767

Kindt R (2020). WorldFlora: An R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. Applications in Plant Sciences 8: e11388. - doi: 10.1002/aps3.11388

Knopff K, Bede LC, Arruda L, Alves T, Simons B (2020). Methods for post disaster impact assessment: a case study of the impacts of the Fundão dam failure on terrestrial species threatened with extinction. Integrated Environmental Assessment and Management 16: 676-680. - doi: 10.1002/ieam.4265

Leclère D, Obersteiner M, Barrett M, Butchart SH, Chaudhary A, De Palma A (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature 585: 551-556. - doi: 10.1038/s41586-020-2705-y

MapBiomas (2023). Projeto MapBiomas [MapBiomas project] - Coleção [V. 7.0] da Série Anual de Mapas de Cobertura e Uso da Terra do Brasil, web site. [in Portuguese] [online] URL: http://plataforma.brasil.mapbiomas.org/analises-temporais

Marques MCM, Grelle CEV (2021). The Atlantic Forest: history, biodiversity, threats and opportunities of the mega-diverse forest. Springer Nature, Cham, Switzerland, pp. 517. - doi: 10.1007/978-3-030-55322-7

McCune B, Grace JB (2002). Analysis of ecological communities. In: "MjM Software Design". Gleneden Beach, OR, USA, pp. 300.

Mesquita RCG, Ickes K, Ganade G, Williamson GB (2001). Alternative successional pathways in the Amazon Basin. Journal of Ecology 89: 528-537. - doi: 10.1046/j.1365-2745.2001.00583.x

Metzger JP (2009). Conservation issues in the Brazilian Atlantic forest. Biological Conservation 142: 1138-1140. - doi: 10.1016/j.biocon.2008.10.011

Miranda CDC, Donato AD, Figueiredo PHA, Bernini TA, Roppa C, Trece IB, Barros LO (2019). Levantamento fitossociológico como ferramenta para a restauração florestal da Mata Atlântica, no Médio Paraíba do Sul [Phytosociological survey as a tool for forest restoration of the Atlantic Forest, in Médio Paraíba do Sul]. Ciência Florestal 29: 1601-1613. - doi: 10.5902/1980509833042

Morellato LP, Haddad CFB (2000). Introduction: the Brazilian Atlantic Forest. Biotropica 32: 786-792. - doi: 10.1111/j.1744-7429.2000.tb00618.x

Mueller-Dombois D, Ellenberg D (1974). Aims and methods of vegetation ecology. Wiley, New York, USA, pp. 547.

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000). Biodiversity hotspots for conservation priorities. Nature 403: 853-858. - doi: 10.1038/35002501

Omachi CY, Siani SM, Chagas FM, Mascagni ML, Cordeiro M, Garcia GD, Thompson CC, Siegle E, Thompson FL (2018). Atlantic Forest loss caused by the world' s largest tailing dam collapse (Fundão Dam, Mariana, Brazil). Remote Sensing Applications: Society and Environment 12: 30-34. - doi: 10.1016/j.rsase.2018.08.003

Pavoine S (2020). adiv: an R package to analyse biodiversity in ecology. Methods in Ecology and Evolution 11: 1106-1112. - doi: 10.1111/2041-210X.13430

Pires AP, Rezende CL, Assad ED, Loyola R, Scarano FR (2017). Forest restoration can increase the Rio Doce watershed resilience. Perspectives in Ecology and Conservation 15: 187-193. - doi: 10.1016/j.pecon.2017.08.003

Prado F (2013). Feeding behavior, bird visitation, and seed dispersal in *Guarea macrophylla* and *Trichilia quadrijuga* (Meliaceae). Ornitologia Neotropical 24: 459-468.

R Core Team (2018). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Web site. [online] URL: http://www.r-project.org/

Rezende CL, Scarano FR, Assad ED, Joly CA, Metzger JP, Strassburg BBN, Tabarelli M, Fonseca GA, Mittermeier RA (2018). From hotspot to hopespot: an opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 164: 208-214. - doi: 10.1016/j.pecon.2018.10.002

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009). The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142: 1141-1153. - doi: 10.1016/j.biocon.2009.02.021

Rodrigues RR, Lima RAF, Gandolfi S, Nave GA (2009). On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. Biological Conservation 142: 1242-1251. - doi: 10.1016/j.biocon.2008.12.008

Rosenfield MF, Jakovac CC, Vieira DLM, Poorter L, Brancalion PHS, Vieira ICG, De Almeida DRA, Massoca P, Schietti J, Albernaz ALM, Ferreira MJ, Mesquita RCG (2022). Ecological integrity of tropical secondary forests: concepts and indicators. Biological Reviews 98 (2): 662-676. - doi: 10.1111/brv.12924

Rozendaal DM, Bongers F, Aide TM, Alvarez-Dávila E, Ascarrunz N, Balvanera P, Becknell

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JM, Bentos TV, Brancalion PH, Cabral GA, Calvo-Rodriguez S, Chave J, César RG, Chazdon RL, Condit R, Dallinga JS, De Almeida-Cortez JS, De Jong B, De Oliveira A, Denslow JS, Dent DH, Dewalt SJ, Dupuy JM, Durán SM, Dutrieux LP, Espírito-Santo MM, Fandino MC, Fernandes GW, Finegan B, García H, Gonzalez N, Moser VG, Hall JS, Hernández-Stefanoni JL, Hubbell S, Jakovac CC, Hernández AJ, Junqueira AB, Kennard D, Larpin D, Letcher SG, Licona JC, Lebrija-Trejos E, Marín-Spiotta E, Martínez-Ramos M, Massoca PE, Meave JA, Mesquita RC, Mora F, Müller SC, Muñoz R, De Oliveira Neto SN, Norden N, Nunes YR, Ochoa-Gaona S, Ortiz-Malavassi E, Ostertag R, Peña-Claros M, Pérez-García EA, Piotto D, Powers JS, Aguilar-Cano J, Rodriguez-Buritica S, Rodríguez-Velázquez J, Romero-Romero MA, Ruíz J, Sanchez-Azofeifa A, De Almeida AS, Silver WL, Schwartz NB, Thomas WW, Toledo M, Uriarte M, De Sá Sampaio EV, Van Breugel M, Van Der Wal H, Martins SV, Veloso MD, Vester HF, Vicentini A, Vieira IC, Villa P, Williamson GB, Zanini KJ, Zimmerman J, Poorter L (2019). Biodiversity recovery of Neotropical secondary forests. Science Advances 5 (3): 7472. - doi: 10.1126/sciadv.aau3114

Silva FC, Eira PA, Van Raij B, Silva CA, Abreu CA, Gianello C, Pérez DV, Quaggio JA, Tedesco MJ, Abreu MF, Barreto WO (1999). Análises químicas para a avaliação da fertilidade do solo [Chemical analyses for the evaluation of soil fertility]. In: "Manual de Análises Químicas de Solos, Plantas e Fertilizantes" (Silva FC ed). Embrapa, Brasília, Brazil, pp. 75-169. [in Portuguese]

Silva-Júnior MC, Pereira BAS (2009). 100 árvores do Cerrado: Matas de Galeria: guia de campo [100 trees of the Cerrado: Matas de Galeria - field guide]. Rede de Sementes do Cerrado, Brasília, Brazil, pp. 288. [in Portuguese]

Shimamoto CY, Padial AA, Da Rosa CM, Marques MCM (2018). Restoration of ecosystem services in tropical forests: a global meta-analysis. PLoS One 13: e0208523. - doi: 10.1371/journal.pone.0208523

Toma TSP, Overbeck GE, Mendonça Jr MS, Fernandes GW (2023). Optimal references for ecological restoration: the need to protect references in the tropics. Perspectives in Ecology and Conservation 21 (1): 25-32. - doi: 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). Web site. - [online] URL: https://digitallibrary.un.org/record/3794317

Van Der Sande MT, Powers JS, Kuyper TW, Norden N, Salgado-Negret B, Almeida JS (2022). Soil resistance and recovery during neotropical forest succession. Philosophical Transactions of the Royal Society B 378: 20210074. - doi: 10.1098/rstb.2021.0074

Wiegand T, Gunatilleke S, Gunatilleke N, Okuda T (2007). Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. Ecology 88: 3088-3102. - doi: 10.1890/06-1350.1

Supplementary Material

Fig. S1 - Sampling sites in riparian forests at the upper Doce River watershed, Bom Jesus do Galho - MG, SE Brazil.

Fig. S2 - Rarefaction curves for species diversity (Gini-Simpson index) as a function of sampling effort (cumulative number of plots).

Tab. S1 - Phytosociological parameters of species from the tree stratum sampled in three sites at riparian forests from the upper Doce River watershed, Bom Jesus do Galho - MG, SE Brazil.

Tab. S2 - Phytosociological parameters of species from the sapling stratum sampled in three sites at riparian forests from the upper Doce River watershed, Bom Jesus do Galho - MG, SE Brazil.

Tab. S3 - Soil parameters for each sampling site (mean ± SE; N=15 plots per site) at riparian forests from the upper Doce River watershed, Bom Jesus do Galho - MG, SE Brazil.

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