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Papers

Mineral-Organic Interactions and Soil Gradients Drive Plant Community Assembly in Brazilian Semiarid Inselbergs

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Abstract
This study investigated a soil catena along a colluvial slope of a southeast-facing granitic inselberg to evaluate the influence of soil property variations on vegetation composition across altitudinal and distance gradients from the inselberg. Four soil profiles were described and sampled along a toposequence. Soil analyses included texture, acidity, exchangeable bases, phosphorus, nitrogen, and organic carbon contents. Total porosity, macroporosity, and microporosity were determined using undisturbed soil samples. Tree and shrub individuals were identified within vegetation plots around the soil profiles, and plant diversity and evenness were subsequently assessed. The toposequence comprised an Umbrisol (SP1), a Phaeozem (SP2), and two Regosols (SP3 e SP4), extending across different geomorphic positions (summit, shoulder, backslope and toeslope). Principal Component Analysis (PCA) and Spearman correlation were applied to assess the bivariate and multivariate relationships between soil, geomorphological, and vegetation variables. Results indicate that soil weathering intensity, leaching processes, and organic carbon contents increase with elevation and proximity to the inselberg. The higher organic carbon contents observed at the summit (C = 9.93% in SP1) and on the shoulder (C = 10.89% in SP2) of the colluvial slope are attributed to reduced accessibility of organic substrates to decomposers, coupled with intensified mineral-organic interactions, including sorption and chelation processes. Species from the Myrtaceae, Rubiaceae, Fabaceae, and Sapindaceae families were predominantly associated with soils rich in organic carbon, whereas species belonging to the Cactaceae and Euphorbiaceae families were more abundant in soils with lower organic carbon contents in the toeslope (SP4). Peripheral areas in inselbergs host more developed soils that support denser and structurally complex vegetation, functioning as ecological microrefugia relative to the surrounding Caatinga landscape. Overall, the findings of this study demonstrate that inselbergs can be considered essential environments for the conservation and maintenance of Caatinga biodiversity.

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INTRODUCTION

South America contains over 50% of the dry forests in the world, including the Caatinga, the largest and most biodiverse Neotropical dry forest. The Caatinga occurs exclusively in Brazil and occupies 845,000 km², approximately 10% of the country total territory (Moro *et al.*, 2024). The climatic seasonality induces the dominance of xeromorphic vegetation, registering 3,340 Angiosperms species, of which around 16% are endemic (Fernandes *et al.*, 2020). Leptosols, Regosols, and Luvisols cover partially eroded pediments and plateaus between 350 and 700 meters above sea level (m.a.s.l.) (Salgado *et al.*, 2015). These soils are dominantly thin, stony, gravelly, shallow, eutrophic, and have low water storage capacity (Araújo Filho *et al.*, 2017).

Studies have contributed to understanding patterns of vegetation in relation to edaphic conditions (Magnago *et al.*, 2012; Rodrigues *et al.*, 2018; Souza *et al.*, 2018). Under similar climatic conditions, soil properties and topography emerge as the primary drivers of variability in plant community composition (Tindano *et al.*, 2023). Spatial heterogeneity in soil physical and chemical properties, even over short distances, promotes the development of distinct vegetation mosaics (Dubuis *et al.*, 2013; Souza *et al.*, 2025). Furthermore, Medinski *et al.* (2010) emphasized the role of soil texture in regulating water storage capacity and availability for plants in semiarid environments. In the Brazilian Savanna, Rodrigues *et al.* (2018) demonstrated that soil fertility varies among soil types and strongly influences plant species distribution, with more fertile areas supporting taller trees, whereas less fertile areas are dominated by grasses and shrubs. In drier regions, water availability is a determinant factor of species distribution, however, associated physical and chemical soil factors can amplify its effects on species richness (Enright *et al.*, 2014; Huston, 2014).

Inselbergs rise abruptly from the typical gently sloping landscapes of the Caatinga. They consist of high-resistance rocks, predominantly granite and granitoid, and have maintained their topographic integrity while the surrounding terrain has been reduced by erosion, leading to the exposure of bedrock (Porembski *et al.*, 2000; Burke, 2003). Inselbergs exhibit some of the most significant and sensitive microhabitats and ecosystems in the world, largely attributed to the differences in plant community composition and soil properties compared to the surrounding areas (Parmentier *et al.*, 2005; Souza *et al.*, 2025).

In inselbergs of semiarid regions, peripheral areas are frequently characterized by vegetation that is taller and denser than that of the surrounding landscape (Porembski *et al.*, 2000; Seine *et al.*, 2000; Souza *et al.*, 2025). The geomorphological arrangement appears to influence water distribution, sediment accumulation, and organic matter deposition, resulting in distinct soil properties that support plant species sensitive to water scarcity (Borges Neto *et al.*, 2025; Souza *et al.*, 2025). Advancing our understanding of the mechanisms facilitating tree layer establishment around inselbergs in semiarid regions is essential for elucidating biogeographic connections and biodiversity patterns in the Caatinga biome. This study investigates the influence of soil properties on plant community composition along elevation gradients in areas peripheral to an inselberg in the Caatinga, Brazil.

MATERIAL AND METHODS

Study Area

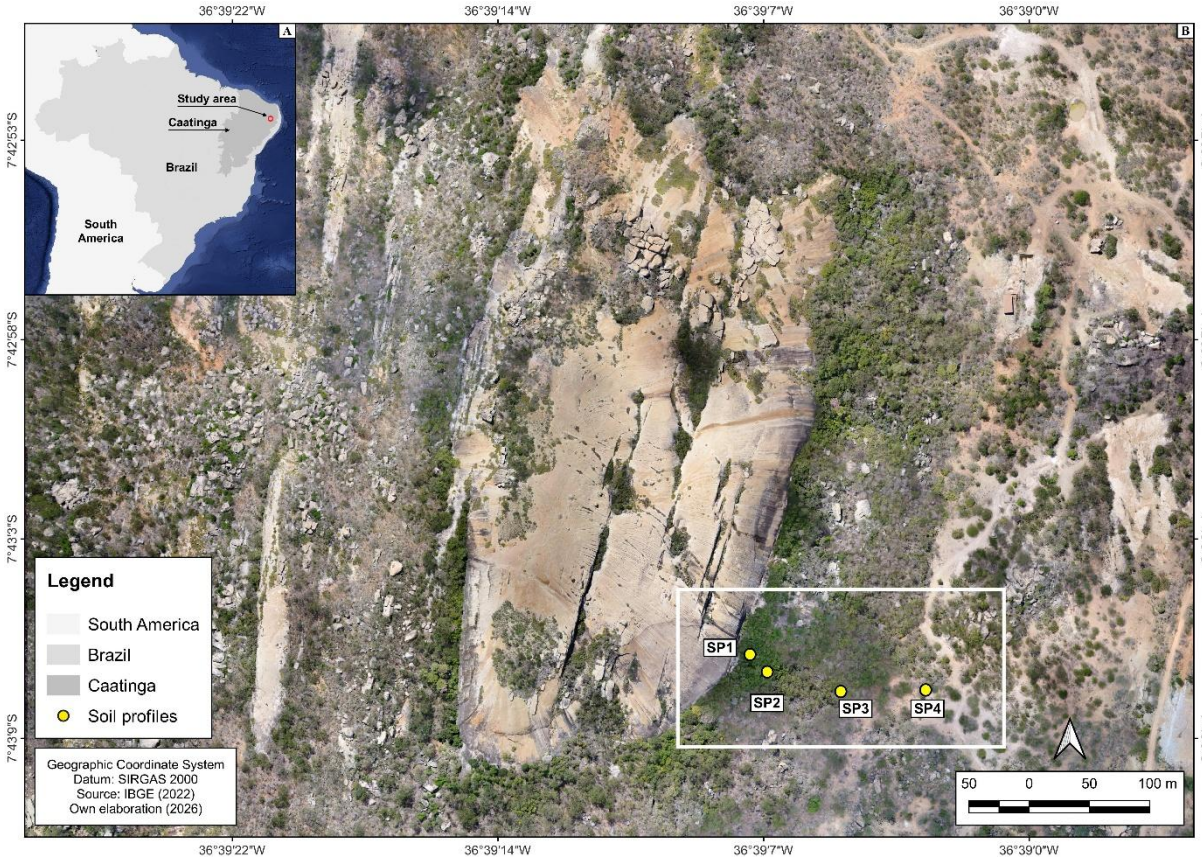
The study area encompasses a southeastern-facing colluvial slope of an inselberg in the Cariris Velhos region, municipality of Congo, Paraíba State, Brazil (Figure 1). The climate is classified as tropical semiarid (BSh), with mean annual precipitation ranging from 350 to 500 mm. The mean annual temperature is 26°C, and potential evapotranspiration can reach values up to four times higher than annual precipitation (Alvares *et al.*, 2013).

Neoproterozoic granite and granitoid outcrop as inselbergs because of pedimentation processes, followed by Cenozoic uplift and subsequent differential erosion (Xavier *et al.*, 2022). An inselberg was chosen for the study due to its minimal human disturbance. The slope exhibits a convex-concave-convex profile, with a maximum elevation of 640 m.a.s.l., a slope gradient of less than 59%, a total area of 22.044 km², and a length of 17.673 km.

The vegetation cover of the study area exhibits high biodiversity and is composed of species well adapted to semiarid climatic conditions. The dominant plant families include Fabaceae and Euphorbiaceae, along with representatives of the Cactaceae family and rupicolous bromeliads, such as *Dyckia spectabilis* (Mart. ex Schult. & Schult.f.) Baker and *Hohenbergia catingae* Ule (Cordeiro *et al.*, 2025; Souza *et al.*, 2025). Luvisols (40.9 % of the total area), Leptosols (35.6 %), and Regosols (3.9 %) are the dominant soil classes in the Cariri

region (Santos *et al.*, 2011). These soils are predominantly loamy, shallow (generally < 1 m in depth), eutrophic, and characterized by low organic carbon contents (Ferreira *et al.*, 2018; Borges Neto *et al.*, 2025).

Figure 1 – Sampled areas along toposequence of a colluvial slope adjacent to an inselberg in the municipality of Congo, Paraíba State, Brazil

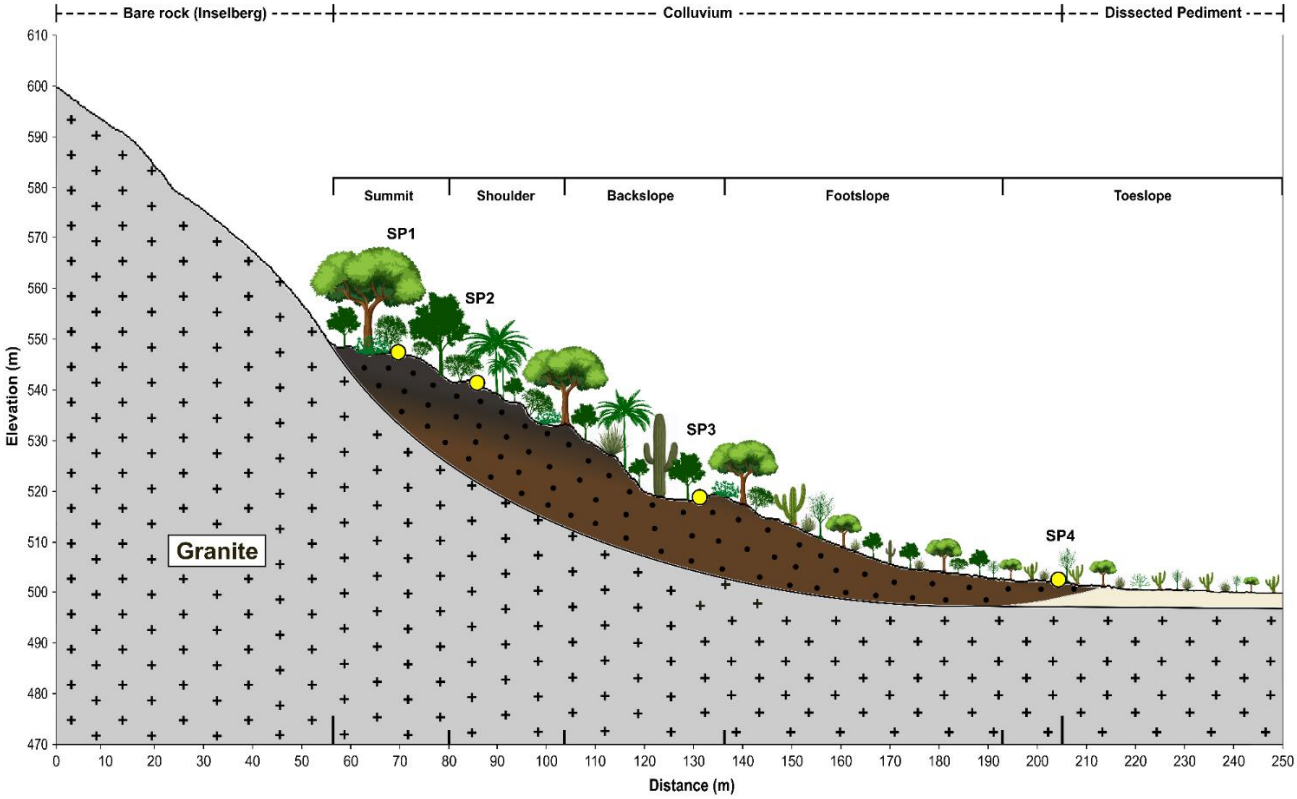


Source: The authors (2026).

Soil Sampling and Analysis

Four soil profiles were opened, described, and classified according to the Brazilian Soil Classification System (Santos *et al.*, 2025) and World Reference Base for Soil Resources (IUSS Working Group WRB, 2022). According to the classification of Zinck (2023), we sampled the different geomorphic surfaces of the slope formed by the colluvial material of the granitic inselberg: summit (SP1), shoulder (SP2), backslope (SP3), and toeslope (SP4) (Figure 2). Standard soil augers were used to sample soil at 10 m intervals.

Figure 2 – Schematic topographic profile of the toposequence and distribution of geomorphic surfaces, soil profiles (yellow points) and tree cover gradient



Source: The authors (2026).

Soil samples were collected to represent each horizon. Samples were air-dried and sieved through a 2.0 mm sieve before texture and chemical analysis according to methods established for tropical soils (Donagema *et al.*, 2011). Sand, silt, and clay were determined by the pipette method after dispersion with 0.1 M NaOH. Soil pH was measured with a glass electrode in a 1:2.5 suspension v/v soil and deionized water (H_2O pH). The potential acidity (H + Al) was extracted by 1 M ammonium acetate solution at pH 7. An atomic absorption spectrometry determined the content of Ca^{2+}, Mg^{2+}, and Al^{3+} after extraction with a 1 M KCl solution. After Melhich-1, the contents of K^+ and Na^+ were determined by flame photometry. From these results, the sum of bases (SB), base saturation (V), and total cation exchange capacity (CEC) were calculated.

A Mehlich-1 extraction solution determined the available phosphorus content (P). The P adsorption (P_{ad}) was calculated as a percentage after 1 hour of stirring with 2.5 g of soil in 0.01 M $CaCl_2$ containing 60 mg P L^{-1}. The suspension was filtered, and the remaining P in solution was determined by photocolorimetry (Alvarez *et al.*, 2017).

Soil organic carbon (SOC) was determined by wet combustion (Yeomans; Bremner, 1988). Total nitrogen (N) was determined by the Kjeldahl method and titration (Teixeira *et al.*, 2017). The carbon-to-nitrogen ratio (C/N) was calculated on a mass basis.

Bulk density, particle density, and macroporosity (-10 kPa tension) were determined in undisturbed soil samples collected by volumetric rings in the surface horizons of each soil profile (Teixeira *et al.*, 2017). Total porosity and microporosity were calculated from these results. The formulae calculated the total organic carbon and nitrogen stocks: Stock (Mg ha^{-1}) = bulk density (kg dm^{-3}) × soil organic carbon (or total nitrogen) content (%) × depth (cm).

Vegetation Cover

To integrate vegetation and soil data, we established four sampling plots corresponding to the locations of soil profiles (SP1, SP2, SP3, and SP4). Each sampling unit consisted of a single plot measuring 50 × 50 m (2,500 m^2). Plant species were recorded from January 2022 to May 2024, covering both dry and wet seasons. The comprehensive species list was derived from vegetation plots and included trees, shrubs, lianas, and members of the Cactaceae and Bromeliaceae families. Herbs, epiphytes, and dead plants were omitted from the inventory. The APG IV classification system was adopted

to define plant families (Angiosperm Phylogeny Group, 2016).

Statistical Procedures

For the vegetation data, we calculated the Shannon diversity index (H′) and the Pielou evenness index (J′). We also used Principal Component Analysis (PCA) to evaluate the multivariate relationships among soil properties, topographic characteristics, and vegetation characteristics. The variables were standardized to minimize the effect of different units and scales of measurement in the data (Hinton, 2014).

The associations between the data were assessed using Spearman's correlation. We chose this nonparametric test because the data did not meet the assumption of normality (Zar, 2014). Correlations were considered statistically significant at $p < 0.05$. All statistical analyses were performed using the R software (R Core Team, 2020).

RESULTS

Soils on Toposequence

Four soil profiles developed from granite-derived colluvium were identified along the slope, comprising three WRB reference soil groups: Endoleptic Chernic Umbrisol (Neossolo Regolítico Distrófico léptico, SP1), Endoleptic Pantochernic Phaeozem (Neossolo Litólico Hístico léptico, SP2), and Hypereutric Regosols (Neossolo Litólico Eutrófico léptico, SP3; Neossolo Regolítico Eutrófico saprolítico léptico arênico, SP4) (Chart1).

Chart 1 – General description of soil and vegetation of the sampled areas

Soil profile	WRB	SiBCS	Altitude (m.a.s.l.)	Description	Dominant species
SP1	Endoleptic Chernic Umbrisol (Pantoloamic, Eutric, Hyperhumic, Pachic)	NEOSSOLO REGOLÍTICO Eutrófico léptico	548	Soil developed on the summit of a colluvial slope. Soil is well-drained without apparent erosion and derived from colluvium. Subangular granite as gravel is abundant in the soil profile. Litter covers the soil surface, and bioturbation is intense. Chernic horizon (O hístico horizon, according to SiBCS) covers an umbric horizon.	*Savia sessiliflora*, *Bauhinia cheilantha*, *Peltogyne pauciflora*, *Rhamnidium molle*, *Cordiera rigida*, *Eugenia* sp., *Anadenanthera colubrina*, *Talisia esculenta*, *Cordia trichotoma*, *Luetzelburgia auriculata*
SP2	Endoleptic Pantochernic Phaeozem (Pantoloamic, Hyperhumic, Pachic)	NEOSSOLO LITÓLICO Hístico fragmentário	542	Soil developed on the shoulder of a colluvial slope. Soil is well-drained without apparent erosion and derived from colluvium. Subangular granite as gravel is abundant in the soil profile. Litter covers the soil surface, and bioturbation is intense. Chernic horizon (O hístico horizon, according to SiBCS) is the surface horizon.	*Luetzelburgia auriculata*, *Combretum leprosum*, *Guapira darwinii*, *Solanum rhytidoandrum*, *Syagrus cearensis*, *Cynophalla flexuosa*, *Croton blanchetianus*, *Eugenia* sp., *Guapira* sp., *Annona leptopetala*
SP3	Hypereutric Epileptic Regosol (Pantoloamic, Ochric)	NEOSSOLO LITÓLICO Eutrófico fragmentário	519	Soil developed on the backslope of a colluvial slope. Soil is well-drained with slight sheet erosion and derived from colluvium. Litter is absent. Ochric horizon (A moderado horizon, according to SiBCS) is the surface horizon.	*Bauhinia cheilantha*, *Croton grewioides*, *Croton blanchetianus*, *Anadenanthera colubrina*, *Peltogyne parvifolia*, *Luetzelburgia auriculata*, *Manihot carthagenensis*, *Cordiera rigida*, *Lippia grata*, *Varronia leucocephala*
SP4	Hypereutric Endoleptic Regosol (Pantoarenic, Ochric)	NEOSSOLO REGOLÍTICO Eutrófico saprolítico léptico arênico	503	Soil developed in the toeslope of a colluvial slope transitioning to a dissected pediment. Soil is well-drained with slight sheet erosion and derived from colluvium and granite. Litter is absent. Ochric horizon (A moderado horizon, according to SiBCS) is the surface horizon.	*Tacinga inamoena*, *Jatropha mollissima*, *Croton blanchetianus*, *Cenostigma nordestinum*, *Herissantia tiubae*, *Jatropha ribifolia*, *Cnidoscolus urens*, *Waltheria indica*, *Jatropha curcas*, *Mimosa ophthalmocentra*

Source: The authors (2026).

Soil depth ranged from 40 to 90 cm, with A–C horizon sequences predominating (Chart S1, Supplementary Materials). Umbric and chernic diagnostic horizons occurred in the summit and shoulder slope positions, whereas Regosols from the backslope and toeslope presented only ochric surface horizons. Soil structure, root abundance, and pore volume decreased downslope.

Soil texture ranged from loamy sand to clay loam, with clay content decreasing toward lower elevations (Tables 1; S1, Supplementary Materials). Exchangeable bases followed the order $Ca^{2+} > Mg^{2+} > K^{+} > Na^{+}$, while extractable P, cation exchange capacity, soil organic carbon, total nitrogen, and P adsorption generally decreased downslope (Table 1). Bulk density increased toward the backslope and toeslope, whereas total porosity, macroporosity, and C and N stocks declined with decreasing elevation, while particle density remained similar among profiles (Table S2, Supplementary Materials).

SP1 and SP2 showed deep, organic matter-rich A horizons with high base status and the highest concentrations of soil organic carbon, nitrogen, exchangeable bases, and extractable phosphorus. In contrast, SP3 and SP4 were shallower, sandier Regosols with weaker structure, lower nutrient availability, and reduced carbon stocks (Chart 1 and Table 1).

Table 1 – Main physical and chemical properties of the sampled soils

Horizon	Depth	CS	FS	Silt	Clay	pH	P	K^+	Na^+	Ca^{2+}	Mg^{2+}	Al^{3+}	H+Al	SB	CEC	V	C	N	C/N	Pad
	cm	---------- % --------				H_2O	mg kg^{-1}	---------- $cmol_c$ kg^{-1} ----------								------- % -------				%
SP1 - Endoleptic Chernic Umbrisol (Pantoloamic, Eutric, Hyperhumic, Pachic) / NEOSSOLO REGOLÍTICO Distrófico léptico																				
Ah	0-35	35.4	12.3	19.3	33.0	5.06	42.2	0.68	0.06	20.41	1.84	<1	10.7	22.99	33.69	68	9.93	0.69	14	49
2Ahb$_1$	35-50	42.0	15.9	15.8	26.44	4.80	13.9	0.49	0.08	3.87	0.99	<1	11.3	5.43	16.73	33	5.92	0.36	16	76
2Ahb$_2$	50-90	44.3	14.0	17.9	23.8	4.72	5.8	0.33	0.06	1.48	0.55	1.43	12.3	2.42	14.72	16	3.82	0.24	15	86
R	90+																			
SP2 - Endoleptic Pantochernic Phaeozem (Pantoloamic, Hyperhumic, Pachic) / NEOSSOLO LITÓLICO Hístico léptico																				
Ah_1	0-5	30.8	12.6	20.9	35.57	5.41	19.7	0.96	0.06	21.77	4.72	<1	6.9	27.51	34.41	80	10.89	0.67	16	29
Ah_2	5-30	37.5	13.9	17.2	31.33	6.00	6.3	1.16	0.10	16.88	4.74	<1	3.9	22.88	26.78	85	5.35	0.40	13	37
Ah_3	30-50	37.6	15.3	16.5	30.7	5.83	5.4	1.11	0.10	15.09	3.96	<1	4.2	20.26	24.46	83	4.96	0.33	15	40
R	50+																			
SP3 - Hypereutric Epileptic Regosol (Pantoloamic, Ochric) / NEOSSOLO LITÓLICO Eutrófico léptico																				
A	0-20	46.5	23.4	15.3	14.8	6.99	9.8	0.65	0.02	4.96	0.94	<1	0.5	6.57	7.07	93	0.84	0.06	13	17
Ce	20-40	51.3	16.6	14.4	17.8	6.19	6.8	0.40	0.06	3.86	0.9	<1	0.6	5.22	5.82	90	0.46	0.04	10	31
R	40+																			
SP4 – Hypereutric Endoleptic Regosol (Pantoarenic, Ochric) / NEOSSOLO REGOLÍTICO Eutrófico léptico																				
A	0-4	57.2	21.5	13.1	8.2	5.32	14.0	0.20	0.00	3.48	0.39	<1	1.4	4.07	5.47	74	1.33	0.06	20	8
C	4-25	60.4	19.0	13.5	7.1	6.03	2.0	0.16	0.00	3.57	0.35	<1	0.8	4.08	4.88	84	0.38	0.02	17	12
2Ahb	25-60	60.3	20.4	12.7	6.5	5.98	1.3	0.15	0.01	2.75	0.25	<1	0.6	3.16	3.76	84	1.07	0.01	107	10
R	60+																			

Source: The authors (2026).

Vegetation Diversity

A total of 1,889 individuals, representing 88 species and 32 families, were recorded at the sampling sites (Table 2). The Shannon-Wiener diversity index (H′) was 3.72, and Pielou's evenness index (J′) was 0.82. Among the recorded species, 37 were trees, 43 shrubs and subshrubs, two lianas, six Cactaceae, and two Bromeliaceae (Table S3, Supplementary Materials).

Table 2 – Number of families, species, individuals, Shannon diversity index (H′), and Pielou evenness index (J′) by sampled areas

	SP1	SP2	SP3	SP4	Total
Families	27	25	25	14	32
Species	47	39	47	31	88
Individuals	418	450	441	580	1,889
Shannon-Wiener (H′)	3.34	2.91	3.00	2.35	3.72
Pielou (J′)	0.86	0.79	0.78	0.68	0.82

Source: The authors (2026).

The tree layer was dominant in SP1 and SP2 (24 species and 455 individuals), with notable dominance of *Luetzelburgia auriculata* (Allemão) Ducke (117 individuals), *Savia sessiliflora* (Sw.) Willd. (48 individuals), *Guapira darwinii* (Hemsl.) E.C.O. Chagas & Costa-Lima (46 individuals), *Peltogyne pauciflora* Benth. (31 individuals), and *Talisia esculenta* (Cambess.) Radlk. (27 individuals). In SP3 and SP4, the tree layer comprised 26 species and 336 individuals, although it was strongly dominated by only two species, *Jatropha mollissima* (Pohl) Baill. (93 individuals) and *Cenostigma nordestinum* Gagnon & G.P. Lewis (59 individuals), which together accounted for 45.2% of all trees recorded in these sites.

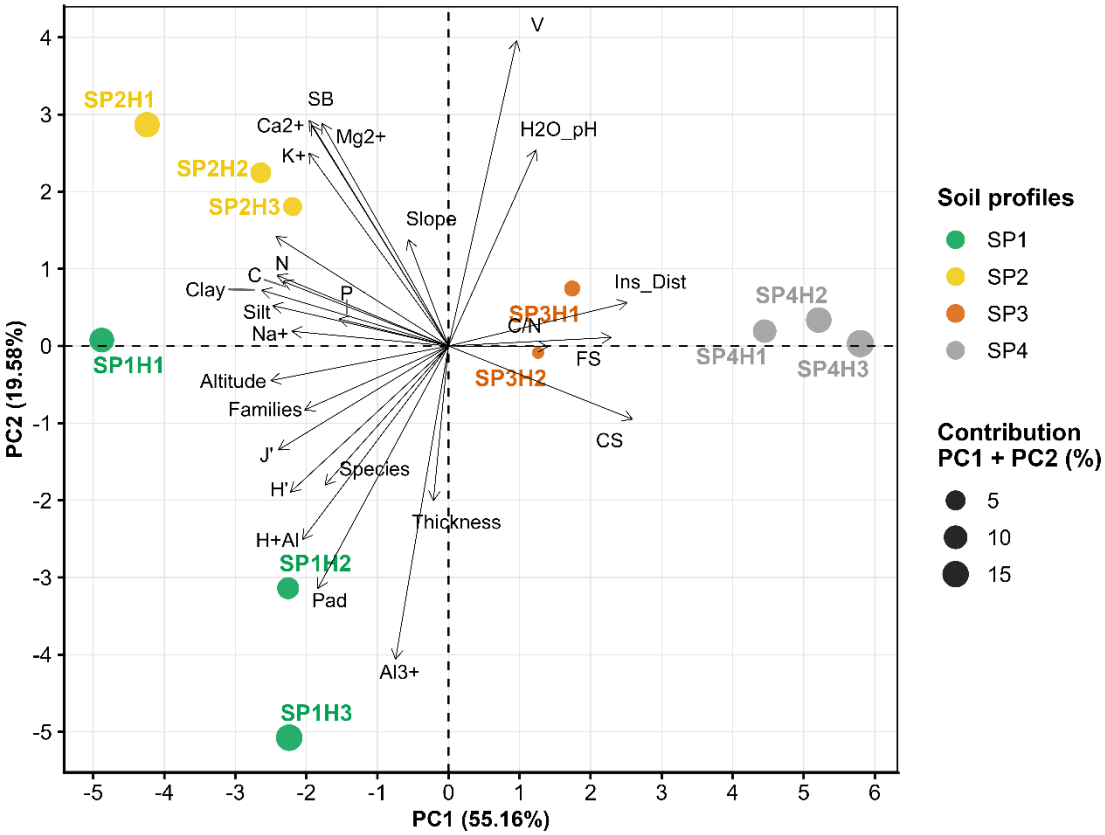
The shrub layer was consistently represented across all sampling units, with species such as *Bauhinia cheilantha* (Bong.) Steud. (133 individuals) and *Croton blanchetianus* Baill. (141 individuals) widely distributed along the colluvial slope. In SP1 and SP2, the most representative shrub species were *Combretum leprosum* Mart. (49 individuals), *Eugenia* sp. (39 individuals), and *B. cheilantha* (37 individuals), whereas in SP3 and SP4, *C. blanchetianus* (114 individuals), *B. cheilantha* (96 individuals), and *Croton grewioides* Baill. (65 individuals) predominated. Cactaceae were represented by six species and 238 individuals and occurred in all sampling units, although with greater abundance in areas closer to the toeslope (181 individuals).

Sampling unit SP1, located near the toeslope, exhibited the highest vegetation diversity, with 27 families, 47 species, $H' = 3.34$, and $J' = 0.86$ (Table 2). As elevation along the slope decreased and distance from the summit toward the toeslope increased, there was a progressive decline in the number of families, species richness, diversity, and evenness, accompanied by an increase in the total number of individuals. Sampling unit SP3, however, functioned as a transitional zone, incorporating species typical of SP1 and SP2 (wetter environments) as well as SP4 (drier environment), which resulted in comparatively high species richness (47 species) and diversity ($H' = 3.00$).

Statistical Analyses

PCA explained 74.74% of the total variance in the data. PC1 explained 55.16% of this variance, and PC2 explained an additional 19.58% (Figure 3). PC1 distinguished the soils in the highest positions of the toposequence (SP1 and SP2) from those at the bottom of the slope (SP3 and SP4). SP3 (orange circles) and SP4 (gray circles) were located on the positive side of PC1 and were strongly associated with distance from the inselberg (Ins_Dist) as well as the contents of coarse sand (CS) and fine sand (FS). SP1 (green circles) and SP2 (yellow circles), located on the negative side of PC1, were more closely aligned with elevation, clay and silt content, C, N, CEC, and Pad (Figure 3).

Figure 3 – Principal component analysis (PCA) biplot illustrating the ordination of soil horizons and environmental variables (edaphic, geomorphic, and vegetational). The circles represent individual soil horizons and are color-coded according to the soil profiles: SP1 (green), SP2 (yellow), SP3 (orange), and SP4 (gray). The size of each circle indicates its relative contribution to the first two principal components (PC1 + PC2). The gray arrows represent vectors of environmental and vegetation variables



Source: The authors (2026).

The second principal component (PC2) distinguished soil chemical fertility and vegetation characteristics (Figure 3). PC2 separated the organic carbon-rich horizons of the Umbrisol (SP1) from the Phaeozem (SP2) horizons, the former of which were more diverse. With the exception of the surface horizon (SP1H1), SP1 was positioned in the lower left quadrant. This group was primarily characterized by soil thickness, H+Al, and Al^{3+}. Additionally, variables related to vegetation and its richness aligned in this quadrant (Figure 3). Conversely, SP2 was located in the upper left quadrant of the graph and showed a stronger association with base-rich chemical properties, including pH in H_2O, V, and the presence of exchangeable Ca^{2+}, Mg^{2+}, and K^{+}.

To better understand these covariations, we analyzed a correlation matrix using Spearman's test (Figure S1, Supplementary Materials). Vegetation diversity appears to be highly sensitive to geomorphic position and edaphic characteristics. There were significant negative correlations between species richness and Shannon diversity (H') and distance from the inselberg (ρ = -0.72 and ρ = -0.86, respectively, both with $p < 0.05$), indicating a decline in vegetation diversity toward lower-lying areas (Figure S1).

Soil texture appears to act as an important primary filter for the plant community. Family richness was positively correlated with clay content (ρ = 0.59, $p < 0.05$) and negatively correlated with the contents of coarse sand and fine sand (ρ = -0.59 and -0.52, respectively, both with $p < 0.05$). Regarding chemical properties, plant diversity was strongly related to the dynamics of carbon and phosphorus sorption in the soil. Family richness showed high positive correlations with C (ρ = 0.60), N (ρ = 0.68), CEC (ρ = 0.59), and Pad (ρ = 0.82), all of which were statistically significant at $p < 0.05$ (Figure S1).

Additionally, the correlation matrix revealed strong relationships between C and soil properties related to their respective retention and stabilization processes in the soil (Figure S1). There were strong positive correlations between C and N (ρ = 0.92), CEC (ρ = 0.87), and

clay and silt contents (ρ = 0.96 and 0.78, respectively). There were also negative correlations with coarse sand (ρ = -0.90) and fine sand (ρ = -0.78) contents. These patterns suggest that C stronger association with more reactive soil fractions likely favors its stabilization in organomineral complexes and contributes to cation exchange capacity.

DISCUSSION

Inselbergs Promote the Development of Fertile, Carbon-Rich Soils in the Brazilian Semiarid

SOC stabilization in semiarid environments is a complex process governed by the interaction among climatic constraints, topographic controls, vegetation inputs, and mineralogical composition (Borges Neto *et al.*, 2025; Souza *et al.*, 2025). In this study, soils on the summit (284.99 Mg ha^{-1} in SP1-Ah) and shoulder (132.41 Mg ha^{-1} in SP2-Ah$_2$) of the colluvial slope have C stock up to seven times higher than the mean of Caatinga (39.2 Mg ha^{-1}, according to Fidalgo *et al.* (2007). According to Figure 3 and Figure S1, the spatial variation in C stocks is reinforced by the positive correlation with altitude (ρ = 0.74) and the negative correlation with distance from the inselberg (ρ = -0.74).

Recent studies have already reported this localized enrichment in the context of the crystalline inselbergs of the Caatinga. An area located approximately 60 km northeast of our study area; soils formed in granitic inselberg fields (44.10 Mg ha^{-1}) had average organic carbon stocks that were three times higher than those of typical Caatinga soils (13.69 Mg ha^{-1}) (Borges Neto *et al.*, 2025).

This geomorphic-pedological mechanism of lateral redistribution and accumulation on slopes and in topographically depressed areas seems similar to patterns observed in other climates and landforms. For example, under a humid subtropical climate, vegetated gnammas with soil depths of up to 98.5 cm accumulate average organic C concentrations of 7.9% in a large granitic dome in Enchanted Rock (Texas, USA). This contrasts sharply with shallow (1-5 cm) and uncovered gnammas, which contain only 2.6% organic C (Pérez, 2023).

Stabilizing soil organic matter (SOM) could be associated with two primary mechanisms: a) reduced access of decomposers, and; b) interactions between mineral and organic compounds. Low soil moisture resulting from high evapotranspiration rates constrains oxidative degradation of organic substrates, thereby slowing decomposition processes (Kang; Choi, 2009). In addition, the presence of strong soil structure and dendritic tubular pores in horizons with elevated organic carbon contents suggests effective physical protection of organic matter through occlusion within soil aggregates (peds). Soil organic matter promotes localized microbial activity (Tang *et al.*, 2011), and these microorganisms secrete extracellular polysaccharides that adhere to soil particles, enhancing aggregation and forming physical barriers around residual organic materials (Tang *et al.*, 2011; Blaud *et al.*, 2014). Although microbial activity was not measured in this study, the role of microbial activity in aggregate formation is well documented in the literature. Here, it is suggested as one possible mechanism contributing to the persistence of SOM. Furthermore, high clay contents combined with abundant polyvalent cations further favor aggregate formation through the flocculation of charged particles (Erktan *et al.*, 2017). This mechanism is most evident in the SP2 surface horizon (Ah1, 0-5 cm), the only horizon in which the clay content (35.7%) exceeds that of coarse sand (30.8%), coinciding with the highest recorded values of exchangeable Ca^{2+} (21.77 $cmol_c$ kg^{-1}) and carbon (10.89%) in topossequence (Table 1).

The importance of cations, particularly Ca, in soil organic matter stabilization is well established. The Ca^{2+} negatively correlates with soil organic matter leaching losses, photo-oxidation and microbial respiration (Minick *et al.*, 2017; Rowley *et al.*, 2018). Besides the positive influence in ped formation, models predict that the Ca^{2+} forms cation bridges with carboxylate, phenolic, and other -OH functional groups, potentially increasing soil organic carbon stability (Czarnes *et al.*, 2000). Both inner- and outer-sphere interactions between the surface of a mineral or metal ion and organic substances act over medium-to-long-time periods (Rowley *et al.*, 2018). Although the Ca content in felsic rocks is lower than limestone, the incipient weathering of granitoid and granite under semiarid climate favors the concentration of enough Ca to stabilize organic carbon compounds. The virtual absence of Al in most horizons indicates that toxicity by Al is not a current mechanism of stabilization of soil organic carbon in the study area.

This study describes the occurrence of Phaeozems in Brazilian semiarid non-associated with limestone in sedimentary areas, where high Ca contents stabilize the accumulated soil organic matter in past climates (Wang *et al.*, 2004). Phaeozems are highly fertile

soils, rich in organic matter and calcium (IUSS Working Group WRB, 2022). The report of the Chernic horizon in soils derived from igneous rocks in Northeastern Brazil is unprecedented. Four mechanisms explain the occurrence of this horizon: i) higher input of organic residues; ii) stabilization of organic compounds; iii) low intensity of erosive processes, and; iv) release of Ca from weathering of primary minerals. Although granitoids are less calcium-rich compared to limestones, the incipient weathering of feldspars under a semiarid climate still provides sufficient Ca to stabilize organic carbon compounds (Silva *et al.*, 2018). The granitic composition thus plays an indirect yet pivotal role in the stabilization of organic matter, fostering more fertile soils that support diverse vegetation communities (Gomes *et al.*, 2026).

Topographic convergence of runoff, sediments, and organic residues from the inselberg likely promotes the accumulation and incorporation of organic matter into soils on the summit and shoulder of colluvial slopes (Patton *et al.*, 2019). The stronger soil structure and abundant dendritic tubular pores observed in SP1 and SP2 further support the physical protection of organic matter within stable aggregates, contributing to long-term carbon storage.

Inselbergs and Edaphic Conditions: Tree Layer Refugia Within a Xerophytic Environment

In this study, inselbergs promote the development of more evolved soils with higher soil organic carbon, nitrogen, and porosity than surrounding Caatinga soils (Figure 3), corroborating previous studies in the Brazilian semiarid (Borges Neto *et al.*, 2025; Souza *et al.*, 2025). For comparison, Borges Neto *et al.* (2025) reported that organic carbon (up to 20% C) accumulates on regional scale within discontinuous "soil pockets" in fractures and gnammas of inseberg bedrock. However, our study shows that these microrefuges can extend to contact areas between the bedrock and the colluvial areas surrounding it.

These conditions support more diverse plant communities dominated by tree species, particularly Myrtaceae, Rubiaceae, Fabaceae, and Sapindaceae, whereas toeslope soils (SP4), with lower SOC, are dominated by shrubs and xerophytic taxa such as Cactaceae and Euphorbiaceae (Tables 2; S3, Supplementary Materials). The higher soil fertility on the summit and shoulder of the colluvial slope likely reduced nutrient limitation and physiological stress, favoring more complex plant communities (Van der Putten *et al.*, 2013). Higher SOC also promotes nutrient cycling and the availability of N and P, two key resources for plant growth in semiarid ecosystems (Reichmann *et al.*, 2013; de-Bashan *et al.*, 2022).

The higher total porosity and macroporosity observed in SP1 and SP2 probably increased soil water availability, favoring tree dominance over xerophytic vegetation (Paloschi *et al.*, 2021; Wright *et al.*, 2024). Water availability acts as a strong environmental filter in dryland ecosystems, limiting the occurrence of drought-sensitive species (Araújo, 2005; Seiler *et al.*, 2015; Moro *et al.*, 2016). Therefore, the similar floristic composition observed between SP1 and SP2 is likely attributable to greater water availability and higher SOC contents at the summit of the colluvial slope. Some drought-sensitive species are also found in SP3, forming a closely related floristic group among the sampling units. In contrast, SP4 is composed exclusively of xerophyte species adapted to semiarid conditions. Within the Caatinga biome, drier environments typically support impoverished plant assemblages and are more susceptible to chronic anthropogenic disturbances, which reduce both species diversity and vegetation structural complexity (Ribeiro *et al.*, 2015; Ribeiro *et al.*, 2016).

These patterns are not unique to the Caatinga biome. Relatively similar dynamics can be observed in other rocky outcrops around the world. In the arid Nama Karoo region of Namibia, for example, soil properties on inselbergs have been shown to be closely related to the underlying geology and relief position. The weathered bedrock there provides most of the parent material for soil development (Burke, 2002). In the Southwest Australian Floristic Region, granitic outcrops act as biodiversity refuges shaped by soil depth and local topography (Clark-Ioannou *et al.*, 2021). At Enchanted Rock in Texas, USA, gnammas and adjacent soils on a granitic dome demonstrate similar interactions between microtopography, soil development, and vegetation cover (Pérez, 2023).

Our results reinforce the role of inselbergs as ecological microrefugia within the Caatinga. Their fertile soils and greater water availability provide suitable habitats for drought-sensitive species that are uncommon in surrounding semiarid landscapes (Souza *et al.*, 2025; Borges Neto *et al.*, 2025; Cordeiro *et al.*, 2025). These communities may represent relict vegetation established under wetter paleoclimatic conditions and subsequently confined to inselbergs after semiarid expansion (Werneck *et*

al., 2011; Sobral-Souza *et al.*, 2015; Souza *et al.*, 2022). Recent phylogeographic studies further support the hypothesis that these refugia contributed to historical connections between the Amazon and Atlantic forests (Bocalini *et al.*, 2023; Machado *et al.*, 2024; Pinto-junior *et al.*, 2024).

FINAL CONSIDERATIONS

The increasing contents of SOC, N, clay, exchangeable base cations, with elevation and proximity to the inselbergs indicate these peripheral positions favor the development of more fertile soils, with a greater capacity to sustain a tree layer relative to the surrounding Caatinga. The accumulation of organic residues in positions closer to inselbergs and bioturbation enhances the incorporation of the organic compounds in soil. Mineral-organic interactions and the formation of metal-organic complexes further limit soil organic matter mineralization, contributing to higher nutrient retention. Increased water availability at higher elevations reduces drought stress and consequently facilitates the establishment of drought-sensitive species, allowing inselbergs to function as ecological microrefugia relative to the surrounding Caatinga landscape. Overall, the findings of this study demonstrate that inselbergs constitute key environments for the conservation and maintenance of Caatinga biodiversity.

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SUPPLEMENTARY MATERIALS

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Bartolomeu Israel de Souza: Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, and Writing – Review & Editing; Rony Lopes Lunguinho: Data curation, Formal analysis, Investigation, Writing – original draft; Daniel Kroehling: Investigation, and Formal analysis; José João Lelis Leal de Souza: Conceptualization, Funding acquisition, Investigation, Methodology, and Writing – Review & Editing; Rubens Teixeira de Queiroz: Data curation, Formal analysis, Investigation; Joseilsom Ramos de Medeiros: Investigation, Writing – original draft; Eini Celly Morais Cardoso: Data curation, Investigation, Writing – original draft; Joel Maciel Pereira Cordeiro: Writing – review & editing; Rafael Albuquerque Xavier: Conceptualization, Methodology, Validation; Inocencio de Oliveira Borges Neto: Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing.

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