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Termite mounds reduce soil microbial diversity by filtering rare microbial taxa

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Originality-Significance Statement

Termites are important terrestrial engineers especially in savanna ecosystems. Here we provide new insights into the role of termite mounds in regulating the distribution and diversity of soil microbial communities. Our results suggest that termite nesting process could potentially enrich the soil dominant taxa while filter the rare taxa. Some copiotrophic taxa e.g., Actinobacteria and Bacteroidetes could take advantage of higher nutrient availability in termite mounds to expand their population, while the oligotrophic taxa may lose their competitiveness and result in a decrease in their abundance. Our study advances the understanding of how termite nesting process shapes the soil microbial communities, which is important to better prediction of ecosystem functions of termite mounds in a changing environment.

Summary

Termites are ubiquitous insects in tropical and subtropical habitats, and some of them construct massive nests (‘mounds’), which substantially promote substrate heterogeneity by altering soil properties. Yet, the role of termite nesting process in regulating the distribution and diversity of soil microbial communities remains poorly understood, which introduces uncertainty in predictions of ecosystem functions of termite mounds in a changing environment. Here, by using amplicon sequencing, we conducted a survey of 134 termite mounds across >1500 km in northern Australia and found that termite mounds significantly differed from bulk soils in the microbial diversity and community compositions. Compared with bulk soils, termite nesting process decreased the microbial diversity and the relative abundance of rare taxa. Rare taxa had a narrower habitat niche

breadth than dominant taxa, and might be easier to be filtered by the potential intensive microbial competition during the nesting processes. We further demonstrated that the shift in pH induced by termite nesting process was a major driver shaping the microbial community profiles in termite mounds. Together, our work provides novel evidence that termite nesting is an important process in regulating soil microbial diversity, which advances our understanding of the functioning of termite mounds.

Introduction

Termites are important terrestrial engineers on Earth, and ubiquitously distributed in tropical and subtropical habitats (Ashton et al., 2019). Some termites, such as fungus-cultivating termites, construct enormous colonies ranging in size from a few hundred to several million individuals and create unique nest structures (i.e., 'mounds') from soil, their saliva and excreta (Singh et al., 2019). This nesting process results in greater soil environmental heterogeneity in terms of elevated soil moisture and nutrient availability and modified soil properties (e.g., pH), with potential consequences for the soil microbial diversity and compositions (Pringle et al., 2010; Singh et al., 2019). It has been estimated that, in tropical ecosystems, termite mound soils constitute an important soil compartment covering ~10% of African soils (Fall et al., 2007). These ubiquitous biotically engineered structures in savannas have significant impacts on multiple ecosystem functions and global methane emissions (Sileshi et al., 2010; Jouquet et al., 2011; Bonachela et al., 2015; Nauer et al., 2018). For example, termite mounds can

enhance the resistance of dryland ecosystems to climatic changes (e.g., drought) by creating “islands of fertility” to support vegetation growth (Sileshi et al., 2010; Jouquet et al., 2011; Bonachela et al., 2015). A recent study demonstrated that termites produce globally significant amounts (~1 – 3%) of methane, half of which is biofiltered before emission by methanotrophic bacteria dwelling in termite mound walls (Nauer et al., 2018). Termite mounds harbor a broad range of soil microbial communities integral to ecosystem functions (Chiri et al., 2020). A recent study demonstrated that the bacterial and fungal community assemblies in termite mounds were driven more by deterministic selection compared with stochasticity (Chen et al., 2021). However, the role of termite nesting process in altering soil microbial diversity and the driving forces shaping the microbial biogeographic pattern in termite mounds remain unclear. Such a knowledge gap impedes our ability to uncover the mechanisms underlying the global patterns of soil microbial diversity, especially in savanna ecosystems, and ultimately to predict the responses of ecosystem functions to future climatic changes.

Termites accumulate a wide range of materials (e.g., wood and leaf litter) and regulate soil moisture by transporting water upward and decreasing transpiration within their mounds (Gautam and Henderson, 2014). Compared with the oligotrophic bulk soil environment, the relatively copiotrophic environment in termite mounds would support more copiotrophic microbial assemblies such as Actinobacteria, Bacteroidetes and Alpha/Gamma-Proteobacteria than oligotrophic assemblages including Acidobacteria and Planctomycetes (Fierer et al., 2007; Fierer et al., 2012; Ho et al., 2017). Microbial species

are not often found alone, and they can affect one another in both positive or negative ways (Hammarlund and Harcombe, 2019). The stress gradient hypothesis (SGH), a framework to predict when positive or negative interactions would be observed, suggests that microbial competitive interactions will increase with the increasing resource levels (Hammarlund and Harcombe, 2019). The expected increase in water and nutrient availability in termite mounds would induce more intensive competition in microbial communities. As dominant microbial taxa generally have a higher genomic potential for resource utilization, competition and stress tolerance, they are known to often have a stronger ability in resource acquisition than rare taxa (Egidi et al., 2019). Thus, we hypothesized that the rare taxa in soil are more vulnerable and may disappear or decrease in their relative abundances due to the more intensive microbial competition processes in termite mounds. To test this hypothesis, we conducted a large-scale (>1500 km) survey of 134 termite mounds across 16 locations from northern Australia (Fig. 1A). By using standard amplicon sequencing to analyze the microbial community diversity and compositions, we aimed to explore the role of termite (*Amitermes meridionalis*) nesting process in regulating the soil microbial diversity, and to identify the dominant drivers in shaping the microbial community assemblies associated with termite mounds.

Results and Discussion

Compared with bulk soils, a significantly higher ($P < 0.001$) microbial abundance of both bacteria and fungi was found in termite mounds (Fig. S1). In contrast, termite

mounds harboured a significantly lower alpha-diversity of both bacteria and fungi than bulk soils (Fig. 1B and Fig. S2). Nonmetric multidimensional scaling (nMDS) ordinations (PERMANOVA, $P = 0.001$ for both bacteria and fungi), together with the ratios of bacteria and fungi ($P < 0.001$) showed that the overall patterns of microbial community in termite mounds were significantly distinct from those in bulk soils (Figs. 1B). Our results are consistent with the findings from a recent study that used the shotgun sequencing technique to profile the bacterial diversity and community structure of termite mounds in South Africa (Enagbonma et al., 2020). In contrast to our results, Delgado-Baquerizo et al. (2019) reported a higher microbial diversity in ant colonies than surrounding soils and argued that ant colonies are an important refugia for microbial diversity (Delgado-Baquerizo et al., 2019). Termites are also known as 'white ants', however they belong to Isoptera at the order level, as compared to ants belonging to Hymenoptera, a completely different insect group. The differences in diet (e.g., *Amitermes meridionalis* feeds wood and grass for carbohydrates, while *Iridomyrmex purpureus* is an omnivore and retrieves food from various insects) and nesting behaviour (e.g., size and structures of their nests) between termites and ants might be a potential explanation for these discrepancies. Nevertheless, these results suggested that termite nesting process is an important biological driving force in shaping the soil microbial diversity. However, some potential limitations should be noticed that in both the present and previous studies (Delgado-Baquerizo et al., 2019), as our sampling strategy did not consider the seasonal effects. In addition, in the present study, the various feeding guilds

(e.g., wood feeding, soil feeding, litter feeding, lichen feeding and fungus growing) of termites were not considered (Donovan et al., 2001). The physical-chemical composition of termite mounds was reported to vary with the feeding modes of termite species (Holt and Lepage, 2000), with potential effects on the microbial community compositions in termite mounds. These potential concerns also necessitate the development of systematic and quantitative approaches in this infant research field.

We further analyzed the shared microbial taxa between termite mounds and bulk soils. A total of 11,118 bacterial and 2,517 fungal phylotypes were shared between termite mounds and bulk soils, which occupied 97.03% and 88.22% of the total soil bacterial and fungal sequences, respectively (Fig. S3). The microbial community compositions in both bulk soils and termite mounds were predominated by the bacterial phyla Actinobacteria, Chloroflexi, Proteobacteria, and the fungal phylum Ascomycota (Fig. 1B). Compared with bulk soils, some dominant phyla were significantly enriched in the termite mounds (Fig. 1C). For example, Ascomycota, a common fungal phylum in soil (Egidi et al., 2019), showed an extremely higher relative abundance in termite mounds (on average 96.21%) than in bulk soils (on average 88.31%). Actinobacteria and Proteobacteria were significantly more abundant in termite mounds (on average 82.22%) compared to bulk soils (on average 58.11%). Conversely, most of the less abundant phyla such as Planctomycetes, Cyanobacteria, WPS2 and Nitrospirae, were more abundant in the corresponding bulk soils than in the termite mounds. At a higher resolution level, the rank abundance curve also showed that abundant species (amplicon sequence variants,

ASVs) increased in abundance, while some less abundant species declined in abundance in termite mounds especially for fungal communities (Fig. S4). Indicator species analysis (Table S1) showed that a total of 9256 bacterial indicator species (ASVs) and 1062 fungal indicator species were identified in bulk soils, which occupied 53.30% and 44.36% of the total bacterial and fungal sequence, respectively. In termite mounds, a total of 711 bacterial and 129 fungal indicator species were identified, which accounted for 33.59% and 58.49% of the total bacterial and fungal sequences, respectively. Most importantly, 8,985 indicator species in bulk soils were classified as rare taxa (ASV with relative abundance below 0.01%) based on previous studies (Jiao and Lu, 2020), which indicated that bulk soils were the ecological preferred habitats for rare taxa. Altogether, our results suggested that rare taxa may be more easily filtered during the nesting process, compared to the dominant taxa. Our finding is challenging to a previous observation that the higher nutrient availability supported more microbial assemblages and promoted the less abundant taxa of bacteria and fungi (Delgado-Baquerizo et al., 2019).

We further calculated the microbial habitat niche breadth, and found that a narrower habitat niche breadth of rare taxa compared with the dominant ones, which could partially explain why rare taxa may be more easily filtered in termite mounds. (Fig. 2A and Fig. S5). In addition, the newly developed SGH predicts that microbial competition would be more intensive at high resource levels (Bertness and Callaway, 1994; Hammarlund and Harcombe, 2019; Piccardi et al., 2019). Our results demonstrated that the nutrient availability was higher in termite mounds than in bulk soils, for example, DOC and DON

in termite mounds were over five-fold than those in bulk soils (Table S2). Therefore, the predicted higher microbial competition (as the observed negative interactions) in termite mounds may have resulted in the more dominance of abundant taxa in the microbial communities (Fig. 2B), while some rare taxa may have been filtered out to be undetectable. It should be noted that, our conclusion is based on observation and modeling, more direct mechanisms underlying the loss of rare taxa in termite mounds are still unclear.

Our results further indicate that the termite nesting process could potentially regulate the microbial functional groups by increasing nutrient availability. For example, Planctomycetes are typically classified as oligotrophs (Lauro et al., 2009) and prefer environments characterized by low nutrient availability, and we found that their relative abundance was negatively related to DON and significantly lower in termite mounds (Fig. 1C; Table 1). Conversely, the relative abundance of Actinobacteria (classified as copiotrophs and prefer high nutrient availability (Fierer et al., 2012)), was positively related to DON and significantly higher in termite mounds (Fig. 1C; Table 1). These findings suggested that during the termite nesting process, copiotrophic taxa may take advantage of higher nutrient availability to expand their population, while the oligotrophic taxa may lose their competitiveness and result in a decrease in their abundance.

Termite nesting process also significantly elevate soil pH from ~6.2 to ~6.7 (Fig. 3). We found that pH was the most important driver for the pattern of bacteria and fungi in

termite mounds, which was in agreement with the observation in global soils (Lauber et al., 2009). The most dominant bacterial and fungal taxa were the strongest responders to pH (Table 1), and microbial community profiles (NMDS1) of both bacteria and fungi were significantly correlated with pH ($P < 0.001$). For example, the relative abundance of Acidobacteria was negatively correlated with pH, which contributes to the decrease of Acidobacteria abundance in termite mounds (Fig. 1C). Nutrient availability driving the diversity of soil bacteria and fungi is widely known (Bending et al., 2002; Delgado-Baquerizo et al., 2017). In the present work, we also found that soil total carbon and nitrogen, mineral nitrogen as well as climatic aridity were importance predictors of microbial compositions in termite mounds (Fig. 3). Furthermore, soil NH_4^+-N and aridity index were the main drivers causing the high dispersion in NMDS2 for both bacteria and fungi in termite mounds (Fig. S6). Nevertheless, the random forest models indicated that the importance of nutrient availability or aridity in regulating the microbial profiles was lower than that of pH in termite mounds (Fig. 3).

Conclusions

Together, we provide novel evidence that termite mounds harbor unique microbial assemblages with a lower relative abundance of rare taxa compared with bulk soils. Termite nesting process is a process of potentially enriching the soil dominant taxa while filtering the rare taxa, which significantly decreases the microbial diversity of both bacteria and fungi. Some taxa (e.g., Actinobacteria and Bacteroidetes) could benefit from

the copiotrophic environment in termite mounds compared to bulk soils. The shift in soil pH is the dominant predictor of microbial assemblages in termite mounds. Our findings have important implications for a better understanding of how termite nesting process shapes the soil microbial communities and potential terrestrial ecosystem functions, especially in savanna ecosystems.

Experimental procedures

Study area and sample collection

We collected termite mound samples in May 2019 from 16 locations spanning > 1500 km in Northern Territory and Queensland of northern Australia (133.36° E to 140.36° E, 22.98° S to 19.25° S) (Fig. 1A). The termite mounds were occupied by *Amitermes meridionalis* were recognized based on the morphological characters. Mean annual precipitation and temperature in the sampling sites randomly ranged from 254 to 583 mm, and from 21.36 to 26.54 ºC, respectively. Soil properties were as follows: Soil pH 4.96 ~ 7.36 (with an average of 6.22), total carbon 0.19% ~ 1.32% (with an average of 0.65%), total nitrogen 0.02% ~ 0.10% (with an average of 0.05%). Spatial geographical coordinates and elevations were recorded using a handheld GPS (eTrex Venture, Garmin, Olathe, KS, USA). Termite mounds (0.5-1.5 m in height, 0.2-1.0 m in diameter in the bottom) were highly abundant and widely distributed in the sampling regions. In order to collect the representative termite mounds, we randomly established a 40 m × 40 m plot at each sampling location, and collected composite samples from the

top, middle and bottom of termite mound walls (5~10 termite mounds in each plot) and three bulk soil samples by mixing five soil cores (0-5 cm) for each sample. A total of 134 termite mound samples and 48 bulk soils were collected in this sampling campaign. All samples were transported to laboratory (sieved < 2 mm) and divided into two fractions. One fraction for molecular analysis was at −80 °C before analysis; the other was stored at 4 ºC for soil physicochemical analyses.

Soil physicochemical analysis

Standard methods from CSIRO were used to characterize soil physicochemical properties (Rayment and Lyons, 2011). Briefly, soil pH was measured in a 1: 2.5 mass: volume of soil and water suspension with a pH meter (Thermo Scientific Inc., Waltham MA, US). Dissolved organic carbon (DOC) and nitrogen (DON) were extracted with Milli-Q water and measured using a TOC analyzer (Shimadzu, Kyoto, Japan). Mineral nitrogen (NO_3^--N and NH_4^+-N) were extracted with 1M KCl and measured using a continuous flow analyser (Skalar Analytical B.V. Tinstraat,Bread, Netherland). Soil total carbon and nitrogen (TC and TN) were determined using Dumas combustion method with a LECO EP628 analyser (LECO Corp, Michigan, USA). All the raw data of nutrient availability and soil properties are available in Supplementary Table S2.

Characterization of microbial community structure

Total genomic DNA of termite mound and bulk soils was extracted using a DNeasy PowerSoil Kit (QIAGEN Pty Ltd., Hilden, Germany) *as per* the manufacturer's instructions. The DNA quality was assessed using a NanoDrop 2000c spectrophotometer

(Thermo Fisher Scientific Inc., Waltham, USA). The DNA concentration was determined with a Qubit™ dsDNA HS Assay kit on a Qubit™ 3.0 fluorometer (Thermo Fisher Scientific Inc., Waltham, USA).

Microbial abundance as represented by the absolute bacterial 16S rRNA and fungal ITS region copy numbers was quantified with the primers of 515FmodF/806RmodR (Walters et al., 2016) and ITS1F/ITS2R (White et al., 1990) on a Bio-Rad CFX384 Real-Time PCR Detection system (Bio-Rad, Hercules, USA). The 20 μl qPCR mixture consisted of 10 μl of 2× SensiMix SYBR No-ROX reagent (Bioline, London, UK), 0.8 μl each primer, 2 μl DNA template and 6.4 μl of nuclease-free PCR-grade water. Plasmids containing a 16S rRNA or ITS region gene fragments were used to generate calibration curves from ten-fold dilutions (Yan et al., 2019; Sun et al., 2021). All qPCRs were performed in technical triplicates with template-free negative controls.

The bacterial 16S rRNA gene and fungal ITS region were amplified with the primers 515FmodF/806RmodR (Walters et al., 2016) and ITS1F/ITS2R (White et al., 1990), respectively, on the CFX96 Touch^{TM} PCR Detection System (Bio-Rad, Herculers, USA). For bacteria, after the initial enzyme activation at 95 °C for 3 min, 28 cycles of the following program were used for amplification: 95°C for 30 s, 55°C for 30 s and 72°C for 45 s, and a final extension at 72 °C for 10 min. For fungi, after the initial enzyme activation at 95 °C for 3 min, 36 cycles of the following program were used for amplification: 95°C for 30 s, 55°C for 30 s and 72°C for 45 s, and a final extension at 72 °C for 10 min. Amplicons of bacteria and fungi were sequenced on an Illumina MiSeq

PE300 platform (Illumina Inc., CA, USA) at the Majorbio Bio-pharm Technology Co., Ltd (Shanghai, China). The obtained raw sequence was checked by filtering raw pair-end reads with a low (Q < 20) average quality score, short reads (< 100 bp), and reads with three or more ambiguous nucleotides, and paired ends were joined for 16S rRNA sequences and ITS reads with FLASH (Magoc and Salzberg, 2011). Default settings were used except that forward reads were truncated to 200 base pairs, and reverse reads were truncated to 175 base pairs before merging. The sequences were processed and analyzed using the Quantitative Insights Into Microbial Ecology 2 (QIIME 2) (Bolyen et al., 2019). DADA2 pipeline was used to generate a feature table of ASVs counts (Callahan et al., 2016). Representative sequences were assigned to taxonomic lineages using the RDP classifier against the SILVA database for bacteria (Quast et al., 2012) and UNITE database for fungi (Nilsson et al., 2018). The proportion of unclassified sequence for fungi was ~6.7% and 0.7% in soil and termite mounds, respectively. In the present work, the sequence data was rarefied at a depth of 30,000 and 25,000 for bacteria and fungi, respectively. Good's coverage was ~98.0% and 99.8% for bacteria and fungi, respectively. Based on previous studies (Mo et al., 2018; Chen et al., 2019; Jiao and Lu, 2020), ASVs with relative abundances below 0.01% were defined as "rare" taxa. All the raw sequencing data were deposited in the National Center for Biotechnology Information Sequence Read Archive under the accession number PRJNA647630.

Statistical analysis

All statistical analyses were performed in the R platform (R Core Team, 2016).

Climatic factors including Mean annual temperature/precipitation, mean temperature/precipitation of wettest quarter and aridity index were obtained from the WorldClim (https://www.worldclim.org/) and Global Aridity Index and Potential Evapotranspiration Climate Database v2 (https://cgiarcsi.community/). To compare the microbial community composition between termite mounds and bulk soils, we calculated the alpha-diversity (Shannon index) and beta-diversity based on the Bray–Curtis distances. Non-metric multidimensional scaling (nMDS) ordinations was performed to evaluate changes in microbial composition between termite mounds and bulk soils. To determine the significance in the difference in microbial community compositions between termite mounds and surrounding soils, PERMANOVA analysis was performed in the 'vegan' package (Oksanen et al., 2017). The significant difference in the relative abundances of specific microbial taxa between termite mounds and soils was identified using one-way ANOVA. Microbial interactions were based on the network analysis by calculating the Spearman rank correlation. Random forest model was constructed with the 'randomForest' and 'rfPermute' packages (Liaw. A and Wiener. M, 2002; Archer, 2018) to identify the major statistically significant predictors for the termite mounds microbial profiles.

Habitat niche breadth is a crucial trait that influences the relative importance of deterministic and stochastic processes in shaping the microbial community assembly (Pandit et al., 2009). We calculated Levins' niche breadth index (B) for both bacteria and fungi according to the formula (Levins, 1968; Pandit et al., 2009):

$$B_j = 1/\sum_{i=1}^{N} P_{ij}^2$$

Where B_j represents the habitat niche breadth of ASV_j in a metacommunity; N is the total number of communities in each metacommunity; P_{ij} is the proportion of ASV_j in community i. A high *B*-value for a given ASV indicates that the ASV occurs widely and has a wide habitat niche breadth. Habitat niche breadth at the community level was estimated as the average *B*-values from all ASVs in a single community (*Bcom*) (Wu et al., 2018). A microbial group with a wider niche breadth is more metabolically flexible at the community level (Jiao et al., 2019).

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Table 1 Correlation (Spearman) between aridity, selected termite mounds and soil properties and microbial attributes.

Microbial group	Variable	pH (TM)	pH (Soil)	DON (TM)	DON (Soil)	DOC (TM)	DOC (Soil)	TC (Soil)	TN (Soil)	NO3-N (Soil)	NH4-N (Soil)	Aridity index
Bacteria	Bacterial NMDS1	0.83***	0.40***	-0.18*	-0.19*					-0.26**		
	Bacterial NMDS2			-0.29***	-0.26**		-0.19*	0.28**	0.29**		-0.43**	0.44***
	Actinobacteria			0.19*	0.17*			-0.40***	-0.36***	0.23*	0.35***	-0.45***
	Acidobacteria	-0.56***										
	Armatimonadetes	0.33***	0.31***	-0.27**	-0.29***	0.18*				-0.35***	-0.23*	0.24*
	Chlamydiae						0.19*					
	Chloroflexi	0.31***	0.21*		-0.25**					-0.33***		
	Cyanobacteria	0.22**			-0.18*			0.22*		-0.27**	-0.22*	0.24*
	Fibrobacteres				-0.27**		-0.22**				-0.36***	
	Firmicutes				-0.17*		-0.18*				-0.31**	0.24*
	Gemmatimonadetes	0.61***	0.36***									
	Margulisbacteria						-0.27**					
	Nitrospirae	0.34***	0.28**	-0.33***	-0.41***					-0.45***	-0.33***	0.30**
	Patescibacteria				0.35***		0.34***				0.39***	
	Planctomycetes			-0.22*	-0.18*					-0.31**		0.23*
	Proteobacteria		-0.24**					0.25**	0.24*		-0.22*	0.28**
	Rokubacteria	0.30***		-0.23**	-0.24**		-0.24**				-0.45***	
	Tenericutes				-0.19*	0.18*	-021*					
	Verrucomicrobia			-0.25*	-0.34***					-0.37***	-0.33***	0.39***
	WPS.2	-0.59***	-0.19*									
Fungi	Fungal NMDS1	0.81***	0.32***	-0.18*								
	Fungal NMDS2		-0.19*	-0.44***	-0.36***		-0.41***	0.37***	0.35***		-0.63***	0.59***

	Ascomycota	0.19*	0.21*		0.29***		0.32***				0.30**	-0.27**
	Basidiomycota	-0.21*	-0.29***		-0.23**		-0.45***				-0.35***	0.28**
	Calcarisporiellomycota	0.28**		-0.20*	-0.30***		-0.28**				-0.36***	0.30**
	Chytridiomycota	0.25**								-0.22*		
	Mortierellomycota	0.36***	0.19*	-0.18*	-0.31***		-0.21*			-0.25*	-0.35***	0.30**

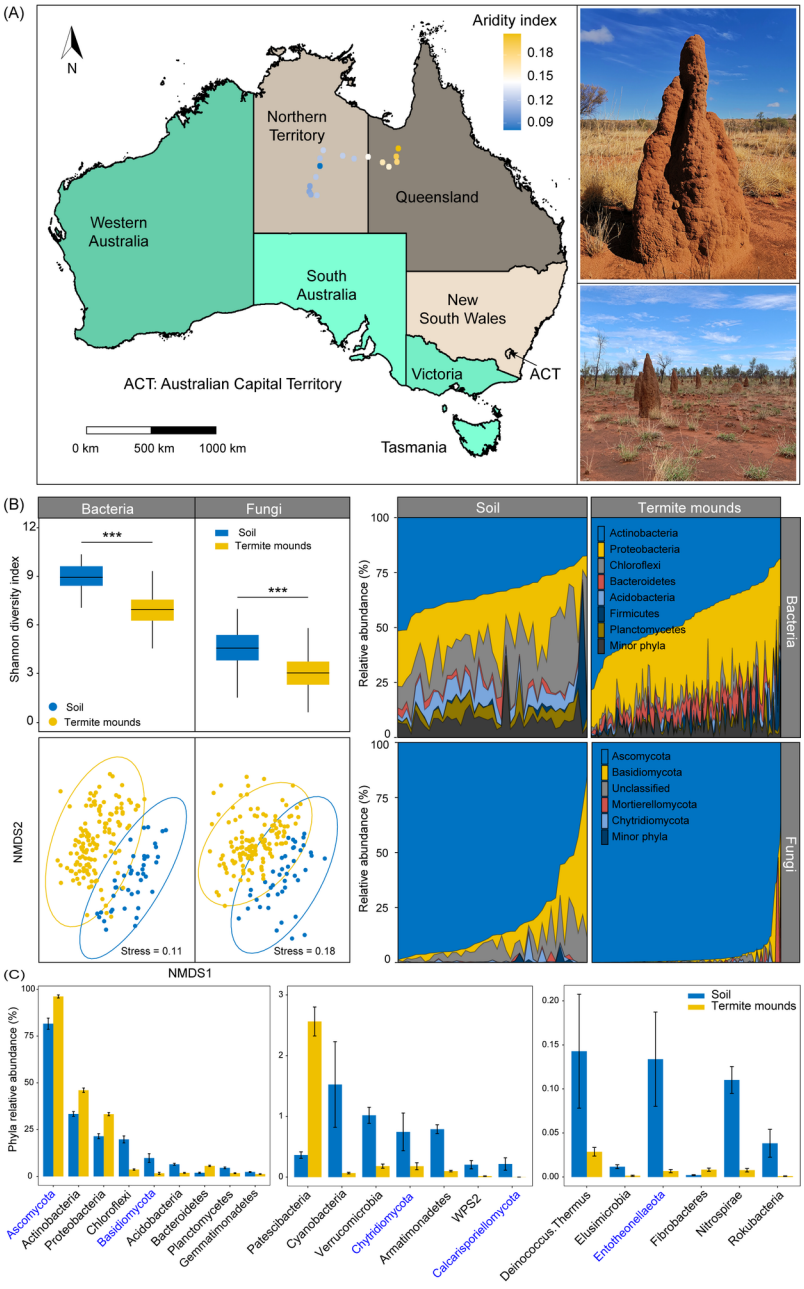
Note: TM, termite mound; DON, dissolved organic nitrogen; DOC, dissolved organic carbon; TC, total carbon; TN total nitrogen

Figure legends

Fig. 1 Sampling locations (n = 16), aridity index of each sties and photos of a representative ecosystem type and termite mounds (A). Microbial community profiles including microbial alpha and beta-diversity, and microbial compositions at the phylum level in termite mounds and bulk soils (B). Relative abundances (mean ± SE) of bacterial and fungal phyla that have significant differences between termite mounds and bulk soils (C). The names of fungal phyla are in blue color, while the names of bacterial phyla in black.

Fig. 2 The relationships between habitat niche breadth (*Bcom*) of taxa and their relative abundances (Log 10 transferred) in termite mounds. The black line indicates the predicted *Bcom* from the logistic model. R^2 and p values were calculated from the ordinary least squares (OLS) regression between measured and predicted *Bcom* value (A). Number of microbial interactions based on the network analysis between termite mounds and bulk soils, the microbial interactions were calculated at the genus level (B).

Fig. 3 Multiple predictors of microbial profiles in termite mounds. Ordinary least square (OLS) regression and nonmetric multidimensional scaling (nMDS) analysis showing the relationships between pH and microbial community compositions. Random Forest mean predictor importance (% of increase of MSE) of edaphic factors and aridity index on microbial profiles in termite mounds. TM, termite mound; DON, dissolved organic nitrogen; DOC, dissolved organic carbon; TC, total carbon; TN total nitrogen.



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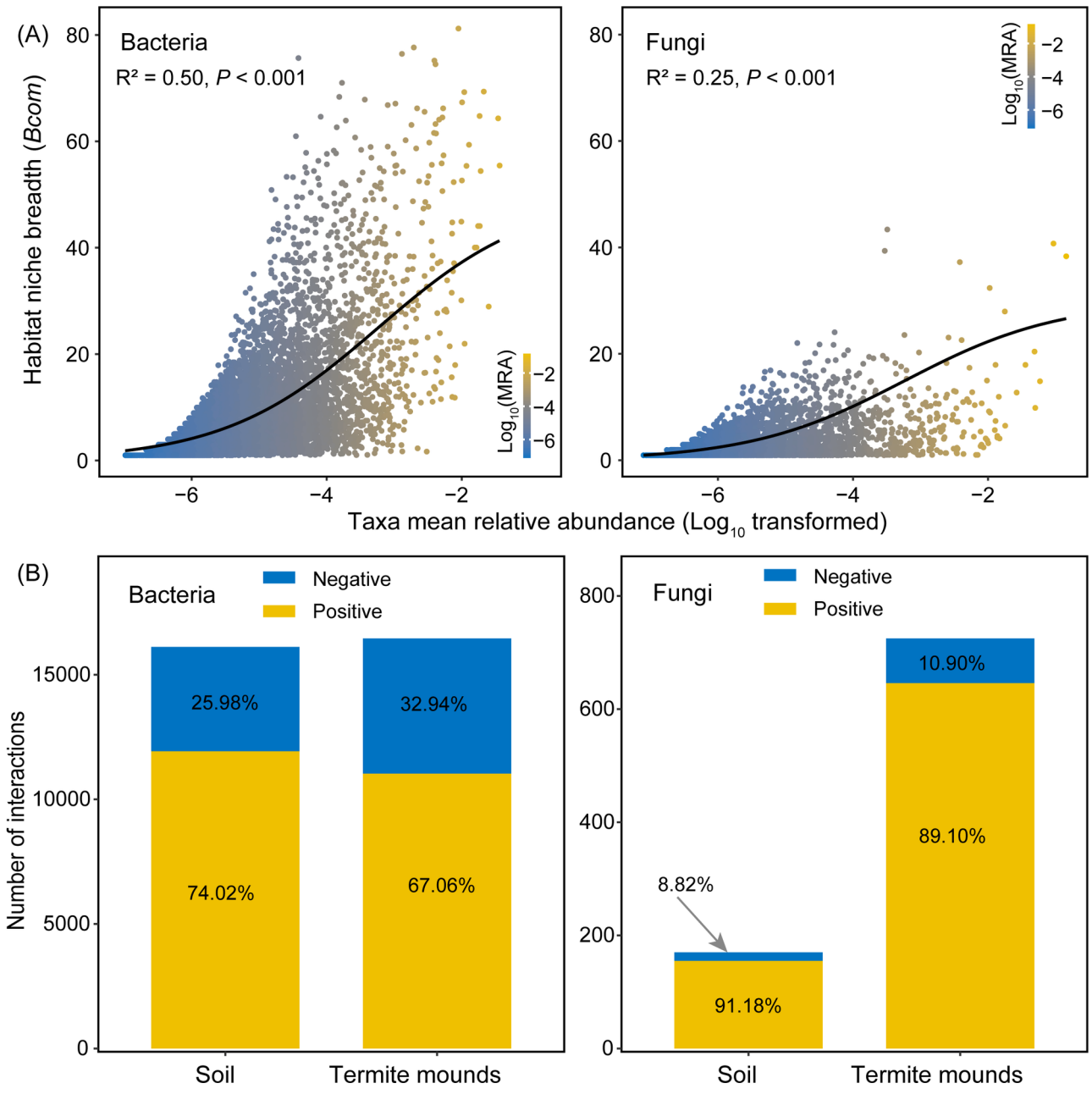

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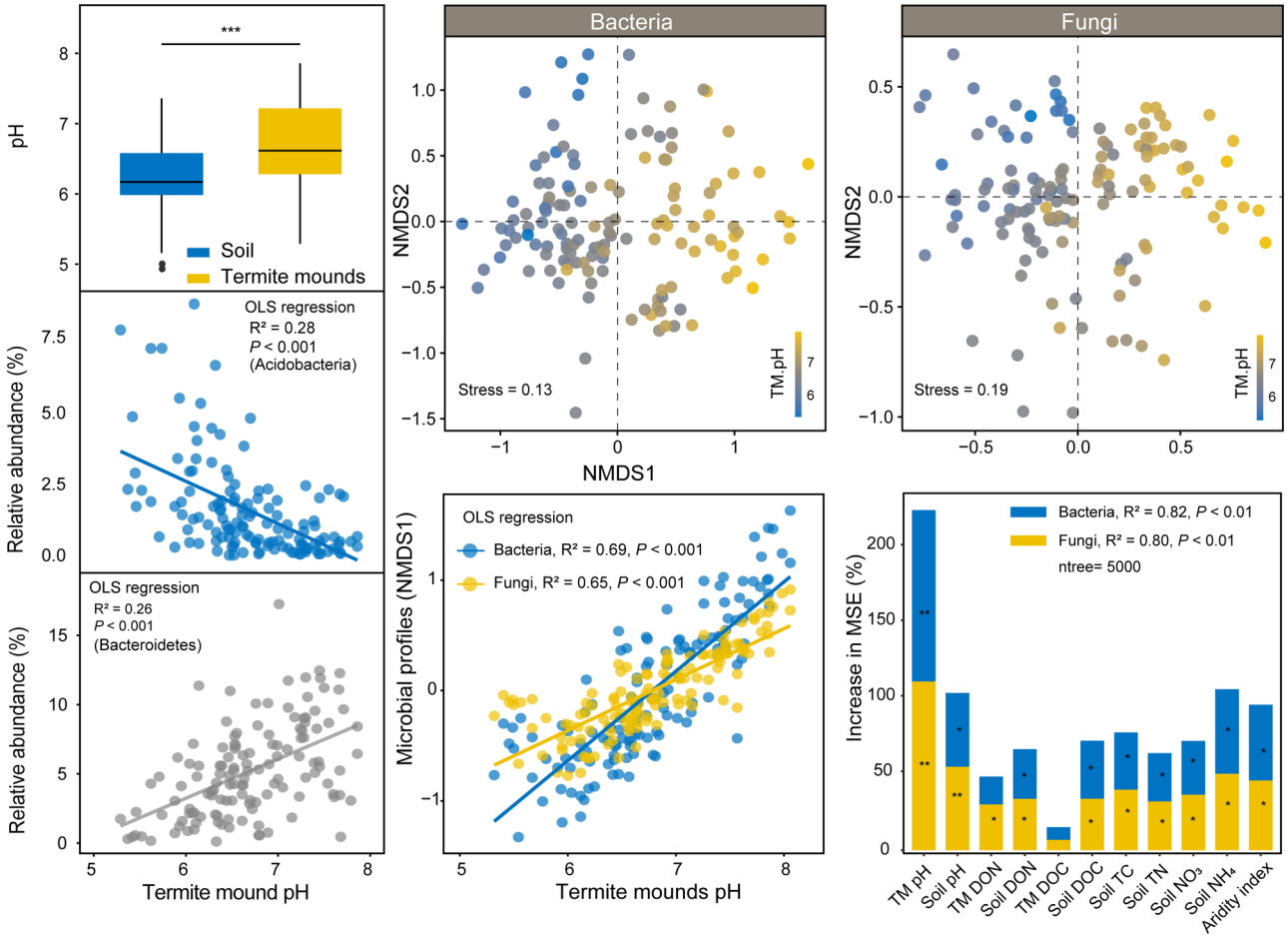

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