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Termite participation in the soil-forming processes of 'murundus' structures in the semi-arid region of Brazil

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ABSTRACT: Regularly spaced earth mounds called "murundus" are scattered in several landscapes in the semi-arid region of Brazil. Although recent evidence indicates that termites are involved in the building of *murundus*, the contribution of these insects to soil-forming processes in those structures remains poorly understood. In this study, we tested a set of hypotheses to examine whether there are consistent evidence for suggesting the participation of termites in the formation of *murundus* soils. Morphological and physicochemical features of *murundus* were compared with adjacent soil profiles in the inter-mounds surface and one epigeic nest built by one species of *Syntermes* Holmgren. The *murundus* soils had a more clayey texture, higher contents of nutrients (C, N, P, K, Ca, and Mg) and organic matter compared with adjacent soils. We identified a set of recent and ancient traces inside the *murundus* that reveals the intense building activity of termite colonies (e.g., galleries, tunnels, and royal chambers), confirming that these structures are not only occupied by these insects but also built-up by them. Taken together, our results provide hard evidence that the long-term activity of mound-building termites was the hierarchically dominant process in producing *murundus* structures in the semi-arid region of Brazil. Based on available empirical data, we propose an explanatory model on how that construction process may have taken place.

Keywords: *Caatinga* biome, ecosystem engineering, landforms, *Syntermes*, soil-forming processes.

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INTRODUCTION

Termites are important ecosystem engineers in tropical and subtropical regions (Bignell and Eggleton, 2000). One of the key roles that these insects play is their ability to build spectacular biogenic structures (Vasconcelos, 2000), which have a significant impact on soil functional processes (Lavelle, 2002; Jouquet et al., 2006). Termite mounds and their associated structures (i.e., galleries, sheeting, and chambers) significantly influence soil physicochemical properties, such as morphology, structure, stability, and organic content (De Bruyn and Conacher, 1990; Fall et al., 2001). Therefore, the set of those structures represents a major functional compartment of tropical soils and can directly or indirectly mediate the supply of resources to other organisms (Lavelle, 2002).

Large (>20 m diameter and 1.5 m in height) and regularly spaced earth mounds encountered in many parts of the world have been historically attributed to the activity of mound-building termites. In most cases, evidence in favor of a termite origin are yet somewhat circumstantial and there is an ongoing debate whether termites are capable of producing such structures (Midgley, 2010; Cramer and Barger, 2014). Examples of those earth mounds include *heuweltjies* in South African savannas (Moore and Picker, 1991) and *murundus* in seasonally flooded savannas and some seasonally dry tropical forests of Brazil (Funch, 2015; Paulino et al., 2015; Souza and Delabie, 2016; Martin et al., 2018) (Figure 1).

Heuweltjies were considered fossilized termite nests (4.000-years-old) by Moore and Picker (1991), but recent evidence suggested their genesis through vegetation induced by aeolian sediment deposition (Cramer and Midgley, 2015). Similarly, *murundus* of

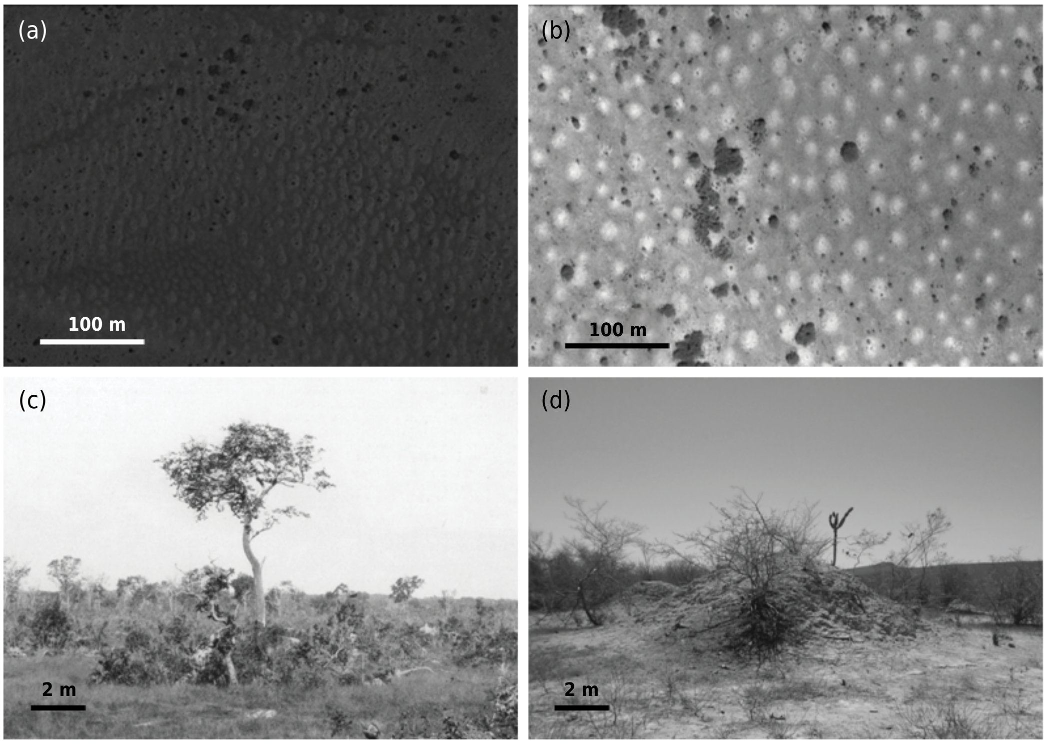


Figure 1. *Murundus* of Brazil. (a) *Campos de murundus* ("mound fields") of seasonally floodplains of central-western region (15° 57′ 59″ S, 47° 58′ 34″ W); (b) densely-packed *murundus* on drylands of the northeastern region (12° 28′ 29″ S, 41° 45′ 40″ W); (c) typical *murundus* densely covered by woody vegetation of *Cerrado* biome (tropical savanna); and (d) typical *murundus* partially covered by woody vegetation of *Caatinga* biome (seasonally dry tropical forest). Images (a) and (b) were obtained from Google Earth' satellite (Google Inc., Mountain View, California, USA); image in (c) was taken from Ponce and Cunha (1993) and corresponds to a *campos de murundus* situated in the Pantanal region (state of Mato Grosso); image (d) was taken during the dry season by Henrique Jesus de Souza in a densely-packed *murundus* in the 'Chapada Diamantina' region (state of Bahia).

seasonally flooded savannas were described as being formed by the localized activity of mound-building termites (Oliveira-Filho, 1992), but soil organic matter isotopic analysis, soil physicochemical, and floristic composition suggested a geomorphological origin through differential erosion of a savanna ecosystem (Silva et al., 2010). On the other hand, recent evidence obtained from micromorphological soil analysis, spatially explicit mapping, predictive modeling, and spatial distribution pattern have raised the possibility of a termite origin for *murundus* occurring in seasonally dry tropical forests of the semi-arid region of Brazil: (i) the occurrence of *murundus* on soils predominantly deep, well-drained and unsaturated with water makes unlikely a geomorphological origin through differential erosion (Souza and Delabie, 2016); (ii) in some locations, *murundus* soils contain microgranular structures similar to “termite pellets” and high levels of phosphorus, indicating biological activity (Antunes et al., 2012; Melo-Júnior, 2012; Simões, 2012); (iii) there are a strong geographical congruence between the potential distributions of densely-packed *murundus* and four mound-building termite species (*Cornitermes bequaerti* Emerson, *Cornitermes silvestrii* Emerson, *Syntermes dirus* [Burmeister] and *Syntermes wheeleri* Emerson) (Souza and Delabie, 2016); and (iv) *murundus* show a significant regular distribution at the distance scale of up to 50 m radius suggesting competition for foraging territories between different termite colonies (Souza and Delabie, 2017).

Despite those preliminary evidence indicating a termite origin for the *murundus* of the semi-arid domain, with structures up to 4,000-year-old in some localities (Martin et al., 2018), the contribution of those insects to soil-forming processes in those structures still remains poorly understood. For example, it is not known whether traces of biological activity in *murundus* soils reflect the action of builder termites or only secondary occupants. The termite genera hypothesized to be the creators of *murundus* build mounds that are relatively smaller (*Cornitermes* Wasmann 1897, approximately 2 m in height and 1 m of diameter; and *Syntermes* Holmgren 1909, 2 m in height and 5 m of diameter) than the size of those structures (1.5 to 3 m in height and 8 to 20 m in diameter at the base), raising doubts whether termites were the responsible for their construction. As a consequence, it has been proposed that successive generations of termites of the same or different species have contributed to the construction of a single unit of *murundu* (Funch, 2015; Souza and Delabie, 2016), but this hypothesis still lacks empirical evidence.

It is well known that in the process of mound building, termites modify the structural, chemical, and biochemical properties of the soil that they use for construction, as well as the soil of nearby areas, so that some elements (particularly C, N, and P), exchangeable cations (K, Ca, and Mg) and clay content are more abundant in the termite mounds than in adjacent soils (De Bruyn and Conacher, 1990; Holt and Lepage, 2000; López-Hernández, 2001; Jouquet et al., 2002; Sarcinelli et al., 2009). In addition, the bioturbation caused by termite workers during the process of mound building can homogenize soil profiles attenuating typical characteristics derived from local pedogenic processes (Schaetzl and Anderson, 2005).

In this study, we examined morphological and physicochemical features of *murundus* and adjacent soil profiles in the inter-mounds surface to investigate whether there are consistent evidence for suggesting the participation of termites in the formation of *murundus* soils in the semi-arid region of Brazil. Specifically, we test the following hypotheses: (i) the morphology of *murundus* soils along the depths of the profiles is more uniform than that of adjacent soils; (ii) the texture of *murundus* soils is more clayey than the texture of adjacent soils; (iii) *murundus* soil profiles have higher contents of nutrients (C, N, P, K, Ca, and Mg) and organic matter than adjacent soils; and (iv) biological traces inside the *murundus* are more consistent with termite construction than secondary occupation only. We assumed that the confirmation of such hypotheses would support that *murundus* were produced by the activity of mound-building termites. On the other hand, the rejection of such hypotheses would suggest that *murundus* are not primarily the product of termite activity, but instead, the consequence of another, not yet identified, hierarchically dominant agent.

MATERIALS AND METHODS

Study area

The study was carried out in four densely-packed *murundus* situated in the Chapada Diamantina region (geographical center of Area 1: 12° 28′ 06″ S 41° 45′ 19″ W; Area 2: 12° 26′ 25″ S 41° 46′ 45″ W; Area 3: 12° 27′ 22″ S 41° 46′ 05″ W; and Area 4: 12° 26′ 58″ S 41° 46′ 54″ W), which is the most prominent within the core area of densely-packed *murundus* in the semi-arid region of Brazil.

The studied areas have a semi-arid climate (Bsw) according to the Köppen's classification system (Köppen and Geiger, 1936), with average annual precipitation ranging from 740 to 880 mm, and average annual temperature from 20 to 22 °C (Hijmans et al., 2005). The geology is characterized by the presence of quartzite and aeolian sandstones, with *Latossolos* (Oxisols) predominantly deep, well-drained, acid, and with low fertility (Velloso et al., 2002; Souza et al., 2003). The biome is *Caatinga* (seasonally dry tropical forest) and the typical plant species belong to the genera *Capparis* L. (Capparaceae Juss.), *Syagrus* Mart. (Arecaceae Schultz Sch.), and *Mimosa* L. (Leguminosae - Mimosoideae). Moderate anthropogenic degradation of the vegetation, mainly through agriculture, grazing, and urbanization, resulted in forested densely-packed *murundus* being substituted by cleared densely-packed *murundus* with secondary grassland and scattered shrubs and trees in most areas.

Soil sampling and analyses

In each of the four areas, we have studied a single *murundu,* and a single soil pit in the inter-mounds surface was excavated for the analysis and description of soil profiles and physicochemical analyses. *Murundus* were excavated using digger and shovel and soil pits in the inter-mounds surface were handling excavated at least 10 m away from the *murundus* to minimize any physicochemical interference with the original soil properties. Additionally, we handling excavated an active nest built by *Syntermes* spp. in the same area to serve as a reference profile (for exploratory purposes only) aiming to compare the morphological and physicochemical features of *murundus* and adjacent soils in the inter-mounds superficies. The samples were taken every 0.20 m depth from the topsoil to bottom/bedrock. In each depth, six soil samples were collected to form composite samples of approximately 2 kg, which were screened by a mesh sieve (2 mm) and air-dried. In total, 80 samples were collected at the beginning of the region's dry season (i.e., May/June 2016).

Morphological characteristics of soil profiles (e.g., horizons, structure, consistency, biological activity, among others) were described following the Brazilian Society of Soil Science's recommendations (Santos et al., 2013). Physicochemical analyses comprised soil texture (by pipette method), pH(H_2O) at a ratio of soil:solution equal to 1:2.5, organic carbon (Walkley-Black method), organic matter content (by multiplying the value of organic carbon by Van Barnmelen factor of 1.724), total nitrogen (Kjeldahl method), exchangeable Ca, Mg, and Al (extractant KCl 1 mol L^{-1}), available K, P, Fe, Zn, Mn, and Cu (extractant Mehlich-1), and H+Al (extractant calcium acetate 0.5 mol L^{-1} at pH 7.0). All variables were performed at the Soil Laboratory of the Cocoa Research Center, CEPLAC, Ilhéus, Brazil following EMBRAPA's standard procedures (Donagemma et al., 2011).

Statistical analyses

Physicochemical soil variables were compared between *murundus* and adjacent soil profiles in the inter-mounds surface with one way Analysis of Variance (ANOVA). We used the mean values of variables in each soil profile to perform the statistical tests at a significance level of 5 %. Phosphorous values were square root transformed to meet the assumption of normality and homogeneity of variance. Additionally, a Principal Component Analysis (PCA) of the physicochemical data was computed to make an ordination of the soil samples of *murundus* (n = 41), inter-mounds surface (n = 33), and the *Syntermes* nest (n = 6). The aim of the PCA was to define hypothetical variables accounting for as much as possible of the variance in the multivariate data. We used correlation matrix for normalize all variables using division by their standard deviations. This was necessary considering that the variables were measured in different units. ‘Scree plot’ (simple plot of eigenvalues) was then used to indicate the number of significant components. We plotted on it the eigenvalues expected under a random model (Broken Stick). All statistical analyses were performed in the software PAST version 2.17 (Hammer et al., 2001).

RESULTS

Morphological properties

Murundus

Murundus soil profiles present a uniform structure without forming genetic horizons (Figure 2a). Stones are absent and roots of a range of sizes (0.1 to 2.0 cm in diameter) are well distributed throughout all structures. There are evident traces of termite activity inside the *murundus*, which suggest that these structures are not only occupied by these insects but also constructed by them (Figures 3 and 4). Heavily cemented galleries and tunnels (0.2 to 4.0 cm in diameter) are abundant along the entire structure, being more preserved in the middle-upper portion (up to 1.50 m depth) where secondary occupants can be found (e.g., termites: *Syntermes praecellens* [Silvestri 1946], *S. molestus* [Burmeister 1839], and *Nasutitermes corniger* [Motschulsky 1855]; ants: *Camponotus* sp., *Pheidole* sp., and *Solenopsis geminata* [Fabricius 1804]; and spiders: *Leprolochus birabeni* [Mello-Leitão 1942], *Camillina minuta* [Mello-Leitão 1941], and *Oxyopes salticus* [Hentz 1845]). Royal chambers (0.60 × 0.50 m in diameter) are differentiated structures with rounded shape, moderate consistency, and darker coloring built by the termites (Figure 3d). More than one royal chamber can be observed in a single *murundu*, suggesting the activity of construction of more than a single colony, sometimes by different species and that have probably occurred at different periods of the mound edification. We observed traces of those structures in the middle part (0.40-0.60 m layer) and basal (0.20-0.30 m below ground surface) of the *murundus* (Figures 3b and 4d). In the last case, royal chambers were edified just above a stone-line typical of the original soil where *murundus* are built.

Inter-mounds surface

Soil profiles in the inter-mounds surface have a typical morphology of Oxisols with genetic horizons of distinct structure and composition (Figure 2b). A horizon (up to 0.60 m depth) is formed by a combination of partially decomposed organic matter and a stone-line of 0.30 to 0.40 m thick formed by gravel with stones of size varying from 1.0 to 15 cm in diameter and irregular in shape to rounded depending on the locality. The ground surface is formed by gravel and pebbles with irregular shapes and a thin layer of leaf-litter that covers the adjacent soil layers. The B horizon (0.60 to 1.60 m depth) is formed by a large layer of weathered minerals of uniform structure. The C horizon (1.60 to 2.00 m depth) is formed by unconsolidated material similar to the bedrock. Finally, R horizon (from 2.00 m) is the bedrock, which is composed of quartz arenite of laminar shape.

Active termite nest

The nest built by *Syntermes* has a conical shape reaching approximately 1 m high and 3 m in diameter at the base, which corresponds to a soil volume of 5.50 m^3 (Figure 5a).

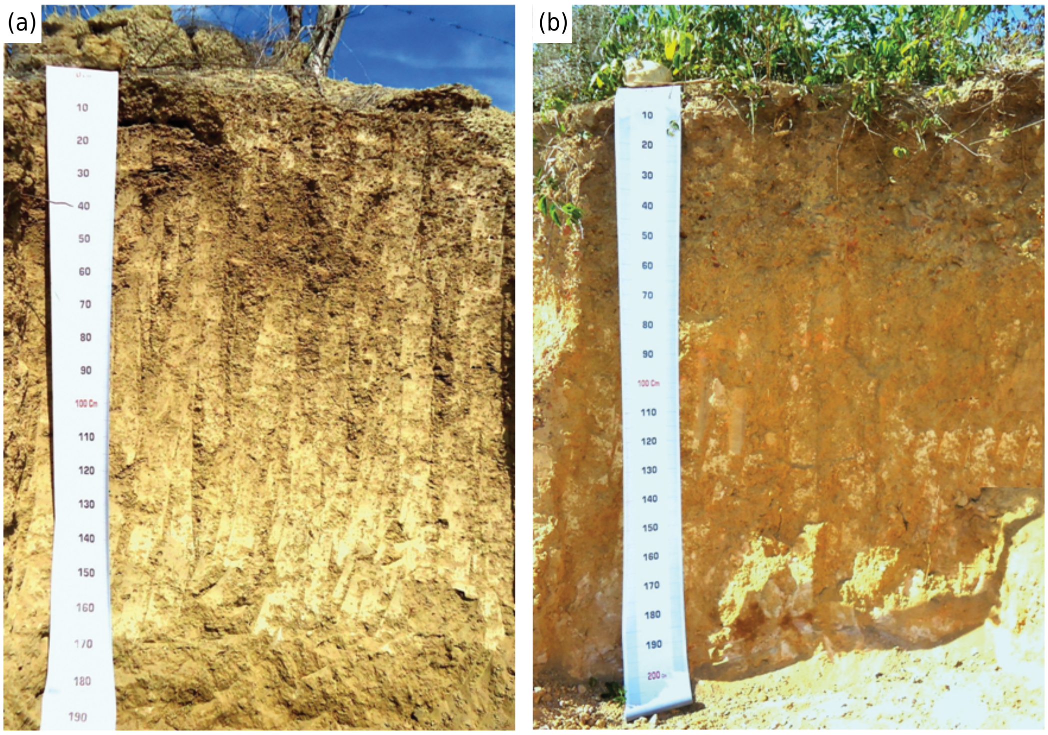


Figure 2. Soil trenches excavated in the semi-arid region of Brazil. Typical soil profile of *murundus* structures (a); and typical soil profile of adjacent soils in the inter-mounds surface (b). The ruler scale is graduated in centimeters.

Figure 3. Evident traces of termite construction inside a recent *murundu* (1.80 m in height and 13.2 m³ of soil volume) excaved in the semi-arid region of Brazil. Side view of a cross section (a); frontal view of same *murundu* (b); preserved galleries in the middle-upper portion (up to 0.90 m depth) (c); remains of a rounded royal chamber in the middle part of the structure (d). The basal part of the structure (from 0.90 m depth) was occupied by a mature colony of *Syntermes molestus*.

It is composed of excavated soil brought to the surface by the workers and can be divided into three main compartments: a thin sandier external layer with fragile granular structure; a larger internal part with many tunnels and horizontal galleries measuring 0.2 to 5.0 cm

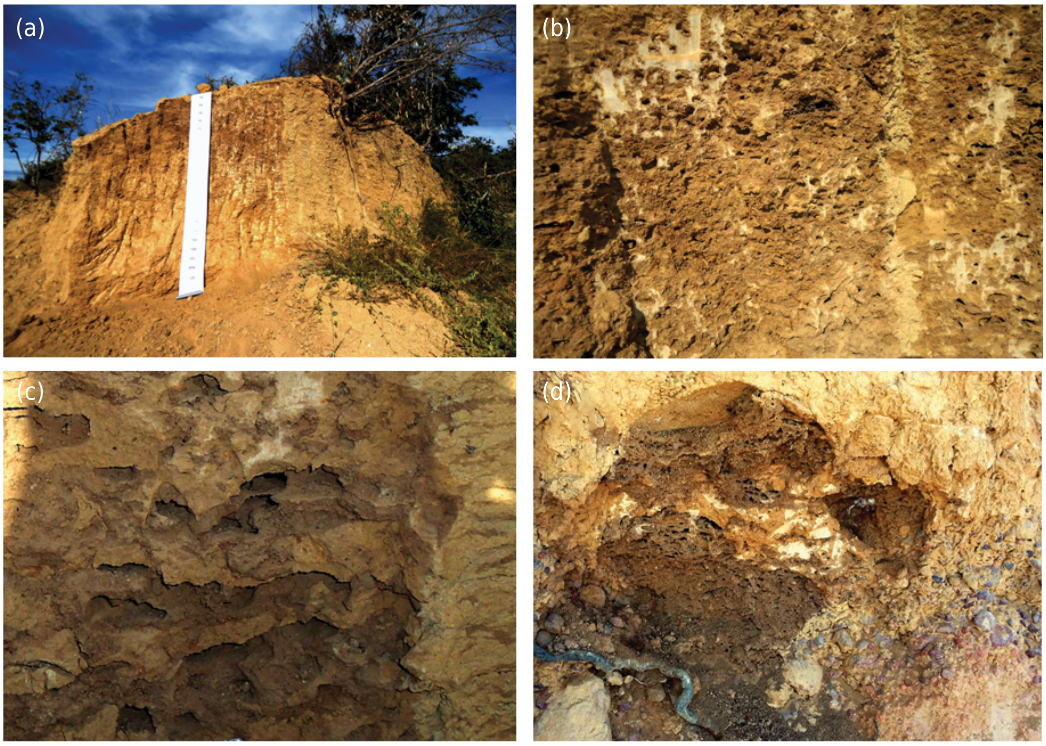


Figure 4. Evident traces of termite construction inside a ancient *murundu* (2 m in height and 34.5 m^3 of soil volume). Frontal view of a cross-section (a); Vestigies of galleries in the middle-upper portion (up to 1.20 m depth) (b); close view of vestigies of galleries (c); remains of a rounded royal chamber situated at the base of the *murundu* just above a stone-line typical of the original soil (0.20 m below the ground surface) (d).

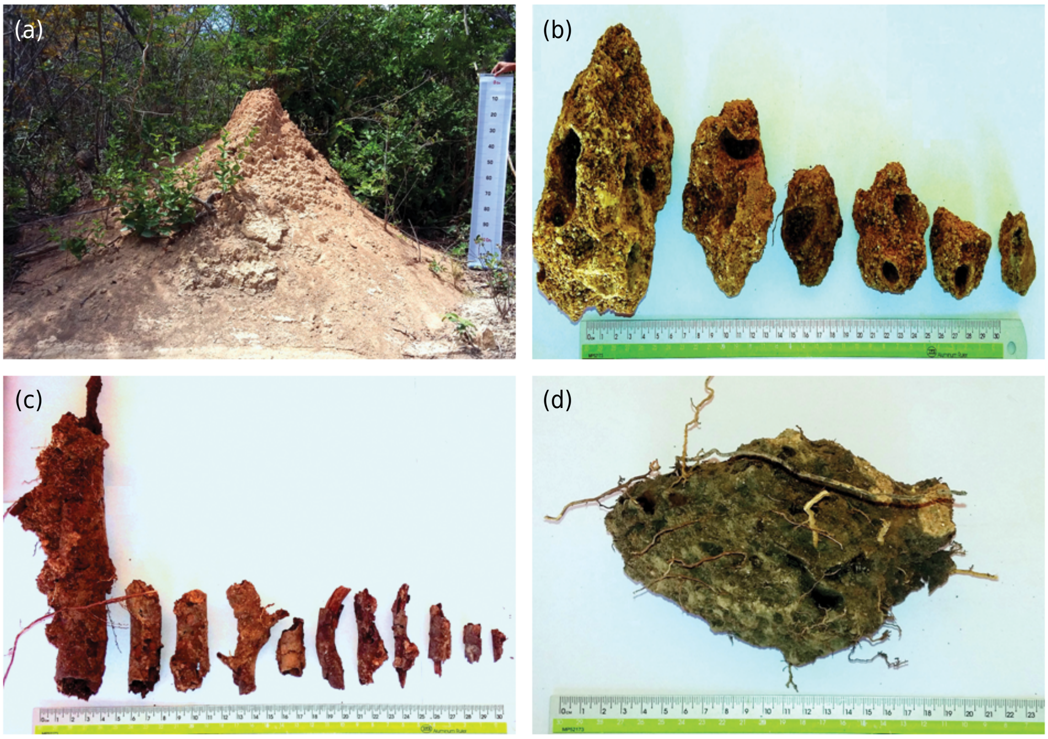


Figure 5. Nest built by *Syntermes* and its associated biostructures in a seasonally dry tropical forest in the semi-arid region of Brazil. Mound formed by a pile of loose soil brought from subsoil by workers (a); soil aggregates with traces of galleries and pores built by workers (b); trunks and twigs used by workers as pillars for the construction of some galleries and tunnels (c); and part of a rounded royal chamber of hard clayey consistency with many roots penetrated (d).

in diameter and sometimes built using trunks and twigs as pillars (Figures 5a and 5b); and a differentiated rounded royal chamber (0.20 m below ground surface and just above the bedrock) of hard clayey consistency with many roots penetrating (Figure 5c). Dry leaves were also found in the *Syntermes* nest, but there was none specific compartment for the storage of this material.

We found two termite species inhabiting the nest: *S. molestus* and *Syntermes dirus* [Burmeister 1839]. Both species occupied only the middle-basal part of the nest (0.50-1.10 m layer), where workers and soldiers were abundant inside galleries and walls, while alates and larvae were rare and confined to the base of the structure near the royal chamber. In addition, the nest was occupied by seedlings of the surrounding vegetation (seasonally dry tropical forest) and occasionally by foraging organisms, such as ants (*Dorymyrmex thoracicus* Gallardo 1916, *Camponotus blandus* [Smith F. 1858], *Ectatomma muticum* Mayr 1870, *Pseudomyrmex termitarius* [Smith F. 1855]), centipedes (unidentified Myriapoda: Chilopoda), and lizards (*Cnemidophorus ocellifer* Spix 1825).

Physicochemical properties

All profiles studied showed acid soils (pH 4.0 to 5.8), with varied texture and nutrient content (Table 1). The results of the one-way ANOVA showed that *murundus* had significantly higher nutrient contents (C, N, and P), soil organic matter (SOM), and exchangeable cations (K^+, Ca^{2+}, and Mg^{2+}), and a more clayey texture than adjacent soils in the inter-mounds surface (Table 2 and Figure 6). *Murundus* showed homogeneous particle-size distribution characterized by little variation in clay fraction across the different depths compared with adjacent soil profiles, which had a homogeneous zone

Table 1. Physicochemical properties of *murundus* structures (n = 4), adjacent soils in the inter-mound surface (n = 4), and *Syntermes* nest (n = 1) in the semi-arid region of Brazil. Values are the average of subsamples (taken every 0.20 m depth) in each soil profile. The standard deviation is indicated in brackets

Property	*Murundus* structures				*Inter-mounds* surface				Syntermes nest
	Profile 1	Profile 2	Profile 3	Profile 4	Profile 5	Profile 6	Profile 7	Profile 8	Profile 9
pH(H_2O)	4.6 (0.3)	4.2 (0.2)	4.5 (0.5)	4.8 (0.7)	4.8 (0.5)	4.8 (0.5)	4.5 (0.3)	4.5 (0.5)	4.8
Al^{3+} ($cmol_c\ dm^{-3}$)	1.1 (0.6)	1.0 (0.4)	1.2 (0.6)	0.6 (0.3)	1.0 (0.4)	1.5 (0.7)	1.0 (0.5)	1.1 (0.4)	1.7
H+Al ($cmol_c\ dm^{-3}$)	5.7 (1.9)	4.3 (1.6)	4.3 (2.2)	4.0 (0.7)	3.7 (1.8)	3.0 (1.1)	2.9 (1.2)	3.6 (1.0)	4.7
Ca^{2+} ($cmol_c\ dm^{-3}$)	1.5 (0.7)	1.5 (0.4)	0.9 (0.3)	1.9 (1.0)	0.5 (0.5)	0.4 (0.5)	0.3 (0.1)	0.4 (0.4)	0.3
Mg^{2+} ($cmol_c\ dm^{-3}$)	0.9 (0.7)	0.7 (0.3)	0.6 (0.3)	0.9 (0.5)	0.2 (0.3)	0.1 (0.1)	0.6 (0.3)	0.1 (0.2)	0.3
K^+ ($cmol_c\ dm^{-3}$)	0.4 (0.1)	0.4 (0.0)	0.1 (0.1)	0.4 (0.0)	0.2 (0.1)	0.1 (0.1)	0.1 (0.0)	0.1 (0.1)	0.2
P ($mg\ kg^{-1}$)	7.6 (16)	4.7 (4.0)	9.3 (20.0)	24.8 (14.0)	3.9 (4.8)	1.3 (1.0)	1.7 (1.0)	2.9 (3.0)	1.3
Fe ($mg\ kg^{-1}$)	63.6 (37.3)	32.2 (12.7)	33.0 (14.1)	71.9 (32.4)	37.1 (24.6)	19.1 (15.0)	29.5 (31.4)	38.5 (14.1)	65.9
Zn ($mg\ kg^{-1}$)	1.3 (0.5)	1.6 (0.3)	1.5 (0.5)	2.2 (0.7)	1.5 (0.4)	1.2 (0.2)	1.5 (0.6)	1.2 (0.2)	0.9
Cu ($mg\ kg^{-1}$)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	0.4 (0.1)	0.4 (0.1)	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	0.3
Mn ($mg\ kg^{-1}$)	10.5 (11.1)	12.7 (3.5)	4.2 (3.2)	13.4 (9.1)	3.3 (4.2)	5.6 (11.7)	1.5 (1.3)	1.4 (2.0)	1.8
C ($g\ dm^{-3}$)	10.5 (5.65)	7.8 (4.1)	8.4 (4.7)	12 (2.8)	7.5 (7.0)	5.3 (3.9)	3.1 (2.1)	6.8 (5.7)	11.4
N ($g\ dm^{-3}$)	0.9 (0.33)	0.7 (0.3)	0.6 (0.4)	1.1 (0.2)	0.7 (0.5)	0.4 (0.3)	0.3 (0.2)	0.5 (0.3)	0.7
SOM ($g\ dm^{-3}$)	18.3 (9.73)	13.5 (7.0)	14.5 (8.1)	20.7 (4.9)	13.0 (12.0)	9.2 (6.7)	5.4 (3.7)	11.8 (9.8)	19.7
Coarse sand ($g\ kg^{-1}$)	87.5 (73.2)	181.0 (38.3)	178.3 (17.9)	274.3 (15.7)	383.9 (162.8)	270.3 (106.7)	291.3 (51.7)	372 (107.1)	273.7
Fine sand ($g\ kg^{-1}$)	211.7 (15.0)	199.6 (13.0)	255.3 (193.4)	269.3 (15.5)	168.6 (58.0)	175.6 (35.3)	165.7 (18.5)	196.9 (42.9)	230.3
Silt ($g\ kg^{-1}$)	278.4 (38.1)	311.5 (46.7)	376.9 (234.5)	203.7 (32.9)	233.9 (71.6)	359.5 (158.8)	330.4 (115.4)	258.1 (112.3)	199.2
Clay ($g\ kg^{-1}$)	422.5 (68.8)	307.9 (66.0)	331.4 (88.9)	252.7 (31.6)	213.7 (131.1)	194.6 (88.6)	212.6 (118.3)	173.4 (117.2)	296.8

Soil texture (pipette method); pH(H_2O) at a ratio of soil:solution equal to 1:2.5; organic carbon (Walkley-Black method), organic matter content (by multiplying the value of organic carbon by Van Barnmelen factor of 1.724); total nitrogen (Kjeldahl method); exchangeable Ca, Mg, and Al (extractant KCl 1 mol L^{-1}); available K, P, Fe, Zn, Mn, and Cu (extractant Mehlich-1); and H+Al (extractant calcium acetate 0.5 mol L^{-1} and pH 7.0).

Table 2. Summary of one-way Analysis of Variance (*F* and *p* values) for 17 physicochemical properties of soil profiles of *murundus* structures (n = 4) and the inter-mounds surface (n = 4). Values in bold indicate statistically significant differences at p<0.05

Physicochemical properties	*F* (Fisher)	*p*
pH(H_2O)	0.6757	0.67
Al^{3+} ($cmol_c$ dm^{-3})	0.9735	0.64
H+Al ($cmol_c$ dm^{-3})	8.6796	**0.03**
Ca^{2+} ($cmol_c$ dm^{-3})	24.9623	**0.01**
Mg^{2+} ($cmol_c$ dm^{-3})	13.9263	**0.01**
K^{+} ($cmol_c$ dm^{-3})	6.4000	**0.04**
P (mg kg^{-1})	9.364	**0.02**
Fe (mg kg^{-1})	2.9114	0.14
Zn (mg kg^{-1})	2.0000	0.21
Cu (mg kg^{-1})	0.2727	0.62
Mn (mg kg^{-1})	9.8202	**0.02**
C (g dm^{-3})	8.4975	**0.03**
N (g dm^{-3})	6.2553	**0.04**
SOM (g dm^{-3})	8.4540	**0.03**
Coarse sand (g kg^{-1})	9.8143	**0.02**
Fine sand (g kg^{-1})	9.9000	**0.02**
Silt (g kg^{-1})	0.0037	0.95

with higher clay content only up to 0.80 m depth. The *Syntermes* nest was characterized by a more variable texture and high levels of nutrients (mainly carbon and nitrogen) only at lower depths of structure (Figure 6).

The first two axes of the PCA were responsible for 70 % of the total variation on the physicochemical properties of the soil samples, in which the axis 1 (PC1) was responsible for 48.2 % and the axis 2 (PC2) for 22.6 % of the data variations. Owing to the sharp decrease of eigenvalues, no other axes were retained for interpretation (Figure 7a). The PC1 revealed two distinct groups between soil samples (*murundus* and basal part of the *Syntermes* nest versus inter-mounds surface and upper part of the *Syntermes* nest), which are influenced positively by soil fertility (i.e., levels of organic nutrients and exchangeable cations) and finer soil fraction (i.e., total clay and fine sand contents). Despite PC2 apparently contributing to a significant proportion of the variance, it showed a rather diffuse grouping making interpretation more difficult (Figure 7b).

DISCUSSION

Most authors have assumed a termite origin for the *murundus*-type that we have studied using a self-evident explanation. It was suggested that the *murundus* are huge termite nests composed primarily of subsurface soils brought to the surface by termite tunneling activity (Oliveira et al., 2014; Funch, 2015). However, the first empirical support in favor of the termite hypothesis was provided by demonstrating that aspects related to the soil micromorphology, geographical distribution, and spatial patterning of *murundus* are consistent with a termite origin (Antunes et al., 2012; Melo-Júnior, 2012; Simões, 2012; Souza and Delabie, 2016, 2017; Martin et al., 2018). Despite those preliminary contributions, it still lacked consistent evidence for supporting the termite participation in the soil-forming processes of *murundus* because one could argue that termites only have secondarily occupied but not built them. Based on morphological and physicochemical analyses, our results demonstrate unambiguously that the *murundus*

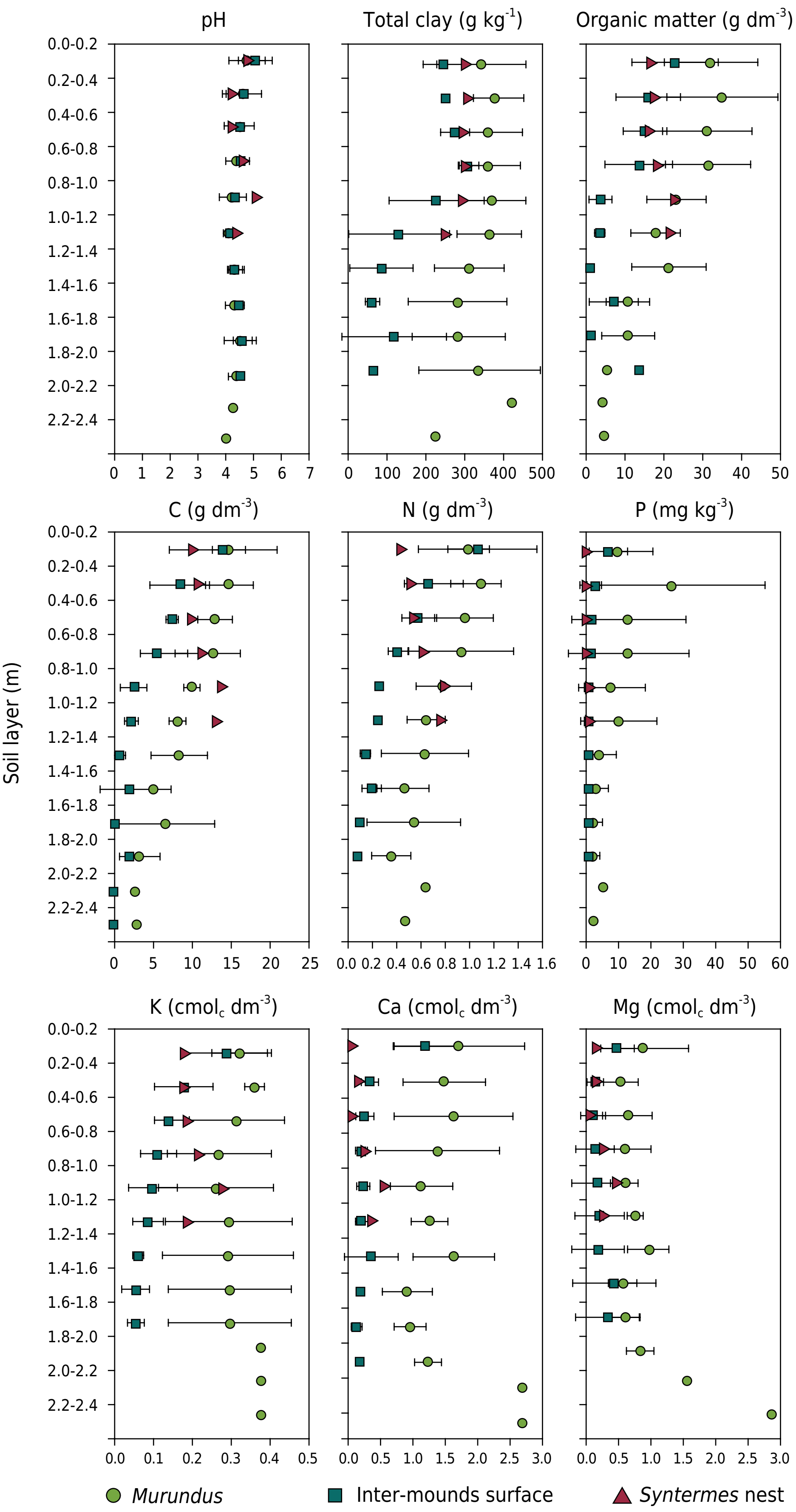


Figure 6. Physicochemical properties of soil profiles of *murundus* structures (black line), inter-mounds surface (dark-grey line), and *Syntermes* nest (light-grey line) in the semi-arid region of Brazil. There were four replicates for *murundus* structures and adjacent soils in the inter-mounds surface and one replicate for the nest built by *Syntermes*. Error bars represent the standard deviation.

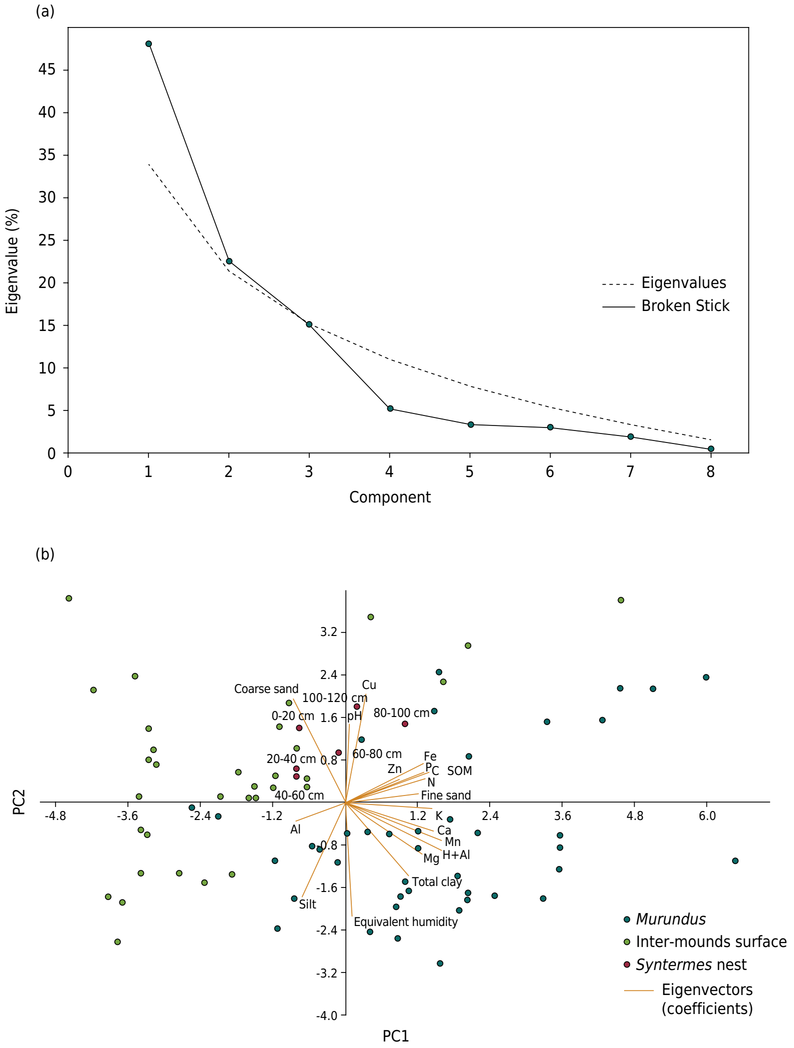


Figure 7. Principal Component Analysis (PCA) for physicochemical properties of soil samples collected in different depths of *murundus* structures (n = 41), inter-mounds surface (n = 33), and *Syntermes* nest (n = 6) in the semi-arid region of Brazil. Scree plot indicating the number of significant components (a). The eigenvalues under the Broken Stick' curve represent non-significant components; and Scattergram showing all soil samples plotted in the coordinate system given by two of the components (b). Orange lines correspond to eigenvectors, which is another visualization of the PCA loadings (coefficients). Depth intervals refer to the samples collected in the *Syntermes* nest.

structures in the semi-arid region of Brazil were constructed by the long-term activity of mound-building termites.

Firstly, the uniformity of the *murundus* soil profiles, as evidenced by morphology, texture, and nutrient content, strongly suggests that they were produced above the original land-surface by a single process that is hierarchically dominant (Figures 2a and 6). If *murundus* were relict soils shredded by differential erosion – as has been suggested for structures of the seasonally flooded savannas of Central Brazil – (Araújo-Neto et al., 1986; Silva et al., 2010), their soil profiles would not be uniform because, as evidenced in adjacent soil profiles, local pedogenic processes tend to produced soils with layers displaying distinct morphological and physicochemical features (Figure 2b). The fact that *murundus* have a clayey texture throughout all their depths and without any stone and gravel inside them strongly supports the hypothesis that termites built *murundus* by displacing finer soil particles upwards. The little variable zone with higher clay content (up to 0.80 m depth) in inter-mounds soils on which *murundus* were built-up indicates that probably termites used material from there for the construction of those structures (Figure 6). Previous studies also have evidenced the termites' preferential use of clay-enriched subsoil material for building their mounds (De Bruyn and Conacher, 1990; Abe et al., 2009, 2011). Generally, these insects enrich those structures with clay particles to improve their structural stability, water holding capacity, and increase foraging resources (Jouquet et al., 2002, 2004; Oberst et al., 2016).

Secondly, *murundus* soil profiles have significantly higher concentrations of nutrients (C, N, P, K^+, Ca^{2+}, and Mg^{2+}), and organic matter compared with adjacent soils in the inter-mounds surface being most similar to the inhabited part of the *Syntermes* nests (Figure 6 and Table 2). It is well documented that during the building process, termites enrich their mounds with organic matter and nutrients altering soil properties (De Bruyn and Conacher, 1990; Holt and Lepage, 2000; Fall et al., 2001; Sarcinelli et al., 2009; Rückamp et al., 2010). Our results showed that *murundus* almost always present double or triple the concentration of nutrients when compared to the adjacent soil profiles in the inter-mounds surface (Table 1). Organic matter and nutrients slightly decreased in samples taken from the deepest of *murundus* reflecting probably the most ancient termite activity. On the other hand, exchangeable cations had higher concentrations in the basal depths of *murundus*, reflecting the mobility of these elements in response to leaching effects. The higher nutrient content in the lower layers of the *Syntermes* nests indicates that there must be a gradual increase in mound fertility as the nest structure evolves in size and soil volume incorporated. As the top of the *Syntermes* nest corresponds to an uninhabited compartment composed of a pile of loose soil with few functional structures, the increase in its fertility should occur with the cumulative activity of the termite colonies over time. This partially explains why, even though they are older structures, *murundus* have higher levels of fertility than active *Syntermes* nests.

The content of C, N, and P in termite mounds is generally associated with organic matter incorporation by workers, as leaf-litter particles and fecal pellets mixed with saliva (Fall et al., 2001; Sarcinelli et al., 2009; Rückamp et al., 2010). The termite genera hypothesized to be main builders of *murundus* – *Syntermes* and *Cornitermes* – (Funch, 2015; Souza and Delabie, 2016; Martin et al., 2018) feed on semi-decomposed wood, leaf-litter, and grasses that they collect on the ground and store usually in subterranean chambers (Constantino, 1995). In fact, we did not observe specific chambers for storing vegetable debris inside the *Syntermes* nest or *murundus* structures indicating that termites should even store the collected material in subterranean chambers. When feeding, the termites break down the vegetal material into minute particles, enhancing the action of fungi and soil bacteria that favor the formation of humic substances of high fertility (Brauman, 2000), which are displaced upwards during the building process of their mounds. The higher concentration of exchangeable cations (K^+, Ca^{2+}, and Mg^{2+}) in *murundus* can be attributed to the turnover of some primary minerals from saprolite source due to soil burrowing, as was suggested also by Schaefer (2001) and Sarcinelli et al. (2009) for termite nests built-up on Oxisols in other regions of Brazil.

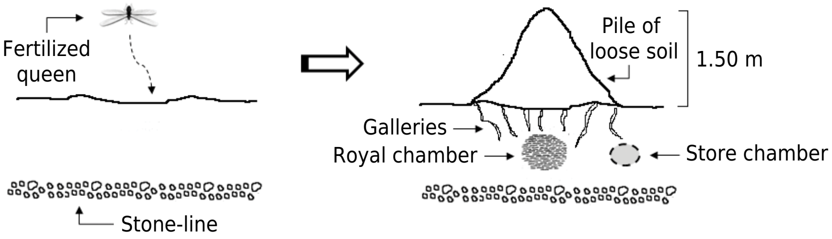
Thirdly, biogenic structures (i.e., galleries, tunnels, and royal chambers) with different degrees of conservation inside *murundus* structures attest to the intense and long-term termite activity (Figures 3 and 4). Foraging galleries, tunnels, and royal chambers were more evident in the upper-middle part of *murundus* possibly reflecting a more recent construction for this region. In addition, the lower soil compaction (i.e., due the lower soil volume) in this part of the *murundus* certainly contribute to keep the biostructures more conserved. In some *murundus*, the characteristics of the biostructures were very similar to those of the *Syntermes* nest that we have described (Figure 5), as well as the *Syntermes* nests reported by other authors (Constantino, 1995). Species of this genus build large and cylindrical galleries and royal chambers with a rounded shape, which have color and consistency distinctly different from the surrounding soil (Constantino, 1995). We found out that more than one royal chamber with distinct degrees of conservation can occur in a single *murundu* (in middle and basal parts). Furthermore, different termite species can coexist in the same *murundu* or *Syntermes* nest.

We observed workers of *Syntermes molestus* and *Nasutitermes corniger* in the same *murundu* in the first hand, while both *Syntermes molestus* and *S. dirus* were present in the same active nest. In the first case, the colony of *S. molestus* occupied the middle-basal part of that structure (0.50-1.80 m layer), whereas workers of *N. corniger* occupied the upper galleries, even those probably built by *Syntermes*. In the active nest, we observed many workers, soldiers, alates, and larvae of *S. molestus* and only some workers of *S. dirus* in the middle-basal part of the structure (0.50-1.10 m layer). These findings are surprising because previous reports describe *S. molestus* as having a subterranean nesting behavior that does not build external mounds (Constantino, 1995). As some individuals of *S. dirus* (which is known to build mounds) were found inside the nest, it is also possible that *S. molestus* has occupied the structure secondarily only after *S. dirus* had built-up it. The same is valid for *N. corniger* in the *murundu* case. However, our observations only allow stating that *S. molestus* can establish mature subterranean colonies within mounds. If it has yet the capacity to build them deserves further studies.

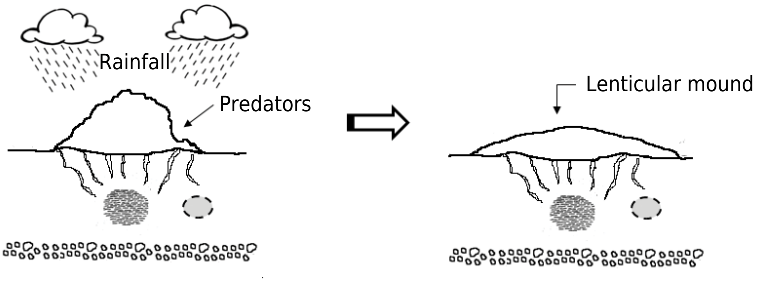
Based on the findings of this study, as well as in available empirical data, we propose an explanatory model for the *murundus* origin. Their formation occurs through the progressive evolution of mounds originally built-up by *Syntermes*, which grow in volume, size, and fertility as they are successively colonized and constructed by other termite colonies of the same or other species, over a long period. The succeeding colonies take advantage of the pre-existing system of galleries and biostructures (storage and royal chambers) likely to optimize access to resources in an oligotrophic environment marked by intense competition for foraging territories between mature colonies (Souza and Delabie, 2017). The figure 8 depicts in detail our interpretation of the formation of the *murundus* in the semi-arid region of Brazil. The construction process begins with smaller *Syntermes* nests [as also proposed by Funch (2015) and Martin et al. (2018)], whose pile of loose soil brought to the surface via tunneling activity form mounds with approximately 1.5 m in height and up to 5 m in basal diameter (Stage 1). The death of the original colony or its partial destruction by rainfalls or excavators (mainly vertebrates such as armadillos, lizards, owls or rodents) deforms part of the mounds making them concave with gentle slopes – something similar to the lenticular mounds built by *Macrotermes* in African savannas (Grassé, 1986; Josens et al., 2016). Physicochemical processes of clay aggregation must contribute to the compaction of the initial pile of loose soil (Stage 2). The lenticular and more compact mounds are then colonized by neighboring colonies of *Syntermes* or other mound-building termites (e.g., *Cornitermes*) (or even strict hypogeal species, not detectable in our study). Foraging and building activities by workers of the new colonies both expand the system of preexisting galleries and biostructures as well as increase the soil volume and fertility of the mounds (Stage 3). From successive cycles of the last two stages, the *murundus* assume their current appearance with volume corresponding up to 60 initial *Syntermes* nests (i.e., up to 600 m^3 of soil for a single structure; stage 4).

Further research is still needed to clarify aspects that remain obscure in the explanatory model that we have described here. For example: (i) the nature of the physicochemical aggregation reactions of the clayey fraction of *murundus* soils, which seem to play a secondary hierarchical role in the formation of those structures; (ii) the nature of the interactions between the termite colonies that coexist as well as succeed each other inside the *murundus*, suggesting these structures represent large termitary complexes like those observed by Grassé (1986) in Africa; (iii) the mechanisms that favored the intense termite activity during the *murundus* formation, as well as those that triggered the senescence of the colonies; and (iv) the *murundus* properties that favor their persistence in the landscapes like hotspots of nutrients until the present day.

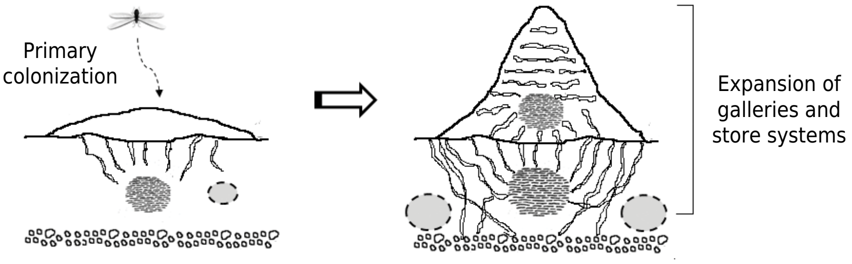
(a) Stage 1



(b) Stage 2



(c) Stage 3



(c) Stage 4

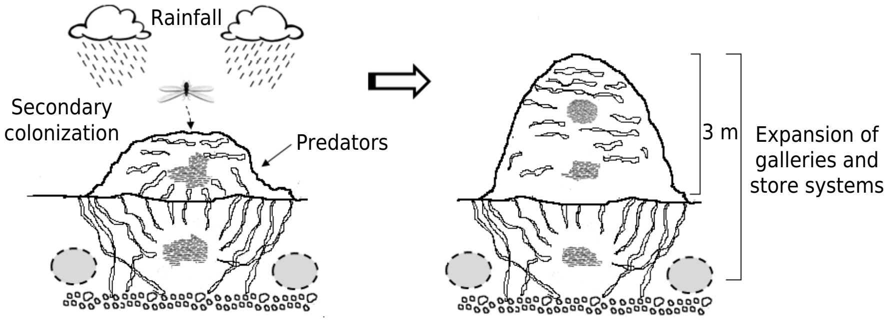


Figure 8. Explanatory model for the formation of *murundus* structures in the semi-arid region of Brazil. Stage 1: Fertilized queen of *Syntermes* colonize the ground surface and builds a royal chamber just above the stone-line (0.30-0.40 m depth) (a). After hatching from the eggs laid by the queen, workers begin to build the system of underground galleries and storage chambers displacing soil particles upwards during their excavation activities; Stage 2: the erosive action of rainfall and excavators (eating-termites fauna and others vertebrates) partially destruct the initial mound resulting in lenticular (concave) mound (b). Physicochemical reactions of clay aggregation contribute to its compactation. Stage 3: again fertilized queen of *Syntermes* or other mound-building termite (e.g. *Cornitermes*) colonize the lenticular mound founding a new colony (c). The forraging and building activities of new colony both expand the system of preexisting galleries and biostructures as well as increase the soil volume of the mound; and Stage 4: illustrates the present physiognomy of *murundus*, which must have arisen only after several repetitions of the mechanisms described in the last two stages (d).

CONCLUSIONS

Our results strongly support that *murundus* structures in the semi-arid region of Brazil are senescent *termitaria* produced by the long-term activity of mound-building termites.

The main evidence that supports their participation in the soil-forming processes of *murundus* can be brought about by: (i) uniform structure and morphology of *murundus* soils without the formation of horizons suggesting the localized activity of termite colonies as a hierarchically dominant process above the land-surface; (ii) *murundus* soils with clayey texture suggesting selection and displacing of finer soil particles upwards by termites from deep soil layers; (iii) *murundus* soils with high levels of nutrients suggesting enrichment of organic matter by termite colonies via feeding and building activities; (iv) evident traces of termite construction (i.e., galleries, tunnels, and royal chambers) suggesting that *murundus* structures were not only occupied by those insects but also built-up by them.

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Methodology: Henrique Jesus de Souza (lead) and George Andrade Sodré (supporting).

Software: Henrique Jesus de Souza (lead) and Jacques Hubert Charles Delabie (supporting).

Validation: Henrique Jesus de Souza (lead) and Jacques Hubert Charles Delabie (supporting).

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Writing – review and editing: Henrique Jesus de Souza (lead), Jacques Hubert Charles Delabie (supporting), and George Andrade Sodré (supporting).

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Supervision: Jacques Hubert Charles Delabie (equal) and George Andrade Sodré (equal).

Project administration: Henrique Jesus de Souza (lead) and Jacques Hubert Charles Delabie (supporting).

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