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Effect of termite mounds on soil microbial communities and microbial processes: Implications for soil carbon and nitrogen cycling

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ABSTRACT

Fungus-feeding termites are considered to be ecosystem engineers because of their ability to construct massive and complex mounds with different soil physicochemical and biological properties in tropical ecosystems. However, the impact of the termite nesting process on soil microbial communities and microbial functions related to nutrient cycling is poorly understood. In this study, we investigated termite-induced changes in soil microbial communities and their nutrient cycling functions within termite mounds (i.e. live mounds and abandoned mounds) in the humid tropical region of Southwest China. We found that the live mounds harbour intermediate microbial community richness (i.e. PLFAs, fungi, bacteria, G+, and G- bacteria) between surrounding topsoils and deep soils, with the ratio of fungi to bacteria (F:B) in mounds being significantly higher than in surrounding soils. However, the microbial communities gradually transformed to resemble the surrounding soils after the mounds were abandoned because of natural weathering and plant invasion. A relatively more uniform distribution of microbial communities was found within live mounds than in abandoned mounds and surrounding soils, suggesting that termites shaped the environment within the mounds, leading to the homogenisation of microbial communities. In addition, the termite-induced changes of soil physicochemical properties (e.g. water content, pH, organic matter, total N and P) were closely linked to microbial communities. We also observed a reduction in microbial processes associated with nutrient cycling, including microbial respiration, and extracellular enzymatic activities, in mounds relative to the surrounding topsoils. These findings have important implications for exploring microbial communities within termite mounds, which is critical to understand the potential role of termites in regulating soil carbon and nitrogen cycling in tropical ecosystems.

1. Introduction

Termites are primary ecosystem engineers that play vital roles in tropical and subtropical ecosystems (Ashton et al., 2019). Some termites, such as fungus-cultivating species, could build magnificent architecture (i.e. termite mounds), which not only provides a comfortable place to feed and escape from predators, but also has been the hot issues for environment research for their contribution to nutrient cycling (Levick et al., 2010; Seymour et al., 2014). Termite mounds are generally recognised as 'fertility islands' because of their nutrient-rich structure, shaping vegetation clustering, and increasing landscape diversity (Levick et al., 2010; Bonachela et al., 2015). Furthermore, nutrient transformations with continuous leaching from mounds can enhance nutrient levels in the surrounding soils and increase the resilience and resistance of the ecosystems to drought (Bonachela et al., 2015; Ashton et al., 2019). Therefore, termite mounds play central roles in nutrient fixation and cycling in terrestrial ecosystems, which has been well documented in the case of C, N, and P cycling (Jouquet et al., 2017; Chen et al., 2018; Jouquet et al., 2020; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c). Previous studies have proposed several hypotheses for differences in nutrient stoichiometry caused by termite mounds, such as the nutrient status of neighbouring soils and their preferential selection, transportation, and ingestion by termites (Jouquet et al., 2007; López-Hernández, 2001; Chen et al., 2018; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c). In this context, mound characteristics may also lead to changes in thriving soil microbial communities and associated microbial processes (Baker et al., 2020); however, termite–microbe interactions and their impact on nutrient cycling processes in tropical ecosystems have been less studied.

Termites can change soil microbial communities and functions by

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feeding, nest building, littering activities, and modifying the physicochemical properties of mounds, which are an integral part of ecosystem functions relevant to global climate change (Harry et al., 2001; Chiri et al., 2021; Yan et al., 2021). Previous studies have demonstrated that a relatively nutrient-rich environment in termite mounds attracts and supports more fungal and bacterial communities than nutrient-poor surrounding soils in savanna systems (Chiri et al., 2021; Yan et al., 2021). Termites can also promote the speciation of microbial communities within mounds. For instance, Chen et al. (2021a) showed that fungal and bacterial communities in mounds have specific ecological niches through deterministic selection (rather than stochastic forces), and the fungi were more influenced by deterministic processes than bacteria, resulting in a higher F:B ratio in mounds in savanna systems. The speciation of microbial communities is mainly attributed to the improvement of soil organic matter and micro- and macro-nutrients in mounds relative to surroundings. Mounds have higher relative abundances of copiotrophic microbes that thrive in nutrient-rich environments and lower abundances of oligotrophic groups that prefer nutrient-limited conditions (Baker et al., 2020). However, this case is not observed in tropical forests, where termite mounds generally have lower concentrations and stocks of nutrients than the surrounding top soils (Jouquet et al., 2015; Chen et al., 2018; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c). Hence, termite mounds in tropical forests may provide nutrient-poor and competitive environments for microbial communities. Moreover, microbial communities and microbial processes may also be influenced by termite-induced changes in physicochemical properties (e.g. soil water content, pH, electrical conductivity), which depend on the underlying soil and climate. Therefore, exploring the changes in soil microbial communities and microbial processes caused by termite mounds in humid tropical forests would be worthwhile.

Changes in the soil microbial and biochemical properties of termite mounds may influence soil nutrient availability because microorganisms play a central role in elemental cycling and are sensitive to alternations in soil conditions (Maharjan et al., 2017). For instance, termites could increase the fungal to bacterial biomass ratio, which can alter organic matter decomposition because fungi have higher decomposition efficiency and greater soil carbon (C) storage potential than bacteria (Malik et al., 2016; Liu et al., 2018, Guo et al., 2020). In addition, microorganisms produce extracellular enzymes involved in organic matter decomposition and nutrient cycling (Arnosti, 2011), and termite mounds may influence these enzyme activities. Thus, exploring changes in microbial processes, such as extracellular enzyme activities linked to carbon, nitrogen, and phosphorus cycles in tropical forest mounds is necessary.

The termite mound becomes aged or abandoned over time because of weathering and the absence of termite building activities, resulting in variations in soil properties relative to live mounds and surrounding soils (Menichetti et al., 2014; Chen et al., 2018; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c). Thus, the impact of live and abandoned mounds on soil microbial communities and microbial processes should be considered to determine their comprehensive role in nutrient cycling. Hence, this study aimed to (1) assess the impact of termite nesting activities on soil microbial communities and microbial biomass using mounds (i.e. live mounds and abandoned mounds) as their niche; and (2) explore the relationship between microbial communities and associated microbial processes related to C and N cycling in termite mounds. We hypothesised that termite would affect the microbial community directly or indirectly by changing physicochemical properties and functions in termite mounds. Changes in microbial communities lead to variations in soil C and N cycling by modifying extracellular enzyme activities in mounds. Moreover, we hypothesised that the microbial community and microbial processes in abandoned mounds tend to resemble surrounding soils because of natural weathering and plant invasion.

2. Materials and methods

2.1. Study site and experimental design

This study was conducted in Menglun Town, Xishuangbanna National Nature Reserve, Southwest China (21°55′39″ N, 101°15′55″ E). The local climate was dominated by the tropical southern monsoon associated with contrasting seasons, that is, the dry season (November–April) and wet season (May–October). The mean precipitation in this region is 1454 mm, and approximately 87 % of the total precipitation occurs during the rainy season. The annual mean temperature is 21.7 °C, with a minimum mean temperature of 16.4 °C (January) and a maximum temperature of 25.9 °C (May). The soil is classified as Ferralic Cambisol (IUSS Working Group, 2014), which develops from alluvial deposits and is derived from sandstones.

Tropical rainforest sites are a part of the long-term ecological observation platform of the rainforest ecosystem in Menglun. The plant community structure in natural forests is complex and can be attributed to different vegetation layers. The conspicuous tree layer is dominated by *Terminalia myriocarpa*, *Lagerstroemia villosa*, and *Barringtonia pendula*; the shrub layer, by *Saprosma ternatum* and *Psychotria yunnanensis*; and the herb layer, by *Pteris cretica* and *Adiantum capillus-veneris*. Historically, natural forests have been almost free from human interference and protected by local governments. The rubber plantation sites are located in the same catchment, 2 km from the tropical rainforest site. The rubber trees at plantation sites were placed in a uniform arrangement with 2 × 4.5 m spacing after the complete clear-cutting of the primary rainforest in 1997. Undergrowth vegetation is scarce because of agronomic practices such as herbicide use, latex extraction, and fertilizer application (mixed N—P—K fertilizer at a rate of approximately 40 kg N ha^{-1} $year^{-1}$).

2.2. Sample collection and processing

This study was conducted in rainforests and on rubber plantation sites in April 2020. Numerous epigeic mounds were constructed here by *O. yunnanensis*; some were abandoned in the absence of termite nest-building activities. The live mounds only had termite activity, which we used as an indicator to identify and account for the live and abandoned mounds. In addition, the live mounds had fully functional structures, such as indurated walls and massive amounts of closely connected channels, galleries, and chambers. By contrast, the abandoned mounds had an incomplete structure with collapsed walls and chambers, owing to erosion and plant invasion. The size of the mounds was closely related to the termite population in their colonies and colonisation age. Consequently, live mounds approximately 2.3 m in width and 1.5 m in height and abandoned mounds approximately 2.5 m in width and 1.3 m in height were used for sampling. Specifically, 12 live and abandoned mounds and 12 reference soils from their surroundings were sampled at each study site. Soil samples were collected along the central vertical line of the mounds at depths of 0–30, 30–60, and 60–90 cm using a long cutting ring. Three samples from each mound in the same sampling layer were thoroughly mixed and homogenized to produce a pooled sample according to mound height (repetitions = 4). Surrounding soils were sampled from three depths (0–30, 30–60, and 60–90 cm) using the same sampling procedure at least 12 m from the mounds to avoid the interference of termites in soil properties. The fresh samples were passed through a 2 mm sieve by hand prior to analyzing PLFA, soil NO_3^- and NH_4^+, enzyme activities, and microbial biomass carbon (MBC) and nitrogen (MBN). The air-dried soils were passed through a 0.1 mm sieve to determine soil organic carbon (SOC), total N, and total P.

2.3. Soil basal respiration

Soil microbial respiration (SMR) was estimated by measuring CO_2

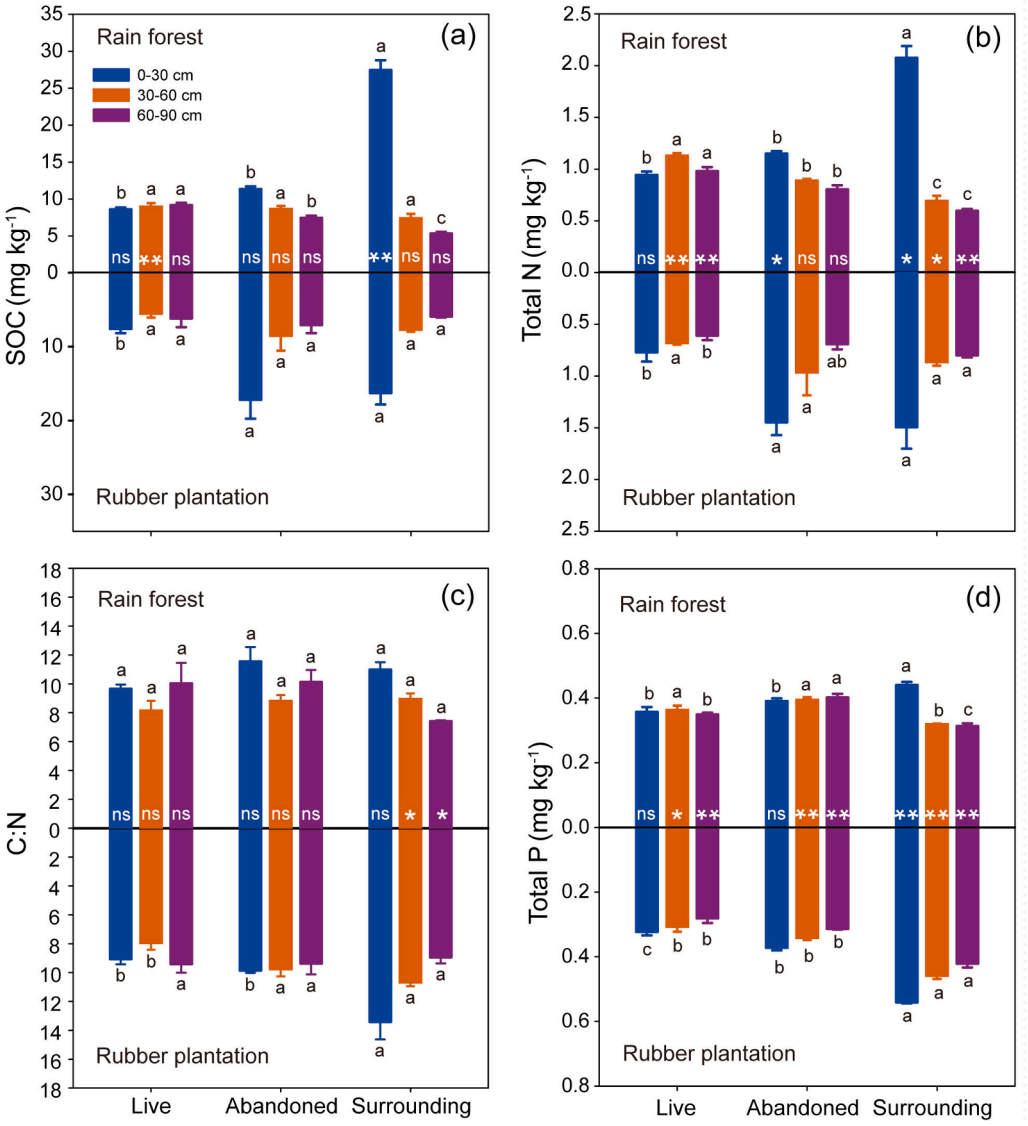

Fig. 1. SOC, total N, C: N, total P concentration of the live and abandoned mounds and surrounding soils. Live, live mounds; Abandoned, abandoned mounds; Surrounding; surrounding soils. The bars are the means with the standard error (SE). The lowercase letters denote significant differences ($P < 0.05$) within each treatment. The asterisks inside the bars indicate the significant differences in the values between the rainforest and rubber plantations. * $p < 0.05$, ** $p < 0.01$, ns, no significant difference.

evolution from incubation (12 days) according to the method proposed by Cheng et al. (2013). In brief, a 10 g (dry weight equivalent) soil sample was pre-incubated at 25 °C for 10 days after adjusting the water content to 60 % of the water-holding capacity. The incubated soil was then transferred to an airtight glass jar (500 ml). After 2 d of incubation, the gas was collected and analyzed using a gas chromatograph (GC-2014; Shimadzu Corporation, Kyoto, Japan). For the control, jars without soil were subjected to the same experimental process.

2.4. Measurement of soil physical and chemical properties

Soil pH and electrical conductivity (EC) were measured using a corresponding pH and EC electrode linked to a digital meter (Accumet AB15/15; Fisher Scientific, UK) in a 1:2.5 soil:water suspension. SOC was analyzed by the vitriol acid–potassium dichromate oxidation method using a mixture of potassium dichromate ($K_2Cr_2O_7$) and sulfuric acid (H_2SO_4) and titrated against ferrous sulfate ($FeSO_4$). Soil total N was analyzed via the dry combustion method using a macro elemental CN analyzer (Vario MAX CN; Germany). Soil total P was analyzed using ICP-AES (Thermo Fisher Scientific, USA) after digestion with H_2SO_4-$HClO_4$. Soil NH_4^+-N and NO_3^--N were measured in 1 M KCl solution using an AutoAnalyzer (Bran Luebbe, Germany). Water content was determined using the oven drying method at 105 °C for 24 h. Microbial biomass C (MBC) and microbial biomass N (MBN) were estimated using the chloroform fumigation-extraction method (Vance et al., 1987) with fresh soil samples.

2.5. Measurement of PLFAs

Microbial communities were assayed by analyzing the PLFA composition according to a modified method (Quideau et al., 2016). In brief, the lipids from 8.0 g freeze-dried soil were extracted using chloroform:methanol:citrate buffer (1:2:0.8, v:v:v) solution. Fatty acids were separated and measured by comparing the individual peak areas in a gas chromatograph (Agilent Technologies, Palo Alto, CA, USA) using an internal standard at 19:00. Fatty acids were identified using MIDI peak identification software (Microbial ID, Newark, DE, USA). The selected PLFA with different biomarkers were then divided into soil organisms: fungi (F), bacteria (B), gram-positive bacteria (G^+), and gram-negative bacteria (G^-) (Table S1, Ma et al., 2020). The ratio of fungal to bacterial biomass (F:B) was calculated as the amount of total fungal PLFA to bacterial PLFA. The ratio of gram-positive bacteria to gram-negative bacteria (G^+:G^-) was calculated as the amount of gram-positive bacterial PLFA to gram-negative bacteria.

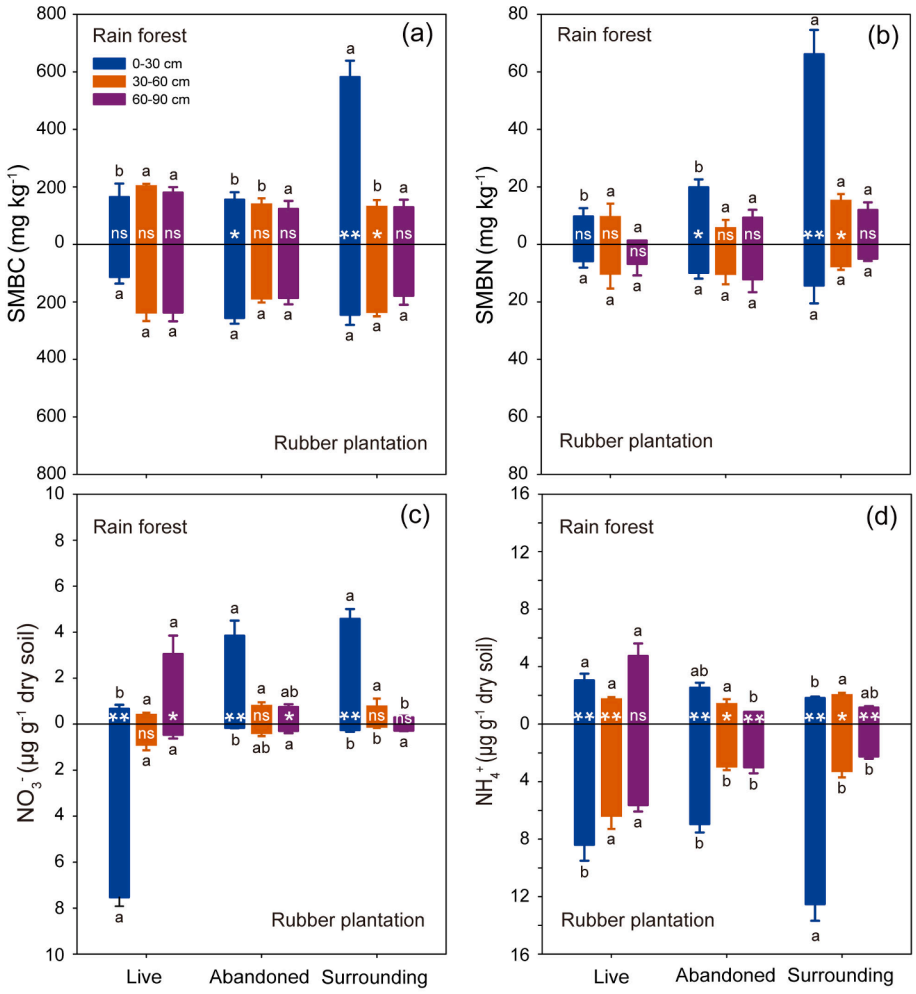

Fig. 2. Soil microbial biomass carbon (MBC), nitrogen (MBN), NO_3^-, and NH_4^+ in the live and abandoned mounds and surrounding soils. Error bars were SE. Means with different lowercase letters denote significant differences ($P < 0.05$) within each treatment. The asterisks inside the bars indicate the significant differences between the rainforest and rubber plantations. * $p < 0.05$, ** $p < 0.01$, ns, no significant difference.

2.6. Measurement of soil microbial enzyme activities

Five extracellular enzymes involved in C, N, and P cycling were investigated. These extracellular enzymes are related to C cycling: β-1,4-glucosidase (BG), β-D-cellobiohydrolase activity (CB), β-1,4-*N*-acetyl-glucosaminidase (NAG), N cycling: leucine aminopeptidase (LAP), and P cycling: acid phosphomonoesterase (AP). Enzyme assays were conducted using fluorogenically labelled substrates: 4-methylumbelliferyl (MUB)-β-D-cellobioside for S-CB, 4-MUB-β-D-glucoside for BG, 4-MUB-*N*-acetyl-β-D glucosaminide for NAG, l-leucine-7-amino-4-methyl - coumarin for S-LAP, and 4-MUB-phosphate (MUF-P) for AP. The detailed method uses the procedure in Dong et al. (2019).

2.7. Statistical analysis and calculations

One-way analysis of variance (ANOVA) was performed to determine the differences in SOC, TN, MBC, MBN, the MBC/MBN ratio, NO_3^-, NH_4^+, SMR, enzyme activities, total PLFAs, fungi, and bacteria among the live and abandoned mounds and the surrounding soils. An independent sample *t* test was conducted to compare the differences in these soil variables between the rainforest systems and rubber plantations. Repeated-measures ANOVA was performed with sampling depth treatments (live and abandoned mounds and surrounding soils) to test for interactive effects on physicochemical and biological properties. Principal coordinate analysis (PCoA) based on the Bray-Curtis distance was conducted to identify similarities and differences in the biological properties of live mounds, abandoned mounds, and surrounding soils in different sampling layers (e.g. 0–90 cm, 0–30 cm, 30–60 cm, 60–90 cm). Redundancy analysis (RDA) was performed to explore the relationships between soil physicochemical properties, enzyme activities, and microbial communities. We also used structural equation models (SEM) approach to evaluate how SMR and microbial communities were influenced by termites and environmental factors and their interactions in the 0–90 cm and 0–30 cm sampling layers, respectively. We considered the effects of termite activities and weathering, and the rating factor varied by '5', '2', and '0' because the weighting assignments were assigned to live mounds, abandoned mounds, and surrounding soils, respectively. Next, SEM was performed using AMOS 22.0 (SPSS Software, Chicago, IL).

3. Results

3.1. Physicochemical properties of termite mounds

Compared with the surrounding soils, the SOC and total N in the live mound were significantly lower in the surface layer (0–30 cm) but relatively comparable or higher in the deep layer (30–90 cm) in the rainforest and rubber plantation sites ($P < 0.05$) (Fig. 1a and b). The SOC of the live and abandoned mounds did not differ between the rainforests and rubber plantations ($P > 0.05$). In the rainforest, the total P in the live

Table 1
Total PLFA concentrations and biomarker-PLFAs for fungi, bacteria, G+ bacteria, G− bacteria, and radio of fungi to bacteria (F/B), and radio of G+ bacteria.

	Rubber plantations			Rain forest		
	Live	Abandoned	Surrounding	Live	Abandoned	Surrounding
0–30 cm						
PLFAs	7.78 ± 0.63c	14.49 ± 0.62b	18.12 ± 1.03a	8.15 ± 1.9b **ns**	22.68 ± 2.18a*	26.34 ± 1.35a **
Fungi	0.95 ± 0.12b	1.65 ± 0.12a	1.93 ± 0.14a	0.88 ± 0.21b **ns**	2.68 ± 0.22a**	2.73 ± 0.16a **
Bacteria	4.7 ± 0.36c	9.35 ± 0.43b	11.92 ± 0.71a	5.16 ± 1.24b **ns**	15.35 ± 1.49a	18.35 ± 0.96a **
G+ bacteria	2.87 ± 0.25c	5.85 ± 0.2b	7.18 ± 0.33a	3.23 ± 0.71b **ns**	8.34 ± 0.73a**	9.6 ± 0.49a **
G- bacteria	1.83 ± 0.15c	3.5 ± 0.24b	4.74 ± 0.39a	1.93 ± 0.54b **ns**	7.02 ± 0.77a*	8.75 ± 0.47a **
F/B	0.2 ± 0.01a	0.18 ± 0.01ab	0.16 ± 0b	0.17 ± 0.01a **ns**	0.18 ± 0a **ns**	0.15 ± 0b *
G+/G-	1.58 ± 0.11a	1.69 ± 0.07a	1.53 ± 0.07a	1.8 ± 0.15a **ns**	1.2 ± 0.04b**	1.1 ± 0.01b **
30–60 cm						
PLFAs	11.27 ± 1.17a	6.81 ± 1.48b	3.22 ± 0.23c	6.16 ± 0.19a **	7.53 ± 1.78a **ns**	5.73 ± 0.7a *
Fungi	1.27 ± 0.15a	0.64 ± 0.19b	0.22 ± 0.03b	0.47 ± 0.03a**	0.53 ± 0.12a **ns**	0.33 ± 0.06a **ns**
Bacteria	7.13 ± 0.75a	4.53 ± 0.94b	2.16 ± 0.13c	3.95 ± 0.15a**	5.53 ± 1.27a **ns**	4.35 ± 0.5a **
G+ bacteria	4.79 ± 0.44a	3.13 ± 0.55b	1.63 ± 0.09c	2.59 ± 0.08a**	3.74 ± 0.71a **ns**	3.13 ± 0.3a **
G- bacteria	2.34 ± 0.32a	1.4 ± 0.39b	0.54 ± 0.05b	1.36 ± 0.09a*	1.8 ± 0.57a **ns**	1.22 ± 0.21a *
F/B	0.18 ± 0.01a	0.13 ± 0.02b	0.1 ± 0.01b	0.12 ± 0a*	0.1 ± 0.01ab **ns**	0.07 ± 0.01b *
G+/G-	2.08 ± 0.09b	2.52 ± 0.35ab	3.06 ± 0.09a	1.92 ± 0.13a **ns**	2.48 ± 0.45a **ns**	2.68 ± 0.26a **ns**
60–90 cm						
PLFAs	12.23 ± 1.16a	6.66 ± 0.84b	2.16 ± 0.36c	5.12 ± 0.27a **	4.12 ± 0.7a **ns**	4.06 ± 0.51a *
Fungi	1.37 ± 0.1a	0.61 ± 0.06b	0.13 ± 0.03c	0.38 ± 0.03a **	0.18 ± 0.05b**	0.18 ± 0.04b ns
Bacteria	7.96 ± 0.85a	4.35 ± 0.58b	1.47 ± 0.21c	3.32 ± 0.16a **	3.22 ± 0.47a **ns**	3.23 ± 0.34a **
G+ bacteria	5.27 ± 0.49a	2.93 ± 0.34b	1.15 ± 0.15c	2.17 ± 0.09a **	2.53 ± 0.3ans	2.58 ± 0.19a **
G- bacteria	2.68 ± 0.36a	1.43 ± 0.24b	0.32 ± 0.06c	1.15 ± 0.1a **	0.69 ± 0.17ab*	0.65 ± 0.15b **ns**
F/B	0.18 ± 0.01a	0.15 ± 0.01a	0.09 ± 0.01b	0.12 ± 0.01a **	0.05 ± 0.01b**	0.05 ± 0.01b **
G+/G-	2.01 ± 0.11b	2.15 ± 0.19b	3.73 ± 0.29a	1.93 ± 0.16b **ns**	3.95 ± 0.43a**	4.31 ± 0.53a **ns**

Means and standard error ($n = 4$). Treatments indicated by the same letter are not significantly different at $P < 0.05$ (one-way ANOVA). The asterisks behind the data represent the significant differences of the values of the same treatment between the rainforest and rubber plantations. * $p < 0.05$, ** $p < 0.01$, ns, no significant difference.

mounds was significantly lower than that in the surrounding soil when compared with that of the surface layer (0–30 cm) but higher than that in deep layers (30–90 cm) (Fig. 1d). However, on the rubber plantations, the total P in the mounds (i.e. live and abandoned mounds) was significantly lower than that in the surrounding soils across all studied depths ($P < 0.05$). In the rainforest, the MBC and MBN in termite mounds were significantly lower than those in the surrounding soil when comparing the surface layer but comparable or higher when comparing deep layers (30–90 cm) ($P < 0.05$). However, on rubber plantations, the MBC and MBN in termite mounds showed no significant differences from the surrounding soils across all sampled depths ($P > 0.05$) (Fig. 2 a and b). In the expected surface soil layer (0–30 cm) in the rainforest, the NO_3^- in the live mounds was considerably higher than that in the surrounding rainforests and rubber plantations (Fig. 2c and d). Except for the surface soil layer (0–30 cm) on the rubber plantations, NH_4^+ in the live mounds was considerably higher than that in the surrounding soils across all sampling depths.

3.2. Distribution of microbial communities in termite mounds

The distribution of the microbial community in the termite mounds and their surroundings is presented in Table 1. Total PLFAs, fungi, bacteria, G + bacteria, and G- bacteria in the live mounds were significantly lower than those in the abandoned mounds and surroundings when comparing the surface layer (0–30 cm) in rainforests and rubber plantations ($P < 0.05$). The ratio of G+ and G- bacteria (G+:G-) in termite mounds was higher than that in the surrounding soils at all studied depths. However, total PLFAs, fungi, bacteria, G+ bacteria, and G- bacteria in live mounds were significantly higher than in abandoned mounds ($P < 0.05$), and those in abandoned mounds were higher than those in surrounding areas when compared with the 30–60 and 60–90 cm soil depths on the rubber plantations. However, the G+:G- ratio showed the opposite and an increasing trend: live mounds < abandoned mounds < surrounding soils on the rubber plantation. In the rainforests, total soil PLFAs, fungi, bacteria, G+ bacteria, and G- bacteria showed the same increasing trend of live mounds > abandoned mounds > surrounding soil. In rainforests and rubber plantations, the ratio of fungi to bacteria (F:B) in live mounds was significantly higher than in the surrounding areas ($P < 0.05$) at all soil depths, but in abandoned mounds, it was slightly higher or comparable to the surrounding areas (Table 1).

3.3. Soil extracellular enzyme activities

The extracellular soil enzyme activities related to C, N, and P cycling (e.g. CB, BG, NAG, LAP, and AP) differed between mounds and surroundings (Fig. 3). The extracellular C-cycling enzymes, that is, the amounts of CB, BG, and NAG, in the live mounds were significantly lower than in the surrounding soils ($P < 0.05$) and were either lower than or similar to those in abandoned mounds (Fig. 3a, b, & c). LAP, an enzyme related to the N cycle, was higher in termite mounds (i.e. both live and abandoned) than in surrounding soils (Fig. 3d). The AP of the P-cycle enzyme in live mounds was higher than that in abandoned mounds but was comparable to that of the surrounding soil ($P > 0.05$) (Fig. 3e).

3.4. Soil respiration in the termite mounds

In the rainforests, soil respiration in the live mounds was significantly lower than that in the abandoned mounds and surroundings when comparing the surface layer (0–30 cm) but did not differ when comparing deep layers (30–90 cm) (Fig. 4). On the rubber plantation, soil respiration in live and abandoned mounds was significantly lower ($P < 0.05$), with no difference ($P > 0.05$), and higher ($P < 0.05$) than that in the surroundings at the 0–30 cm, 30–60 cm, and 60–90 cm depths, respectively. Soil respiration declined precipitously with increasing soil depth in all the three treatments.

3.5. Multivariate analysis

PCoA was used to measure the similarities or discrimination of physicochemical properties and microbial community structure between live mounds and abandoned mounds and between mounds and surroundings (Fig. 5). The PCoA analysis showed a narrower distribution of microbial communities within the live mounds than those found in the abundant mounds and surrounding soil in the average 0–90 cm

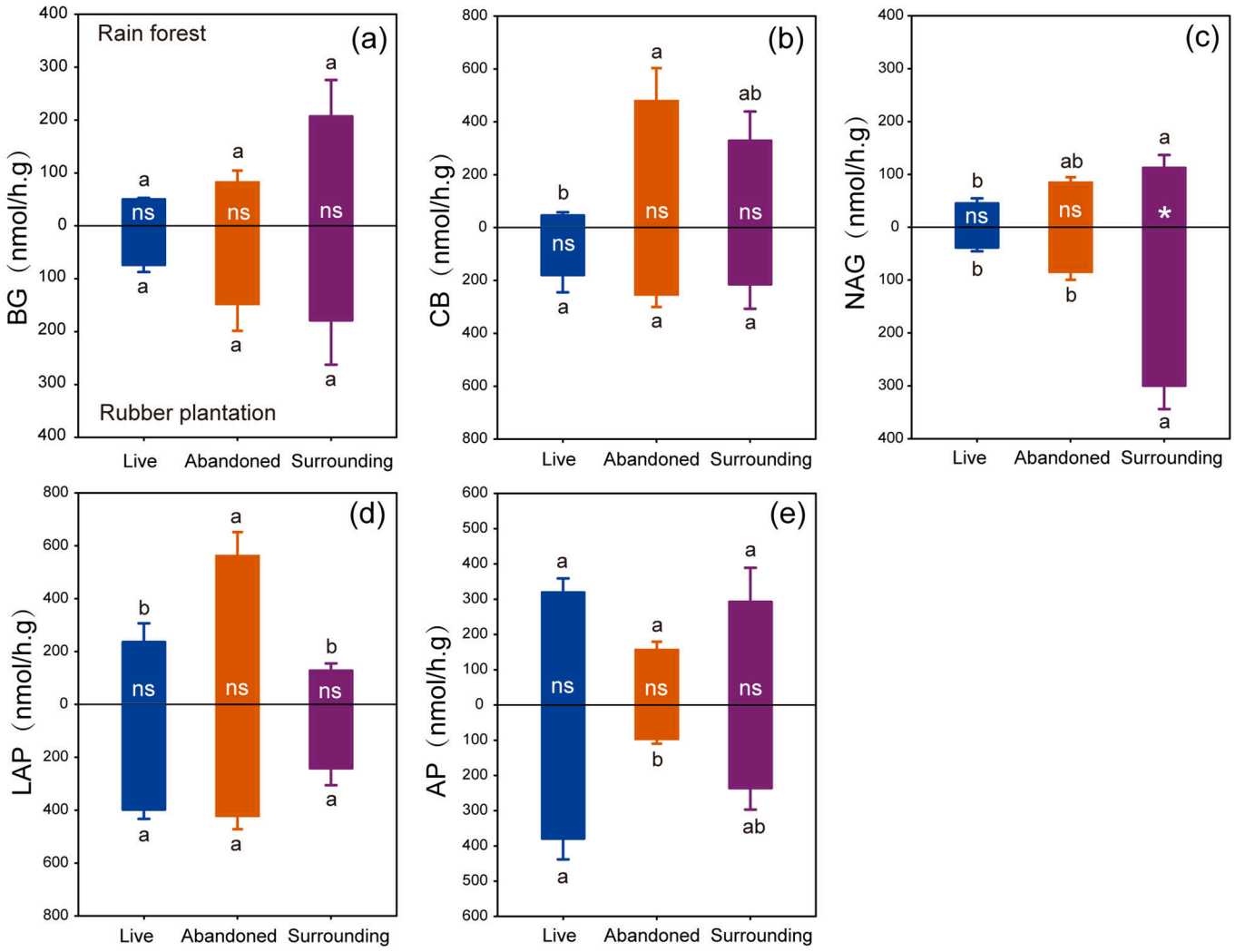

Fig. 3. Extracellular soil enzyme activities in the live and abandoned mounds and surrounding soils. Error bars were SE. Means with different lowercase letters denote significant differences ($P < 0.05$) within each treatment. Live, live mounds; Abandoned, abandoned mounds; Surrounding; surrounding soils. BG: β-1,4-glucosidase, CB: β-D-cellobiohydrolase activity, NAG: β-1,4-*N*-acetyl-glucosaminidase, LAP: leucine aminopeptidase, AP: acid phosphomonoesterase.

layer (Fig. 5a). In the surface layer (0–30 cm), microbial communities in live mounds showed significant differences from those in abandoned mounds and surrounding soils, and abandoned mounds showed partial overlap with surrounding soils (Fig. 5b). In the deep layer (30–90 cm), the two-axis biplot for the microbial community clearly showed a small overlap between live mounds and surrounding soils, whereas the abandoned mounds showed partial overlap with live mounds and surrounding soils (Fig. 5c and d).

3.6. Correlation between soil abiotic, biotic variables, and soil respiration

The Pearson correlation matrix revealed that the biochemical variables correlated significantly with soil physicochemical properties at different depths in the different treatments (Figs. S1 and S2). The PLFA-derived microbial communities, including total biomass, fungi, bacteria, G+ bacteria, and G- bacteria, were significantly positively correlated with EC, soil respiration, SOC, and TN in each treatment (live and abandoned mounds and surrounding soils). However, the microbial communities were significantly positively correlated with water content and pH in live mounds (Fig. S2b) but not in abandoned mounds and surrounding soils (Fig. S2c and d). In addition, the microbial communities were significantly associated with TP in the live mounds; NO_3^- and MBN in the abandoned mounds; and TN, NO_3^-, MBC, and MBN in the surrounding soils. The related correlation coefficient in live mounds was lower than that in surrounding soils. RDA analysis revealed that the microbial community structures (PLFAs; total fungi, bacterial, G+ bacteria, and G- bacteria, and the F/B ratio) were significantly positively correlated with pH, EC, SOC, total N, and total P in live mounds (Fig. S3).

SEM demonstrated that termite mounds negatively affected microbial respiration directly ($\beta_{total} = -0.19$, $\beta_{0\text{-}30\ cm} = -0.3$, $\beta_{60\text{-}90\ cm} = -0.37$) (Fig. 6 and Fig. S4). Termite mounds also indirectly influenced microbial respiration via their effects on soil physicochemical properties and environmental factors (e.g. organic matter, water content, pH, and EC). In addition, termite mounds had positive direct and/or indirect effects on the ratio of fungi to bacteria (F:B) at each sampling depth ($\beta_{total} = 0.50$, $\beta_{30\text{-}60\ cm} = 0.16$, $\beta_{60\text{-}90\ cm} = 0.39$) (Fig. 6 and Fig. S4). Soil microorganisms (PLFAs) were directly and negatively affected by the termite mounds in surface soils ($\beta_{0\text{-}30\ cm} = -1.04$) and were directly and positively affected in deep soils ($\beta_{0\text{-}30\ cm} = 0.29$). In addition, the soil microorganisms were indirectly influenced by termite mounds through their effects on soil physicochemical properties and environmental factors (e.g. organic matter, water content, pH, and EC).

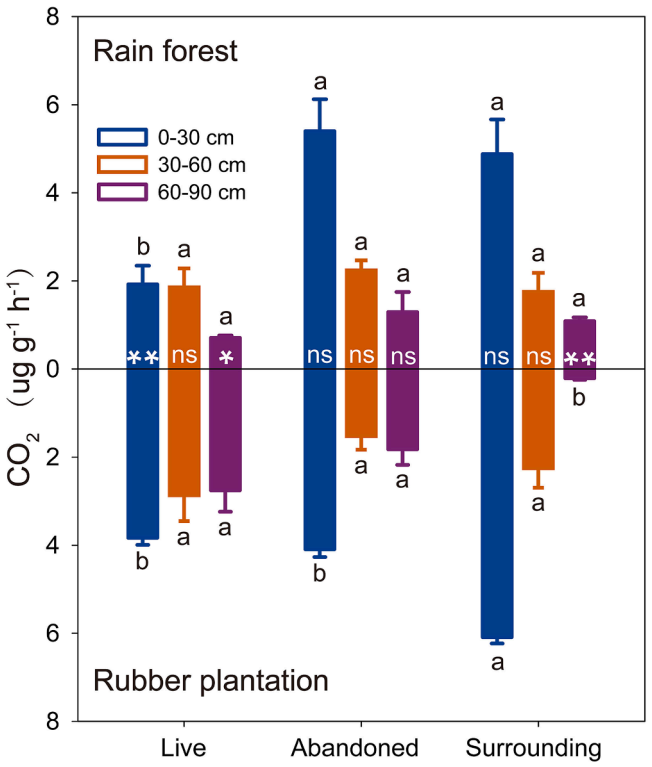

Fig. 4. Soil microbial respiration in the live and abandoned mounds and surrounding soils. Error bars were SE. Means with different lowercase letters denote significant differences ($P < 0.05$) within each treatment. The asterisks inside the bars indicate the significant differences in the values between the rainforest and rubber plantations. * $p < 0.05$, ** $p < 0.01$, ns, no significant difference.

4. Discussion

4.1. Termites regulate microbial community structure and function within mounds

In live mounds, microbial communities (i.e. PLFAs; total biomass, fungi, bacteria, G+ bacteria, and G- bacteria) significantly decreased relative to the surrounding surface soils (Table 1). These results are consistent with those of studies that found a lower distribution of microbial communities in termite mounds than in surrounding surface soils in tropical savanna systems (Chen et al., 2021b; Yan et al., 2021). This phenomenon is based on at least three types of evidence. First, the quantity and quality of soil organic matter and nitrogen inputs are the primary sources of soil microbial biomass and activity (Kallenbach and Grandy, 2011; Selosse et al., 2017; Yanardağ et al., 2017). In contrast with surrounding surface soils with continuous inputs of organic materials from vegetation sources (i.e. root exudates and litter), live mounds are nearly bare and impermeable because of the absence of plants (Ackerman et al., 2007; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c), resulting in lower organic matter available for microbial growth and activity (Fig. 1). Second, live mounds generally provide harsh conditions for microorganisms, with low soil water content, high clay content, unsuitable soil pH, and high bulk density, for their survival and growth (Ackerman et al., 2007; Chen et al., 2018). Third, termite mounds are protective enclosures that can fend off predators and provide suitable places for feeding and foraging with structural integrity and stability to support optimum microbial growth and biomass (Jouquet et al., 2006).

Conversely, the termite mounds supported higher microbial richness and biomass than the surrounding deep soils (Table 1). Previous studies have shown that the materials of the termite mounds were selected and transported from deep soils, and the termite-driven changes in organic matter and nutrients were mostly positive (Jiménez et al., 2008; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c). The elevated nutrients in the mounds may provide more energy and primary carbon sources for the growth of microorganisms, resulting in a greater increase in the microbial communities in live mounds than in surrounding deep soils.

In agreement with the previous finding (Fierer et al., 2003), our PCoA analysis showed a narrower distribution of microbial communities (i.e. PLFAs; total biomass, fungi, bacteria, G+ bacteria, and G- bacteria) within the live mounds than those found in the abundant mounds and surrounding soil (Fig. 5), suggesting that termites provide a homogeneous environment for the microorganisms, leading to the perpetuation of a specific range of microbial communities. It also suggested that live termite mounds are not only homogeneous in physicochemical properties, as we showed in our previous study in this region (Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c), but also show uniformity among thriving microbial communities. The uniform distribution of microbial communities within live mounds was primarily due to the nesting activities of termites and their survival strategies. Another reason is that the materials for the construction of mounds were isolated and used from the deeper soils by the termites (Jiménez et al., 2008; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c); these exclusive selections might result in high spatial homogeneity in nutrients in the live mounds, contributing to uniformity in the microbial communities. Moreover, termites ensure the stability of mound walls by repairing cracks and other unsolicited destruction caused by natural weathering forces. Such recurrent management by termites prevents the spatial heterogeneity of nutrients within mounds by decelerating rainfall erosion, accumulating mobile elements, and plant invading the mound (Erens et al., 2015b; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c).

Termites also enhance the speciation of different groups of microorganisms within mounds. Notably, the F:B ratio was always significantly higher in the mound than in the surrounding soil (Table 1). This probably occurred because fungi and bacteria differ in their biomass turnover rates when limited C substrates are available. Unlike bacteria, fungi prefer to use the soil C substrate in mounds, which do not receive organic matter input from plants or organic matter residues, resulting in a higher F:B ratio. Another explanation is that termites maintain a symbiotic relationship with fungi as primary food decomposers in the chambers and selectively facilitate their richness over bacteria when building their mound structures. Moisture availability can also regulate the composition of soil microorganisms, because bacteria are more sensitive to water stress than fungi, resulting in the bacterial community being rapidly outcompeted by the fungal community (Manzoni et al., 2012). pH is another important driver probably associated with decreased bacterial richness and other microbial traits in termite mounds (Fig. 6). This result is consistent with those found by Yan et al. (2021) that the ratio of F:B in termite mounds was significantly lower than that in surrounding surface soils, which was attributed to the narrow pH optimum for the soil bacterial taxa relative to fungi (Xiao et al., 2016). Moreover, the ratio of G+:G- in the live mounds was generally higher and lower than that in the surrounding surface soils and subsoils, respectively, and the G+: G- ratio was significantly correlated with soil nutrients. These results indicate that the ratio of G+ to G- bacteria reflects the nutritional state of the soil, with a higher percentage of G+ bacteria suggesting a poor nutrient state (Xia et al., 2019).

Another finding was that the abandoned mounds had intermediate levels of microbial biomass (MBC and MBN) and microbial community richness (i.e. PLFAs; total biomass, fungi, bacteria, F:B, G+ bacteria, G- bacteria, and G+:G-) that ranged between those of live mounds and surrounding soils (Table 1). Microbial communities were significantly correlated with physicochemical and biological properties of mounds and surrounding soils (Fig. 6), suggesting that organic matter content and nutrient availability play an essential role in microbe growth. In this

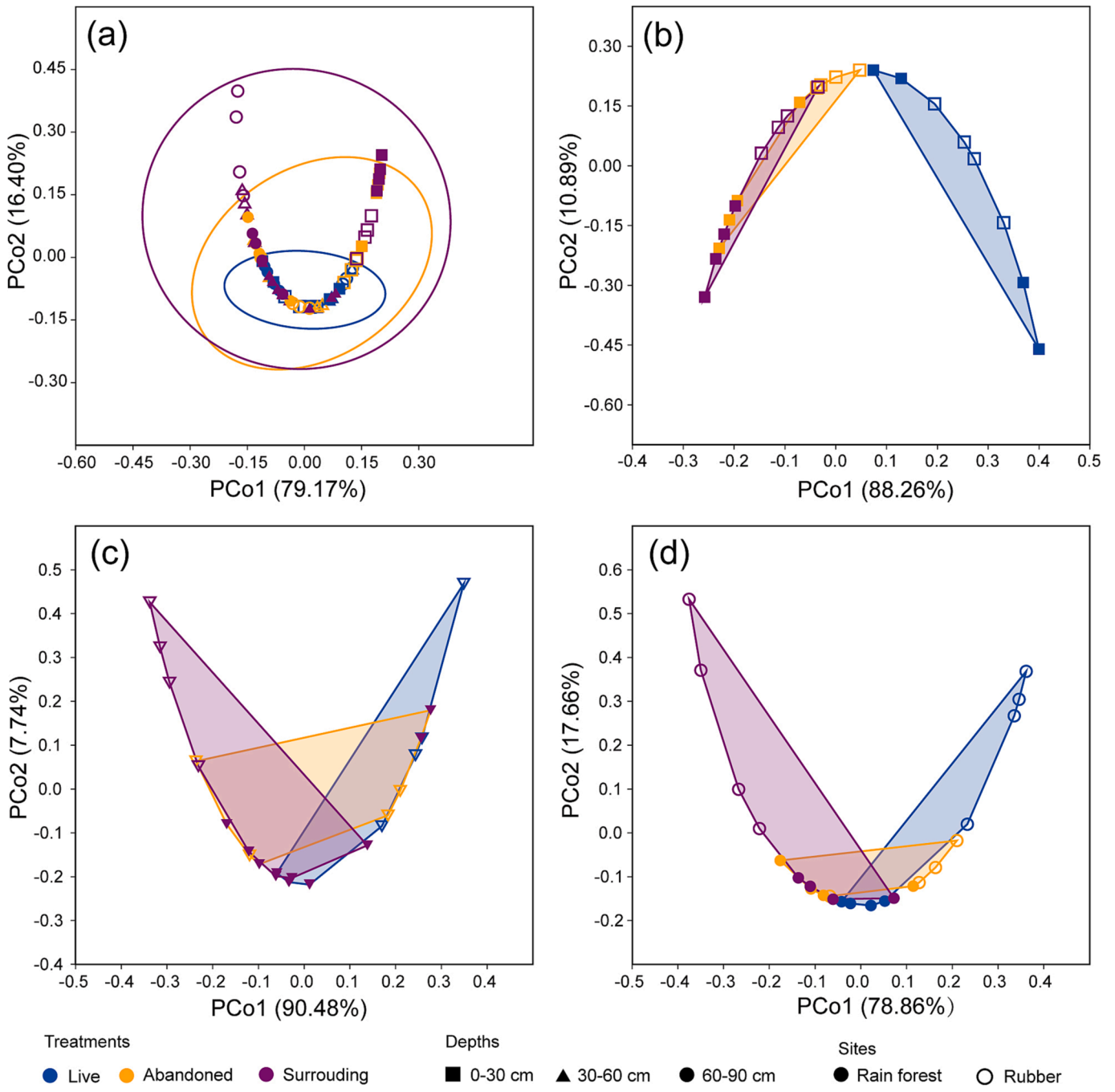

Fig. 5. Principal coordinate analysis based on the Bray-Curtis distances shows the differences in microbial community structure among the live and abandoned mounds and surrounding soils in (a) the average 0–90 cm layer, (b) 0–30 cm layer, (c) 30–60 cm layer, and (d) 60–90 cm layer. Different colors represent different treatments; symbols indicate different sampling depths, and the solid one indicates rainforest, while the hollow one indicates rubber plantation.

study, the organic matter and nutrient status may have gradually resembled natural soil because of natural weathering and plant invasion once the termite mounds were abandoned (Figs. 1 and 2; Chen et al., 2018; Chen et al., 2021a; Chen et al., 2021b; Chen et al., 2021c), resulting in an intermediate grade of microbial communities.

4.2. Implication of microbial community structure and function on soil carbon and nitrogen cycling

Termite-induced nutrient cycling depends not only on the ingestion, selection, and translocation of organic and inorganic materials to the mounds (Sarcinelli et al., 2009; Levick et al., 2010) but also on the microbial biomass and microbial communities present. Moreover, microbial biomass (through mineralisation) and sink (through immobilisation) are vital components of C and N cycling in ecosystems as the source (MBC and MBN) of C and N cycling in ecosystems (Xu and Yuan, 2017). In our study, the MBC and MBN in live mounds were significantly lower than those in surrounding topsoils (Fig. 2), indicating a lower role of microbial biomass of termite mounds in C and N sequestration in the tropical forest ecosystem. As a result, the SMR in live mounds was also significantly lower than that in surrounding topsoils, having a significant positive correlation with the microbial biomass (MBC and MBN) and microbial communities (total PLFA, fungi, bacteria, G+, and G- bacteria) (Fig. 6 and Fig. S2). The lower soil respiration in mounds was

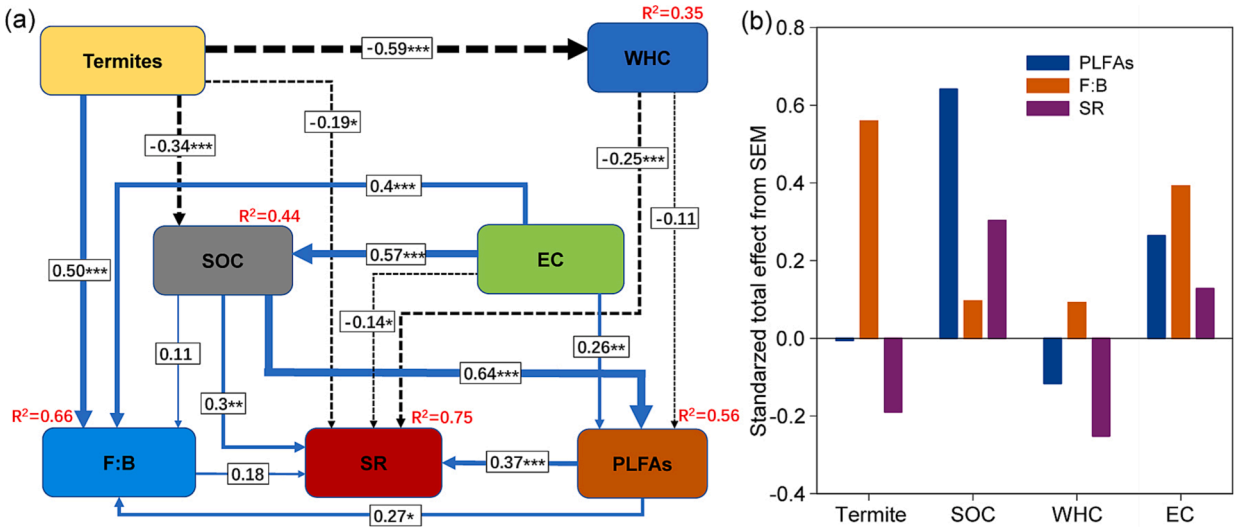

Fig. 6. Structural equation model showing relationships among the termite mounds, physicochemical properties, microbial communities, the ratio of fungi to bacteria (F: B), and carbon mineralization (CO_2) (a), and their standardized total effects (direct plus indirect effects) derived from the structural equation model (b). Arrow thickness is scaled proportionally to the standardized path coefficients (numbers on arrows). Solid lines represent positive relationships and dotted lines represent negative relationships. Numbers beside the arrows are standardized coefficients and asterisks behind the numbers represent significance (* < 0.05, ** < 0.01, *** < 0.001). The proportion of variation explained by the model (R^2) are shown next to each endogenous variable.

primarily related to the limited exogenous organic matter inputs, fewer microbial communities, and less microbial biomass richness (Fig. S4a). Recent studies have demonstrated that the surface soil layer in the present region annually receives 9.21 and 11.20 Mg ha^{-1} $year^{-1}$ of leaf litter on rubber plantations and in rainforests, respectively (Zhu et al., 2019), and mounds do not receive any measurable input, because plant litter cannot adhere to the surface of the mounds with a pyramid-shaped structure (Chen et al., 2018). These may force microbes to use inorganic nutrients available in mounds rather than complex organic substrates (Enagbonma et al., 2021) and reduce the accessibility of microbes and exoenzymes to the substrate, which may be the primary degrading organic matter to obtain nutrients in termite mounds. For instance, the elevated *N*-acquiring enzyme (i.e. LAP) in termite mounds (Fig. 3) reflects the presence of complex and recalcitrant substrates (e.g. chitin), because this enzyme is involved in breaking down proteins and polypeptides that are relatively persistent in nature. By contrast, lower C-acquiring enzymes (i.e. CB, BG, and NAG) in live mounds indicate less use of labile substrates to obtain nutrients because these enzymes are involved in the decomposition of easily accessible substrates.

Fungal biomass provides higher C-to-N stoichiometry, slower turnover rates, and potentially higher carbon use efficiency than bacteria (Waring et al., 2013). In this study, the higher F:B ratio within the mounds demonstrated that the microorganisms in the young or live mounds possibly used stable carbon in response to limited inputs of exogenous organic matter. G- bacteria preferentially use easily degradable organic substances primarily originating from plants, whereas G+ bacteria use recalcitrant C as the energy source and have a greater inherent resistance to environmental stress than G^- bacteria (Zhang et al., 2018; Fanin et al., 2019).

In this study, the ratio of G+ to G- bacteria in termite mounds (live and abandoned mounds) was significantly higher than that in surrounding topsoils (Table 1) but gradually increased in order of live mounds, abandoned mounds, and surrounding deep soils. These results highlight that the microbes in the live mounds tended to use complex, residual organic substrates as the energy source rather than plant-derived organic matter. However, microbes acquire energy identical to the pre-existing recalcitrant C of mounds and easily degradable organic materials from plant sources when mounds are abandoned.

Mounds were enriched in NH_4^+ but depleted in NO_3^- at rainforest sites. By contrast, termite mounds on rubber plantations were enriched in NO_3^- but depleted in NH_4^+ (Fig. 2). These differences are probably observed because of mound pH that mounds in rainforests and on rubber plantations had an acidic range (pH = 6.4) and an alkaline range (pH = 7.3), respectively. Studies have also found that mounds in an acidic environment were enriched in NH_4^+ (López-Hernández, 2001), whereas those in an alkaline environment were enriched in NO_3^- (Seymour et al., 2014; Chen et al., 2018). Microorganisms in an alkaline environment can facilitate the soil nitrification process controlled by the Nitrobacter community (Seymour et al., 2014), and NH_4^+ and ammonifying bacteria are usually dominant in an acidic environment.

4.3. Limitations

In this study, we have examined the spatial distributions of microbial communities and their related functions on nutrient cycling in different mound stages (live mounds and abandoned mounds). Consistent with the majority of previous studies, we compared the microbial communities between the active and abandoned mounds without considering the effects of the ages of the mounds (Menichetti et al., 2014; Chen et al., 2018), which may influence the development of soil physicochemical properties and microbial communities in the termite mounds (Erens et al., 2015a). Therefore, the future investigation should focus on the effects of the chronological development of the mounds on the microbial communities and their related functions on nutrient cycling.

We demonstrated the changes in spatial distribution pattern of microbial community composition and structure in the termite mounds using PLFAs method, which has been regarded as a vital approach to inferring the presence of specific microbial groups (Quideau et al., 2016; Ma et al., 2020). However, the PLFAs method has some limitations, such as lower precision in identifying microbial groups due to overlap in phospholipid structure, and does not provide information for specific microbial communities. Thus, more approaches, such as ^{13}C PLFAs and genome-based microbial community profiling, should be used to characterise the specific microbial communities.

5. Conclusions

We have shown that live termite mounds harbour unique microbial communities with an intermediate abundance between surrounding topsoils and deep soils and a higher F:B ratio in live mounds relative to

surrounding soils. However, the microbial communities tended to resemble surrounding soils when the mounds were abandoned. This study also provided evidence supporting the conjecture of homogenization in the microbial community structure within the mound. The microbial communities in the mounds may be influenced by the redistribution of the organic nutrients by termites or subsequent changes in the physiochemical properties (water content, pH, and EC). In addition, termite-induced changes in soil microbial communities could affect soil carbon and nitrogen cycling by modifying microbial respiration and extracellular enzymatic activities in the mounds. Overall, our results demonstrated that termite nesting behaviour and its effect on the physicochemical properties shape the microbial communities and microbial processes in termite mounds and subsequently contribute to soil nutrient cycling in tropical ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2023.116368.

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