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**RESEARCH PAPER** 

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Chemical properties associated with guts, soil and materials of Odontotermes and Macrotermes species from Kenya

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**Key words:** Termites, mineralization, tropical soils, *Macrotermitinae*.

## **Abstract**

Termites play important roles in carbon and nitrogen cycles thus affecting soil functioning and ecosystem activities. The study focused on analyzing levels of nitrogen, carbon and pH in the guts, soil and mound materials associated with Odontotermes and Macrotermes termites' species. Macro- and micro-elements were also evaluated using spectrophotometer methods. The standard soil analyses and concentrations of various forms of nitrogen and carbon were performed using calometric and Bremmer's methods. Results showed higher clay content in the mounds than the surrounding soil. Most concentrations of ammonia, nitrate and total organic carbon between the termites and within the gut sections were significantly different (p < 0.05). Levels of ammonia (3.00 - 6.00 ppm) and nitrate (6.00 - 11.50 ppm) were highest in the hindguts of all termites analyzed than the respective foreguts and midguts sections. Ammonia (6.00 - 14.50 ppm), nitrate (16.00 - 83.00 ppm) and organic carbon (31.00 - 37.00 %) levels were highest in the fungus comb samples. The levels of all macroand micro-elements investigated were highest in the fungus combs. It can be concluded that fungus-growing termites accumulate different levels of nitrogenous compounds in their guts and modify soil properties in terms of clay, C, N and mineral contents.

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#### Introduction

Termites (Isoptera) are a large and diverse group of terrestrial social insects comprising of over 2600 species worldwide (Ahmed et al., 2011). Termites live from temperate to tropical regions, but the greatest termite diversity is in Africa, where they play diverse roles in semi-arid and humid ecosystems (Eggleton, 2000). They efficiently biodegrade plant biomass and other lignocellulosic material thereby contributing to the global carbon and nitrogen cycles (Freymann et al., 2008; DeSouza et al., 2009). Furthermore, they are recognized as a key group for their impact on soil properties in the tropics which is attributed by their mound construction activities (Holt and Lepage, 2000; Lopez- Hernandez, 2001). As soil engineers, termites have an impact on the soil structure which modifies the soil environment thereby controlling diversity and activity of other soil organisms (Jones et al., 1997; Lavelle et al., 1997). Their major construction activities of complex galleries and mounds partly contribute to soil heterogeneity in the tropical regions and also affect the soil microbial communities (de Bruyn et al., 1990; Manuwa, 2009) Owing to the intensification of agriculture over recent decades and the social and environmental imperative to develop sustainable agricultural practices, there has been increasing attention on the role of soil biodiversity in mediating the main ecological functions of the system (Lavelle et al., 2006). Amongst the soil organisms, fungus-growing termites (Isoptera, sub-family Macrotermitinae) apparently play an important role in soil fertility in tropical ecosystems because of their strong impact on soil physical and chemical properties (Black and Okwakol, 1997; Mora et al., 2003). The fungus-growing termites (subfamily Macrotermitinae) build their mounds using soil and clay cemented by salivary secretions, which make the mounds enriched with clay particles but impoverished in carbon (Harry et al., 2001). The nest-walls consist of organo-mineral aggregates, characterized by a low stability and thus mineralize easily (Garnier-Sillam et al., 1988). They have a wider range of activity on the surrounding soil of 1-3 m in depth and within a range of a 2-8 m, which may influence the soil properties and fertility (Harry et al., 2001; Jouquet et al., 2002a).

Studies regarding the impact of termites on soil properties have previously focused more on soil feeding termites than fungus cultivating termites (Brouman, 2000; Ji and Brune, 2006). Due to the high abundance of the fungus cultivating termites and their major activities in African savannas, the question arises whether these termites can impact soil properties as those observed in soil-feeders (Harry et al., 2001; Fall et al., 2004; Roose-Amsaleg et al., 2004; Fall et al., 2007). Literature indicates that the proportion of clay in the termite-built structures is always greater than that in the bulk soil (Holt and Lepage, 2000) and conspicuous differences have also been observed in their mineralogical properties (Mahaney et al., 1999). Subterranean fungus-growing termites play a major role in maintenance of tropical soil fertility, in terms of clay, C and N contents, as compared to the surrounding soil (Jouquet et al., 2002a,2002b, 2004, 2005). Jouquet et al. (2005) reported a greater impact on soil properties by Odontotermes compared to the Ancistrotermes. Their study concluded that different species within the Macrotermitinae subfamily play different roles in soil organic matter content and clay distribution. However, this has to be confirmed through others similar studies. This study therefore was aimed at determining the levels of different chemical properties associated with guts, mound (nest) materials and soils of some fungus cultivating termites (Odontotermes and Macrotermes species). The results can be applied in agriculture to improve soil properties.

## Materials and methods

Study site and collection of samples

Samples were collected randomly from ten active termite nests around Jomo Kenyatta University of Agriculture and Technology (JKUAT) compound, Juja in Kiambu County (latitude 10 5' 54.68" N, longitude 1' 1.10" W). Termite mounds (nests) (approximately between 1 and 3 km far apart), which

were colonized by Odontotermes and Macrotermes species were excavated to a depth of  $\approx 0.5 - 1.0$  m as described elsewhere (Makonde et al., 2013). Termites (n = 100 workers) were collected and put into sterile plastic boxes. Worker-caste termites were used in the experiments due to their foraging activities during formation and renewal of the fungus gardens. Mound materials (fungus combs) were collected and put into sterile plastic bags. In addition, soil samples from the nests and their surrounding (3 m away from the nest) were collected and put into sterile plastic bags. Collection of all samples was performed in triplicates.

## Physico-chemical analyses

Standard physical soil analyses, which involved texture and bulk density analyses of the soil samples, were performed according to Ackerman et al. (2007). Particle size distribution was determined by the hydrometer method for determining the silt and clay fraction as described by Manuwa (2009). Determination of pH and inorganic nitrogen of the samples were performed according to the methods described by Tanaka (1986). Carbon content was determined by the WalkleyBlack method (Walkley et al., 1934) while ammonia and nitrate concentrations were determined by calometric methods as described by Chaney and Marbach (1962) and Okalebo et al. (2002), respectively. Phosphorus and potassium concentrations were determined by using a spectrophotometer (UV-VIS Spectrophotometer 1240 SHIMADZU-JAPAN) and flame photometry (Flame photometer 410 CORNING-JAPAN), respectively. Concentrations of other elements (calcium, magnesium, iron, manganese, zinc and copper) were determined by using atomic absorption spectrophotometry (AA-62000 SHIMADZU-JAPAN).

## Statistical analyses

The data obtained from the experiments were subjected to statistical analyses using ANOVA as implemented in SARS software (Version 9.0).

#### **Results**

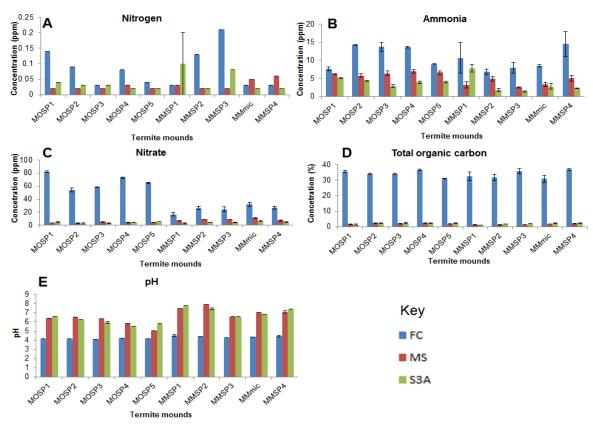
Physico-chemical properties of the soils

The results from the physical properties of the soil generally showed that the texture grade of the soils ranged between sandy clay loamy to loamy across the samples analyzed (Supplementary Table 1). Notably the bulk density (0.61-0.93 gcm3) and the clay content in most of the mounds (Sites 3, 5, 6, 7, 9 and 10) were slightly higher than those in the surrounding soil samples (Supplementary Table 1).

Key: 'FC' denotes fungus comb, 'MS' denotes soil taken from mound, 'S3A' denotes soil taken 3m away from mound. 'MOSP1-MOSP5' denotes different mounds of Odontotermes spp., 'MMSP1-MMSP4' denotes different mounds of Macrotermes spp. and 'MMmic" denotes mound of Macrotermes michaelseni.

Concentrations of inorganic nitrogen forms, carbon and pH in the mounds and surrounding soils

The levels of ammonia (6-15 ppm), nitrate (16-82 ppm) and total organic carbon (31-37 %) in the fungus comb materials were often higher than their corresponding soil samples from the mounds and surroundings (Fig. 1B, C & D). Most of these levels were significantly different (p < 0.05) in the fungus combs across the samples analyzed (Fig. 1B, C & D). The levels of the nitrate (3-11 ppm) in the mound samples were different across the samples but did not differ significantly with those of corresponding surrounding soil samples (2-7 ppm) within a single mound (Fig. 1C). The levels of total organic carbon (TOC) were lower (1-3 %) in all the mound and surrounding soil samples (Fig. 1D). The same trend was also observed for the levels of nitrate in the mound and surrounding soil samples. Nitrogen levels were the least (<0.3 ppm) in all samples but differed significantly in most of the samples. The pH levels were between the acidic to neutral range (pH 5-7) and were significantly different (p < 0.05) between and within most samples analyzed. The results also showed that the pH levels were the least in the fungus combs samples ranging from pH 4-5 (Fig. 1E).



**Fig. 1.** Levels of pH, inorganic and organic minerals in different parts across termite mounds. Key: 'FC' denotes fungus comb, 'MS' denotes soil taken from mound, 'S3A' denotes soil taken 3m away from mound. 'MOSP1-MOSP5' denotes different mounds of Odontotermes spp., 'MMSP1-MMSP4' denotes different

mounds of Macrotermes spp. and 'MMmic" denotes mound of Macrotermes michaelseni.

Table 1. Levels of mineral elements in different parts across termite mounds.

			Termite s	pecies							
Mineral elements (pmm)		s OSP1	OSP2	OSP3	OSP4	OSP5	MSP1	MSP2	MSP3	Mmic	MSP4
K	FC	3.40±0.0°a	3.00±0.0ea	$2.20{\pm}0.0^{h}{}_{b}$	$2.10\pm0.0^{i}_{a}$	2.60±0.0ga	$2.81{\pm}0.0^{f}_{a}$	3.00±0.0ea	3.58±0.0ba	$3.78{\pm}0.0^{a}_{a}$	3.39±0.0da
	MS	1.60±0.0°c	1.50±0.0 <sup>d</sup> c	1.40±0.0°c	1.50±0.0 <sup>d</sup> b	1.50±0.0 <sup>d</sup> b	2.42±0.0 <sup>b</sup> b	0.87±0.0h	1.06±0.0g <sub>b</sub>	3.00±0.0a <sub>b</sub>	1.26±0.0fc
Ca Mg	S3A FC MS S3A FC	4.58±0.1 <sup>h</sup> a 2.67±0.2 <sup>f</sup> b 2.44±0.1 <sup>f</sup> b	5.91±0.0 <sup>cd</sup> a 4.20±0.0 <sup>e</sup> b 4.07±0.0 <sup>d</sup> c	7.78±0.0 <sup>a</sup> <sub>a</sub> 5.51±0.0 <sup>c</sup> <sub>b</sub> 5.58±0.0 <sup>a</sup> <sub>b</sub>	$6.35\pm0.1^{b}{}_{a}$ $4.65\pm0.1^{d}{}_{b}$ $4.55\pm0.1^{b}{}_{b}$	5.94±0.0 <sup>c</sup> a 5.81±0.0 <sup>b</sup> b 5.42±0.0 <sup>a</sup> c	$5.48 \pm 0.0 ^{g}_{a}$ $2.66 \pm 0.0 ^{f}_{b}$ $2.73 \pm 0.1 ^{e}_{b}$	5.63±0.0 <sup>f</sup> a 4.32±0.1 <sup>e</sup> b 4.28±0.1 <sup>c</sup> b	7.90±0.0 <sup>a</sup> a 4.39±0.1 <sup>e</sup> b 4.41±0.0 <sup>bc</sup> t	$2.03\pm0.0^{d}_{c}$ $5.78\pm0.0^{de}_{a}$ $2.73\pm0.0^{f}_{c}$ $2.80\pm0.0^{e}_{b}$ $2.89\pm0.5^{bc}_{a}$	5.74±0.0 <sup>ef</sup> l 7.29±0.0 <sup>a</sup> a 2.76±0.1 <sup>e</sup> c
Zn	MS S3A FC MS S3A	2.45±0.1 <sup>abc</sup> b 0.25±0.0 <sup>e</sup> a 0.17±0.0 <sup>c</sup> c	0.45±0.0° <sub>c</sub> 0.45±0.0° <sub>a</sub> 0.14±0.0° <sub>b</sub>	2.09±0.0 <sup>d</sup> b 0.26±0.0 <sup>e</sup> a 0.11±0.0 <sup>e</sup> b	$2.08\pm0.0^{d}_{b}$ $0.87\pm0.1^{a}_{a}$ $0.25\pm0.0^{b}_{b}$	2.71±0.1 <sup>a</sup> a 0.37±0.0 <sup>d</sup> a 0.12±0.0 <sup>e</sup> b	$2.34\pm0.3^{bcd}$ $0.28\pm0.0^{e_{a}}$ $0.15\pm0.0^{cd}$	0.59±0.0 <sup>a</sup> a	$2.07\pm0.1^{d}_{b}$ $0.26\pm0.0^{e}_{a}$ $0.10\pm0.0^{e}_{c}$	$\begin{aligned} 2.26 &\pm 0.4^{cd}{}_{al} \\ 2.13 &\pm 0.6^{cd}{}_{b} \\ 0.24 &\pm 0.0^{e}{}_{b} \\ 0.17 &\pm 0.0^{c}{}_{c} \\ 0.34 &\pm 0.0^{a}{}_{a} \end{aligned}$	2.61±0.0 <sup>ab</sup> 0.37±0.0 <sup>d</sup> 0.17±0.0 <sup>cd</sup>

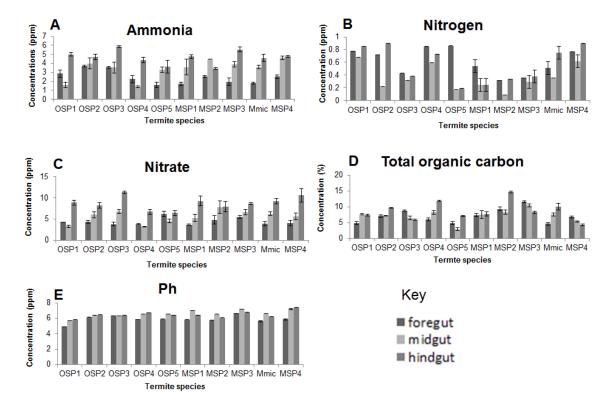
Key: Values indicate means ± standard deviation. FC' denotes fungus comb, 'MS' denotes soil taken from mound, 'S3A' denotes soil taken 3m away from mound. 'MOSP1-MOSP5' denotes different mounds (1-5) of Odontotermes spp., 'MMSP1-MMSP4' denotes different mounds (1-4) of Macrotermes spp. and 'MMmic' denotes mound of Macrotermes michaelseni.

<sup>\*</sup>Superscript letter - indicates difference between termite mounds.

\*Subscript letter – indicates difference within termite mounds. Concentrations of inorganic nitrogen forms, carbon and pH in the gut sections

The concentrations of inorganic nitrogen forms, for instance ammonia (3-6 ppm) and nitrate (6-12 ppm) were generally higher in the hind guts (Fig. 2A & C). Notably, most ammonia and nitrate concentrations differed significantly (p<0.05) between gut sections. The nitrogen levels were generally low (<1 ppm) in all

samples with variations slightly between and within gut sections (Fig. 2B). The levels TOC ranged from 4 to 15 % but varied significantly (p<0.05) across most samples analyzed. The pH levels of most of the gut sections were within the acidic range (pH 5-6) and differed significantly between some termite's species (Fig. 2E).



**Fig. 2.** Levels of pH, inorganic and organic minerals in different gut sections across termite species. Key: 'Foregut, midgut, hindgut' denotes gut sections of the termite. 'OSP1-OSP5' denotes different Odontotermes spp., 'MSP1-MSP4' denotes different Macrotermes spp. and 'Mmic" denotes Macrotermes michaelseni.

Levels of mineral elements in samples associated with different termite mounds. The levels of all mineral elements investigated were relatively higher in the fungus combs compared to the soils samples from the mounds and their surroundings (Table 1). This trend was observed for all the analyzed samples. Most of the zinc (0.2-0.9 ppm), iron (1-6 ppm) and phosphorous (1-3 ppm) levels in the fungus combs between the samples were almost the same. For instance, the levels of zinc in the fungus combs of mounds (MOSP1 [0.25 ppm], MOSP2 [0.45 ppm] and MOPS3 [0.26

ppm]), which were colonized by Odontotermes species and mounds (MMSP1 [0.28 ppm] and MMSP3 [0.26 ppm] of Macrotermes species and that of M. michaelseni (MMmic [0.24 ppm] were not significantly different from one another (Table 1). Of the eight mineral elements determined, manganese (8-21 ppm) had the highest concentration while copper (0.10-0.3 ppm) had the least levels, followed by zinc (0.2-0.9 ppm) in the fungus combs.

There were significant differences in levels of copper, manganese, potassium, calcium and magnesium between the samples but most calcium and magnesium levels were almost the same within the mound and surrounding soil samples analyzed (Table 1). For example, the levels of calcium in the mound and surrounding soil samples of mounds (MOSP1, MOSP3 and MOSP4 belonging to Odontotermes species and mounds (MMSP1, MMSP2 and MMSP3 of Macrotermes species were different. The differences in levels of the mineral elements in the various soil samples investigated indicate that the distribution of these elements in the soils is not homogenous.

### Discussion

The construction activities of termites play an important role in soil heterogeneity and fertility in tropical ecosystems due to the impact on soil physical and chemical properties. Our results indicate some changes on the physical properties of the soil samples analyzed. The texture grade of the soils ranged between sandy clay loamy to loamy across the samples, but the clay content in most mounds was relatively higher than in the surrounding soil (Supplementary Table 1). This shows that the soils in the mounds are enriched with clay particles as a result of termite activities due to preferred selection of clay particles by termites (Harry et al., 2001). This is in consistent with other findings by Manuwa (2009). Literature indicates that fungus growing termites build their mounds using soil and clay cemented by salivary secretions, which make the mounds enriched with clay particles impoverished in carbon (Harry et al., 2001). This underlines the influence of construction activities of termites on the physical properties of the soil (Holt, 2000; Manuwa, 2009), which may have a positive influence in organic matter content and water holding capacity of the soil within the mound compared to the surrounding soils (Lavelle et al., 1994).

There were significant differences concentrations of most inorganic nitrogen forms (such as ammonia, nitrates and total inorganic nitrogen) between the termite species and within the gut sections (Fig. 2A - D). Notably, ammonia and nitrates concentrations of the individual gut sections significantly differed and were often detected in higher levels within the hindguts than the corresponding gut sections (fore- and mid-guts) of all termite species analyzed (Fig. 2A, C) Nitrogen levels were relatively low but significantly different between some termite species and within some gut sections (Fig. 2B). Likewise, the levels of total organic carbon varied significantly across most of the samples (Fig. 2D). These results may demonstrate that different termites accumulate different levels of inorganic minerals in their respective gut sections in the course of their diet (Ji and Brune, 2006). However, there were insignificant differences in the pH values of the gut sections of most termites' species (Fig. 2E), which partly contradicts other findings elsewhere (Bignell and Eggleton, 1995) that reported different pH levels in gut sections of different termite species.

Levels of most inorganic nitrogen forms and organic carbon differed significantly amongst the comb materials and soil samples collected on the mound and 3m away (Fig. 1A-D). Remarkably, the levels of ammonia, nitrate and organic carbon were often higher in the comb materials than the corresponding soil samples for all mounds studied. A similar trend was also observed for levels of nitrogen in some mounds (Fig. 1B). This demonstrates that comb materials are rich in nitrogenous wastes and other organic carbon, which accumulate in the comb materials as the termites use their feces to make the fungus combs (Eggleton and Tayasu, 2001). The pH values ranged from acidic to neutral range (ph5-7) and were significantly different between and within most mounds (Fig. 1E). Similar pH values were observed in the gut sections, however, it should be noted that pH values were the least in the fungus combs samples. This may partly be due to the high levels of nitrate and organic carbon present in the fungus combs that tend to lower the pH. These findings show that fungus combs and soil in mounds

of different termites accumulate different amount of inorganic material and organic carbon during renewal and establishment of mounds.

The micro- and macro-elements investigated were relatively higher in the fungus combs compared to the soils samples from the mounds and their corresponding surroundings (Table 1). However, there were insignificant differences of zinc, iron and phosphorous levels in the fungus combs between the mound samples. For instance, the levels of zinc in the fungus combs from mounds MOSP1, MOSP2 and MOSP3 (colonized by Odontotermes species) and mounds MMSP1, MMSP3 and Mmic (colonized by Macrotermes species) were almost similar (Table 1). Of the eight elements determined, manganese had the highest concentration while copper had the least levels, followed by zinc in the fungus combs (Table 1). The accumulation of these elements may have important roles in the fungus combs. Literature indicates that fungus combs harbor termites and their mutualistic fungi mostly from the genera Xylaria and Termitomyces (Moriya et al., 2005; Makonde et al., 2013). Therefore, the micro- and macro-elements present in the combs may be crucial for growth and survival of these mutualistic fungi. Notably, significant differences in levels of copper, manganese, potassium, calcium and magnesium were observed between the samples analyzed (Table 1). For example, the levels of calcium in the mound and surrounding soil samples of mounds MOSP1, MOSP3 and MOSP4 (colonized by Odontotermes species) and mounds MMSP1, MMSP2 and MMSP3 (colonized by Macrotermes species) differed significantly. These results indicate that the distribution of these elements in the soils is not homogenous.

It has been reported that the modifications in soil organic matter, clay content, and soil quality as a result of termites' activities lead to a decrease in soil porosity, a stimulation of microbial activity and an enrichment in mineral nutrients like NH4+ and NO3- and exchangeable cations such as Ca2+, Mg2+, K+ and Na+, as compared to the surrounding soil (Holt and Lepage, 2000; Jouquet et al., 2004). Organic compounds particularly carbon and nitrogen also become more abundant in the fungus combs than in the surrounding soils as observed in this study (Fig. 1B and D).

#### Conclusion

Termites and the termitosphere play a crucial role in the cycling of nutrients in their ecosystems. Comparing the nutrient concentrations from the surrounding soils to the mound samples, it is clear that termite activity increases the amount of nutrients and therefore influences nutrient availability in their ecosystems. Soil analysis showed an increase in clay percent in the mound soils as compared to the surrounding soils. One reason of this may be related to preferred selection of clay particles by termites during establishment of mounds. Our results, therefore, underscore the major role played by fungus-growing termites in the maintenance of tropical soil fertility, in terms of clay, C and N contents in relation to the surrounding soil.

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#### References

Aanen DK, Eggleton P, Rouland-Lefevre C, Guldberg-Froslev T, Rosendahl S, Boomsma JJ. 2002. The evolution of fungus growing termites and their mutualistic fungal symbionts. Proceedings of the National Academy of Sciences 99, 14887-14892.

Ackerman IL, Wenceslau GT, Susan JR, Johannes L, Erick CM. 2007. The impact of mound-building termites on surface soil properties in a secondary forest of Central Amazonia. Applied Soil Ecolology 37, 267-276.

Ahmed BM, Nkunika POY, Sileshi WG, French JRJ, Nyeko P, Jain S. 2011. Potential Impact of Climate Change on Termite Distribution in Africa. British Journal of Environment and Climate Change 1, 172-189.

Bignell DE, Eggleton P. 1995. On the elevated intestinal pH of higher termites (Isoptera: Termitidae). Insect Sociaux 42, 57-69.

Black HIJ, Okwakol MJN. 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites. Applied Soil Ecology **6**, 37–53.

Brauman A. 2000. Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: Annual review. European Journal of Soil Biology 36, 117-125.

Chaney AL, Marbach EP. 1962. Modified reagents for the determination of urea and ammonia. Clinical Chemistry 8, 130-132.

DeSouza O, Araújo APA, Reis-Jr R. 2009. Trophic controls delaying foraging by termites: reasons for the ground being brown? Bulleting in Entomological Response 99, 603-609.

Eggleton P, Tayasu I. 2001. Feeding groups, life types and the global ecology of termites. Ecolological Response 16, 941-960.

Eggleton P. 2000. Global patterns of termite diversity. In Abe T, Bignell DE Higashi M, ed. Termites: evolution, sociality, symbioses, ecology volume one. Dordrecht, The Netherlands: Kluwer Academic publisher. 25-51.

Fall S, Hamelin J, Ndiaye F, Assigbetse K, Aragno M, Chotte JL, Brauman A. 2007. Differences between bacterial communities in the Gut of a Soil-Feeding Termite (Cubitermes niokoloensis) and Its Mounds. Applied Environmental Microbiology 73, 5199-5208.

Fall S, Nazaret S, Chotte JL, Brauman A. 2004. Bacterial density and community structure associated with aggregate size fractions of soil-feeding termite mounds. Microbial Ecolology 28, 191-199.

Freymann BP, Buitenwerf R, DeSouza O, Olff H. 2008. The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review. European Journal Entomology 105, 165-173.

Garnier-Sillam E, Toutain F, Renoux J. 1988. Comparaison de l'influence de deux termitie`res (humivore et champignonniste) surla stabilite' structurale des sols forestiers tropicaux. Pedobiology **32**, 89-97.

Harry M, Jusseaume N, Gambier B, Garnier-Sillam E. 2001. Use of RAPD markers for the study of microbial community similarity from termite mounds and tropical soils. Soil Biolology and Biochemistry **33**, 417–427.

Holt JA, Lepage M. 2000. Termites and soil properties. In: Abe T, Bignell DE, Higashi M, eds. Termites: Evolution, Sociality, Symbioses, Ecology volume one. Dordrecht, The Netherlands: Kluwer Academic Publishers. 25-51.

Ji R, Brune A. 2006. Nitrogen mineralization, ammonia accumulation and emmision of gaseous NH<sub>3</sub> by soil feeding termites. Biogeochemistry **78**, 267-283.

Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946-1957.

Jouquet P, Lepage M, Velde B. 2002a. Termite soil preferences and particle selections: strategies related to ecological requirements. Insect Sociaux 49, 1-7.

Jouquet P, Mamou L, Lepage M, Velde B. 2002b. Effect of termites on clay minerals in tropical soils: fungus-growing termites as weathering agents. European Journal of Soil Science 53, 521-527.

Jouquet P, Mery T, Rouland C, Lepage M. 2003. Modulated effect of the termite *Ancistrotermes* cavithorax (Isoptera, Macrotermitinae) on soil properties according to the structures built. Sociobiology **42**, 403-412.

Jouquet P, Tessier D, Lepage M. 2004. The soil structural stability of termite nests: role of clays in Macrotermes bellicosus (Isoptera, Macrotermitinae) mound soils. European Journal of Soil Biolology 40, 23-29.

Katoh H, Miura T, Maekawa K, Shinzato N, Matsumoto T. 2002. Genetic variation of symbiotic fungi cultivated by the macrotermitinae termite Odontotermes formosanus (Isoptera: Termitidae) in the Ryukyu Archipelago. Molecular Ecology 11, 1565-1572.

Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillion S. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology 33, 159-193.

Lavelle Ρ, Dangefield C, Fragoso С, Eschenbrenner D, Lopez HD, Pashanasi B, Brussard L. 1994. The relationship between soil macro fauna and tropical soil fertility. In: Woomer PL, Swift MJ, ed. The biological management of tropical soil fertility. UK: John Wiley and sons. 137-169.

Lavelle PT, Decaëns M, Aubert S, Barot M, Blouin F, Bureau P, Margerie P, Mora, J-P Rossi. 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology 42, (Suppl. 1) S3eS15 ICSZ-Soil Animals and Ecosystems Services, Proceedings of the XIVth International Colloquium on Soil Biology.

Lopez-Hernandez D. 2001. Nutrient dynamics (C, N, P) in termite mounds of Nasutitermes ephratae from savannas of the Orinoco Lia nos (Venezuela). Siol Biollogy and Biochemistry 33, 747-753.

Makonde HM, Boga HI, Osiemo Z, Mwirichia R, Stielow JB, Göker M, Klenk H-P. 2013. Diversity of Termitomyces Associated with Fungus-Farming Termites Assessed by Cultural and Culture-Independent Methods. PLoS ONE 8(2), e56464. doi:10.1371/journal.pone.0056464.

Manuwa SI. 2009. Physico-chemical and dynamic properties of termite mound soil Relevant in sustainable food production. African Crop Science Society 9, 356-369.

Mora P, Seugé C, Chotte JL, Rouland C. 2003. Physico-chemical typology of the biogenic structures of termites and earthworms: a comparative analysis. Biology of Fertile Soil 37, 245-249.

Moriya S, Inoue T, Ohkuma M, Yaovapa T, Johjima T, Suwanarit P, Sangwani U, Vongkaluang C, Noparatnaraporn N, Kudo T. 2005. Fungal Community Analysis of Fungus gardens in termite nests. Microbes Environment 20, 243-252.

Noirot C. 1992. From wood- to humus-feeding: an important trend in termite evolution. In: Billen J, ed. Biology and Evolution of Social Insects. Leuven, Belgium: Leuven University Press. 107-119.

Okalebo JR, Githua WG, Wooma P. 2002. Laboratoty methods of soil and plant analysis: A working manual. 2nd edition. TSBF- CIAT and sacred Africa.

**Roose-Amsaleg C, Brygoo Y, Harry M.** 2004. Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest. Environmental Microbiology **6**, 462–469.

**Tanaka U.** 1986. Procedures for Soil Analysis. Technical cooperation project of JKUAT, Kenya. 19-57.

**Walkley A, Black IA.** 1934. An examination of the Degtjareff method for determining soil organic matter and proposed modification of the chromic acid titration method. Soil Science **37**, 29–38.

Supplementary Table 1: Soil physical properties data.

Site	Sample	Average tex	ture class	Bulk density gcm <sup>-3</sup>	Texture Grade
1	Soil	% SANDY	59.1		
		% CLAY	30		
		% SILT	10.9	0.83	SANDY CLAY LOAMY
	Mound	% SANDY	59.1		
		% CLAY	34		
		% SILT	10.9	0.61	SANDY CLAY LOAMY
2	Soil	% SANDY	61.6		
		% CLAY	32.5		
	_	% SILT	5.9	0.92	SANDY CLAY LOAM
	Mound	% SANDY	49.1		
		% CLAY	40	_	
		% SILT	10.9	0.8	SANDY CLAY
3	Soil	% SANDY	69.1		
		% CLAY	27.5		
	3.5 1	% SILT	3.4	0.73	SANDY CLAY LOAM
	Mound	% SANDY	66.6		
		% CLAY	30		GT 1777 G 177
	a 11	% SILT	3.4	0.68	CLAY LOAM
4	Soil	% SANDY	69.1		
		% CLAY	27.5		
	3.6 1	% SILT	27.5	1.01	SANDY CLAY LOAMY
	Mound	% SANDY	69.1		
		% CLAY	30	0.00	CANDYCIAVIOAMY
_	0-:1	% SILT	5.9	0.93	SANDY CLAY LOAMY
5	Soil	% SANDY	61.6		
		% CLAY	32.5	0.60	CANDYLOAM
	Mound	% SILT	3.4	0.69	SANDY LOAM
	Mound	% SANDY	56.6		
		% CLAY	40	0.50	CANDVCIAVICANA
		% SILT	5.9	0.59	SANDY CLAY LOAM

Continuation of Supplementary **Table 1**, soil physical properties data.

Site	Sample	Average texture	e class	Bulk density gcm <sup>-3</sup>	Texture Grade
6	Soil	% SANDY	81.6		
		% CLAY	10		
		% SILT	8.4	0.71	LOAMY SAND
	Mound	% SANDY	79.1		
		% CLAY	15		
		% SILT	5.9	0.62	SANDY CLAY LOAM
7	Soil	% SANDY	84.1		
		% CLAY	10		
		% SILT	5.9	0.81	LOAMY SAND
	Mound	% SANDY	71.6		
		% CLAY	20		
_		% SILT	8.4	0.89	SANDY CLAY LOAM
8	Soil	% SANDY	74.1		
		% CLAY	12.5		
		% SILT	13.4	0.69	SAND LOAM
	Mound	% SANDY	74.1		
		% CLAY	20		
	- ••	% SILT	5.9	0.67	SANDY CLAY LOAMY
9	Soil	% SANDY	84.1		
		% CLAY	7.5		
		% SILT	8.4	0.75	LOAMY SAND
	Mound	% SANDY	86.6		
		% CLAY	10		
	~ !!	% SILT	3.4	0.66	LOAMY SAND
10	Soil	% SANDY	89.1		
		% CLAY	7.5		G.1375
	3.6	% SILT	3.4	1.26	SAND
	Mound	% SANDY	81.6		
		% CLAY	10		
		% SILT	8.4	0.9	LOAMY SAND