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# 1 **Termite constructions as patches of soil fertility in**

## 2 **Cambodian paddy fields**

3

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1 **Abstract**

2 In Cambodia, termite mounds are commonly used by farmers as amendments to increase the  
3 fertility of their paddy fields. However, despite their utilization, their chemical and physical  
4 properties have not been described yet. Therefore, the aim of this study was to analyze the  
5 chemical and physical properties of two termite constructions commonly found in paddy fields:  
6 (a) termitaria built and occupied by the fungus-growing termite *Macrotermes gilvus* and (b)  
7 lenticular mounds that are initially built by termites but host a large diversity of other  
8 invertebrates and plants. This study shows that these biogenic structures have very specific  
9 properties. Termitaria were characterized by higher clay, phosphorus and electrical  
10 conductivity than the surrounding soil. However, their effect on carbon dynamics was limited  
11 to a modification of the interactions between soil organic matter and minerals and to the  
12 presence of carbonates. At the same time, lenticular mounds appeared as patches of nutrients  
13 in paddy fields because they were always enriched in carbon, nitrogen, and phosphorus in  
14 comparison with the surrounding cultivated soil. Lenticular mounds were also enriched in clay,  
15 although this effect was only measured when the sand content in the surrounding environment  
16 was > 60%. Together with these changes, lenticular mounds were characterized by a lower bulk  
17 density, higher saturated hydraulic conductivity ( $K_{sat}$ ), and higher water holding capacity. In  
18 conclusion, this study shows that termite constructions can be considered fertility and  
19 biogeochemical hotspots in paddy fields, thus explaining their use by farmers for improving  
20 the fertility of their lands.

21 **Keywords:** Bioturbation, ecosystem services, water holding capacity, C sequestration, gley  
22 soil

## 1 **1. Introduction**

2 Termites are among the most important soil invertebrates across the tropics (Wood and Sands  
3 1978) due to their high abundance and impact on the decomposition of litter and other plant-  
4 derived materials (Collins 1981; Schuurman 2005; Griffiths et al. 2019). However, what makes  
5 termites almost unique among soil invertebrates is their capacity to regulate soil biological,  
6 chemical, and physical properties through the construction of soil biogenic structures, such as  
7 galleries, sheeting, and mounds (Jouquet et al. 2016b). For this reason, termites are commonly  
8 considered key soil bioturbators and soil engineers (Dangerfield et al. 1988; Black and  
9 Okwakol 1997; Jouquet et al. 2006).

10 Through their bioturbation activity, termites impact the dynamics of soil and water at  
11 different spatial and temporal scales (Bottinelli et al. 2015; Jouquet et al. 2016a). At a small  
12 scale, termites have been compared to weathering agents because they influence the mineralogy  
13 of clay and the properties of soil aggregates, which in turn influence soil organic matter and  
14 nutrient dynamics (Abbadie and Lepage 1989; Jouquet et al. 2002) as well as soil water-holding  
15 capacity (Konaté et al. 1999; Suzuki et al. 2007; Traoré et al. 2019). At the soil profile scale,  
16 termites use soils from various soil depths or specifically select soil particles of small sizes (i.e.,  
17 clays) for the construction of their nest structures (Abe et al. 2009; Jouquet et al. 2017, 2002).  
18 If the capacity of termites to enrich the soil in clay particles seems to be the rule (Holt and  
19 Lepage 2000), their impact on soil organic matter is highly variable. For instance, several  
20 studies showed higher C content in termite mounds than in the surrounding soil (De Souza et  
21 al. 2020; Chen et al. 2021; Wakbulcho and Kenea 2021), while Cheik et al. (2018) found a  
22 negative or neutral effect of termite bioturbation activity. Finally, termites act as heterogeneity  
23 drivers and shape the distribution of natural resources such as water and nutrients at the  
24 landscape scale through the edification of mounds that are comparable to nutrient patches or

1 fertility islands (Dangerfield et al. 1988; Sileshi et al. 2010; Van der Plas et al. 2013; Cramer  
2 and Midgley 2015; Davies et al. 2016; Jouquet et al. 2016a, 2011; Muvengwi et al. 2017;  
3 Muvengwi and Witkowski 2020; Chen et al. 2021).

4 The specific soil biological, chemical, and physical properties of termite mounds have  
5 largely been described, especially in Africa, where they play a key role in the dynamics of  
6 vegetation (e.g., Traoré et al. 2008) and increase the robustness and resilience of African  
7 dryland ecosystems against water shortages and desertification (Bonachela et al. 2015). In  
8 Brazil, termite activity is considered to be at the origin of the “*murundus*” structures, which  
9 represent a quantity of soil equivalent to approximately 4,000 great pyramids of Giza (De Souza  
10 and Delabie 2018; Martin et al. 2018; De Souza et al. 2020). In Asia, studies considering the  
11 properties of termite mounds have mainly been restricted to India (Jouquet et al. 2020, 2017,  
12 2015) and China (Chen et al. 2021). However, termite mounds are also conspicuous features  
13 of the landscapes in the Lower Mekong Basin (Choosai et al. 2009; Miyagawa et al. 2011). In  
14 Laos, lenticular mounds provide numerous ecosystem services, and their soil is also used for  
15 growing vegetables or as an amendment for increasing the soil fertility of paddy fields  
16 (Miyagawa et al. 2011). In northeastern Thailand, their higher concentrations of C and nutrients  
17 and higher clay content in comparison with the surrounding topsoil explain why farmers spread  
18 termite mound soil in their lands to increase their soil fertility (Noble et al. 2004; Suzuki et al.  
19 2007; Choosai 2010). Despite the fact that termite mounds are also commonly observed in  
20 paddy fields in Cambodia and that their soil is often used as an amendment for increasing the  
21 soil fertility of paddy fields or for growing vegetables (Muon pers. com.), there is a dearth of  
22 information on their chemical and physical properties. The question of the impact of termites  
23 on soil properties is, however, very important in paddy fields in Cambodia, where soils are  
24 mainly sandy and are characterized by low soil fertility and poor soil physical properties (i.e.,  
25 soils are highly compact with a low water-holding capacity) (White et al. 2006; Seng et al.

1 2007). In this environment, any enrichment in clay particles is likely to have a positive impact  
2 on soil chemical and physical properties, especially the retention of organic matter and water  
3 (Noble et al. 2004).

4 Therefore, the aim of this study was to analyse the impact of termite bioturbation on soil  
5 properties in Cambodian paddy fields. Our main hypothesis was that termite mounds can be  
6 considered biogeochemical hotspots in paddy fields with higher clay, organic matter, and  
7 nutrient contents, as well as higher water hydraulic conductivity and a higher water-holding  
8 capacity.

9

## 10 **2. Materials and methods**

### 11 **2.1. Study site and sampling procedure**

12 The study was carried out in the Chrey Bak catchment, Cambodia, a long-term observatory and  
13 research infrastructure of the Institute of Technology of Cambodia. This catchment is located  
14 in the watershed of Tonle Sap Lake (12°15'3.62"N, 104°40'6.21"E) and in the southwest of the  
15 provincial capital of Kampong Chhnang Province. It is covered by two districts, namely Tuek  
16 Phos and Rolea Biér, approximately 700 km<sup>2</sup>. 34% of the catchment is covered by forests, and  
17 the remaining is used for agriculture (32%) or consists of shrublands (27.4%) and grasslands  
18 (5.4%) (JICA, 2003). The catchment is influenced by the tropical monsoon and has two distinct  
19 seasons: the dry season from November to April and the rainy season from May to October,  
20 with annual rainfall varying between 1400 and 2000 mm (MOWRAM 2014). Soils are mainly  
21 Gleysols (Bridges et al. 1998) with varying sand contents (Muon, 2022). Soils were sampled  
22 in three positions in the catchment (see supplementary file 1). Three soil categories were  
23 identified based on their sand contents: Group I (GI, very sandy soils with > 80% sand), Group  
24 II (GII, moderately sandy, ~60% sand), and Group III (GIII, low sandy soils, ~40% sand) (see

1 supplementary file 2. GI was found in the lower part of the catchment, while GIII was found in  
2 the upper reaches of the soil gradient. GII was sampled in both the lowland and upland. The  
3 slope of the catchment is variable and high (~37% on average) in the mountainous area in the  
4 southwest region, while it is very gentle (slope < 12%) or almost flat in the cultivated area  
5 (Mekong River Commission 2003), which is dominated by rain-fed paddy fields. Rice plots  
6 were separated by small dikes for irrigation purposes. In this environment, soil bioturbation is  
7 mainly carried out by termites, especially *Macrotermes gilvus* (Bathellier, 1927) which builds  
8 termite mound nests, also called termitaria (TN) that are only occupied by *M. gilvus* (i.e., they  
9 do not host inquiline species) and which are usually found on large lenticular mounds (LM, ~6  
10 m<sup>3</sup> and 16.88 m<sup>2</sup> on average) (see Josens et al., 2016; Harit and Jouquet, 2021 for examples of  
11 ‘termite lenticular mounds’; see supplementary file 3 for a description of the method used for  
12 the identification of *M. gilvus*). Although the origin and dynamics of LM are unknown, it is  
13 commonly considered by local villagers that they come from the degradation and colonization  
14 of abandoned TN by other termite species (e.g., *Odontotermes* spp. and *Globitermes*  
15 *sulphureus*), invertebrates (e.g., ants and earthworms) and plants (Figure 1; and see Inoue et al.  
16 1997 for a description of LM), then suggesting very different properties and dynamics than  
17 those of TN.

18 Soil sampling occurred during the dry season in February 2020 because sampling sites  
19 are unavailable during the rainy season when paddy fields are flooded. Five LM were selected  
20 per soil group based on the presence of TN (n = 5 per soil group). The influence of termite  
21 bioturbation on soil properties was measured via the sampling of soil in three locations: (i) in  
22 the topsoil (0–10 cm depth) of LM, (ii) from the outer wall of TN located on LM, and (iii) in  
23 the surrounding soil environment in the paddy field (CTRL) at 0–10 cm depth and at a distance  
24 of ~5 m ahead of each LM (Figure 1). The same procedure was repeated in the three soil groups  
25 (GI, II and III), giving a total of 3 soil groups × 3 locations (LM, TN and CTRL) × 5 replicates

1 = 45 soil samples. Soil samples were air-dried in shade at air temperature for one week and  
2 then sieved to 2 mm and stored in air tight plastic bags.

3

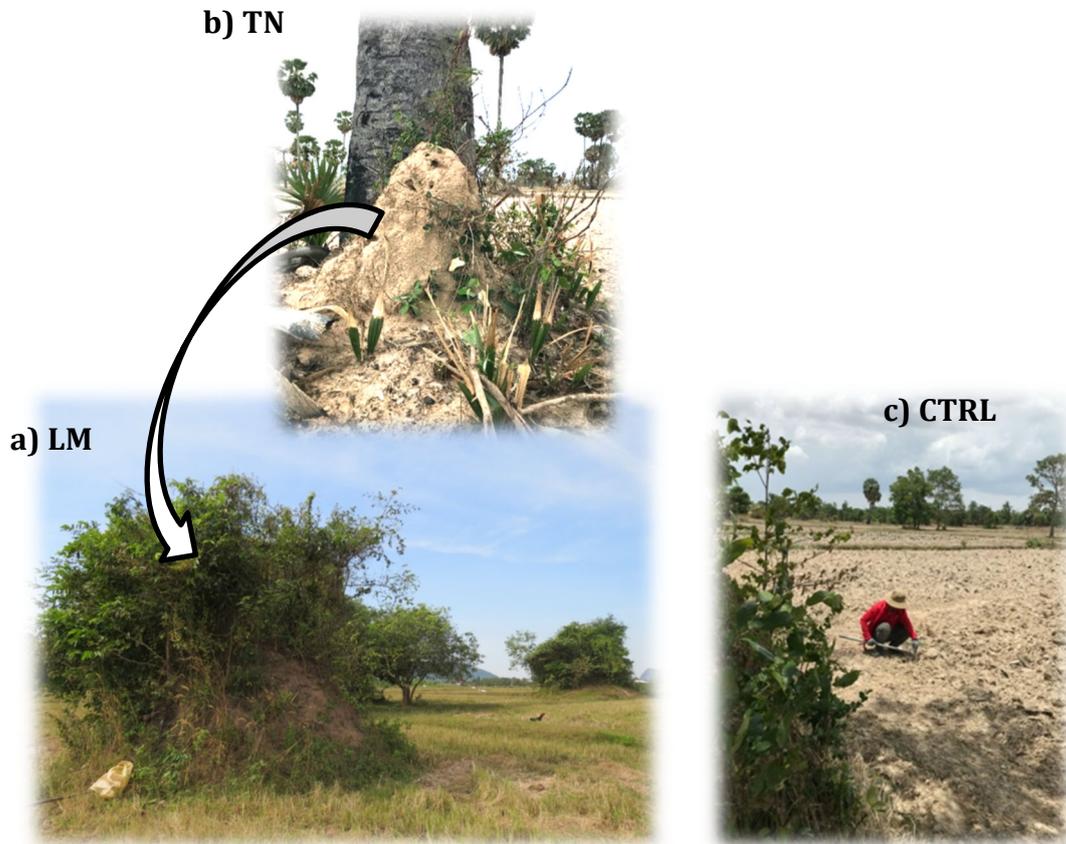
## 4 2.2. Soil chemical and physical analyses

5 The soil pH and electrical conductivity (EC) were determined in a 1:5 soil:water suspension  
6 (Pansu and Gautheyrou, 2006) with portable pH and EC devices. The soil particle size  
7 distribution was measured after the destruction of organic matter by 30% hydrogen peroxide  
8 ( $H_2O_2$ ) and dispersion with sodium hexametaphosphate ( $Na_6O_{18}P_6$ ). The proportion of sand  
9 (50–2000  $\mu m$ ) was obtained by sieving, while the proportions of silt (2–50  $\mu m$ ) and clay (< 2  
10  $\mu m$ ) were obtained by using ASTM 152H hydrometers (Gee and Or, 2002). The bulk densities  
11 of LM and CTRL were measured using 100  $cm^3$  sample rings and dried at 105°C for 48 h.  
12 Because of the hardness of TN soil, this method could not be used for measuring the soil bulk  
13 density of TN, that is why the paraffin-clod method (Blake 1965) was used for TN using large  
14 size soil samples (~20-25 g in average). Concentrations of C and N were analysed using a  
15 Thermo Scientific Flash 2000 organic elemental analyser. Total P was analysed by a  
16 spectrophotometer using a blank and standards prepared in the Olsen P extracting solution  
17 (Estefan et al. 2013) with a Thermo Scientific GENESYS 30 Visible Spectrophotometer.  
18 Exchangeable K was measured by the flame photometer method (Black et al. 1965) using S20  
19 Superspec Series flame photometers. The saturated hydraulic conductivity ( $K_{sat}$ ) of CTRL and  
20 LM soils was analysed in the laboratory using the falling head method (Reynolds and Elrick  
21 2002) with a  $K_{sat}$  device. Finally, the soil water holding capacity was determined at pF 0 by  
22 the sand box (Eijkelkamp) and pF 2.5, 3, 3.2, and 4.2 by the pressure plate method (Dane and  
23 Hopmans 2002) using “Richards” pressure plate extractors. Because of the hardness of TN soil

1 and the difficulty to collect non-disturbed TN soil samples, *Ksat* and the soil water holding  
2 capacity were measured only for CTRL and LM.

3         Soil samples were analysed at IFPEN laboratory (Institut Français du Pétrole Énergies  
4 Nouvelles) with a Rock-Eval 6 device. This technique has been recommended for  
5 characterizing soil organic matter (Derenne and Quéné 2015; Disnar et al. 2003) and has proven  
6 relevance in various contexts (Malou et al. 2020; Romanens et al. 2019; Sebag et al. 2016;  
7 Thoumazeau et al. 2020), and for studying the impact of soil engineering organisms  
8 (Schomburg et al. 2019, 2018; Le Mer et al. 2020). The method uses ramped pyrolysis of  
9 organic matter under an artificial air supply (N<sub>2</sub>) between 200 and 650°C and then the  
10 combustion of residual carbon under oxidative conditions between 200 and 850°C. The  
11 released gases are quantified using a flame ionization detector (FID) for hydrocarbon  
12 compounds (HC) and infrared detectors (IR) for CO and CO<sub>2</sub>. Qualitative and quantitative  
13 parameters are calculated by integrating the amounts of HC, CO, and CO<sub>2</sub> produced during  
14 thermal cracking of organic matter between defined temperature limits (Behar et al. 2001;  
15 Lafargue et al. 1998). Carbon contents were calculated by integrating the C moieties produced  
16 during thermal cracking and combustion-defined temperature limits, with TOC (%) calculated  
17 as the sum of all released carbon released at low temperatures from organic compounds and  
18 OrgC and MinC (%) consisting of organic and mineral carbon pools released at high  
19 temperatures. Soil organic matter quality was assessed with the hydrogen index (HI in mg HC/g  
20 TOC), calculated as the total amount of HC normalized to the TOC content. Soil organic matter  
21 thermal stability was assessed by combining two indices (denoted R- and I-index) calculated  
22 from five subdivided areas of the S2 thermograms related to HC (Sebag et al. 2016). By  
23 construction, the R-index relates to the thermally resistant and refractory pools of organic  
24 matter, while the I-index is related to the ratio between the thermally labile and resistant pools.  
25 As derived from a mathematical construct, these two indices may be inversely correlated when

1 OM stabilization results from progressive decomposition of labile organic compounds and  
2 relative enrichment in refractory compounds. Then, in the I/R diagram, the same  
3 “decomposition line model” describes the decreasing labile pools and concomitant increase in  
4 more thermally stable pools, as observed in compost (Albrecht et al. 2015) and in soils (Sebag  
5 et al. 2016; Matteodo et al. 2018; Thoumazeau et al. 2020). I/R diagrams were used to calculate  
6 the deviation of I-index values from LM and TN to those predicted from the regression line of  
7 the control soil.  
8



9 **Figure 1.** Termite constructions in paddy fields in the Chrey Bak catchment, Cambodia: (a)  
10 Lenticular mounds covered by vegetation (LM), (b) Termitaria built by *M. gilvus* on the  
11 top of a lenticular mounds (TN), (c) control soil (photos: R. Muon, 2021; Jouquet, 2022).  
12

### 1 2.3. Statistical analyses

2 Since soils were sampled in different locations in the catchment, linear mixed models with  
3 elevation as random factor and Tukey tests were performed to assess differences between  
4 means for the different soil structures (TN, LM and CTRL) and soil groups (GI to III). Prior to  
5 running linear mixed models, data were tested for homogeneity of variance and normality using  
6 Levene and Shapiro-Wilk tests. Differences among treatments were declared significant at the  
7  $P < 0.05$  probability level. All statistical analyses and visualizations were carried out with R  
8 version 4.1.1 (<https://www.r-project.org/>) using mainly lme4, ggplot2 and emmeans packages.

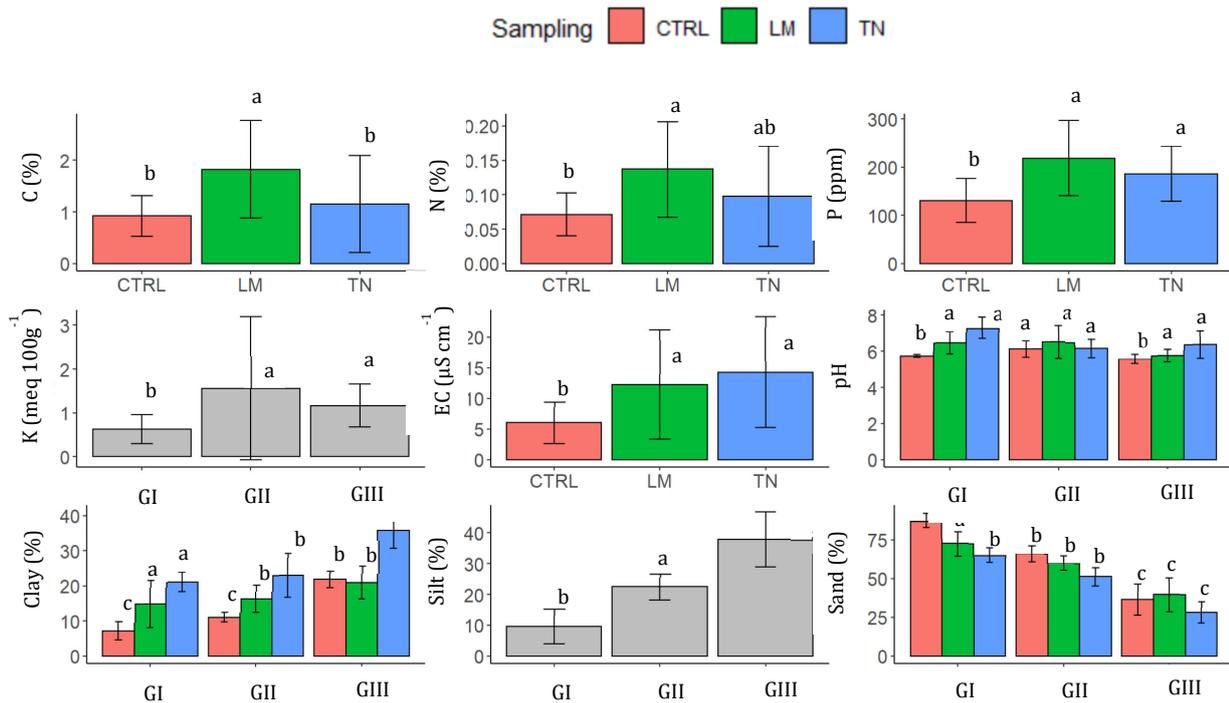
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## 10 3. Results

### 11 3.1 Soil physical and chemical properties

12 The three soil groups were mostly differentiated from their soil particle size distribution (i.e.,  
13 no significant differences in C, N, or P contents, C:N ratio, pH or EC) (Figure 2 and Table 1).  
14 The K content was higher in GIII than in GI, with intermediate value for GII. Conversely, the  
15 amount of sand was the highest in GI and the lowest in GIII, while intermediate sand contents  
16 were measured in GII. The opposite was found for the clay and silt contents, which were the  
17 highest in GIII and the lowest in GI.

1



2 **Figure 2.** Histograms showing the impact of termite bioturbation (control soil “CTRL” in  
3 orange, lenticular mounds “LM” in green, and termitaria “TN” in blue) in the three soil  
4 groups (GI, GII and GIII) on the C, N, and P contents, pH and electrical conductivity (EC),  
5 and soil particle sizes (clay and sand contents) (n = 5), and on K and silt contents (no  
6 termite bioturbation effect, n = 10). Histograms with different letters are significantly  
7 different at  $P < 0.05$  (mixed linear model with elevation as random factor).

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1 **Table 1** Results of the linear mixed models testing the influence of termite bioturbation  
 2 (i.e., termite mound nests, lenticular mounds, and reference soil) and soil groups  
 3 (i.e., GI, GII and GIII) on soil properties with elevation as random factor.  
 4 \*\*\* < 0.001, \*\* < 0.01, \* < 0.05

	Bioturbation (a)		Soil Groups (b)		(a) × (b)	
	<i>F</i> -values	<i>P</i> -values	<i>F</i> -values	<i>P</i> -values	<i>F</i> -values	<i>P</i> -values
C (%)	5.53	0.008 **	2.30	0.302	32.87	0.829
N (%)	5.20	0.011 *	5.42	0.156	0.46	0.760
C:N	1.68	0.201	4.64	0.177	0.10	0.980
P (ppm)	9.028	< 0.001 ***	0.15	0.899	1.09	0.377
K (meq 100g <sup>-1</sup> )	3.67	0.036 *	2.05	0.328	4.09	0.008 **
EC (μS cm <sup>-1</sup> )	6.32	0.005 **	1.18	0.458	1.60	0.197
pH	8.92	< 0.001 ***	4.47	0.182	3.21	0.024 *
Clay (%)	35.02	< 0.001 ***	11.75	0.078	3.15	0.026 *
Silt (%)	0.45	0.637	32.18	0.030 *	1.61	0.193
Sand (%)	16.48	< 0.001 ***	115.74	< 0.001 ***	2.14	0.096

5  
 6  
 7 Bioturbation by termites significantly influenced soil properties apart from the C:N  
 8 ratio, which was influenced neither by termite bioturbation nor by the soil groups (Table 1).  
 9 The C, N and P contents and EC were only influenced by termite bioturbation (i.e., not  
 10 influenced by soil groups). Higher C, N and P contents were measured in LM than in CTRL  
 11 (Figure 2). LM was also characterized by intermediate EC value between those measured in  
 12 CTRL and TN ( $P > 0.05$  for both CTRL and TN). TN had similar C content to CTRL but  
 13 intermediate N content to those measured in CTRL and LM ( $P > 0.05$  for both). TN was also  
 14 characterized by a higher P content and a higher EC than that of CTRL ( $P < 0.05$  for both).

15 Termite bioturbation did not influence the soil pH, except in the sandiest soil group (GI)  
 16 where a higher soil pH was measured in TN than in CTRL (Figure 2). In GI, LM had  
 17 intermediate soil pH values between those of CTRL and TN ( $P > 0.05$  in both cases). Clay and  
 18 sand contents were also influenced by termite bioturbation. The clay content was always higher

1 in TN than in CTRL, while the enrichment in clay was only measured in GI and GII for LM.  
2 Conversely, the sand content was reduced in TN in comparison with CTRL, although this  
3 impact was only measured in the first soil group (i.e.,  $P > 0.05$  for GII and GIII).

### 5 3.2 Carbon pools measured by Rock-Eval<sup>®</sup> analysis

6 Soil groups had no influence on the soil properties measured by Rock-Eval (Table 2). Higher  
7 OrgC content was measured in LM than in TN and CTRL ( $P > 0.05$  between TN and CTRL).  
8 In general, MinC content was very low. However, their concentrations were the highest in TN  
9 in comparison with the other treatments for all soil groups ( $P > 0.05$  in all cases). While HI was  
10 lower in TN than in LM and CTRL, the differences were nonsignificant. Finally, no significant  
11 differences in R-index values were measured ( $P > 0.05$ ).

12 Comparatively, I/R values from LM and CTRL were lower than those of the general  
13 regression model (Figure 3). The distribution of the data was more variable for TN, with values  
14 both higher and lower than those of the general model. This difference in variability shows a  
15 higher deviation of the I-index from control soils for TN than for LM (Figure 4).

### 17 3.3 Soil porosity and water dynamics

18 The soil bulk density (BD) reached between 1.4 and almost 1.7 g cm<sup>-3</sup> in CTRL. The BD value  
19 was influenced by both the location (i.e., soil group effect,  $P < 0.001$ ) and the termite  
20 bioturbation ( $P < 0.001$ ) (Table 3). CTRL and TN had similar BD values, independent of the  
21 soil groups. Conversely, the soil BD was lower in LM than in CTRL and TN, except in GI,  
22 where BD in TN was similar to that in LM and CTRL. The lower BD in LM was also associated  
23 with a higher  $K_{sat}$  in LM soil than in CTRL ( $P = 0.005$ ), independent of the soil groups ( $P =$   
24 0.084) (Figure 5). Water-holding capacity was also significantly higher in LM than in CTRL

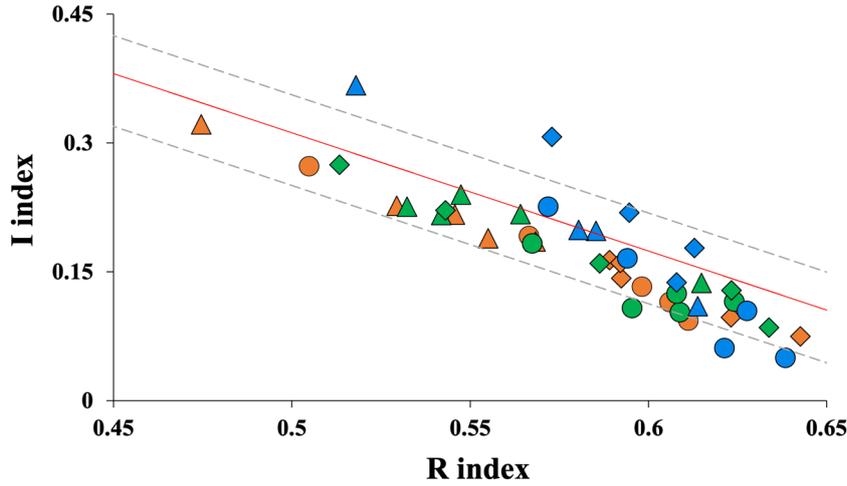
1 at pF 4.2, 3.2 and 2.5, independent of the location (soil group effect,  $P > 0.05$ ) (Table 4 and  
2 Figure 6).

3 **Table 2.** Results from the Rock Eval analysis showing the percentages of organic (OrgC) and  
4 mineral C contents (MinC) and HI (in mg HC g<sup>-1</sup> TOC) and the R index for termite mound  
5 nests (TN), lenticular mounds (LM), and the surrounding paddy field (control, CTRL) found  
6 in the three soil groups (GI, GII, and GIII) in the Chrey Bak catchment. Numbers in parentheses  
7 are standard errors of the means (n = 5).

8  $P$ -values correspond to the results of the linear mixed models testing the influence of termite  
9 bioturbation (i.e., LM, TN, and CTRL) and soil groups (i.e., groups I, II and III) on soil  
10 properties with elevation as random factor. Values with similar letters are significantly similar  
11 at  $P > 0.05$ .

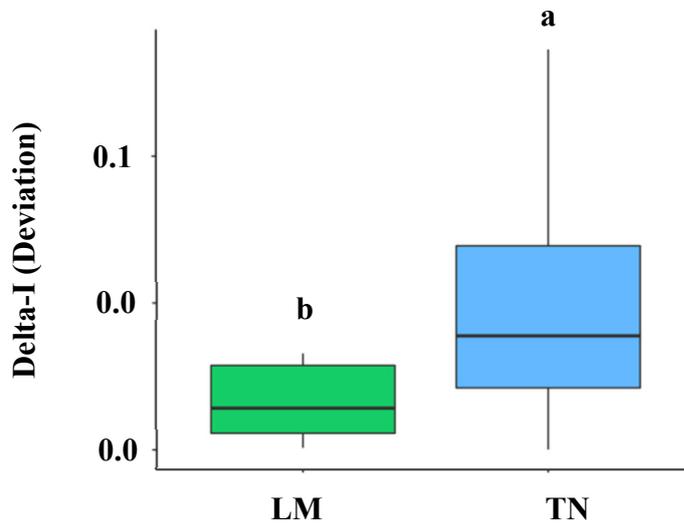
12 \*\*\*  $P < 0.001$ , \*  $P < 0.05$

	Soil types	OrgC (%)	MinC (%)	HI (mg HC g <sup>-1</sup> TOC)	R index
GI	CTRL	0.49 <sup>b</sup> (0.12)	0.01 <sup>b</sup> (0.00)	238.6 (9.15)	0.58 (0.02)
	LM	1.06 <sup>a</sup> (0.16)	0.00 <sup>b</sup> (0.01)	215.8 (10.28)	0.60 (0.01)
	TN	0.62 <sup>b</sup> (0.06)	0.07 <sup>a</sup> (0.02)	191.0 (20.60)	0.61 (0.01)
GII	CTRL	0.85 <sup>b</sup> (0.09)	0.00 <sup>b</sup> (0.00)	253.4 (14.22)	0.53 (0.02)
	LM	1.63 <sup>a</sup> (0.40)	0.02 <sup>b</sup> (0.02)	215.4 (23.63)	0.56 (0.01)
	TN	0.74 <sup>b</sup> (0.19)	0.03 <sup>a</sup> (0.00)	158.6 (10.43)	0.55 (0.03)
GIII	CTRL	1.08 <sup>b</sup> (0.11)	0.00 <sup>b</sup> (0.00)	191.2 (7.96)	0.61 (0.01)
	LM	1.94 <sup>a</sup> (0.45)	0.01 <sup>b</sup> (0.00)	197.4 (18.72)	0.58 (0.02)
	TN	1.60 <sup>b</sup> (0.59)	0.05 <sup>a</sup> (0.01)	136.6 (28.48)	0.61 (0.01)
Bioturbation (a)		$P = 0.011$ *	$P < 0.001$ ***	$P = 0.7531$	$P = 0.490$
Soil groups (b)		$P = 0.285$	$P = 0.117$	$P = 0.139$	$P = 0.092$
(a) × (b)		$P = 0.786$	$P = 0.320$	$P = 0.489$	$P = 0.435$



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**Figure 3.** I- vs. R-index diagram for termitaria and lenticular mounds, and control soils. The dashed line represents the ‘humic trend’ measured by Sebag et al. (2016). The I-index is shown on the vertical axis (control ‘CTRL’ in orange, lenticular mounds ‘LM’ in green, and termitaria ‘TN’ in blue). Soil groups are GI in circles, GII in triangles, and GIII in squares.



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**Figure 4.** Histogram showing the deviation of I-index values of lenticular mounds (LM) and termitaria (TN) from those of the control soils (CTRL) (average values for the three soil groups). Vertical bars are standard errors (n = 15). Differences are significantly different

1 at  $P < 0.05$ .

2 **Table 3** Differences in soil bulk density (BD, in  $\text{g cm}^{-3}$ ) in termite mound nests (TN), lenticular  
 3 mounds (LM), and control soils (CTRL) in the three groups of soil. Numbers in parentheses  
 4 are standard errors of the mean.  $P$ -values correspond to the results of the linear mixed models  
 5 testing the influence of termite bioturbation (i.e., LM, TN, and CTRL) and soil groups (i.e., GI,  
 6 GII and GIII) on soil properties with elevation as random factor. Values with similar letters are  
 7 significantly similar at  $P > 0.05$ . \*\*\*  $P < 0.001$

	Soil types	BD ( $\text{g cm}^{-3}$ )
GI	CTRL	1.66 <sup>a</sup> (0.08)
	LM	1.41 <sup>ab</sup> (0.06)
	TN	1.58 <sup>a</sup> (0.05)
GII	CTRL	1.51 <sup>a</sup> (0.03)
	LM	1.18 <sup>b</sup> (0.10)
	TN	1.54 <sup>a</sup> (0.04)
GIII	CTRL	1.38 <sup>ab</sup> (0.04)
	LM	1.21 <sup>b</sup> (0.06)
	TN	1.45 <sup>ab</sup> (0.06)
Bioturbation (a)		$P < 0.001$ ***
Soil groups (b)		$P < 0.001$ ***
(a) × (b)		$P = 0.436$

8

## 9 **4. Discussion**

### 10 **4.1 Termite constructions as nutrient patches**

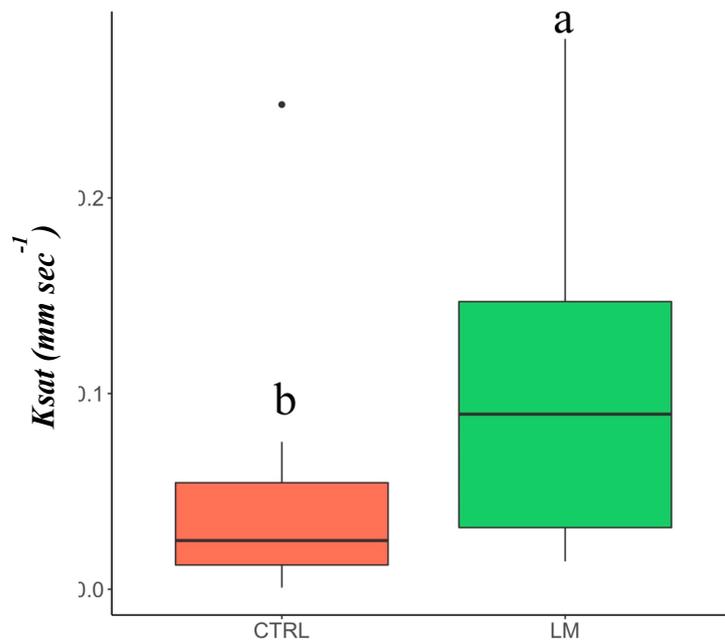
11 In the Lower Mekong Basin, LM are conspicuous features of the landscape. At our study site,  
 12 their density was not influenced by the location within the catchment or by the soil types,  
 13 reaching 2 mounds  $\text{ha}^{-1}$ , which corresponds to  $\sim 6 \text{ m}^3$  soil  $\text{ha}^{-1}$  on average. One striking  
 14 conclusion of this study is that LM always constitutes patches of nutrients in paddy fields, with  
 15 higher C and nutrient (N and P) contents than the surrounding topsoil. TN was also enriched in

1 P in comparison with the reference soil, but no difference in C or N content was found.  
2 Enhancement in C content in LM was confirmed by Rock-Eval<sup>®</sup> analysis. However, termite  
3 bioturbation did not influence the R- index and HI value, suggesting similar soil organic matter  
4 quality (Barré et al., 2016; Sebag et al., 2016). Nevertheless, the I/R diagram showed specific  
5 SOM-mineral interactions in TN in comparison with both LM and CTRL. Indeed, while LM  
6 and CTRL samples were distributed along the ‘decomposition line’ (i.e., the red line in Figure  
7 3), TN samples were characterized by high variability. This result suggests the presence of  
8 variable proportions of labile but unstable organic matter fractions in TN, most likely of saliva  
9 origin and/or of organic fractions stabilized by adsorption on mineral surfaces. Such changes  
10 could be attributed to the total reorganization of the interactions between SOM and minerals  
11 during the molding of individual soil pellets by termites, as well as the enrichment of clay  
12 particles in TN. Indeed, TN was always enriched in clay in comparison with the surrounding  
13 soil, although a reduction in sand was only measured when the sand content of the paddy field  
14 was > 80% (i.e., GI). LM was also enriched in clay, but this effect was only measured when  
15 the sand content of the paddy field was > 60% (i.e., GI and GII). Therefore, these findings  
16 confirm the general assumption that termites’ impact on soil texture is preponderant in sandy  
17 and poor soils, while it is more limited in more clayey soil (e.g., Jouquet et al. 2015; Bera et al.  
18 2020). In sandy soil, the construction of termitaria usually requires the selection of clay  
19 particles, which might come from the deeper soil layers (Abe et al., 2009; Jouquet et al., 2017),  
20 and the incorporation of organic matter (C and N), *i.e.*, mostly saliva that fungus-growing  
21 termites use for ensuring cohesion between particles (Holt and Lepage, 2000; Jouquet et al.,  
22 2022; Zachariah et al., 2017).

23 As observed by others (Bera et al. 2020; Cheik et al. 2018; Jouquet et al. 2015; Subi and  
24 Sheela 2020), a higher soil pH was found in termite constructions in comparison with the  
25 surrounding soil in GI. Interestingly, this higher soil pH was associated with the highest MinC

1 values in TN. Although its concentration was very low ( $< 1\%$ ), the presence of mineral C was  
2 highly surprising in the Chrey Bak catchment, where the soil is acidic. Since a Pisoplinthic  
3 horizon was found at approximately 80 cm depth, we consider it unlikely that mineral C came  
4 from the deeper soil layers. Examination of the thermograms measuring the fluxes of  $\text{CO}_2$  and  
5  $\text{CO}$  during pyrolysis shows the presence of 2 synchronous peaks between 500 and 525  $^\circ\text{C}$ ,  
6 observed in oxalate-rich samples (see supplementary file 4). These peaks are not observed in  
7 CTRL and suggest that high MinC value in TN could correspond to biogenic carbonate, which  
8 could be derived from the oxalotrophic activity of termite-associated fungi and bacteria feeding  
9 on decaying oxalogenic plant tissues (Cailleau et al. 2011; Mujinya et al. 2011; Suryavanshi et  
10 al. 2016; Francis and Poch 2019; Jouquet et al. 2022). Additionally, these oxalate crystals could  
11 also have a bacterial (Hervé et al. 2016) or fungal origin (Hervé et al. 2021). Since termite  
12 constructions harbour microbial communities distinct from those present in the surrounding  
13 soil (Baker et al. 2020), oxalogenic microorganisms could be more abundant in termite  
14 constructions than in soil. To form  $\text{CaCO}_3$  from the oxidation of calcium oxalate, the soil pH  
15 needs to reach the stability of calcite, i.e., pH 8.4 under conventional surface conditions of  
16 temperature and pressure. This pH is likely to be reached during the digestion of organic  
17 residues by termites (pH = 9.5 in the paunch of *Macrotermes subhyalinus*, Anklin-Mühlemann  
18 et al. 1995). Even if the soil pH is lower than 8.4 in TN, it is also possible that such a value  
19 could be reached at a very small scale (e.g., Kim and Or 2019) within the soil pellets produced  
20 by termites by building their nests. Finally, the oxidation of oxalate by oxalotrophic bacteria  
21 can also locally increase the soil pH, making  $\text{CaCO}_3$  precipitation possible in an overall acidic  
22 environment. Enhancement in soil pH increases the cationic exchange capacity of soil organic  
23 matter and 1:1 minerals in soil (Brady and Weil 2010) and therefore its ability to hold nutrients.  
24 Indeed, together with these enrichments in clay, C and N contents, termites also enhanced the  
25 concentrations of exchangeable basic cations and nutrients in their constructions (Jouquet et al.

1 2011; Abe et al. 2011; Bera et al. 2020; Chisanga et al. 2020). Our study confirmed this increase  
2 in soil fertility with higher amount of total P in termite constructs. The impact of termite  
3 bioturbation activity on the amount of available P is usually related to the functional groups to  
4 which termite species belong (López-Hernández et al. 2006). Previous studies showed that  
5 fungus-growing termites increase the sorption of P in soil (i.e., reduce the amount of available  
6 P) in comparison with the surrounding soil (López-Hernández et al. 2006; Bera et al. 2020).  
7 Therefore, more research is needed to determine whether the higher amount of total P in LM  
8 and TN is associated with a higher availability of P in soil.



9 **Figure 5.** Saturated hydraulic conductivity ( $K_{sat}$ ) in lenticular mounds (LM) and control soil  
10 (CTRL) (average values for the three soil groups). Vertical bars are standard errors ( $n =$   
11 13). Histograms with different letters for the same location are significantly different at  $P$   
12  $< 0.05$ .

13

1 **Table 4.** Results of the linear mixed models testing the influence of termite bioturbation (i.e.,  
 2 termite mound nests, lenticular mounds, and reference soil) and soil groups (i.e., GI, GII and  
 3 GIII) on water the content at pF 0, 2.5, 3, 3.5 and 4.2 with elevation as random factor.

4 \*\*\* < 0.001, \*\* < 0.01, \* < 0.05

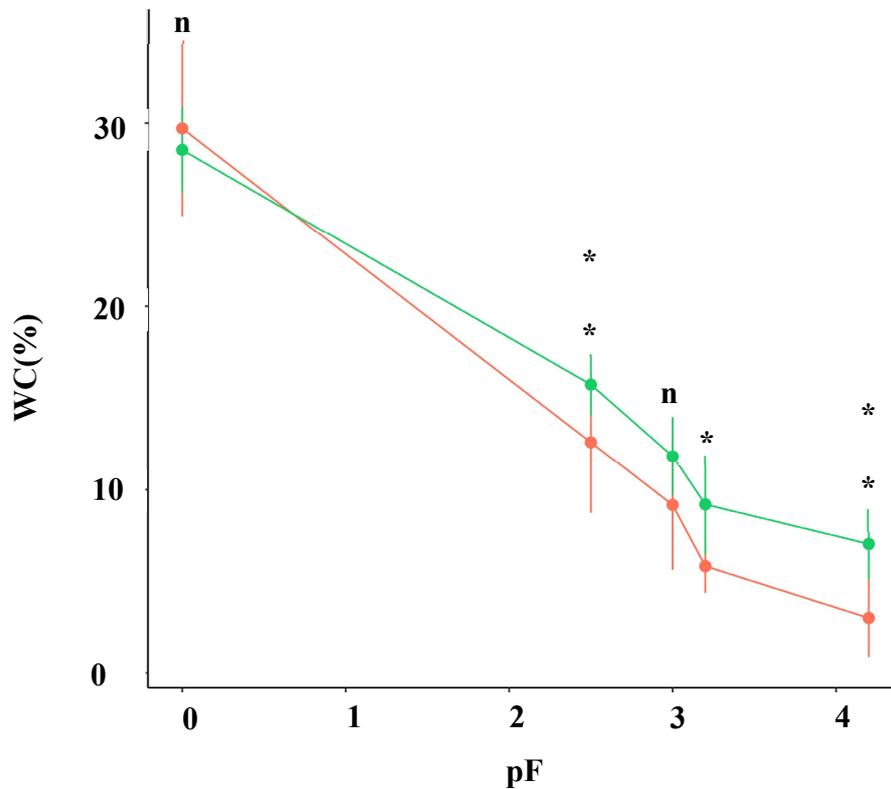
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	Bioturbation (a)		Soil Groups (b)		(a) × (b)	
	<i>F</i> -values	<i>P</i> -values	<i>F</i> -values	<i>P</i> -values	<i>F</i> -values	<i>P</i> -values
pF0	0.38	0.545	0.69	0.590	0.81	0.455
pF2.5	8.24	0.009 **	7.79	0.114	0.02	0.975
pF3	3.31	0.082	13.74	0.068	0.02	0.978
pF3.2	4.95	0.036 *	12.66	0.073	0.11	0.893
pF4.2	14.71	< 0.001 ***	5.96	0.144	0.46	0.638

7

1



2 **Figure 6.** Soil water content at different pFs for the lenticular mound (LM) in green and control  
 3 soils (CTRL) in orange in the different soil groups. Vertical bars are the standard errors,  
 4 and the stars are significantly different at  $P < 0.05$ .

5

## 6 4.2 Termite bioturbation improves soil water dynamics

7 As shown in other ecosystems, sandy soils can be highly susceptible to compaction (Huang and  
 8 Hartemink, 2020). This is especially true in the Lower Mekong Basin when the ploughing of  
 9 soil and the harvesting of rice are mechanized (Gürsoy 2021). At our study site, the high  
 10 compaction of soil is unlikely to be a problem for the cultivation of rice when it is submerged  
 11 by water, and it can even be looked at to avoid the leaching of nutrients (Patel and Singh 1981).  
 12 However, a high bulk density can become a real issue in periods of water shortage (Hoque and  
 13 Kobata 2000) because of the hardness of soil, which can reduce the ability of rice roots to grow

1 (Hasegawa et al., 1985; Iijima et al., 1991). In Cambodia, agriculture is hampered by erratic  
2 rainfall at the beginning of the rainy season, with a temporary period of drought threatening the  
3 seedlings and the growth of rice and thus, rice productivity (Tsubo et al. 2009). Therefore, the  
4 lower bulk density measured in lenticular mounds is interesting because it shows that  
5 bioturbation (i.e., the production of subterranean tunnels by termites and other invertebrates  
6 and the production of macropores by roots) associated with a limited increase in clay particles  
7 and organic matter can significantly improve soil structure and both the infiltration of water  
8 and the water-holding capacity of soil. This was evidenced by the higher values of *K<sub>sat</sub>*  
9 measured in lenticular mounds in comparison with the surrounding topsoil, as well as by the  
10 significantly higher water retention measured at pF 2.5, 3.2, and 4.2.

11 The high compaction (i.e., extremely low soil porosity) of *Macrotermes* spp. termitaria  
12 has been described in several ecosystems (Holt and Lepage 2000; Abe et al. 2009; Traoré et al.  
13 2019; Bera et al. 2020) and explains the extremely high resistance of these soil structures to the  
14 attack of predators and to the weathering impact of rain (Jouquet et al. 2004). Our study  
15 confirmed the very high bulk density of *M. gilvus* termitaria. The water retention curves and  
16 *K<sub>sat</sub>* could not be measured from TN samples. However, the higher clay content in TN but  
17 similar soil bulk density than in CTRL suggested a very specific organization of the soil  
18 porosity and a very low diffusion of water within termitaria.

19

## 20 **5. Conclusion**

21 Two key conclusions and perspectives came out from this study. First, we confirmed that  
22 termite constructions could be seen as nutrient patches in paddy fields, explaining why farmers  
23 use these soil types to improve the fertility of their lands (Noble et al. 2004; Suzuki et al. 2007;  
24 Sarcinelli et al. 2013; Subi and Sheela 2020; Chisanga et al. 2020). In addition to increasing

1 the chemical fertility of soil, the amendment of LM and TN by farmers is also likely to improve  
2 the physical properties of soil. More research is now needed to determine if the amendment of  
3 LM soil can also enhance the water holding capacity of cultivated soils. This impact could be  
4 very important in Cambodian paddy fields, where the management of water is considered to be  
5 a key issue (Chem et al. 2011).

6 Second, we evidenced the presence of carbonates in TN, most likely due to the  
7 stimulation of specific bacteria and fungi associated with the production of carbonate nodules  
8 within microhabitats. This result is especially interesting because, although the concentration  
9 of carbonate is very low, it can favourably impact both the soil fertility and the sequestration  
10 of C in paddy fields, which are known to be important emitters of methane (Li 2010). Therefore,  
11 more research is also needed to identify the ecological processes and biological actors  
12 associated with the production of carbonates in TN and to determine if they could be used to  
13 increase the soil fertility and the sequestration of C in cultivated soils.

14

## 15 **Acknowledgements**

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22 program ARTS).

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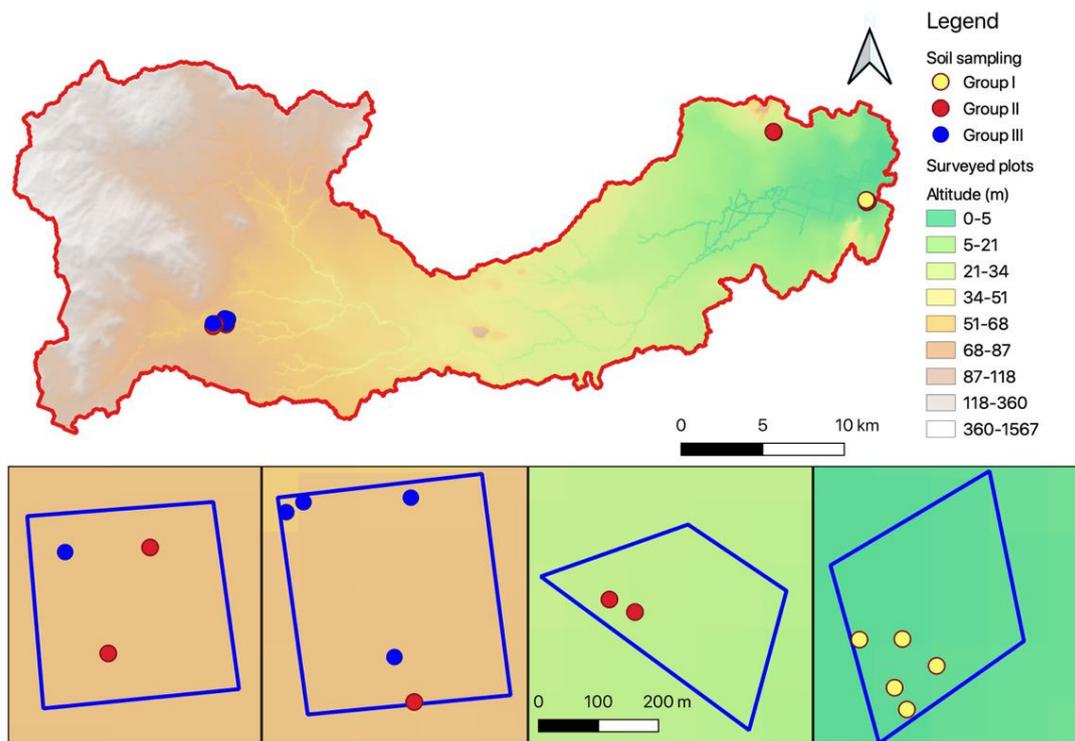
1 **Conflict of interest**

2 Authors declare no competing interests.

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1 **Supplementary file.**

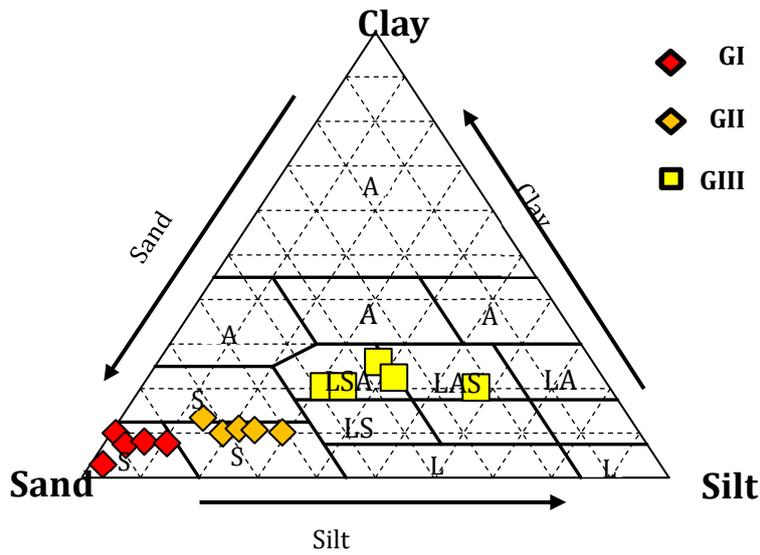


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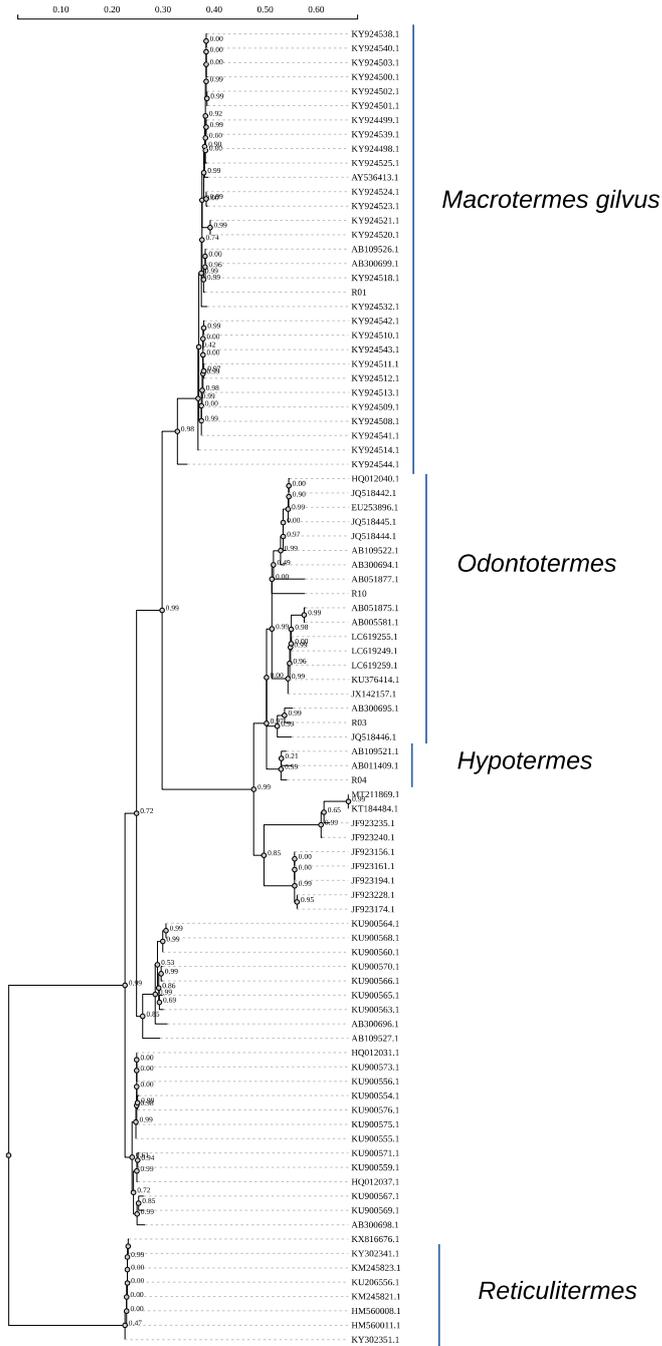
3 S1. Map of the Chrey Bak catchment showing the location of the sampling plots for the three

4 soil groups. The coordinate positions of the centre of the plots are displayed.

1

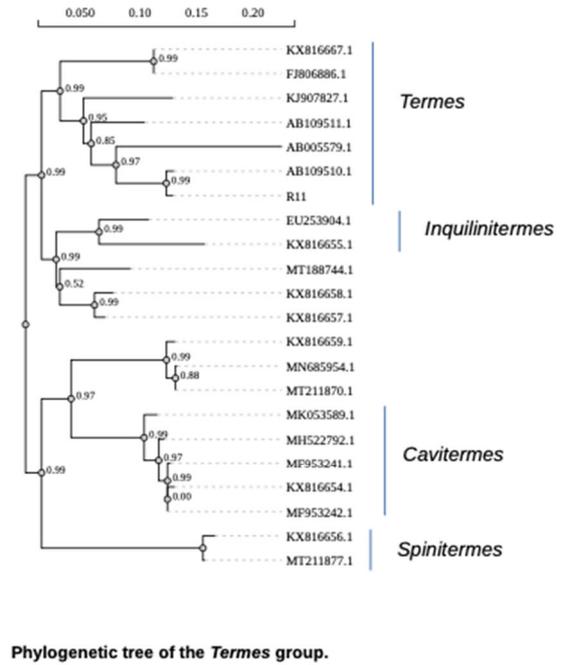
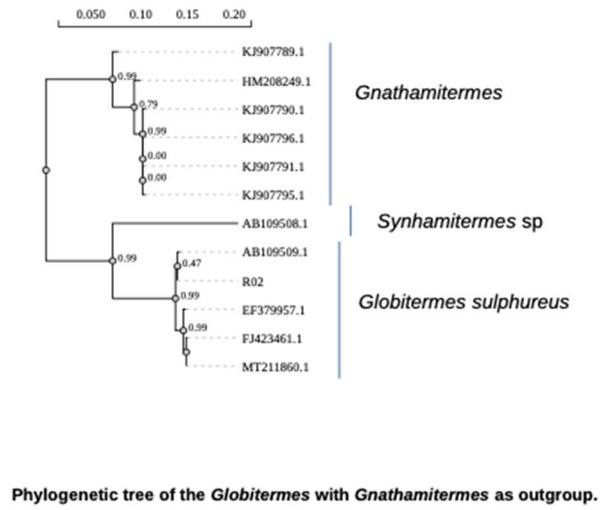


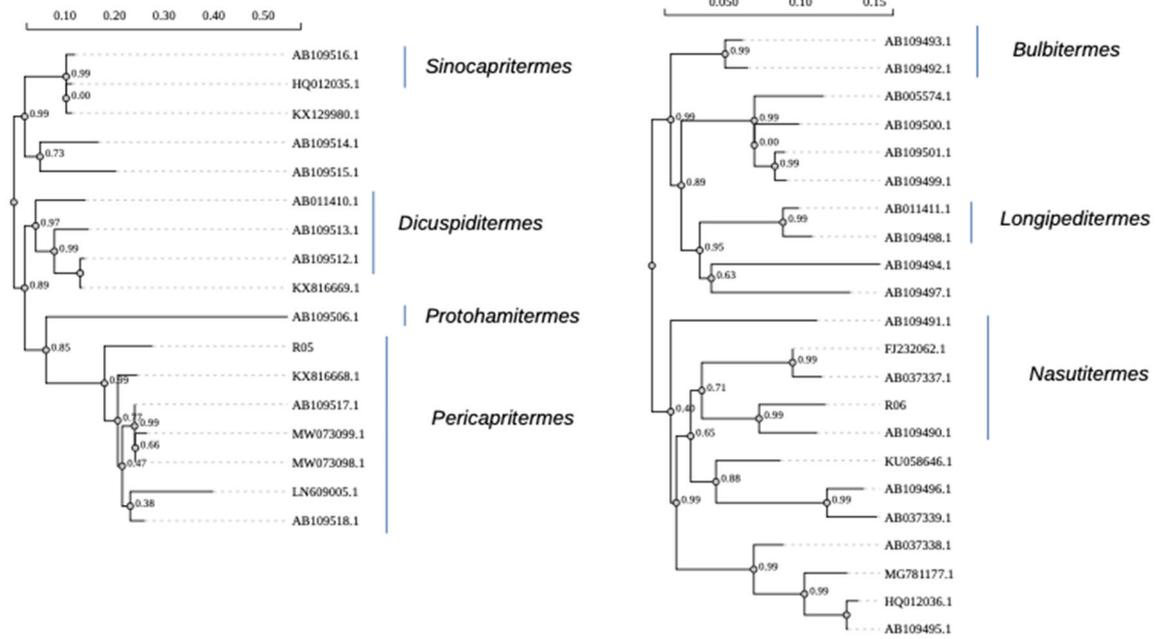
2 S2. Soil texture triangle showing the different soil groups (GI to GIII)



1

Phylogenetic tree of the Macrotermitinae with *Reticulitermes* as outgroup.

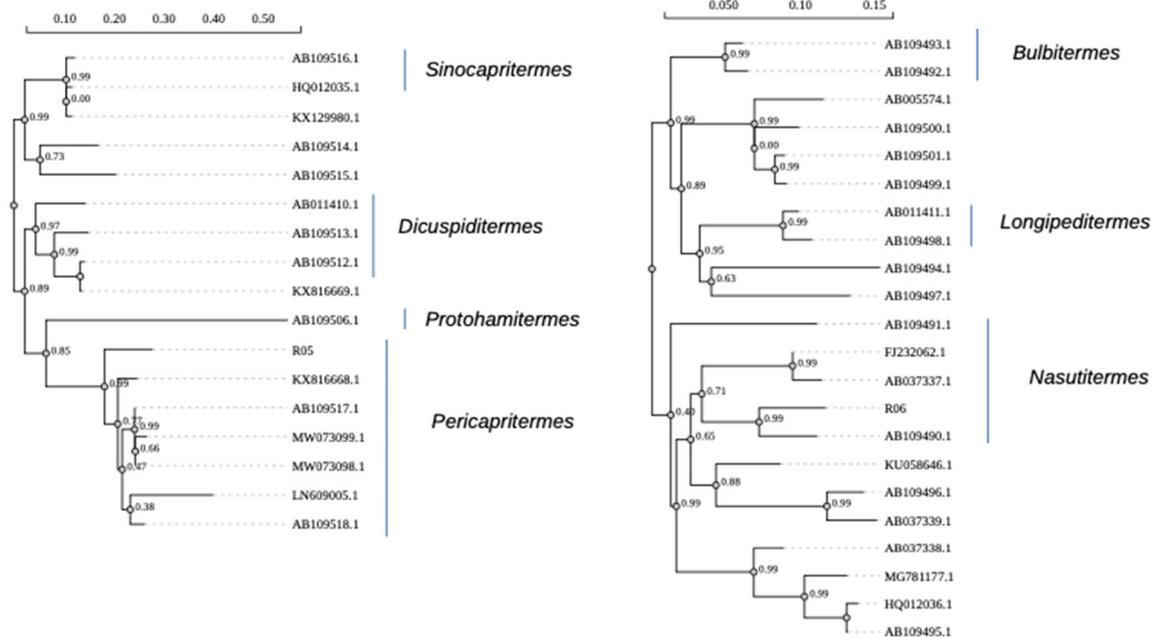




Phylogenetic tree of the *Pericapritermes* group.

Phylogenetic tree of the *Nasutitermes* group.

1

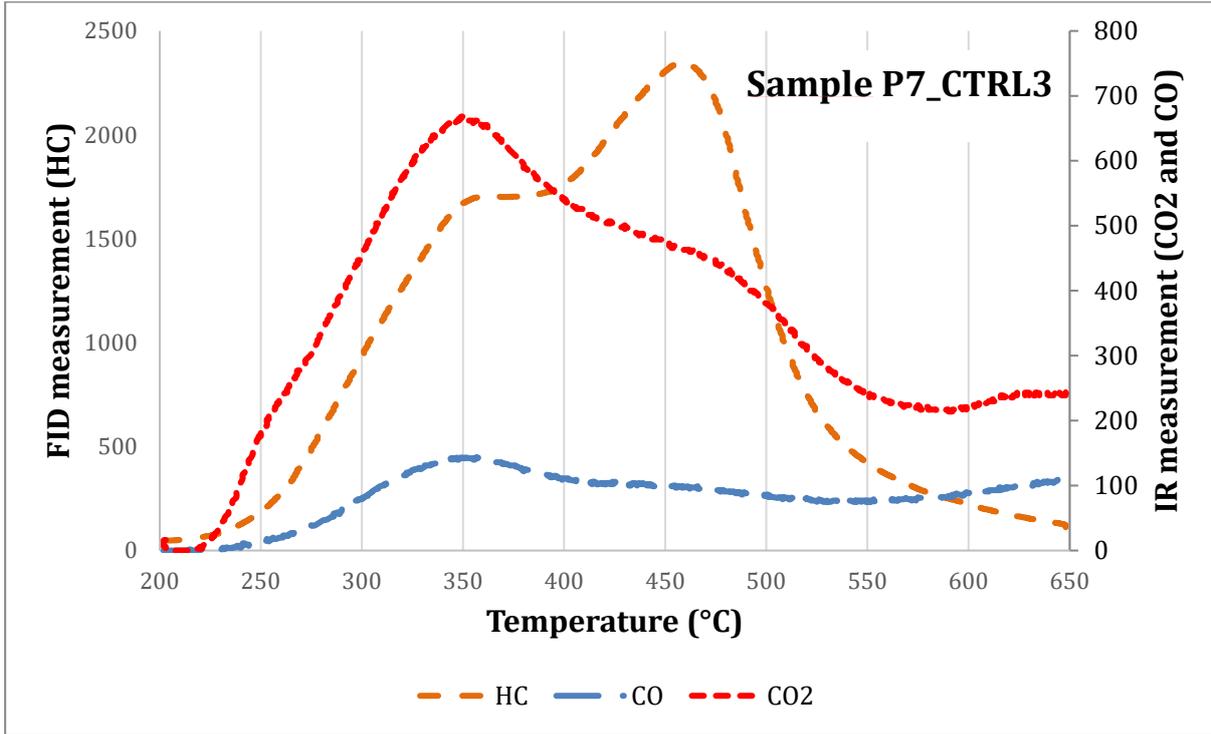


Phylogenetic tree of the *Pericapritermes* group.

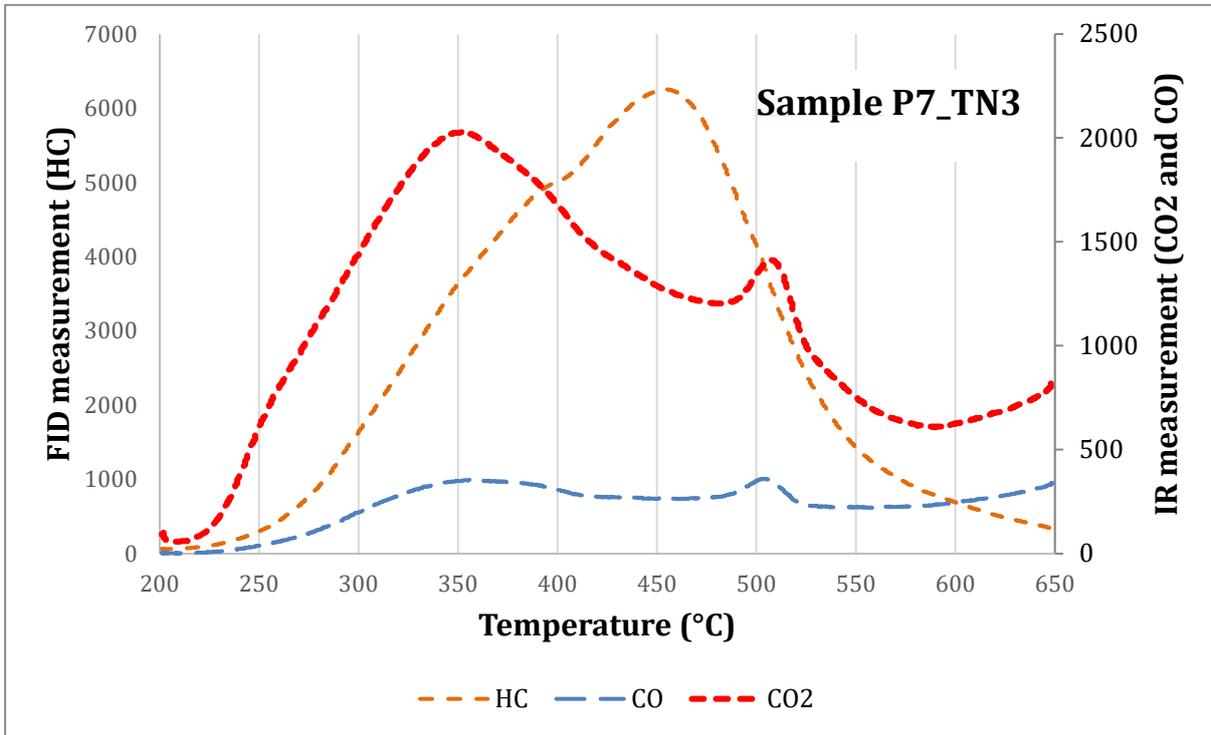
Phylogenetic tree of the *Nasutitermes* group.

2

3 S3. DNA extraction and termite identification



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2



3

4 S4. Examples of thermograms (S2HC, S3CO and S3CO2) obtained by Rock-Eval® pyrolysis  
5 of (A) CTRL samples and (B) TN samples. The existence of a sharp peak between 500 and

1 525°C on the S3CO and S3CO<sub>2</sub> thermograms of the N sample is characteristic of the presence  
2 of oxalates, most likely CaC<sub>2</sub>O<sub>4</sub>.

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