

Research article

Pedogeomorphology of a Mound-building termite savanna in Roraima, Brazilian Amazonia

Pedogeomorfologia de uma savana com murundus em Roraima, Amazônia Brasileira

Meiriane Nunes de Oliveria¹, José Frutuoso do Vale Júnior², Hugo Galvão Candido³, Agno Nonato Serrão Acioli⁴, Matheus Gonçalves Matos⁵ e Carlos Ernesto Gonçalves Reynaud Schaefer⁶

¹ Universidade Federal de Roraima, Departamento PRONAT, Boa Vista, Brasil. meirianeprofissional@gmail.com.

ORCID: <https://orcid.org/0009-0003-5497-5073>

² Universidade Federal de Roraima, Departamento de Solos e Irrigação, Boa Vista, Brasil. valejr51@gmail.com

ORCID: <https://orcid.org/0000-0003-3327-6444>

³ Universidade Federal de Viçosa, Departamento de Biologia Vegetal, Viçosa, Brasil. hugogalvaocandido@gmail.com.

ORCID: <https://orcid.org/0000-0003-1209-6292>

⁴ Universidade Federal do Amazonas, Faculdade de Ciências Agrárias, Manaus, Brasil. acioli@ufam.edu.br.

ORCID: <https://orcid.org/0000-0002-8482-0932>

⁵ Universidade Federal de Viçosa, Departamento de Biologia Vegetal, Viçosa, Brasil. matheus.g.matos@ufv.br.

ORCID: <https://orcid.org/0000-0002-4787-6814>

⁶ Universidade Federal do Rio de Janeiro, Instituto de Geociências, Rio de Janeiro, Brasil. carlosschaefer@igeo.ufrj.br.

ORCID: <https://orcid.org/0000-0001-7060-1598>

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Abstract: Termite mounds are key biogeomorphological structures in tropical drylands, yet their role in Amazonian savannas remains poorly documented. We assessed termite diversity, nesting habits, mound morphology, and soil attributes across Plinthosols and Acrisols in the Surumu Depression, northeastern Roraima, an extensive murundu field in a savanna-caatinga ecotone. Transect sampling recorded 16 species/morphospecies from eight genera and two families, with Termitidae representing most encounters. Frequent species were shared across soil classes, whereas rare species differed. Although *Amitermes excellens* was not numerically dominant in the assemblage, it was the main builder of the large conical and cathedral-shaped mounds that structure the local landscape. Mounds showed marked physical and chemical contrasts with adjacent soils, especially selective incorporation of fine particles and enrichment in bases, nitrogen, and organic matter. Mound density was higher on poorly drained Plinthosols, whereas larger and older mounds occurred on better-drained Acrisols, where erosion and vegetation succession were more advanced. These results show that *A. excellens* acts as a major pedobioturbation agent, redistributing subsurface materials, creating fertility islands, and maintaining pedogeomorphological heterogeneity in the northern Amazonian savanna. Their spatial pattern therefore records hydrogeomorphic controls, with first-order bioturbation estimates of 47.5-85.3 mm ka⁻¹ along the toposequence.

Keywords: Termite diversity, pedobioturbation, nutrient cycling, pedogenesis, landscape ecology, biogeomorphology, zoogeomorphology; hydrogeomorphology; termite mounds.

Resumo: Murundus de cupins constituem estruturas biogeomorfológicas relevantes em ambientes tropicais secos, mas seu papel nas savanas amazônicas ainda é pouco documentado. Avaliamos a diversidade de cupins, os hábitos de nidificação, a morfologia dos murundus e os atributos do solo em Plinthosols e Acrisols da Depressão do Surumu, nordeste de Roraima, extensa área de campos de murundus em ecótono savana-caatinga. A amostragem registrou 16 espécies/morfoespécies, distribuídas em oito gêneros e duas famílias, com predominância de Termitidae. As espécies frequentes foram semelhantes entre as classes de solo, enquanto as raras diferiram. Embora *Amitermes excellens* não tenha sido numericamente dominante,

foi a principal espécie construtora dos grandes murundus cônicos e em forma de catedral que estruturam a paisagem local. Os murundus apresentaram contrastes físicos e químicos em relação aos solos adjacentes, especialmente pela incorporação seletiva de partículas finas e pelo enriquecimento em bases, nitrogênio e matéria orgânica. A densidade foi maior em Plinthosols mal drenados, enquanto estruturas maiores e mais antigas ocorreram em Acrisols bem drenados, com maior erosão e sucessão vegetal. Os resultados indicam que *A. excellens* atua como importante agente de pedobioturbação, criando ilhas de fertilidade e mantendo a heterogeneidade pedogeomorfológica da savana amazônica setentrional. Também registram controles hidrogeomorfológicos toposequenciais.

Palavras-chave: Diversidade de cupins, pedobioturbação, ciclagem de nutrientes, pedogênese, ecologia de paisagem, biogeomorfologia, zoogeomorfologia; hidrogeomorfologia; campos de murundus.

1. Introduction

Termites, classified within the order Blattodea and suborder Isoptera (Krishna et al., 2013), are vital components of tropical ecosystems, occurring in rainforests, savannas, and, to a lesser extent, arid regions (Jouquet et al., 2004; Ferreira et al., 2011a). Globally, they are represented by about 295 genera and 2,937 species across nine families, including Mastotermitidae, Termitidae, and Rhinotermitidae, occupying diverse ecological niches (Krishna et al., 2013; Chouvenc et al., 2016). Climate strongly influences termite distribution, with the highest diversity in tropical and subtropical regions and a decrease toward higher latitudes (Cancello et al., 2014). As geomorphic agents, termites are ecosystem engineers that promote extensive reorganization of soils and landforms (Bétard, 2020; Schaefer and Oliveira, 2022; Viles, 2022). In this sense, termite mounds can be interpreted within the framework of zoogeomorphology, in which animals act as agents of erosion, sediment transfer, soil mixing, and landform construction (Butler, 1995; Bétard, 2021; Viles, 2022). For mound-building termites, the geomorphic effect is not restricted to the mound body itself: galleries, foraging openings, selective particle transport, and repeated cycles of mound construction and decay create microrelief, modify surface roughness, and influence runoff, infiltration, and sediment redistribution at plot and hillslope scales (Léonard and Rajot, 2001; Bétard, 2021; Viles, 2022). Thus, termite ecology and geomorphology are linked through feedback between colony activity, soil physical properties, drainage, vegetation establishment, and local erosional stability.

As detritivores, termites play crucial roles in nutrient cycling and soil formation, especially in savannas, where they affect soil and vegetation dynamics (Gosling et al., 2012). Their trophic groups, including geophagous, humivorous, xylophagous, and harvester termites, feed on soil, plant material, manure, lichens, and fungi, shaping nest composition (Arveti et al., 2012; Seymour et al., 2014; Rezende, 2012; Souza et al., 2012). Nest construction also impacts ecosystems, as termite mounds (murundus) alter soil properties, decomposition, nutrient cycling, hydrology, drainage, and microtopography. Built from organic or mineral material mixed with feces and saliva, these biogenic structures often contain more clay and organic matter than surrounding soils (Arveti et al., 2012; Mujinya et al., 2013; Peres Filho et al., 2012; Abe et al., 2012).

In the Amazon, part of the Neotropical zone, termite fauna is highly diverse, with about 553 species described, although much remains undocumented (Constantino, 1999; Carrijo et al., 2015; Chouvenc et al., 2016). Termitidae, representing 85% of Brazilian species, dominate tropical and subtropical regions (Constantino, 1999). Yet, termite ecology in Roraima is poorly studied, with little data on richness and ecological roles (Constantino and Cancello, 1992).

The pedo-biogeomorphological importance of termites has been recognized since the seminal works of Smeathman (1781) and Drummond (1888), the latter noting that tropical soils are in a state of continuous movement through the circulation of earth. Goudie (1988) and Viles (2022) highlighted the biogeomorphological role of termites in the formation and denudation of tropical landscapes. Nevertheless, little research on this topic has been conducted in Brazil, as indicated by Schaefer and Oliveira (2022), and termites are still underrepresented in textbooks and syntheses on tropical geomorphology (e.g., Thomas, 1994; Faniran and Jeje, 1983; Büdel, 1982). Tricart (1972) also emphasized this topic in tropical geomorphology, and Bétard (2020) recently reinforced the role of insects, especially termites and ants, in Earth surface processes and landforms.

Recent studies have moved this field from qualitative descriptions of termite constructions toward spatially explicit and process-based biogeomorphology. Airborne and satellite analyses showed that mound spacing, mound height, and vegetation islands may reveal hidrogeomorphic gradients and subsurface controls in savanna

catenas (Levick et al., 2010; Davies et al., 2014). Other studies demonstrated that substrate geology and local geomorphology condition mound density and architecture (Muvengwi et al., 2018), while OSL and radiocarbon approaches have quantified the time scales of termite bioturbation and mound persistence in savanna and semiarid landscapes (Kristensen et al., 2015; Freitas et al., 2021). These advances provide the conceptual basis for interpreting murundus as biogenic landforms and not only as ecological nesting structures.

Northeastern Roraima contains the most extensive planation surface associated with prominent mound-building termites in the upper Rio Branco pediplain: the Surumu Depression (Schaefer, 1994; Schaefer and Dalrymple, 1996) (Figure 1). There, two mound morphologies are commonly observed: cone-shaped mounds, with height/width ratios typically >3 and a protruding peak above a strong conical base; and cathedral-shaped mounds, with complex forms, thin walls, buttresses, and multiple peaks.

Geomorphologically, the Surumu Depression is a low-relief, pediplanated compartment of the upper Rio Branco region, developed over volcanic and volcano-sedimentary materials and punctuated by residual inselbergs and gently dissected drainage axes (Schaefer, 1994; Schaefer and Dalrymple, 1996; Vale Júnior and Schaefer, 2010). Within this surface, small differences in relative elevation and drainage separate semi-hydromorphic Plinthosols from better-drained Acrisols, forming a hydropedological catena in which mound density, mound size, erosion, and vegetation succession vary systematically. The mound field therefore represents a suitable natural system for testing how termite activity interacts with pediplanation surfaces, lateral drainage, soil textural differentiation, and the maintenance of biogenic microrelief.

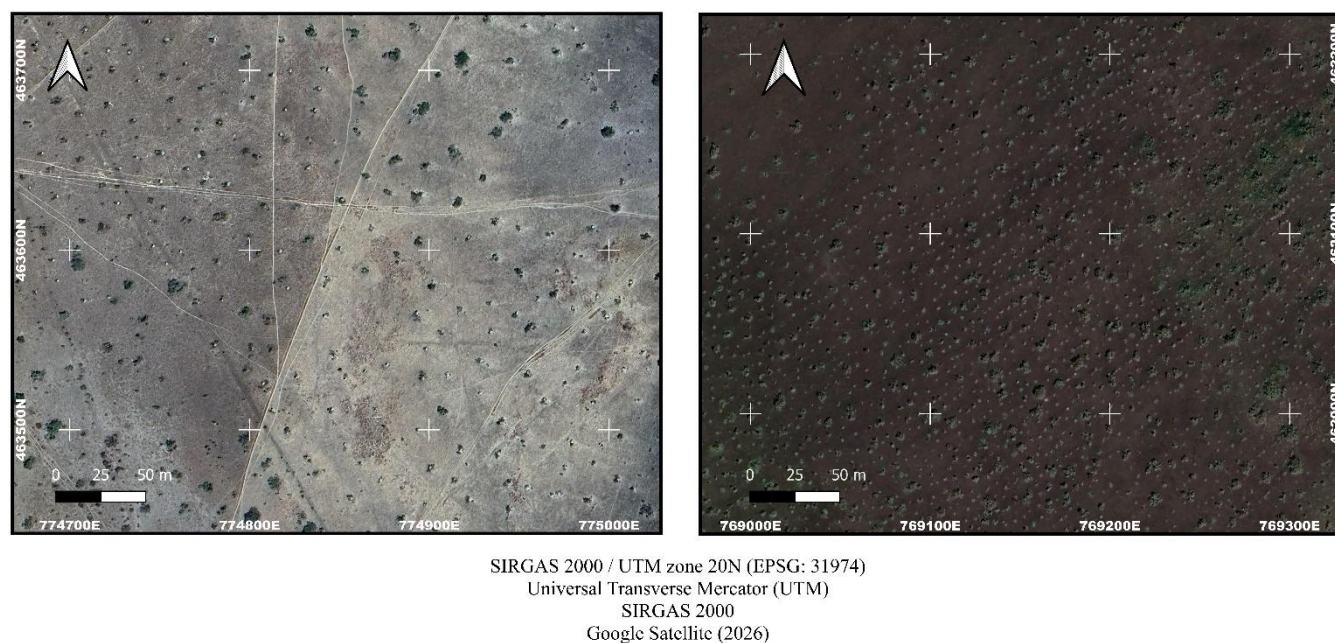


Figure 1. Satellite images adjacent the studied sites (Fig. 2), at the Surumu Depression showing mound-building termite structures (conical and cathedral-shaped) on a pediplanated surface, with contrasting stages of mound age and vegetation development: A) well-drained Acrisol (sites 1 and 2); B) hydromorphic Plinthosol (sites 3 and 4).

This study addresses this gap by analyzing termite diversity and termite influence on soil properties and landforms in the dry savannas of the Surumu Depression, Roraima. By estimating diversity and abundance, identifying functional groups, and evaluating mound and soil attributes, we aimed to clarify termite-soil-landform interactions and their ecological significance in this unique Amazonian dry environment.

Specifically, we asked whether the distribution and morphology of *A. excellens* mounds record hydropedological and geomorphological contrasts between Plinthosols and Acrisols, and whether mound volume can be translated into first-order estimates of soil reworking comparable with zoogeomorphological studies. By explicitly linking termite assemblages, mound morphometry, soil properties, drainage, and catena position, the study contributes to the geomorphological interpretation of murundu landscapes in the northern Amazonian savanna.

2. Study Area

The research was conducted in the Surumu plain, northeastern Roraima (4.186, -60.5335), within a dry savanna characterized by Na-affected soils and Plinthosols (Vale Júnior and Schaefer, 2010) (Figure 2). The landscape consists of a pediplanated surface with inselbergs (200–600 m altitude), where Na-affected soils show stone pavements over acid-volcanic saprolite (andesites, dacites, rhyolites), forming dryland, desert-like conditions (Schaefer and Dalrymple, 1996). Vegetation belongs to a Cerrado-caatinga ecotonal formation, with cacti, sucupira-do-campo (*Bowdichia vigilioides*), pau-rainha (*Centrolobium paraense*), and aroeira (*Astronium ulei*), species adapted to semi-arid climates. Termite mounds occur mainly in semi-hydromorphic soils, especially Plinthosols, across the landscape (Schaefer, 1997; Schaefer and Vale Júnior, 1997; Vale Júnior and Schaefer, 2010).

The studied plots occupy a gently undulating pediplanated surface in which local relief contrasts are small but geomorphologically important. The lower and intermediate positions are seasonally wetter and favor plinthic horizons, mottling, and surface hydromorphism, whereas slightly higher positions have better drainage, stronger textural differentiation, and deeper Acrisol profiles. Field observations and satellite images indicate that mound fields are concentrated on these transitional surfaces rather than on steep slopes, suggesting that mound establishment is controlled by a balance between seasonal waterlogging, surface stability, and access to subsurface fine material. Consequently, the Plinthosol-Acrisol contrast is treated here as a pedogeomorphological gradient, not only as a taxonomic soil contrast.

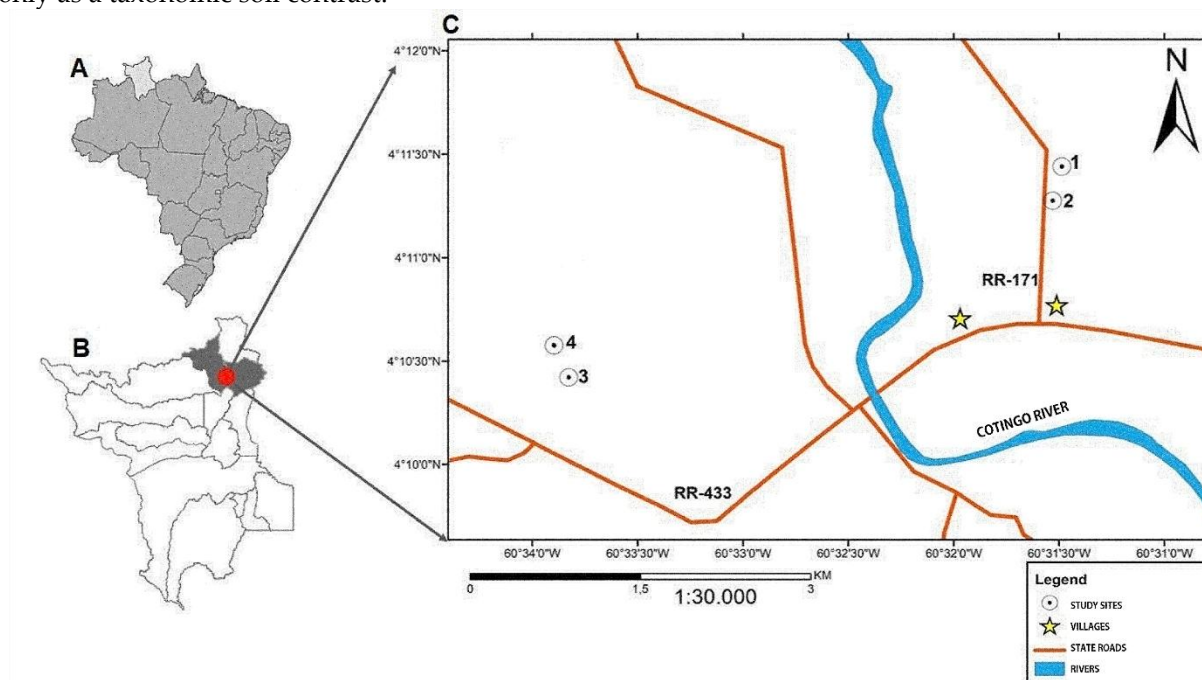


Figure 2. Location map of the study area with the main soil classes in the Surumu Formation, between the municipalities of Normandia and Pacaraima, northeastern Roraima. A) Brazil and Roraima; B) Roraima and the location of the Surumu plains in Pacaraima and Normandia; C) Location of sites 1 to 4, near the RR 433 and RR 171 roads (Coordination System: WGS 1998 Web Mercator Auxiliary Sphere, Datum: WGS 1984).

3. Materiais e Métodos

3.1. Termites and Soil Sampling

Termites were collected during September–October 2017 using a modified Biodiversity Rapid Assessment protocol (Jones and Eggleton, 2000). Transects (100 × 2 m) were established in 1-ha plots, divided into 20 sections (5 × 2 m). Each section was inspected for grass microhabitats, epigeal termites, nests, and shrubs. Twelve topsoil samples (12 × 12 cm, 15 cm depth) were collected for termite exploration (Jones and Eggleton, 2000). Soldiers, workers, and fertile specimens were preserved in 70% alcohol (Constantino, 2016), with multiple individuals from the same plot stored as a single sample (Bignell et al., 2012).

3.2. Soil Morphological Characterization

The Surumu depression plain hosts Natric Planosols, Acrisols, Argiluvic Plinthosols, Gleysols, Luvisols, and Leptosols. Natric Planosols, with hardened Btn horizons, result from dispersible clays, hydromorphism, and Na, leading to waterlogging and clayey textures; they are endoeutrophic with high Na and Mg, and show columnar or prismatic peds (Schaefer et al., 1993).

Sites 1 and 2 contain dystrophic Haplic Plinthosols, derived from dacite/rhyodacites, with eroded A horizons and mottling below 90 cm, classified as dystrophic Tb Haplic Plinthosols in the Brazilian Soil Classification System and corresponding to Plinthosols in the WRB (Figure 3A) (EMBRAPA, 2025; IUSS Working Group WRB, 2022). Sites 3 and 4 host dystrophic Yellow Acrisols, developed from pre-weathered saprolite, with A, E, and Bt horizons to 90 cm and moderately deep, drained profiles (Figure 3B) (EMBRAPA, 2025; IUSS Working Group WRB, 2022). These two soil groups also represent different positions and evolutionary stages within the local catena. The Plinthosols at sites 1 and 2 occur on lower to intermediate, imperfectly drained surfaces where seasonal saturation and plinthite formation constrain vertical drainage. The Acrisols at sites 3 and 4 occupy slightly higher, better-drained surfaces where eluviation-illuviation processes, deeper Bt development, and more advanced erosion of older mound surfaces are more evident. This spatial arrangement provides the basis for interpreting mound density and morphology as responses to hydropedological position along the pediplanated landscape.

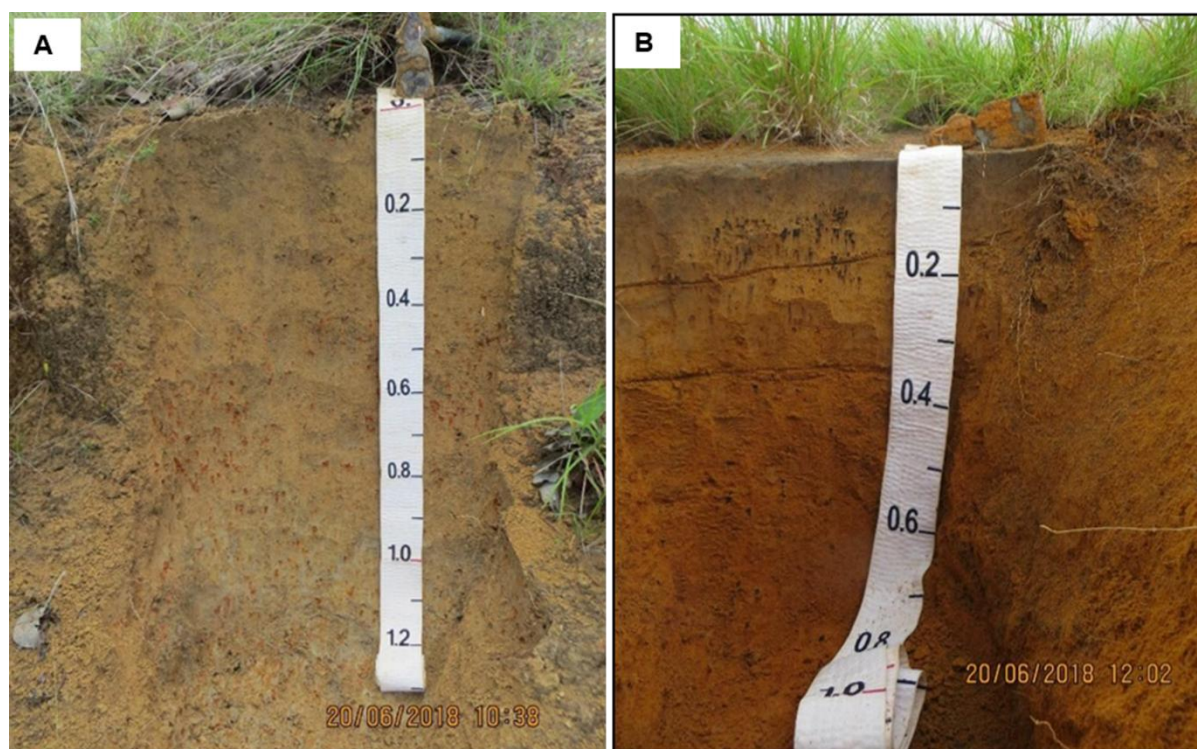


Figure 3. Soil profiles in the studied sites. A) Dystrophic Haplic Plinthosols at sites 1 and 2 (Plintossolo Háplico Tb distrófico in the Brazilian Soil Classification System); B) dystrophic Yellow Acrisol at sites 3 and 4 (Argissolo Amarelo in the Brazilian Soil Classification System).

3.3. Termites Nesting Patterns and Diversity Assessment

Nesting patterns were classified as epigeal, hypogaeal, arboreal, intermediate, or diffuse (Constantino, 1999; Ferreira et al., 2011a; Krishna et al., 2013). Termites were grouped into humivorous, xylophages, reapers, or intermediaries (Donovan et al., 2001; Rezende, 2012; Souza et al., 2012). Twelve active mounds per site were measured (height, circumference; Vasconcellos et al., 2010). Samples from base, center, and top of each mound were collected in triplicate (Sarcinelli et al., 2008). Control soils were taken at 0–10, 10–20, and 20–30 cm depth, 5 m from mounds, also in triplicate (Seymour et al., 2014; Jouquet et al., 2016).

Soil analyses followed EMBRAPA (2025), determining pH, K, P, Na, Ca²⁺, Mg²⁺, Al³⁺, potential acidity (H⁺ + Al³⁺), total N, and organic matter. Mound density and volume were calculated according to the formulae

reported by Sarcinelli et al. (2009), compared between soil classes using paired t-tests, and related to soil attributes by linear regression (Jouquet et al., 2016).

Geomorphological interpretation combined field pedological descriptions, mound morphometry, mound density, satellite-image interpretation, and the relative position of the four sites along the Plinthosol-Acrisol toposequence. Because the original field campaign did not include differential GPS surveys, detailed DEM-derived slope values, or mound-to-channel distances for each mound, the present revision uses conservative, site-level geomorphological interpretations rather than point-scale morphometric modelling. To respond to the need for quantitative zoogeomorphological metrics, standing mound volume ($m^3 ha^{-1}$) was converted into first-order soil-reworking estimates by assuming a mean mound life of 30 years, as already adopted in Table 5. The annual volumetric flux was estimated as $Q_v = V/L$, where V is standing mound volume per hectare and L is mound life span. Vertical-equivalent reworking rates were then calculated by dividing Q_v by $10,000 m^2 ha^{-1}$ and converting to $mm ka^{-1}$. These estimates are not direct denudation rates; they represent the potential volume of subsurface material returned to the surface by mound construction and should be interpreted as minimum comparative indices of termite bioturbation (Bétard, 2021; Kristensen et al., 2015).

The species dominance was calculated for each transect, and for the total area, based on Silveira Neto et al. (1976), using the following formula:

$$Dominance = i / t \times 100 \quad (1)$$

i = total number of nests/species

t = total nest

A dominance $> 10\%$ indicated an Eudominant species. Dominant species showed values from 5 to 10%, and the Subdominant between 2 to 5%. Recessive species were considered between 1 to 2%. Finally, a $D < 1\%$ was classified as rare species (Núñez et al., 2011).

We also calculated the Shannon Wiener diversity index (H') and Simpson (D) for the four transects (Bignell et al., 2012).

3.4. Statistical Analysis

To compare chemical and physical attributes, treating termite mounds, surface soil samples, and soil classes as sample units, a Principal Components Analysis (PCA) was applied. This analysis aimed to reduce dimensionality for a more compact representation and order the most relevant information (Hongyu et al., 2016). A F test (ANOVA) for replicates was conducted for the first principal component (PC1) and second main component (PC2), using the mound as a random factor. A Tukey post-test was further applied to test differences between mound sections and adjacent soil.

For physical and chemical variables showing significant differences in the PCA results, a relative increase (RI) was calculated using the formula:

$$RI = (\text{soil concentration}) / (\text{mound concentration} - \text{soil concentration}) \quad (2)$$

After calculating the RI, a simple linear regression was applied between RI and chemical/physical variables in different soil classes to investigate the relationship between them (Faria, 2012). All statistical analyses were performed using the R 4.0.0 Program (R Development Core Team, 2020), adopting a level of statistical significance of $P \leq 0.05$.

4. Resultados

4.1. Termitofauna Composition

The investigation of termitofauna across the four transects (66 samples) revealed a diverse assemblage comprising 16 species and morphospecies, distributed among 8 genera and two families. The family Termitidae dominated, constituting 94.12% of the total abundance, and included three subfamilies: Apicotermitinae (7 species), Nasutitermitinae (5 species), and Termitinae (3 species). The family Rhinotermitidae was represented by a single species (*Heterotermes* sp. A) accounting for 5.88% of the total abundance (Table 1). *Anoplotermes* emerged

as the most abundant genus, housing 5 species, with *Anoplotermes* sp. A, *Anoplotermes* sp. D, and *Nasutitermes* sp. A ranking as the most abundant species.

Table 1. Termite Richness and index of diversity at the four transects.

Species	Transect 1	Transect 2	Transect 3	Transect 4	Total of encounters
Family Rhinotermitidae					
<i>Heterotermes</i> sp.A	0	0	0	1	1
Family Termitidae					
Subfamily Apicitermitinae					
<i>Anoplotermes</i> spA	53	10	17	42	122
<i>Anoplotermes</i> spB	9	7	2	9	27
<i>Anoplotermes</i> spC	5	7	4	12	28
<i>Anoplotermes</i> spD	24	57	9	22	112
<i>Anoplotermes</i> spE	20	47	13	1	81
<i>Grigiotermes</i> spA	3	0	0	0	3
<i>Rupititermes franciscoi</i> (Snyder, 1946)	17	24	6	10	57
Subfamily Nasutitermitinae					
<i>Cortaritermes intermedius</i> (Banks, 1919)	25	13	18	9	65
<i>Nasutitermes</i> spA	25	17	54	34	130
<i>Nasutitermes</i> spB	5	4	9	8	26
<i>Nasutitermes</i> spC	1	0	1	2	4
<i>Velocitermes</i> spA	0	0	1	0	1
Subfamily Termitinae					
<i>Amitermes excellens</i> (Silvestre, 1923)	3	1	0	5	9
<i>Termes</i> spA	0	0	1	0	1
<i>Termes</i> spB	0	0	0	1	1
Sample (total)	190	187	135	156	668
Species (total)	12	11	12	13	-
Shannon div. ind. (H')	2.1	1.9	1.75	2.02	-
Simpson div. Ind. (D)	0.84	0.81	0.78	0.84	-

The species accumulation curve indicated sufficient sampling effort for both soils. Transects 1 and 2 (Plinthosol) showed a stabilization trend around section 12, while transects 3 and 4 (Acrisol) displayed no further

species increase after section 23 (Figure 4). This stabilization contrasts with the expectation of continual diversity increase suggested by Carrijo et al. (2009).

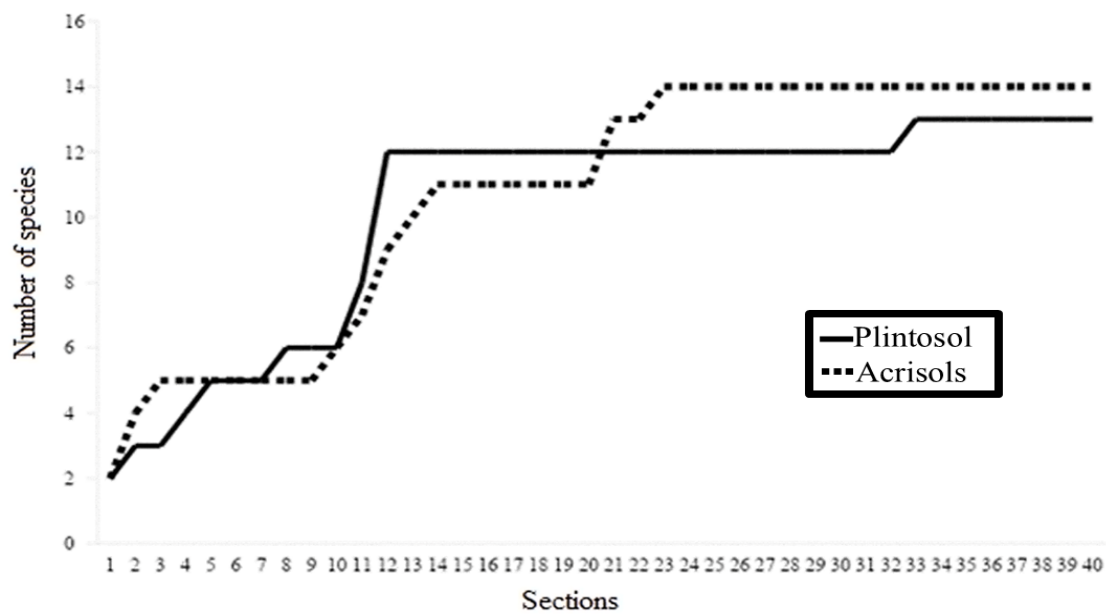


Figure 4. Species accumulation curve for the two soil classes sampled across the four transects.

Species occurrence patterns demonstrated that 56.24% of species were common across all transects, while 43.75% were rare, with fewer than 4 samples. Dominant species constituted 66.62% of the total abundance, with two species at 18.26%, three species as subdominant (12.12%), one as recessive (1.35%), and six as rare (1.80%) (Table 2). Eudominant species were also the most abundant.

Table 2. Termite dominance in the 4 transects.

Species	Trans. 1 (%)	Trans. 2 (%)	Trans. 3 (%)	Trans. 4 (%)	% total	Dominance
Nasutitermes sp A	19.23	12.31	41.54	26.15	19.46	
Anoplotermes sp D	21.43	50.89	8.04	19.64	18.26	Eudominant
Anoplotermes sp E	24.69	58.02	16.05	1.23	16.77	(66.62%)
Anoplotermes sp A	43.44	8.20	13.93	34.43	12.13	
Cortaritermes intermedius	38.46	20	27.69	13.85	9.73	Dominant
Rupititermes franciscoi	29.82	42.11	10.53	17.54	8.53	(18.26%)
Anoplotermes sp C	17.86	25.00	14.29	42.86	4.19	Subdomina
Anoplotermes sp B	33.33	25.93	7.41	33.33	4.04	nt
Nasutitermes sp B	19.23	15.38	34.62	30.77	3.89	(12.12%)
Amitermes excellens	33.33	11.11	0	55.56	1.35	Recessive (1.35%)
Nasutitermes sp C	25	0	25	50	0.60	
Grigiotermes sp A	100	0	0	0	0.45	Rare
Heteroterme sp A	0	0	0	100	0.15	(1.80%)

<i>Termes</i> sp A	0	100	0	0	0.15
<i>Termes</i> sp B	0	0	100	0	0.15
<i>Velocitermes</i> sp A	0	0	100	0	0.15

Several rare species, including *Grigiotermes* sp. A, *Heterotermes* sp. A, *Termes* sp. A, *Termes* sp. B, and *Velocitermes* sp. A, were recorded with few or single encounters. Although *Amitermes excellens* is not among the most abundant taxa in the transect samples and was classified as recessive in the dominance analysis, its large epigeal mounds make it a disproportionally important species for landscape structure and pedobioturbation.

No significant differences were observed in the termitofauna composition among eudominant, dominant, and subdominant species between the two soils. However, in the rare species category, Plinthosol showed 3 species, and Acrisol showed 4 species, with *Nasutitermes* sp. C being a common species in both. Plinthosol exhibited a higher total termite abundance, with 377 samples (56.44%), compared to Acrisol with 291 samples (43.56%).

4.2. Diversity Indices

The Shannon-Wiener diversity index (H') revealed greater diversity of epigeal termitofauna in transect 1 ($H' = 2.10$), followed by transects 4 ($H' = 2.02$), 2 ($H' = 1.90$), and 3 ($H' = 1.75$) (Table 1). The index's sensitivity to rare species indicated a higher percentage of rare species in transect 3, followed by transects 2, 4, and 1.

The Simpson index or species dominance (D) showcased greater diversity of epigeal termitofauna in transect 3 ($D = 0.78$), followed by transects 2 ($D = 0.81$), and equal values for transects 1 and 4 ($D = 0.84$). The index captured abundance variation, emphasizing the stabilization of sampling across the four transects, with less weight assigned to rare species.

4.3. Nesting Patterns

The nesting pattern in the study area revealed six species building diffuse nests in the soil (40%), six species building hypogeous nests (40%), and three species constructing epigeal nests (20%). Arboreal nests were absent in the transects, and *Grigiotermes* sp. A was identified as an inquiline of *A. excellens* mounds. *A. excellens*, *Cortaritermes intermedius*, and *Nasutitermes* sp. A were the main species constructing epigeal nests, characterized by small (15 to 25 cm), grayish mounds (Figure 5C and D; Supplementary material 1).

A. excellens mounds played a significant role in reshaping the study area, reaching heights of up to 4 m in the savanna environment. The conical or complex cathedral mounds, with hard consistency and gray colors, displayed phenotypic plasticity according to environmental conditions. The architecture, particularly the conical shape of *A. excellens* nests, acts as a strategy against natural erosion caused by wind and rain (Figure 5A). The species also exhibits phenotypic plasticity, favoring epigeal nest construction in open savannas, in contrast to forest environments (Figure 5B).

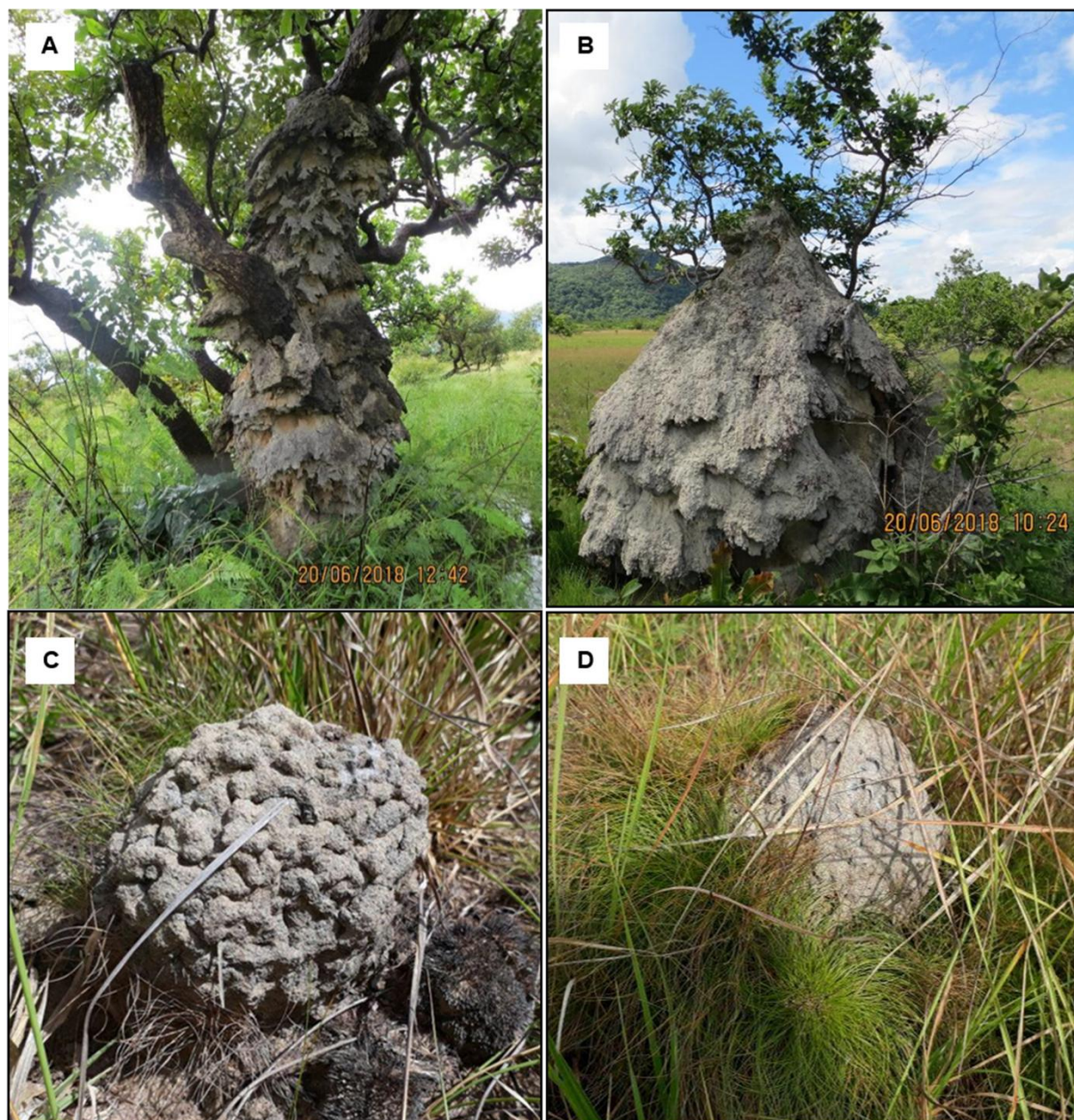


Figure 5. A) Arboreal nests of *Amitermes excellens* in a Caimbé tree on a Natric Planosol; B) epigeal nest of *Amitermes excellens* in a Haplic Plinthosol, with shrubs and trees on the mound top; C) epigeal nest of *Cortaritermes intermedius*; D) epigeal nest of *Nasutitermes* sp. A.

4.4. Feeding Habits

Termites exhibited four *trophic* groups, with humivorous being the most common (6 species or 37.5% of the total), followed by xylophagous (5 species, 31.25%), intermediate (3 species, 18.75%), and harvesters (2 species, 12.5%) (Table 1). Nest-building was closely related to trophic groups, with epigeal mounds predominantly constructed by xylophagous or intermediate species (Bourguignon et al., 2015).

4.5. Soil Attributes

The Principal Component Analysis (PCA) elucidated 70% of the variation based on 22 physicochemical variables in the first two components. PC1, explaining 59.93% of the variation, indicated strong positive correlations for P, K, N, Na, Ca^{2+} , Mg^{2+} , H⁺, Al, SB, t, T, V, ISNA, MO, and Prem. Negative correlations were

observed for pH, Al³⁺, m, coarse sand, fine sand, and soil density. PC2 captured variation in physical attributes, such as coarse sand, fine sand, silt, and clay (Table 3).

Table 3. Score values for the physico-chemical variables in mounds and soils at the PC1 and PC2.

Variables	Score Values		Variables	Score Values	
	PC1	PC2		PC1	PC2
pH	-0.08366571	0.07236063	T	0.26646913	-0.08026420
P	0.23414359	-0.01999062	V	0.23037824	0.29726071
K	0.26025751	0.04036531	M	-0.23734417	-0.21513837
N	0.24163206	-0.10197946	ISNa	0.21876624	0.10444109
Na	0.20577679	0.10589565	MO	0.24419871	-0.15818571
Ca²⁺	0.24882411	0.11463004	Prem	0.24419871	0.06743143
Mg²⁺	0.24684616	0.12059319	Coarse sand	-0.04170014	0.06658522
Al³⁺	-0.1583479	-0.37872683	Fine sand	-0.12225967	0.42035965
H+Al	0.23026678	-0.22302914	Silt	0.16996493	-0.35713302
SB	0.25988257	0.10586790	Clay	0.06513837	-0.42370177
T	0.24781022	0.03497137	Density	-0.23193359	0.26088314

Tukey post-test results showed no significant differences in physical-chemical variables between termite mound segments in axes 1 and 2 of the PCA. However, differences were observed between mounds and adjacent soils. The graphical representation of the second axis revealed greater physical variation between soil classes, which also affected mound samples. Mound walls exhibited higher nutrient concentrations, as discussed further (Figure 6).

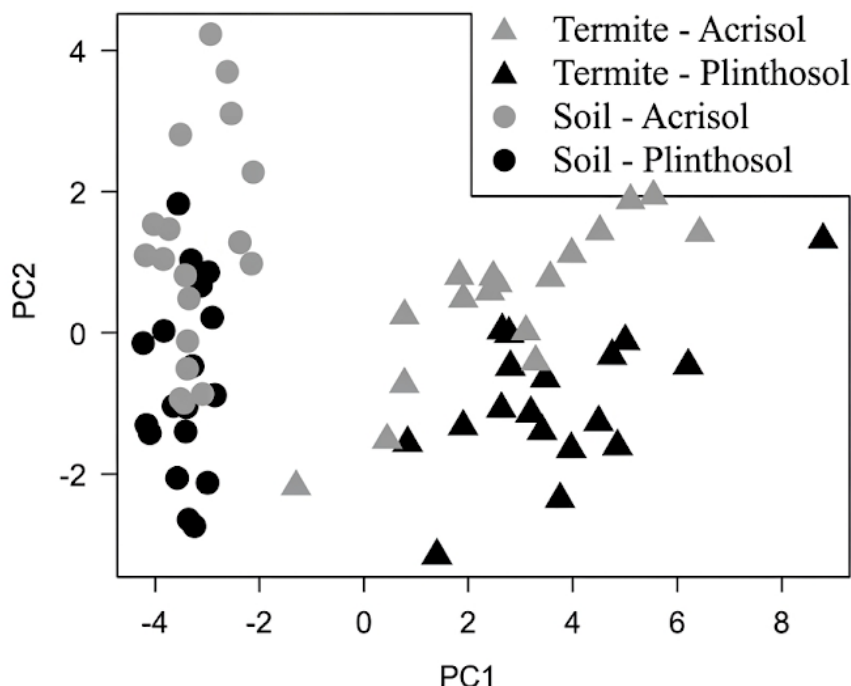


Figure 6. PCA ordination of physical and chemical attributes in termite mounds and adjacent soils according to soil class. Triangles represent mound samples and circles represent adjacent soil samples; gray symbols represent Acrisols and black symbols represent Plinthosols.

Nutrient concentrations in termite mounds across all sections (top, middle, and bottom) were much higher than in control soils, with no significant differences between the three geomorphic sections (Figure 7). However, a significant difference in PC1 was noted between termite mound sections and the three depths of control soils. Higher score values indicated greater differences between mound and soil. Scores up to the first half represented soil contents (1-3), while the second half illustrated mound contents (4-6).

Pedogenetically, the selective incorporation of fine particles into mound material links bioturbation to argilluviation and subsurface horizon development. By moving clay-rich and base-enriched material upward, termites partially reverse the downward redistribution of fines, exposing subsurface materials to biological cycling and surface erosion. On Plinthosols, this upward transport interacts with seasonal redox dynamics and impeded drainage; on Acrisols, it interacts with eluviation-illuviation and the progressive development of Bt horizons. Therefore, termite activity contributes to a lateral pedogeomorphological mosaic in which soil horization, microrelief, fertility islands, and erosional susceptibility are co-produced over repeated mound cycles.

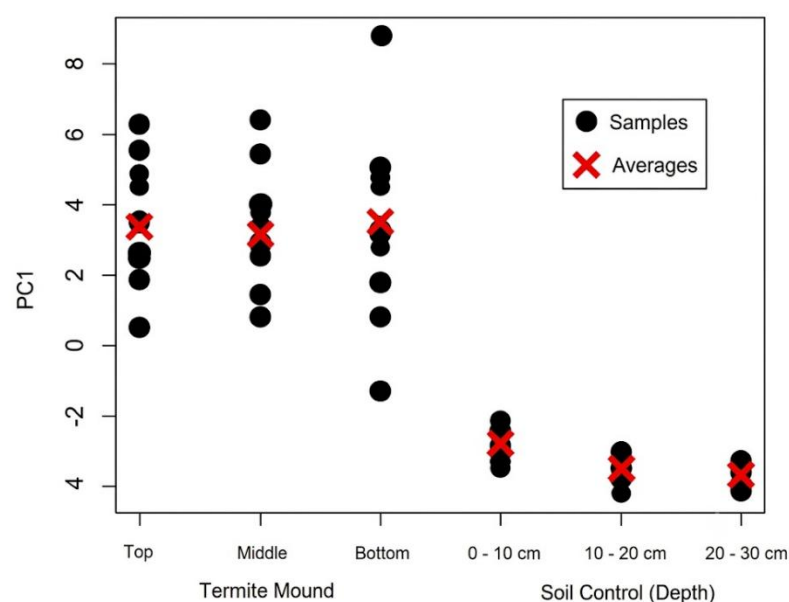


Figure 7. Result of scores of the First axe of the PCA for physical-chemical variables as a function of different.

4.6. Linear Regression Analysis Between Soil Attributes

Although Mg^{2+} , P, pH, and Al^{3+} showed higher levels in termite mounds, significant linear regressions between the Relative Increment (RI) and soil contents were not observed. However, simple linear regression for the RI of mound content in relation to soil contents was significant for potassium ($R^2 = 76\%$, $P < 0.001$), calcium ($R^2 = 78\%$, $P < 0.001$), and total nitrogen ($R^2 = 48\%$, $P < 0.001$). These results indicated that higher RI corresponded to lower concentration in control soil, signifying a strong negative correlation. Enrichment of termite mounds by cations (Ca^{2+} and Mg^{2+}) resulted in higher sum of bases values ($R^2 = 53\%$, $P < 0.001$). The linear regression for the RI of effective cation exchange capacity ($R^2 = 26\%$, $P < 0.001$) showed a low but significant value. The linear regression of the RI of organic matter ($R^2 = 44\%$, $P < 0.001$) displayed negative correlations, albeit with a low R^2 value (Figure 8).

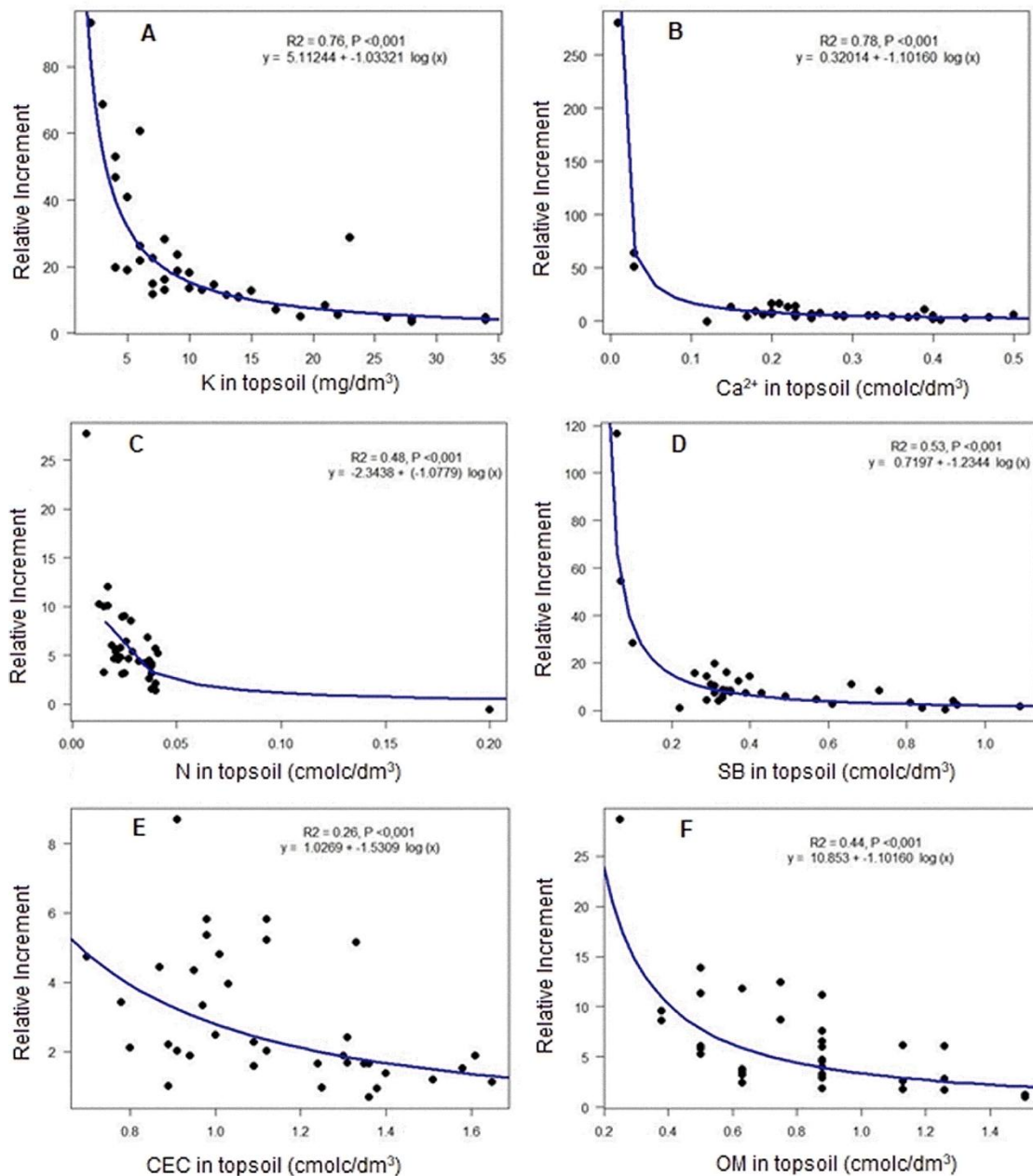


Figure 8. Simple linear regression between RI (%) of chemical attributes in mounds and soils. A) K; B) Ca; C) N; D) sum of bases; E) CEC; F) organic matter.

Contrary to findings by Sarcinelli et al. (2009) and Faria (2012), who studied soils with greater dystrophy and different phytophysionomies, we found no significant concentration of some nutrients (P, K, Ca²⁺, and Mg²⁺) and organic matter by epigeal termites when compared with adjacent soils. This discrepancy highlights the influence of specific environmental and pedological conditions on termite-mediated soil modifications.

In addition, regressions between clay and silt contents and relative increment for both soils indicated that basal mound sections had a decreasing trend with higher silt and clay, whereas mound tops showed the opposite pattern (Figure 9).

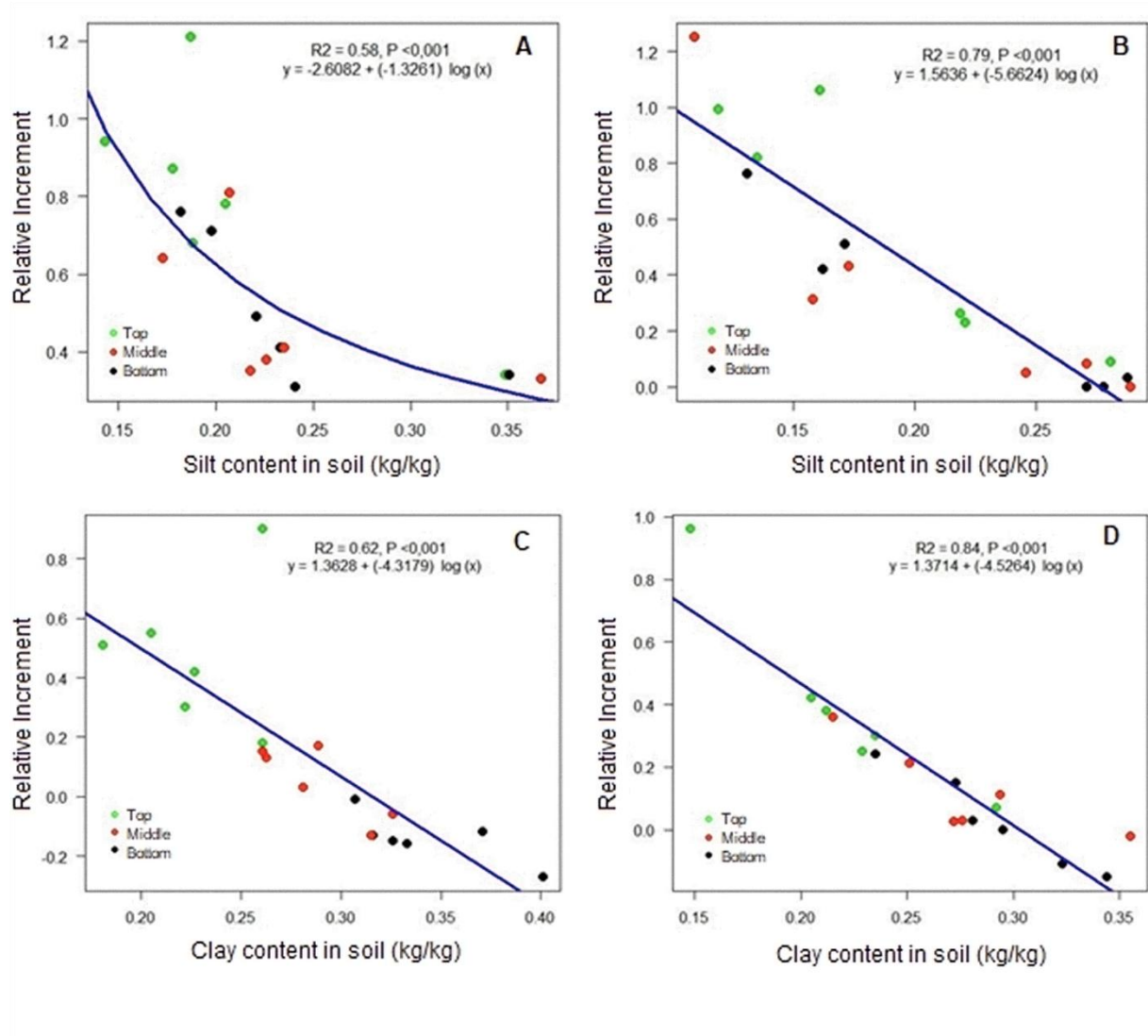


Figure 9. Simple linear regression between RI (%) of physical attributes in mounds and soils. A) Silt contents in Plinthosol; B) silt contents in Acrisol; C) clay contents in Plinthosol; D) clay contents in Acrisol.

4.7. Pedological Attributes and Termite Density

Dominant soils in the studied region included Natric Planosol, Haplic Plinthosol, Yellow Acrisols, and Yellow Ferralsols, with other inclusions (Figure 10). The sampling procedure distinctly revealed landscapes with abundant termite mounds, featuring varying mound density of *A. excellens* (Table 5). In the ill-drained Haplic Plinthosol, mean mound density averaged 40 mounds ha⁻¹, while in Acrisol it was 13.5 mounds ha⁻¹, indicating significant differences in mound density between the two soil types, with different drainage conditions ($t = -23.702; P < 0.001$).

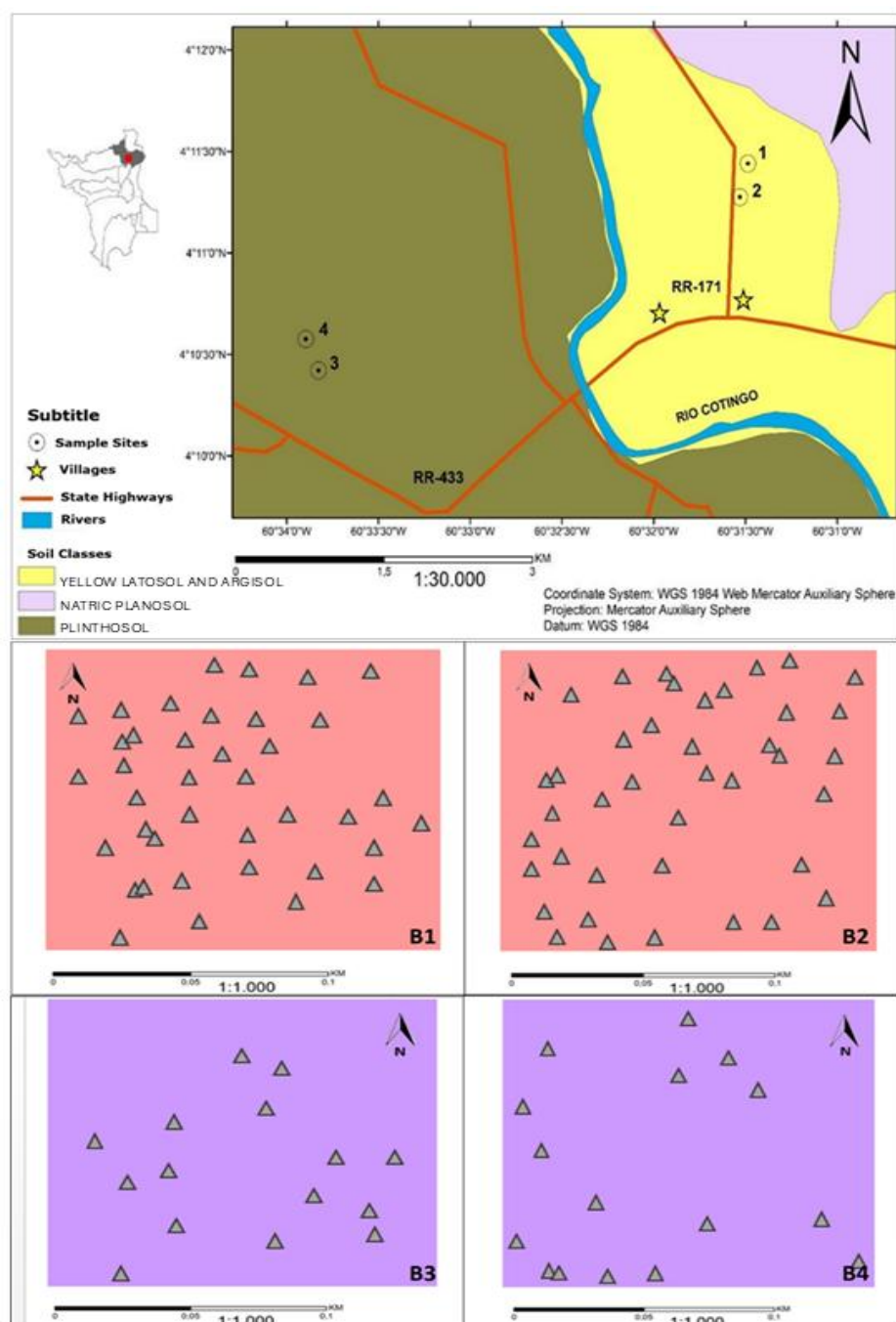


Figure 10. A - Main soils at the studied áreas; B.1 and B.2 - Mounds distribution in the Haplic Plinthosol at sites 1 and 2 respectively; B.3 and B.4 - Mounds distribution in the Red-Yellow Argisols at sites 3 and 4 respectively.

Table 5. Estimates of density and volume of mounds for different soils.

Soil	Density (ha ⁻¹)	Volume (m ³ ha ⁻¹)	Average soil volume (m ³ ha ⁻¹) ^{1/}	Soil layer (cm) ^{2/}
Plinthosol (Site 1)	39	12	0.31	15.61
Plinthosol (Site 2)	41	16.5	0.40	22.56
Average	40	14.25	0.35	18.89
Sites 1 and 2				
Acrisol (Site 3)	13	28.3	2.17	12.25
Acrisol (Site 4)	14	22.9	1.63	10.68
Average	13.5	25.6	1.89	11.46
Sites 3 and 4				

^{1/} Average termite mound soil volume, estimated by volume divided by density; ^{2/} soil layer that returns to the surface in a period of 10,000 years, considering an average life of 30 years for termite mounds.

At the intermediate land surface, 1.5-2.0 m above the lower plain, the highest mound density was observed, representing the highest pedobioturbation activity in Plinthosol without sodicity. The higher flat surface, with better drainage, featured Acrisols with decayed and less frequent mounds, accompanied by greater erosion and redistribution of mound materials (Figure 11), as well as greater vegetation succession on mounds.

This contrast indicates two complementary geomorphic patterns. On Plinthosols, the higher density of smaller mounds suggests more frequent colony establishment on seasonally wet, relatively stable surfaces where epigeal construction may help colonies escape waterlogging. On Acrisols, the lower density but greater mound height and volume suggest longer persistence of individual structures, more advanced surface erosion around mound flanks, and greater vegetation succession on older biogenic landforms. Thus, drainage and relative catena position appear to regulate not only where mounds are built, but also their life cycle, erosional exposure, and contribution to microtopographic roughness.

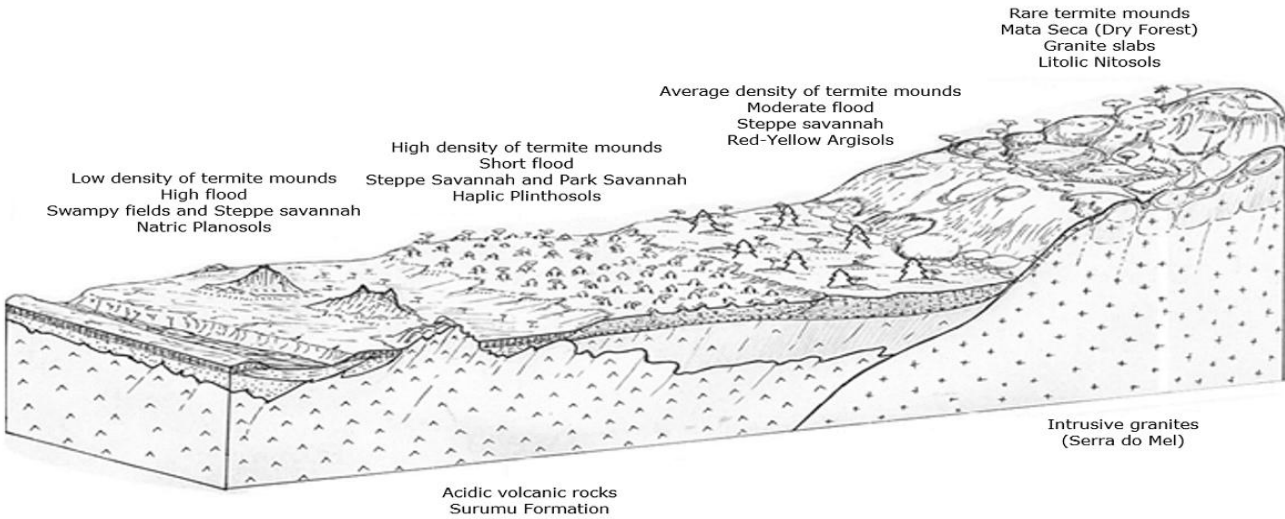


Figure 11. Schematic diagram illustrating the mounds of *A. excellens* in the studied area, NE Roraima. This is a conceptual illustration based on field observations and does not represent a real topographic profile or DEM-derived erosion indicators. Drawing by C. Schaefer.

The height of termite mounds of *A. excellens* differed significantly between soil classes, with mean height of 2.08 m in Acrisols and 1.57 m in Plinthosols ($t = 5.0822$, $P < 0.001$). Mean mound volume in Acrisols was $25.48 \text{ m}^3 \text{ ha}^{-1}$, while Plinthosols showed $14.31 \text{ m}^3 \text{ ha}^{-1}$ ($t = 6.6005$, $df = 105$, $P < 0.001$), as depicted in Figure 12. This is likely related to younger termite mounds on Plinthosols and greater maturity and erosional redistribution with advancing mound age in Acrisols. The recent alluvial plain has very few termite mounds, with smaller sizes and extensive inundation and erosion.

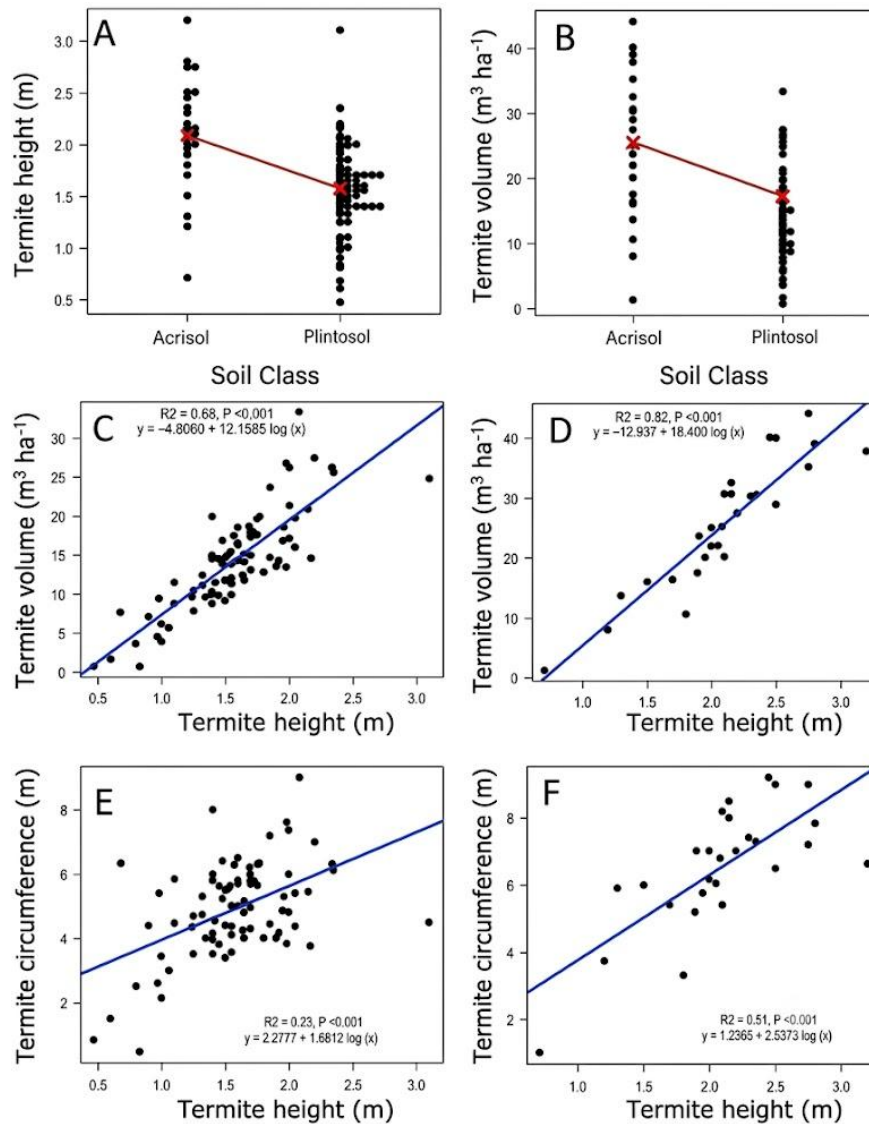


Figure 12. Averages and graphical representations: A) mound height in the studied soils; B) mound volume in the studied soils; C and D) simple linear regression between mound volume and height in Haplic Plinthosol and Yellow Acrisol, respectively; E and F) simple linear regression between mound circumference and height in Haplic Plinthosol and Yellow Acrisol, respectively.

Using the standing-volume approach, the mean mound volume reported for Plinthosols ($14.25 \text{ m}^3 \text{ ha}^{-1}$) corresponds to an estimated soil-reworking flux of $0.48 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$, equivalent to 47.5 mm ka^{-1} when expressed as a vertical layer over one hectare. For Acrisols, the larger mean standing volume ($25.6 \text{ m}^3 \text{ ha}^{-1}$) corresponds to $0.85 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$, or 85.3 mm ka^{-1} . These figures are first-order bioturbation indices derived from standing mound volume and an assumed mean mound life, not directly observed transport or denudation rates. They show that Plinthosols concentrate more mound-building events per unit area, whereas Acrisols stores and recycle more mound material in fewer, larger, and apparently older structures. The conservative soil-layer values already shown in Table 5, 18.89 cm for Plinthosols and 11.46 cm for Acrisols over 10,000 years, correspond to 18.9 and 11.5 mm

ka-1, respectively, and highlight the sensitivity of long-term estimates to assumptions about mound life span, mound abandonment, erosion, and reoccupation.

Similar conical mounds have been reported by Funch (2014) in dystrophic Acrisols of *Syntermes dirus* from Bahia, characterized by large biogenic structures (9 meters in diameter at ground level and 2 to 4 meters high) with mean volumes of 24 m³ ha⁻¹. Both areas of high mound density are situated in a transitional semi-arid zone, exhibiting convergent environmental conditions with the Surumu Depression, in terms of vegetation and climate.

5. Discussion

Generally, the Shannon-Wiener (H') and Simpson (D) indices exhibit remarkable similarity across the four transects and two soil types, suggesting minimal variations in termite diversity between the soils. Contrary to expectations, differences in diversity are more pronounced when comparing distinct phytophysiognomies, landscapes, or areas with varying degrees of degradation and preservation.

The infrequent presence of the Rhinotermitidae family aligns with expectations due to its primarily subterranean nature. Conversely, the higher occurrence of the Termitidae family is consistent with its status as the most diverse termite family in Brazil, distributed widely in tropical and subtropical regions (Constantino, 1999; Bourguignon et al., 2011; Rezende, 2012; Azevedo et al., 2013). The elusive Kalotermitidae family, with nests concealed in dry and hard wood, proves challenging to detect in soil, emphasizing the need for more comprehensive investigations (Constantino and Cancelllo, 1992; Donovan et al., 2001; Viana-Júnior et al., 2014).

This study on epigeal termitofauna in Roraima's dry savannas is pioneering. Constantino and Cancelllo (1992) rightly pointed out that precise insights into Amazonian biodiversity patterns necessitate thorough investigations into habitat preferences and termite community factors. The research site lies within the largest isolated expanse of Amazonian savannas, an area underrepresented in termite studies compared to the more explored core savanna biome in central Brazil.

For instance, in Cerrado pastures, Cunha and Orlando (2011) identified 17 genera, with 19 species of Kalotermitidae, Rhinotermitidae, and Termitidae. Similarly, Carrijo et al. (2009) reported 21 and 17 termite species in native Cerrado and converted grazing areas, respectively, with a shared pool of nine species. In the Caatinga of Pernambuco, Vasconcellos et al. (2010) identified 26 termite species in areas under conservation. The richness reported in our study aligns with Viana-Júnior et al.' (2014) findings, emphasizing the influence of soil depth, climate, and vegetation on termite diversity (Arveti et al., 2012; Cunha et al., 2006; Dambros et al., 2012; Araújo et al., 2015; Couto et al., 2015).

From a geomorphological perspective, *A. excellens* functions as a zoogeomorphic engineer whose activity converts dispersed subsurface material into persistent, meter-scale landforms. Although the species was recessive in the faunal abundance data, its geomorphic dominance results from the size, volume, and durability of its constructions. This mismatch between ecological abundance and geomorphic effect is important because the species that most modifies relief, sediment storage, and surface hydrology is not necessarily the most frequent species in biodiversity transects.

Northeast Roraima experiences a transitional climate, contributing to unique habitats for various termites. The interplay between climate and savanna vegetation shapes termite habitats, especially for *A. excellens*, which constructs epigeal nests due to the scarcity of trees. The low primary productivity in open savannas influences termite richness, density, and composition, where soil attributes play a crucial role (Alves et al., 2011; Viana-Júnior et al., 2014). Chemical attributes, particularly in chemically poor soils, influence termite species, with more demanding ones requiring specific niches (Araújo et al., 2015; Bourguignon et al., 2015; Silva et al., 2015).

Although *A. excellens* was not the numerically dominant taxon in the sampled termite assemblage, its large epigeal mounds confer a disproportionate influence on local pedogeomorphology. By occupying space, modifying soil structure, and creating long-lived biogenic features, this species may affect resource distribution and the availability of microhabitats for other termites and associated organisms (Davies et al., 2014; Araújo et al., 2015).

Large nests of *A. excellens* are associated with specific tree species in the dry savanna. These nests, documented as ecosystem-engineering structures, support a diverse range of organisms, including mosses and lichens on older mounds (Bonachela et al., 2015; Gosling et al., 2012; Davies et al., 2014). While previous studies have observed several inquilines in large termite nests, our sampling limitations suggest the possibility of more cohabitants in abandoned or active nests (Junqueira et al., 2015). This includes ants, two scorpions, and a rattlesnake (*Crotalus durissus roraima*), reinforcing the role of termite mounds as habitats for various vertebrate and invertebrate species

(Moreira et al., 2009; Leitner et al., 2020). Vegetation succession on mounds is strongly influenced by the age of these biogenic structures: higher mound fields in well-drained areas have greater plant diversity.

The dominance of humivorous termites in Roraima's savannas aligns with findings in other open habitats in Brazil, influencing termite distribution based on humification gradients (Cunha et al., 2006; Carrijo et al., 2009; Oliveira et al., 2013). Soil-dwelling termites exhibit preferences based on soil chemical composition, with Apicotermitinae termites showing varied foraging patterns regardless of soil attributes, while some species select specific substrates, such as organic matter-rich soils (Bourguignon et al., 2015).

In low-vegetation density environments like the Roraima savannas, the abundance of xylophagous termites and their limited representation reflect the availability of wood for feeding (Viana-Júnior et al., 2014). This contrasts with dense forest environments where xylophagous termites are more diverse (Oliveira et al., 2013). The scarcity of humivorous termites in the study area is attributed to low organic matter availability, reinforcing the group's prevalence in forested regions (Souza et al., 2012; Azevedo et al., 2013).

While most termite species in the studied savannas exhibit wide distribution, epigeal *A. excellens* is endemic to the Amazon region. Its high density in Amazonian savannas makes it a crucial ecological component (Constantino, 1999). Other species exclusive to open environments include *Cortaritermes intermedius*, *Grigiotermes* sp., and *Velocitermes* sp., with regional restrictions in Brazil (Constantino, 1999). Despite advancements in neotropical termitofauna studies, there's a persistent need for more comprehensive research to enhance our understanding of termite diversity (Carrijo et al., 2015; Chouvenc et al., 2016). The significance of our results underscores the necessity for further investigations in the ecotonal Caatinga/Savanna/Forest region of northeast Roraima. This mosaic of soils and vegetation offers a unique opportunity to unravel biological and evolutionary processes in one of the driest parts of Brazilian Amazonia.

Nutrient concentrations in termite mounds across all sections (top, middle, and bottom) were much higher than in control soils, with no significant differences between the three geomorphic sections (Figure 7). However, a significant difference in PC1 was noted between termite mound sections and the three depths of control soils. Higher score values indicated greater differences between mound and soil. Scores up to the first half represented soil contents (1-3), while the second half illustrated mound contents (4-6).

As in other Brazilian studies, *A. excellens* mounds contain more organic C and N than adjacent soils (Sarcinelli et al., 2009; Rückamp et al., 2012). Their carbon storage capacity highlights their role in savanna cycles (Alves et al., 2011; Bezerra-Gusmão et al., 2011). Different termite species select soil materials for nest construction, affecting organic matter, microbial activity, and mound stability (Jouquet et al., 2007; Arveti et al., 2012; Pinheiro et al., 2013). The granulometry of Acrisol mounds enhances cation exchange capacity (CEC) and reduces leaching (Abe et al., 2009). Soil transport by termites shapes mineral composition, hydrology, and topography (Peres Filho et al., 2012; Schaefer and Oliveira, 2022).

Mound density is higher in Plinthosols than in Planosols, influenced by nesting age, dominant species, colony size (Krishna et al., 2013), and the need to escape flooding and waterlogging in extensive floodplains, as reported by Goudie (1988). Larger nests enhance soil turnover and nutrient cycling (Ferreira et al., 2011b). Higher clay contents in Acrisols contribute to larger and more robust mounds, in agreement with Jouquet et al. (2004) and Pequeno et al. (2015). Erosion from mounds can create a deep soil mantle, influencing soil genesis and fertility (Goudie, 1988; Mujinya et al., 2013). Thus, *A. excellens* mounds function as fertility islands, buffering savanna ecosystems and promoting vegetation recovery after fire or inundation disturbances (Bonachela et al., 2015; Van der Plas et al., 2013; Joseph et al., 2014).

The differential termite activity under varying drainage conditions agrees with Goudie (1988) and Viles (2022), who reviewed the effects of soil drainage and hydrology on mound density, highlighting that some species build abundant mounds in low-lying, ill-drained areas to escape waterlogging (Grigg, 1973). Goudie (1988) also stressed that the pH reaction of mound material depends on the subsurface layer from which it is taken up, so varying results can be expected across soils and drainage conditions. Aged termite mounds also show greater vegetation succession and biomass, forming a special type of dry park savanna.

The mounds also have implications for runoff, infiltration, and erosion. Termite macropores and galleries can increase infiltration and intercept runoff in crusted dryland soils (Léonard and Rajot, 2001), while mound-associated vegetation patches may further enhance preferential flow and soil infiltrability in semiarid savannas (Bargués Tobella et al., 2014). In Surumu, this effect is likely spatially variable: Plinthosol areas are seasonally saturated and promote mound construction as refuges from hydromorphism, whereas better-drained Acrisol

surfaces allow mounds to persist longer but expose them to flank erosion, surface lowering, and progressive vegetation colonization. Comparable Brazilian murundu systems show that mound origin and persistence commonly involve interactions among hydropedology, termite occupation, erosion, and soil micromorphology rather than a purely biological or purely geomorphic origin (Oliveira Junior et al., 2017; Freitas et al., 2021; Sales et al., 2021).

The Surumu mound field also fits the broader hydrogeomorphological model proposed for savanna termite landscapes. In African savannas, mound distribution and morphology are strongly associated with catena position, drainage, and subsurface resource gradients (Levick et al., 2010; Davies et al., 2014). In the Surumu Depression, the higher density of smaller mounds on Plinthosols and the occurrence of larger, older, more eroded mounds on Acrisols indicate a comparable control by relative elevation and drainage. However, the controlling factors are expressed through Amazonian savanna soils developed on pediplanated volcanic substrates rather than through the granitic or alluvial settings described in much of the African literature. This comparison reinforces that mound fields are geomorphic indicators whose spatial patterns must be interpreted in relation to local substrate, hydrology, and surface stability (Muvengwi et al., 2018; Hosseinzadeh et al., 2023).

5. Conclusion

This study demonstrates that the Surumu Depression, in northeastern Roraima, is a distinctive Amazonian murundu landscape in which termite activity links soil formation, mound morphology, drainage conditions, and vegetation succession. The termite assemblage comprised 16 species/morphospecies from eight genera and two families, with frequent species shared between Plinthosols and Acrisols and clearer differences among rare species.

Although *Amitermes excellens* was not numerically dominant in the transect samples, it was the main mound-building species responsible for the conspicuous conical and cathedral-shaped structures that organize the local landscape. Its mounds differ from adjacent soils through selective incorporation of fine particles and enrichment in bases, nitrogen, organic matter, and exchange properties, thereby creating fertility islands and favoring vegetation establishment on older structures.

Mound distribution and morphology varied along the topographic and hydropedological gradient. Poorly drained Plinthosols supported higher mound densities, whereas better-drained Acrisols had fewer but larger and older mounds, with more evident erosion, soil redistribution, and succession of vegetation. These patterns indicate that mound density, mound volume, soil texture, drainage, colony age, and disturbance history jointly control termite-mediated pedobioturbation.

Taken together, the results support the interpretation of *A. excellens* as a key biogeomorphological agent in northern Amazonian savannas. By transporting subsurface material to the surface and modifying local soil fertility and microtopography, this species contributes to pedogeomorphological heterogeneity, ecosystem resilience, and biodiversity maintenance in one of the driest ecotonal sectors of Brazilian Amazonia.

The first-order estimates of soil reworking, 47.5 mm ka⁻¹ for Plinthosols and 85.3 mm ka⁻¹ for Acrisols using standing mound volume and a 30-year mound life, indicate that the geomorphic contribution of *A. excellens* is measurable at landform and pedon scales. These values should be interpreted as potential bioturbation indices rather than direct erosion or denudation rates, but they demonstrate that termite activity contributes to the medium- and long-term sediment budget of the pediplanated Surumu surface.

Future Directions

Future research should prioritize: long-term monitoring of mound growth, decay, soil redistribution, and vegetation succession; microbial and biogeochemical studies of active and abandoned mounds; evaluation of mound effects on plant and animal assemblages and on savanna resilience to fire and climate variability; chronological studies using ¹⁴C or luminescence dating to estimate mound age and pedobioturbation rates; and comparative studies across Amazonian, Cerrado, and Caatinga savannas to distinguish general patterns from local controls. Future work should also include high-resolution DEMs, hillshade maps, topographic profiles, mound-to-channel distances, local slope measurements, and repeated surveys of active, abandoned, and eroded mounds. These data would allow the qualitative catena model proposed here to be tested with quantitative geomorphometry and would directly address the spatial controls of mound establishment, persistence, and decay.

Conflict of Interest: The authors have no conflict of interest to disclose.

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