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Scientific Article

LANDSCAPE ENVIRONMENTAL HETEROGENEITY SHAPING TREE COMMUNITY COMPOSITION AND STRUCTURE IN RIPARIAN FORESTS

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ABSTRACT

Although riparian vegetation is widely recognized for its positive impact on soil and water quality and its role in ecological conservation, there is still a gap in understanding the effect of environmental heterogeneity on tree community composition and structure in riparian landscapes. Riparian forests are ecosystems with abrupt variations in topographic, edaphic, and hydrological features, resulting in the formation of microenvironments with specific plant compositions. We evaluated the influence of the topographical gradient on edaphic and hydrological attributes and their association with tree species composition, diversity, and structure in three remnants of riparian forests in Minas Gerais, at high slope, low slope and alluvium positions. Ten 400 m² plots were set up in each area. All trees and shrubs within the plots with diameter at breast height (DBH) greater than 5 cm were recorded. The abundance was correlated with the topographic, edaphic, and hydrological variables of the plots through multivariate analysis. The highest species richness (122) and diversity (H' 3.99) were associated with the low slope, while the alluvium had the highest tree density (3005 trees ha^{-1}) and basal area (43.99 m^2 ha^{-1}). Cluster analysis and canonical correspondence indicated that the species distribution is mainly influenced by soil moisture and fertility. Understanding the dynamics of riparian forests is essential for strategic decision-making in tropical forest management towards the promotion of ecosystem services, forest restoration and sustainable development goals.

Keywords: Alluvium forest; Ttopographic gradient; Microenvironment; Relationship species-environment; Edaphic conditions; Quantitative ecology

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HETEROGENEIDADE AMBIENTAL DA PAISAGEM MOLDANDO A COMPOSIÇÃO E A ESTRUTURA DA COMUNIDADE DE ÁRVORES EM FLORESTAS RIPÁRIAS

RESUMO Embora a vegetação ripária seja amplamente reconhecida por seu impacto positivo na qualidade do solo e da água, bem como por seu papel na conservação ecológica, ainda há lacunas na compreensão do efeito da heterogeneidade ambiental na composição e estrutura das comunidades arbóreas em paisagens ripárias. As florestas ripárias são ecossistemas com variações abruptas em características topográficas, edáficas e hidrológicas, resultando na formação de microambientes com composições vegetais específicas. Avaliamos a influência do gradiente topográfico nos atributos edáficos e hidrológicos e sua associação com a composição, diversidade e estrutura de espécies arbóreas em três remanescentes de florestas ripárias em Minas Gerais, em posições de encosta alta, encosta baixa e de aluvião. Foram plotadas dez parcelas de 400 m² em cada área. Todos os indivíduos arbóreos com diâmetro à altura do peito (DAP) ≥ 5 cm foram registrados. A abundância foi correlacionada com as variáveis topográficas, edáficas e hidrológicas das parcelas por meio de análise multivariada. A maior riqueza de espécies (122) e diversidades (H' 3,99) estiveram associadas à encosta baixa, enquanto o aluvião apresentou a maior densidade de árvores (3005 árvores ha^{-1}) e área basal (43,99 m^2 ha^{-1}). A análise de agrupamentos e a correspondência canônica indicaram que a distribuição das espécies é influenciada principalmente pela umidade e fertilidade do solo. Compreender a dinâmica das florestas ripárias é fundamental para a tomada de decisões estratégicas na gestão de florestas tropicais, visando a promoção dos serviços ecossistêmicos, a restauração florestal e os objetivos de desenvolvimento sustentável.

Palavras-Chave: Floresta de aluvião; Gradiente topográfico; Microambiente; Relação espécie-ambiente; Condições edáficas; Ecologia quantitativa

1. INTRODUCTION

Riparian zones are transitions between aquatic and land ecosystems, widely recognized as hotspots of multifunctional ecosystem services (Kowalska et al., 2021). They provide fundamental hydrological and ecological services for the maintenance of the health and resilience of watersheds (Pert et al., 2010) including: (1) regulation of the water flux and quality (Attanasio et al., 2012; Saklaurs et al., 2022); (2) reduction of sediments, fertilizers, and pesticides concentrations in the water (Nieminen et al., 2020; Stefanidis et al., 2022); (3) the maintenance of the thermal balance of the water; and (4) stability of river banks. In addition, their forests provide refuge, shelter, and food for terrestrial and aquatic fauna (Graeff et al., 2018; Stutter et al., 2021).

Studies with forest species, especially riparian forests, are fundamental to promoting the restoration in Brazil and worldwide. Brazil has set a goal of reducing greenhouse gas (GHG) emissions by 43% by 2030, compared to 2005 levels (Brasil, 2015; UNCC, 2017). In this context, Brazilian states have defined their GHG reduction or neutralization goals. For instance, in the state of Minas Gerais (MG), strengthening carbon stocks through forest restoration is aimed at reducing or neutralizing GHG emissions, with the goal of achieving emission neutrality by 2050 (EMG, 2023; Morais Júnior et al., 2024).

Forests along riverbanks, streams, lagoons, lakes, and headwaters of the drainage network are heterogeneous and dynamic ecosystems (Pero & Quiroga, 2019). They are mainly the result of topographic, edaphic and flooding regime variations, which lead to the deposition of sediments and removal of litter (You and Liu, 2018). Topography and soil play an important role in the heterogeneity of riparian forest, contributing to their differentiation (Baldeck et al., 2013) at different scales (Arruda et al., 2015). At the local scale, the relative height along a hillside slope affects solar radiation incidence (Jiang et al., 2015) and microclimatic, drainage and edaphic conditions (Reynolds and Haubensak 2009; Chadwick & Asner, 2016). All of them impact the distribution, abundance, diversity, and structure of the tree community (Zuquim et al., 2020), as well as its function and dynamics (Muscarella et al., 2020).

The occurrence of environmental heterogeneity in short distances along riparian forests in the central plateau of the Brazilian southeastern region was reported by Oliveira Filho et al. (1997). However, the link between the tree species distribution and environmental factors in these riparian forests has not yet been established. This information is fundamental to guide forest restoration actions, supporting the selection of species to be used in programs directed to this most endangered Brazilian ecosystem (Brancalion et al., 2020; Fremout et al., 2022). Currently, this selection is carried out generically and empirically without taking into account the specificity of the edaphic, topographic, and hydrological features along the riparian ecosystems.

To contribute with information about the link between tree species distribution and environmental factors and about the eventual selection of restoration species, this study aims to: i) quantify the influence of the topographical gradient on the edaphic and hydrological attributes of three riparian forest areas; ii) evaluate the association of these attributes with composition and structure of the tree communities in these areas; and iii) identify species that are associated with different sites based on their edaphic, topographic and hydrological characteristics. The study is based on the hypothesis that the diversity of tree species increases as soil fertility increases and flooding occurrences decrease.

2. MATERIAL AND METHODS

2.1 Study areas

The study was carried out in three riparian forest fragments located in Bocaina de Minas municipality, Minas Gerais state, Brazil (Figure 1). The fragments are distributed along a 15 km stretch downstream the Grande River headwater, on the continental side of the Mantiqueira mountain range. The first fragment consists of a riparian forest of approximately 15 ha, at an altitude superior to 1,500 m above sea level (masl) and around the coordinates 22º 13' 31.796" S and 44º 34' 24.413" W, further referred as U (corresponding to uphill). It is located at the left margin of the Rio Grande, about 5 km downstream of its headwaters (Figure 1). It has abrupt borders with a pasture area and a road. The definition according to CONAMA resolution 392 is Secondary Forest in the medium stage of regeneration.

The second riparian forest fragment covers approximately 10 ha area at an altitude ranging from 1200 to 1300 meters and around 22º 13' 1.841" S and 44º 32' 20.317" W and it is designated as D (downhill). It is located at the left margin of the Rio Grande, 10 km downstream from its headwater, with abrupt borders with pasture areas (Figure 1). The definition according to CONAMA resolution 392 is primary vegetation.

The third riparian fragment is located on an alluvial plain, at an altitude of around 1,200 masl and 22º 9' 41.328" S and 44º 28' 1.16" W, and it is designated as A (from alluvium). It has approximately 3 ha along both margins of the Rio Grande, about 15 km downstream from its headwaters, bordering on pastures and nearby roads. The definition according to CONAMA resolution 392 is Secondary Forest in the medium stage of regeneration.

The topographic profile showed elevation differences of ~200 m between U and D and ~350 m between U and A (Figure 2). The profile also indicates significant slope variations, ranging from 7.5° to 80.2° and the presence of valleys with a U-D-A orientation. The soils in U and D were classified as Oxisols Xanthic and in A as Entisols Fluvents.

The vegetation and the soil in all the fragments showed no signs of recent human disturbance. In each fragment, ten 400 m² (20 x 20 m in D and U; 10 x 40 in A) plots were set up following random in the range of 0 to 50 meters from the river banks. The plots were installed at a maximum distance of 50 m from the river margin, which limits the strip of vegetation legally preserved along rivers which are 10 to 50 m wide.

2.2 Topographic and environmental variables

The physical characterization of the areas was based on the altimetry and slope

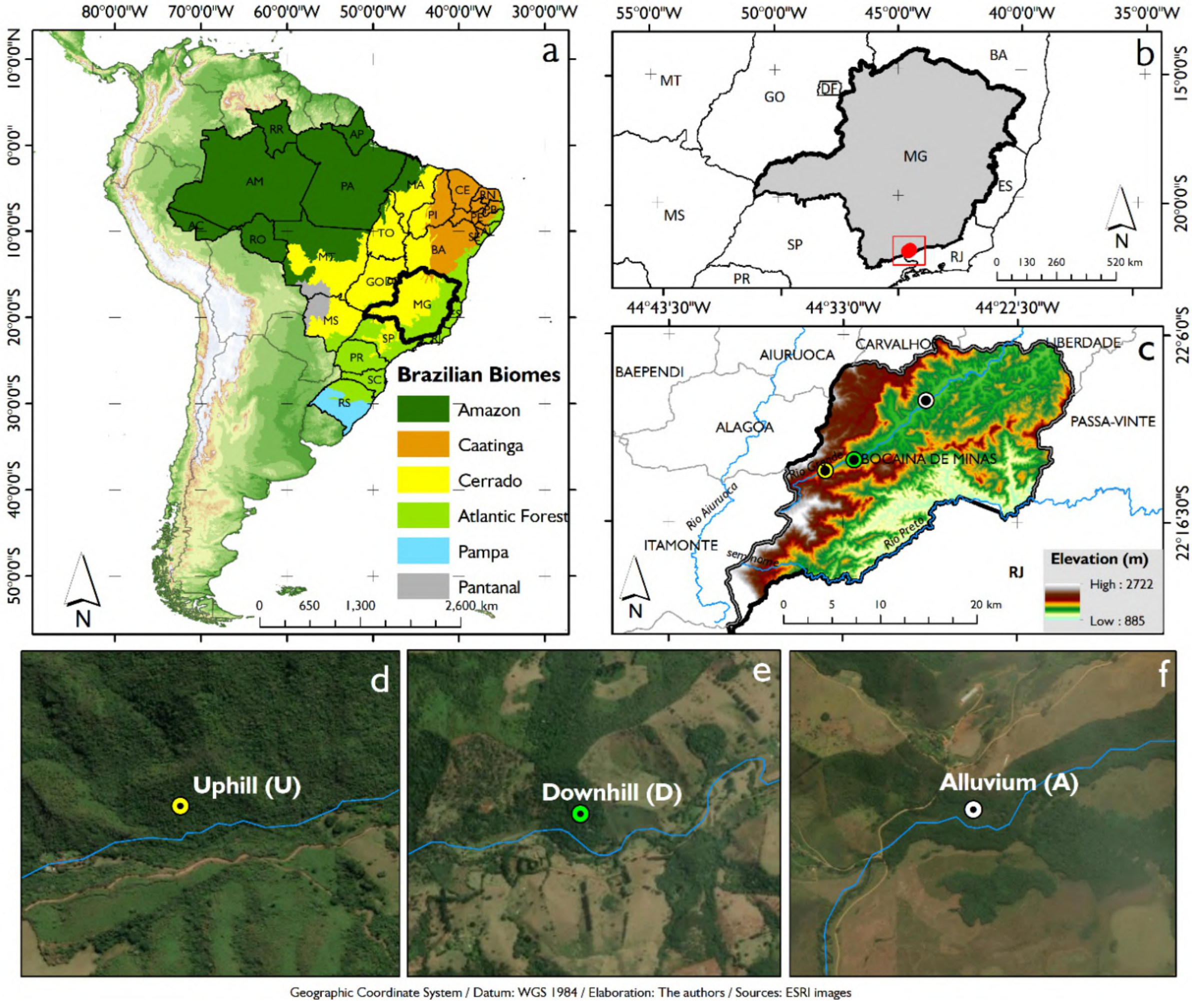

Figure 1. Location of the study area showing the biomes of Brazil (a); State of Minas Gerais (b); Municipality of Bocaina de Minas (c); Uphill area (d); Downhill area (e) and Alluvium area (f)
Figura 1. Localização da área de estudo mostrando os biomas do Brasil (a); Estado de Minas Gerais (b); município de Bocaina de Minas (c); área de alta encosta (d); área de encosta baixa (e) e área de Aluvião (f)

maps from ALOS PALSAR satellite images (Advanced Land Observation Satellite - Phased Array type L-band Synthetic Aperture Radar) with 12.5 meters of spatial resolution (ASF 2020). At plot level, the slope was determined with a Blume-Leiss hypsometer allowing the construction of contour maps 1-m equidistant. For each plot, three topographic variables were computed: (1) vertical distance from the river - the difference between the average altimetric levels of the four vertices of the plot and the altimetric level of the river; (2) topographic difference - difference between the maximum and minimum altimetric level of the plot; (3) average slope - average slope on the four sides of the plot. The predominant soil types in each plot were classified according to the Brazilian System of Soil Classification (EMBRAPA, 2018) with correspondence to USDA (1999), up to the level of subgroup (or 4th categoric level) including the textural group and classes of drainage. Superficial soil samples (0-20 cm depth) excluding litter were collected in the centre of each plot. Chemical and textural analyses were carried out at the UFLA's Laboratory of Soil Analysis, determining pH, organic matter (OM), extractable P, K, Ca, Mg, and Al concentrations, base saturation (V), sum of exchangeable bases (SB), and sand, silt, and clay proportions (Teixeira et al., 2017).

2.3 Vegetation sampling and data

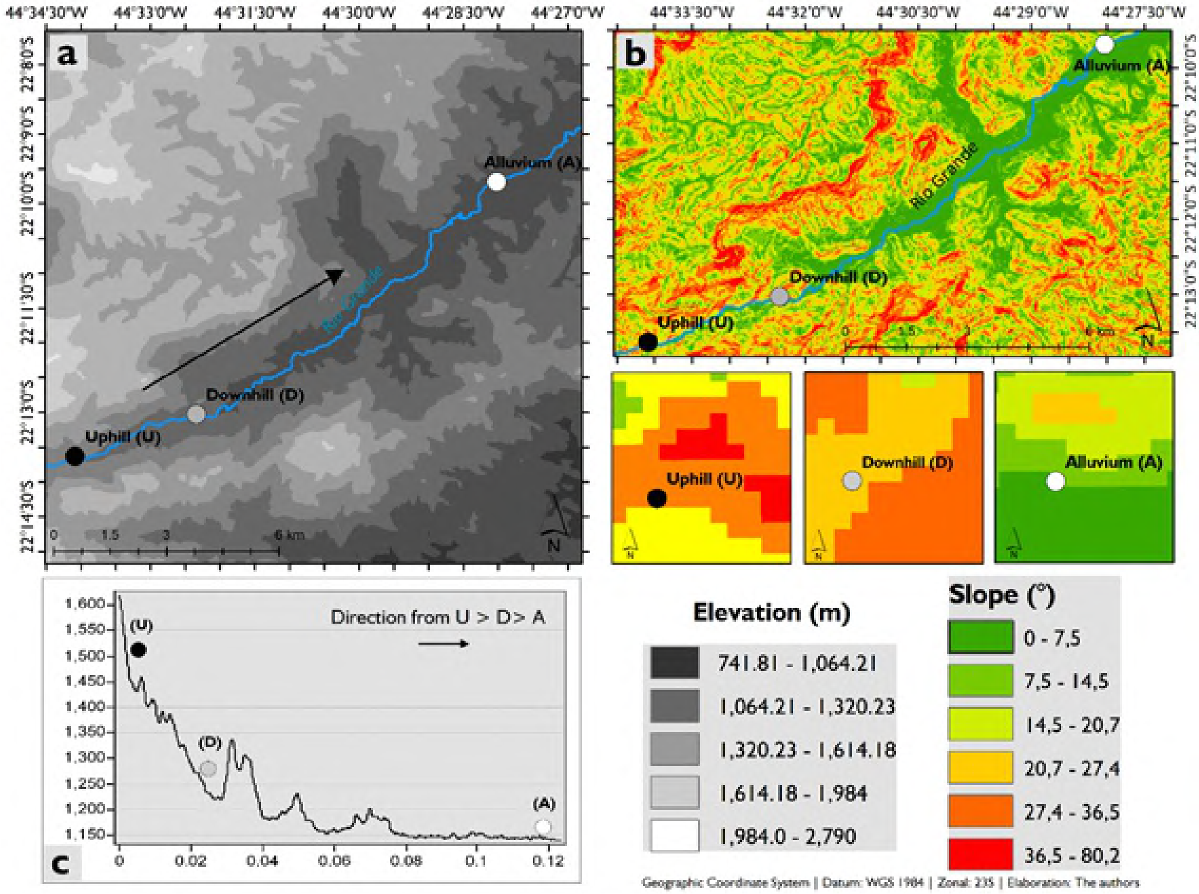

Figure 2. Relief characterization of the study area. Elevation map (a); terrain slope map (b); and topographic profile between points U, D and A - (axis x: distance (km); axis y: elevation (m) (c)
Figura 2. Caracterização do relevo da área de estudo. Mapa de elevação (a); Mapa de declividade do terreno (b); e Perfil topográfico entre os pontos U, D e A - (eixo x: distância (km); eixo y: elevação (m) (c)

Every living arboreal plant within the plots with a circumference at breast height (CBH) of 15.7 cm or higher (corresponding to a diameter at breast height equal to or greater than 5 cm) was recorded, labelled, and identified. Trees with multiple stems were included when the square root of the sum of the square of the CBH values of all the stems was equal to or higher than 15.7 cm. The trees were identified in the field or by comparison with vouchers deposited in two herbariums (Federal University of Lavras or Rio de Janeiro Botanic Garden). When necessary, the botanical identification was performed by a scientific expert.

Density (tree ha^{-1}) and basal area (m^2 ha^{-1}) were determined and compared between areas using variance analysis and Tukey's test (Zar, 2010). Shannon (H ') and Pielou (J') diversity indices were also calculated on a natural logarithmic basis (Brower et al., 1997). The values of the Shannon diversity index for the three areas were compared using Hutcheson´s t-test (Zar, 2010).

2.4 Data analysis

Principal Component Analysis (PCA) was performed to identify existing gradients related to environmental data. Association between environmental and vegetational gradients were determined using Canonical Correspondence (CCA) analyses (McCune and Mefford, 2011). The environmental variables matrix used in PCA and CCA considered 16 variables, being 12 edaphic (pH, Al, OM, K, P, Ca, Mg, V, SB) and percentage of sand, silt, and clay), one hydrological (soil drainage classes) and three topographic variables (distance from the river, unevenness of the terrain and elevation). The soil drainage classes were expressed as an ordinal variable, with scores attributed to the categories described by EMBRAPA (2018): poorly drained (1); moderately drained (2) and well-drained (3).

The species abundance matrix was composed of the number of trees per plot from the species with ten or more trees in at least one area. The indicator species was used for determining species preferences for the three fragments (Dufrêne & Legendre, 1997). The method combined the concentration of the abundance of a species in a certain group of sample units with the fidelity of the occurrence of this species in this same group. An indicator value (ValInd) is computed for each species and the significance of the difference concerning ($p>0.05$) a value generated by the Monte Carlo permutation test. As a result, a species is only considered an indicator of habitat when it has a high and significant ValInd value. The rarefaction curves were calculated using the Past 4.03 software (Hammer et al., 2001). Univariate and multivariate analysis were performed in the PC-ORD for Windows (McCune & Mefford, 2011) and R (R DEVELOPMENT 2021) including the Vegan (Oksanen et al., 2022) and labdsv packages (Roberts, 2023).

3. RESULTS

3.1 Soil

The soil in fragment A has higher cation nutrient concentratons (K, Ca, and Mg) than the other areas, reflected in higher values of the sum of bases (SB) and base saturation (V), and also higher organic matter and P concentrations. However, being an alluvial area, it has worse drainage than U and D. The soil in fragment D is more clayish and acidic than those of the other fragments. Area U differed from the others due to its higher altitude (Table 1 and Figure 3).

Table 1. Values of confidence intervals (n = 10) of the chemical and physical attributes of the soils in the three riparian forest fragments, along a 15 km stretch of Rio Grande, Minas Gerais state, Brazil
Tabela 1. Valores dos intervalos de confiança (n = 10) dos atributos químicos e físicos dos solos dos três fragmentos de mata ciliar, ao longo de um trecho de 15 km do Rio Grande, Minas Gerais, Brasil

Soil properties	Environments		
Chemical	**Uphill**	**Downhill**	**Alluvium**
pH	4.60±0.1a	4.33±0.1b	4.57±0.1a
P (mg dm^{-3})	1.38±0.4b	1.78±0.3b	3.01± 0.3a
K (mg dm^{-3})	29.43±11.5a	14.73±6.3b	40.70±7.9a
Ca (Cmoc dm^{-3})	0.37±0.1b	0.29±0.1b	0.75±0.1a
Mg (Cmoc dm^{-3})	0.13±0.05b	0.10±0.01b	0.30±0.02a
Al (Cmoc dm^{-3})	1.77±0.2ab	2.02±0.19a	1.69±0.26b
SB (Cmoc dm^{-3})	0.59±0.14b	0.41±0.12c	1.24±0.34a
V (%)	6.9±1.34b	3.69±0.72c	11.01±3.27a
OM (dag kg)	1.70±0.19c	3.10±0.47b	4.16±0.36a
Texture	**Uphill**	**Downhill**	**Alluvium**
Sand (%)	61.40±4.6a	52. 90±3.54b	41.50±12.0c
Silt (%)	13.40.1±5.6b	12.0±3.65b	30.10±6.6a
Clay (%)	25.20±3.53b	35.10±4.36a	28.40±6.5b

Where: P, K, Ca, Mg, Al are extractable concentrations of phosphorus, potassium, calcium, magnesium, and aluminum; SB is sum of exchangeable bases; V is base saturation; and OM is organic matter concentration.

Onde: P, K, Ca, Mg, Al são concentrações extraíveis de fósforo, potássio, cálcio, magnésio e alumínio; SB é a soma de bases trocáveis; V é a saturação de bases; e OM é a concentração de matéria orgânica.

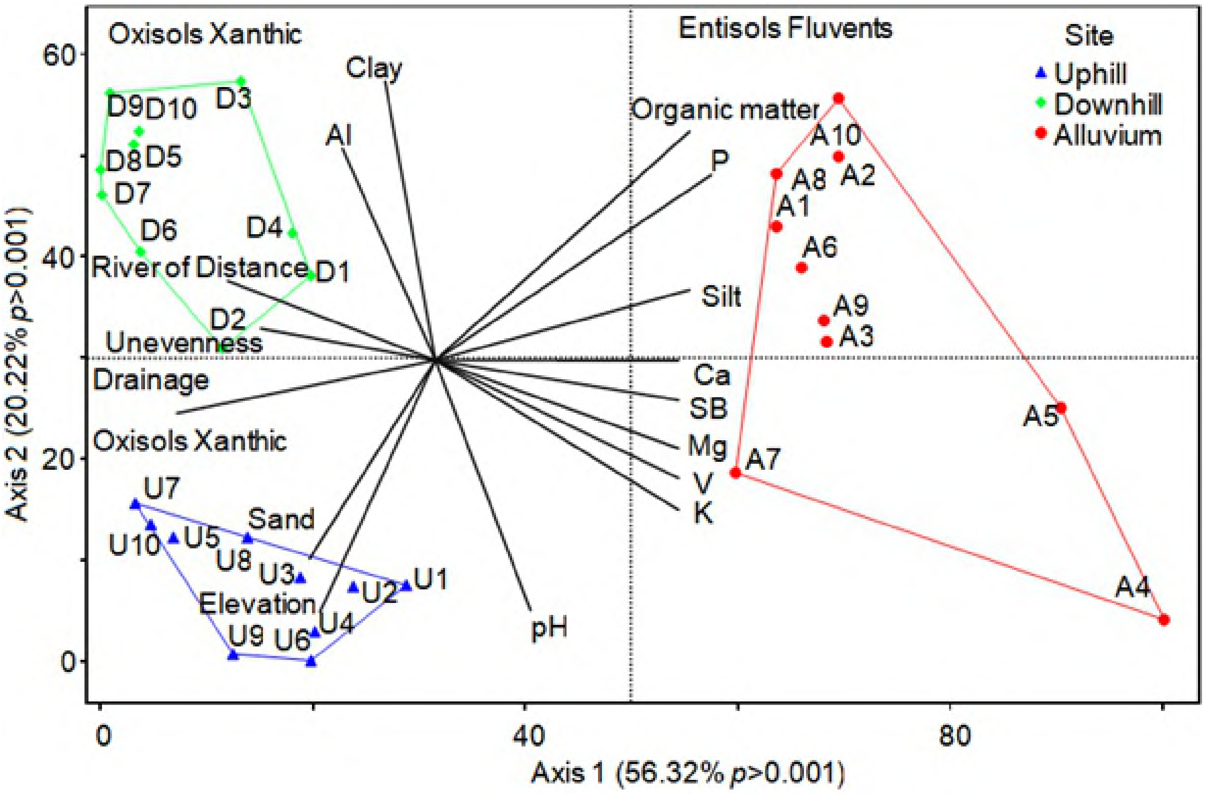

Figure 3. Principal component analysis (PCA) of the environmental variables collected in 30 plots in three areas of riparian forest along a 15 km stretch of Rio Grande, Minas Gerais - Brazil. Where: U = Uphill; D = Downhill and A = Alluvium

Figura 3. Análise de componentes principais (ACP) das variáveis ambientais coletadas em 30 parcelas em três áreas de mata ciliar ao longo de um trecho de 15 km do Rio Grande, Minas Gerais - Brasil. Onde: U = encosta alta; D = encosta baixa e A = Aluvião

3.2 Composition and structure of vegetation

The 206 registered species were distributed in 112 genera and 50 families. Area A had the lowest richness, with 69 species, 50 genera, and 28 families, followed by U, with 90 species, 58 genera, and 34 families, and D, with 112 species, 77 genera, and 41 families. The rarefaction curves indicate a significant difference in species richness among the three areas (Figure 4). At the point of equal sampling effort, U had a richness of 90 species (95% CI: ± 0.29), D of 109 species (95% CI: ± 1.69) and A of 62 species (95% CI: ± 2.17). The Shannon diversity indices (H') were 3.184, 3.408, and 3.909 and the Pielou indices (J') 0.752, 0.757, and 0.828, for A, U, and D, respectively. The H' values were significantly different between A and U (Hutcheson's t = -3.929, p<0.001); A and D (Hutcheson t = 13,647; p <0.001); and D and U (Hutcheson's t = -8,341; p <0.001).

The densities were 2125, 2405 and 3005 trees ha^{-1}, respectively in U, D, and A (Table 2), being significantly higher in the alluvial fragment than in the two upper ones (U, p <0.01; and D, p <0.05), which did not differ. Considering the basal area, all the three areas were different among themselves (p <0.001), with U, D, and A having, respectively, 16.675 m^2 ha^{-1}, 31.027 m^2 ha^{-1}, and 43.993 m^2 ha^{-1} (Table 2). The diametric distribution of the number of trees by diameter class was different in all areas (p< 0.05, Table 2). Area A had the largest number of trees in all classes (except for the class with diameters > 10 to 15 cm) (Figure 5).

The three areas are floristic dissimilar (Figure 6A), as evidenced by the Venn diagram, in which only four species were shared by the three areas (1.94%). The greatest similarity (45 species; 21.8%) was between D and U (Figure 6A and 6B) and the

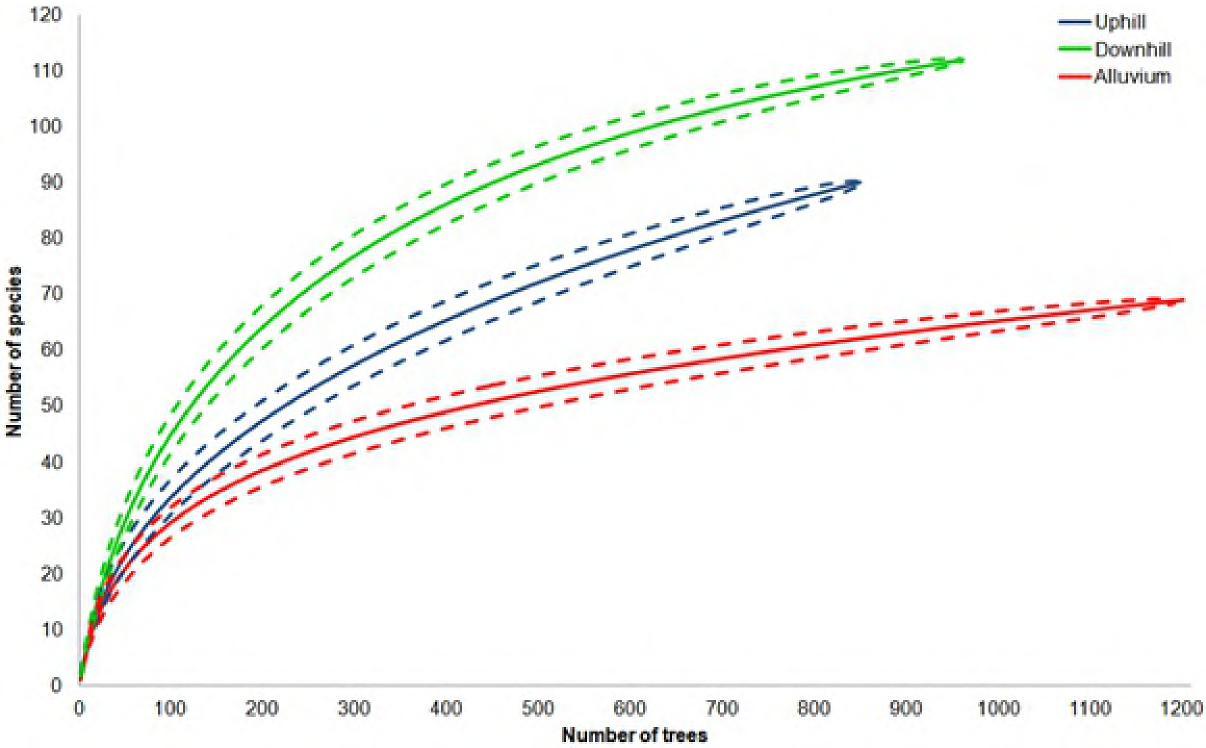

Figure 4. Rarefaction curves representing the expected number of tree species for three areas along a 15 km stretch of Rio Grande, Minas Gerais - Brazil. Dashed lines represent the confidence interval (95%)
Figura 4. Curvas de rarefação representando o número esperado de espécies arbóreas para três áreas ao longo de um trecho de 15 km do Rio Grande, Minas Gerais - Brasil. As linhas tracejadas representam o intervalo de confiança (95%)

Table 2. Values of the structural parameters (basal area and density) and diversity (H' and J) for the three riparian forests, Minas Gerais - Brazil
Tabela 2. Valores dos parâmetros estruturais (área basal e densidade) e diversidade (H' e J) para as três matas ciliares, Minas Gerais - Brasil

Variables	Uphill	Downhill	Alluvium
Trees per hectare	2125±57 b	2405 ± 29 b	3005±37 a
Basal area (m^2 ha^{-1})	15.93±0.75 c	31.10±0.66 b	43.99±1.29 a
Shannon-Weaver index (H')	3.41±0.08	3.91±0.07	3.18±0.07
Pielou's Equability Index (J')	0.76±0.02	0.83±0.01	0.76±0.02

lowest ones between areas A and D (11 species; 5.3%) and A and U (13 species; 6.3%).

3.3 Relationship between environmental variables and vegetation

The Analysis of Indicator Species (IndVal) showed 18 indicator species for area A, 12 species for area D and seven species for area U (Table 3).

4. DISCUSSION

4.1 Topographic and soil variation

Although spatially close, the three studied areas had different tree species composition, diversity, and structure. Species composition and abundance were mainly related to soil fertility and drainage (A versus U and D), and elevation (U versus A and D). Area A has the most superficial water table and the worst drainage, which appeared as an

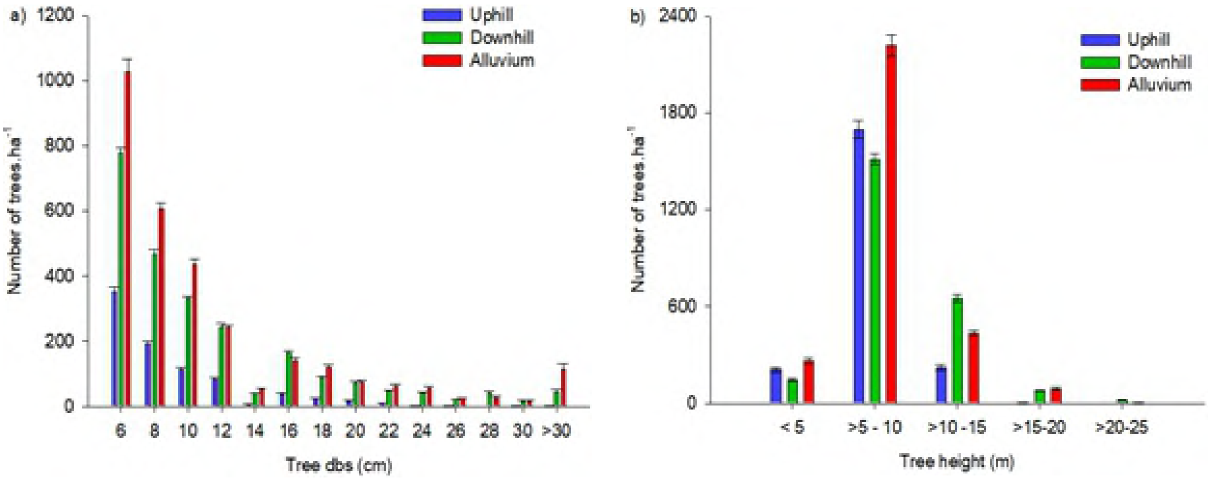

Figure 5. Distribution of the number of trees per hectare in diameter classes (a) and height (b) in three riparian forests along a 15 km stretch of Rio Grande, Minas Gerais - Brazil
Figura 5. Distribuição do número de árvores por hectare em classes de diâmetro (a) e altura (b) em três matas ciliares ao longo de um trecho de 15 km do Rio Grande, Minas Gerais - Brasil

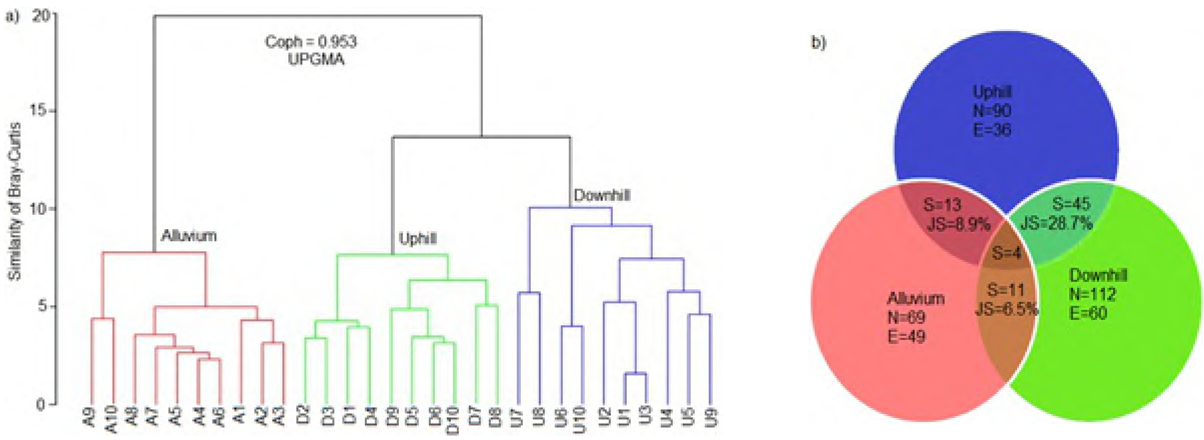

Figure 6. Venn diagram (a) and similarity dendrogram (b), using the Jaccard index as a coefficient and grouping the plots by the group average method (UPGMA), extracted from the floristic composition of the three riparian forests along a 15 km stretch of Rio Grande, Minas Gerais - Brazil. E = exclusive species; S = shared species between areas; N = total number of species recorded in the area; JS = Jaccard Similarity; U = Uphill; D = Downhill and A = Alluvium
Figura 6. Diagrama de Venn (a) e dendrograma de similaridade (b), utilizando o índice de Jaccard como coeficiente e agrupando as parcelas pelo método da média de grupos (UPGMA), extraídos da composição florística das três áreas de mata ciliar ao longo de um trecho de 15 km do Rio Grande, Minas Gerais - Brasil. Onde: E = espécies exclusivas; S = espécies compartilhadas entre as áreas; N = número total de espécies registradas na área; JS = Similaridade de Jaccard; U = encosta alta; D = encosta baixa e A = Aluvião

important factor in the formation of groups in PCA and CCA. The soil in area A is the most fertile and has the highest P, K, Mg, Ca, and organic matter concentrations and SB and V values, while the sandy soils from U had the lowest nutrients levels.

Our results suggest that the sites located in the steepest terrains are associated with lower nutrient levels and acidic and drier soils (as observed in the U and D). Soil accumulates in the lower parts of the terrain, as seen in area A, resulting in more fertile and moist soil. Topography has been associated with many ecological characteristics through its influence on both soil moisture and soil chemistry (Seibert et

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Table 3. List of 59 species used in the analysis of indicator species (ISA) in three riparian forests along a 15 km stretch of Rio Grande in Bocaina de Minas, Minas Gerais - Brazil. Where: IndVal = indicator value and p = significance value; sig = level of significance (ns = not significant and * = significant), U = Uphill; D = Downhill and A = Alluvium

Tabela 3. Lista de 59 espécies utilizadas na análise de espécies indicadoras (ISA) em três matas ciliares ao longo de um trecho de 15 km do Rio Grande, em Bocaina de Minas, Minas Gerais - Brasil. Onde: IndVal = valor indicador e p = valor de significância; sig = nível de significância (ns = não significativo e * = significativo), U = encosta alta; D = encosta baixa e A = Aluvião

Species	Code	Group	IndVal	p	sig
Clethra scabra Pers.	14	U	45.50	0.085	ns
Croton organensis Baillon	16	U	58.34	0.003	*
Eremanthus erythropappus (DC.) MacLeish	22	U	30.00	0.035	*
Guatteria australis A.St.-Hil.	24	U	22.29	0.306	ns
Miconia cinnamomifolia (DC.) Naudin	31	U	22.45	0.146	ns
Miconia sellowiana Naudin	34	U	77.86	0.001	*
Miconia theaezans (Bonpl.) Cogn	35	U	60.00	0.001	*
Myrsine coriacea (Swartz) R.Br.	40	U	38.17	0.050	ns
Myrsine umbellata Mart.	42	U	69.60	0.001	*
Piptocarpha regnellii (Sch.Bip.) Cabrera	44	U	58.90	0.002	*
Psychotria vellosiana Benth.	46	U	46.15	0.120	ns
Pleroma arboreum Gardner	53	U	73.62	0.002	*
Vernonanthura discolor (Less.) H.Robinson	55	D	14.76	0.695	ns
Alchornea sidifolia Müll.Arg.	1	D	57.69	0.012	*
Alchornea triplinervia (Sprengel) Müll.Arg.	2	D	37.35	0.208	ns
Amaioua guianensis Aublet	4	D	29.03	0.174	ns
Cabralea canjerana (Vell.) Mart.	7	D	50.22	0.009	*
Calyptranthes widgreniana O.Berg	8	D	12.38	0.637	ns
Casearia arborea (L.C.Rich.) Urban	9	D	38.46	0.018	*
Casearia decandra Jacquin	10	D	46.15	0.009	*
Casearia obliqua Sprengel	11	D	61.54	0.002	*
Croton floribundus Sprengel	15	D	13.08	0.649	ns
Croton salutaris Casar.	17	D	53.85	0.007	*
Guapira opposita (Vell.) Reitz	23	D	34.19	0.211	ns
Guatteria pohliana Schltdl.	25	D	53.85	0.007	*
Lamanonia ternata Vell.	28	D	63.53	0.004	*
Miconia latecrenata (DC.) Naudin	33	D	29.84	0.056	ns
Mollinedia longifolia Tul.	36	D	61.54	0.002	*
Myrceugenia bracteosa (DC.) D.Legrand & Kausel	37	D	21.54	0.170	ns
Myrcia detergens Miq.	38	D	23.08	0.194	ns
Myrcia splendens (Sw.) DC.	39	D	30.13	0.203	ns
Prunus myrtifolia (L.) Urban	45	D	25.23	0.794	ns
Sapium glandulosum (L.) Morong	47	D	24.40	0.416	ns
Solanum cinnamomeum Sendt.	50	D	28.46	0.111	ns
Tetrorchidium parvulum Müll.Arg.	52	D	45.43	0.028	*
Pleroma raddianum (DC.) Gardner	54	D	54.20	0.009	*
Vernonanthura divaricata (Spreng.) H.Rob.	56	D	35.64	0.119	ns
Vochysia magnifica Warm.	58	D	76.92	0.001	*
Allophylus edulis (A.St.-Hil.) Radlk.	3	A	52.56	0.007	*
Anadenanthera colubrina (Vell.) Brenan	5	A	79.57	0.001	*
Annona emarginata (Schltdl.) H.Rainer	6	A	59.50	0.003	*
Cassia ferruginea (Schrad.) Schrad.	12	A	93.50	0.001	*
Chomelia brasiliana A.Rich.	13	A	95.92	0.001	*
Cupania vernalis Cambess.	18	A	57.34	0.006	*

Cont...

Cont...

Species	Code	Group	IndVal	p	sig
Daphnopsis fasciculata (Meisner) Nevling	19	A	18.57	0.328	ns
Daphnopsis sellowiana Taub.	20	A	71.43	0.001	*
Duranta vestita Cham.	21	A	80.88	0.001	*
Ilex theezans Mart.	26	A	50.72	0.006	*
Inga vulpina Mart.	27	A	20.63	0.354	ns
Machaerium hirtum (Vell.) Stellfeld	29	A	19.38	0.413	ns
Matayba elaeagnoides Radlk.	30	A	93.75	0.001	*
Miconia cubatanensis Hoehne	32	A	40.56	0.011	*
Myrsine gardneriana A.DC.	41	A	67.20	0.001	*
Nectandra lanceolata Nees	43	A	34.82	0.021	*
Sebastiania brasiliensis Sprengel	48	A	72.31	0.001	*
Sebastiania commersoniana (Baill.) L.B. Sm. & Downs	49	A	84.19	0.001	*
Symplocos celastrinea Mart.	51	A	81.30	0.001	*
Vitex megapotamica (Sprengel) Moldenke	57	A	70.43	0.002	*
Xylosma prockia (Turcz.) Turcz.	59	A	53.92	0.003	*

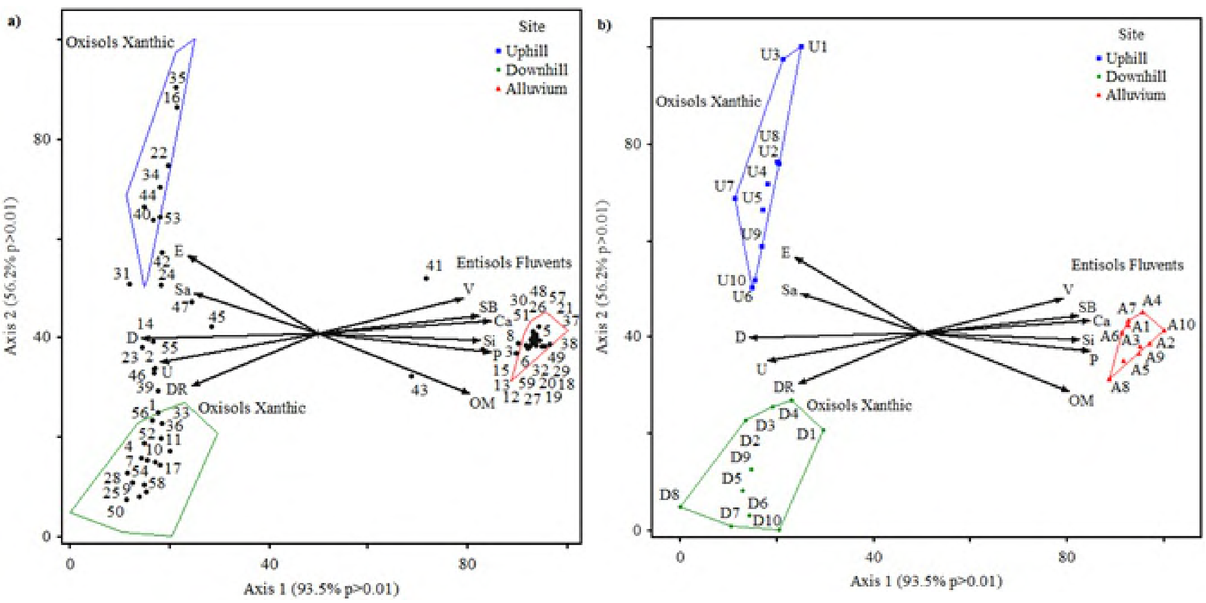

Figure 7. Canonical correspondence analysis: ordination diagram of plots (a) and species (b) based on the distribution of the number of trees of 59 species (species full names in the Table 3) in ten plots in riparian forests along a 15 km stretch of Rio Grande, in Bocaína de Minas municipality, Minas Gerais state, Brazil, and their correlations with the 11 environmental variables (arrows) with correlation above 50% on one of two axes. Where: DR = distance from the river, D = Drainage, U = unevenness of the terrain; El= elevation; Sa= sand, Si= silt, OM = organic matter, Ca = Calcium, P = Phosphorus, SB = Base sum and V = Base saturation.

Figura 7. Análise de correspondência canônica: diagrama de ordenação das parcelas (a) e espécies (b) com base na distribuição do número de indivíduos de 59 espécies (nomes completos das espécies na Tabela 3) em dez parcelas de mata ciliar ao longo de um trecho de 15 km do Rio Grande, em Bocaína de Minas, Minas Gerais - Brasil, e suas correlações com as 16 variáveis ambientais utilizadas (setas). Onde: U = encosta alta; D = encosta baixa e A = Aluvião

al., 2007). Soil and organic matter loss associated with higher areas contribute to high nutrient concentrations in the lower positions of the terrain. This is a relevant factor to habitat heterogeneity (Werner & Homeier, 2015), resulting in high richness of vascular plant species along topographic gradients in tropical forests (Seibert et al.,

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2007). Wilson et al. (2004) found that topography explains between 26 and 64% of soil moisture variation. Slope position was also related to soil water retention in several areas in the USA (Rawls & Pachepsky, 2002).

4.2 Vegetation composition and structure

The lowest richness found in area A is associated with the occurrence of periodic flooding. The seasonal variation in the water level at the soil surface works as a disturbance, altering the soil physical, chemical, and biological properties (Pezeshki & Delaune, 2012). In periodically flooded sites only specialized species with physiological and morphological adaptations can maintain a viable population, which consequently results in a low richness and diversity when compared to non-flooded areas in the same region (Silva et al., 2010). This pattern is repeated in neotropical forests in general (Prance et al., 1976), including the Brazilian Southeast (Silva et al., 2010) and South regions (Gonçalvez et al., 2018).

Also, the lower species richness found in the alluvial fragment is likely related to the greater degree of disturbance and the smaller size of this fragment. Studies in tropical forests generally suggest a positive relationship between the size of the fragment and the number of species, as larger areas tend to host a greater number of species (Pessoa & Araujo, 2020; Hending et al., 2023).

Area D area had a Shannon diversity index (3.992) close to those reported for the areas around the headsprings (H' 3.90 to 4.20) (Rocha et al., 2005). The diversity index for riparian forest associated with alluvial soils (3.178) was higher than those recorded in other areas of similar vegetation type in Brazil: Minas Gerais (H' 2.36, in Silva et al., 2009); Paraná (H' 1.59 to 3.44, in Bardal et al., 2004), Santa Catarina (H' 2.96, in Gonçalves et al., 2018) and São Paulo (H' 2.81, in Marques et al., 2003). The Pielou equability indices found in the present study are similar to those reported for forests around headsprings and along rivers (Gonçalves et al., 2018). The lower values of equability in area A indicate a high ecological dominance of some species, probably due to the alluvial influence (Arellano et al., 2016). The density values of tree species (2178 to 3005 trees ha^{-1}) are among the highest recorded in 20 surveys carried out in the upper part of the Rio Grande basin (969 trees ha^{-1}, in Pereira et al., 2007; 2,683 trees ha^{-1}, in Botrel et al., 2002 and Pereira et al., 2012). Basal areas (D 31.10 m^2 ha^{-1} in D and 43.39 m^2 ha^{-1} in A) were also high compared to other areas (19.79 m^2 ha^{-1} to 34.16 m^2 ha^{-1} in Pereira et al., 2007).

There is still no record in the literature about the dominance of *Anadenanthera colubrina* in alluvial areas. This species is a native tree with wide distribution in Brazil, Paraguay, Bolivia, and Argentina, from 100 to 2000 m above sea level (Giamminola et al., 2020) and it is considered one of the most representative species of the South American Seasonally Deciduous Tropical Forests. Gusson et al. (2011) evaluated the interference of increased soil moisture in populations of *Myracrodruon urundeuva* and *Anadenanthera colubrina* in artificial reservoirs of hydroelectric powerplants and found that *A. colubrina* proved to the species most adapted to this condition. The species has a high seed germination rate, rapid seedling growth, high regeneration speed, and capacity of symbiotic atmospheric nitrogen fixation (Ciaccio et al., 2017), factors that may justify its high abundance.

The low number of species shared among the three areas indicates that the riparian forests of the studied 15 km stretch of Rio Grande are floristically distinct, with high Beta diversity. Floristic comparisons between remnants of riparian forests show that these forest formations have great diversity and low similarity values, even in near areas (Durigan & Leitão Filho 1995). In the present case, the environmental differences between the areas are certainly the main cause for this.

The studied riparian forest sites showed different horizontal and vertical structure, reflecting the influence of the contrasting environmental factors (topographic, edaphic, and hydrological) on plant density and basal area. Topography is considered the most important variable in the structure of tropical forests (Werner & Homeier, 2015), since its variation modifies drainage conditions and soil properties (Fujii et al., 2018; Meireles et al., 2018).

4.3 Relationship between vegetation and environmental variables

The indicator species for area D are: Alchornea sidifolia (1), Cabralea canjerana (7), Casearia arborea (9), Casearia decandra (10), Casearia obliqua (11), Croton salutaris (17), Guatteria pohliana (25), Lamanonia ternata (28), Mollinedia longifolia (36), Tetrorchidium parvulum (52), Pleroma raddianum (54) and Vochysia magnifica (58) (Table 3). They were more abundant on well-drained, high clay and aluminum content soils (Figure 4). These species may be suitable for restoration of riparian forests on intermediate slopes with an altitudinal elevation between 1,200 and 1,300 m.

The indicator species for area U are: Croton organensis (16), Eremanthus erythropappus (22), Miconia sellowiana (34), Miconia theaezans (35), Myrsine umbellata (42), Piptocarpha regnellii (44) and Pleroma arboretum (53) (Table 3). They tend to be more abundant in areas with better drainage conditions (Figure 7) and could be indicated for forest restoration of low fertility sites in steep areas with altitudes above 1,500 m.

The indicator species for area A were: Allophylus edulis (3), Anadenanthera colubrina (5), Annona emarginata (6), Cassia ferruginea (12), Chomelia brasiliana (13), Cupania vernalis (18), Daphnopsis sellowiana (20), Duranta vestita (21), Ilex theezans (26), Matayba elaeagnoides (30), Miconia cubatanensis (32), Myrsine gardneriana (41), Nectandra lanceolata (43), Sebastiania brasiliensis (48), Sebastiania commersoniana (49), Symplocos celastrinea (51), Vitex megapotamica (57) and Xylosma prockia (59) (Table 3). Their abundances are correlated to alluvial soils located closer to the river, periodically flooded (Figure 7). Such species can be indicated for restoration of riparian forest in alluvial sites susceptible to periodic flooding, in altitudinal elevation below 1,200 m in the region of the present study.

Our results show that altitude, drainage, and soil fertility were responsible for the variations in the vegetation composition and structure. The influence of topographic variables such as elevation and slope affect the hydrological and ecological processes (Fujii et al., 2018). Despite the climate being considered the main determining factor in the global patterns of vegetation distribution (Uriarte et al., 2018), soil properties are highly determinant at the biome or even at the community level (Fujii et al., 2018). The combined use of climate-soil factors allows a better understanding of the spatial arrangement by vegetation (Fujii et al., 2018).

Our results may assist restoration protocols and their premises based on the Environmental Regularization Program (PRA), established in the Forest Code (Law 12.651/2012), especially in the selection of species discussed in this study, according to their best spatial and structural suitability. Minas Gerais assumes great importance in forest restoration in southeastern Brazil. The state suffered the largest deforestation of the Atlantic Forest in Brazil in recent years (SOS Mata Atlântica, 2021) and consequently the state will need to invest significant efforts to restore ~3.7 million hectares (Mha) of land in the coming years to meet the requirements of the LPVN (Legislation for the Protection of Native Vegetation) (Morais Júnior et al., 2024). We also highlight that in our findings, some identified species are of high value for conservation, since several genera and species present some degree of threat of extinction, following the list of threatened species of the Ministry of Environment and Climate Change, together with MMA ordinance no. 148, of June 7, 2022.

5. CONCLUSION

Despite spatially close, the riparian forests had significant floristic and structural differences. The species distribution was significantly correlated with altitude, soil fertility and water regime (distance from the river and drainage). Therefore, indication of species to compose forest restoration actions in riparian forests must be defined according to the characteristics of the sites and the adaptation of the species.

Although riparian vegetation is widely recognized for its positive impact on soil and water quality and its role in ecological conservation, there is still a gap in understanding the effect of environmental heterogeneity on tree community composition and structure in riparian landscapes. Understanding the dynamics of riparian forests is essential for strategic decision-making in tropical forest management towards the promotion of ecosystem services, forest restoration and sustainable development goals.

The results obtained in our study may considerably help in increasing the lists of species recommended for forest restoration in areas with characteristics of those evaluated, although the aspect of seedling production and their adaptability in the field were not objects of evaluation in our study, however future research may provide answers on this.

AUTHOR CONTRIBUTIONS

Pereira, I. M.: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review and editing; Botelho, S. A.: Research supervision; Machado, E. L. M., Gorgens, E. B., Oliveira, M. L. R., van den Berg, E., Farnezi, M. M. M., França, L. C. J., and Gonzaga, A. P. D.: Writing – review and editing; Sampaio, E. V. S. B.: Validation, Writing – original draft, Writing – review and editing; Oliveira-Filho, A. T.: Validation, Writing – original draft, Writing – review and editing.

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