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Highlights

1. Termite mounds associated microbial communities exhibited a significant distance-decay pattern.
2. Deterministic selection predominated the microbial community assembly in termite mounds.
3. Mean annual temperature is the most important predictor of microbial profiles in termite mounds.
4. Deterministic processes exhibited a weaker impact on bacteria than fungi.

Deterministic selection dominates microbial community assembly in termite mounds

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Abstract

Termite mounds are an important habitat for an enormous diversity of microorganisms. However, the microbial community assembly processes in termite mounds remain unresolved, which impeded our ability to predict the biological functions of these mound-associated microbiota under the global changes. Here we conducted a large-scale investigation in northern Australia to explore biogeographical patterns of microbial community in termite mounds and identify the role of deterministic and stochastic processes in microbial community assembly. Microbial communities in termite mounds exhibited a significant distance-decay pattern, and fungi had a stronger distance-decay relationship than bacteria. The neutral community model and normalized stochasticity ratio index (*NST*) revealed that the deterministic selection, rather than stochastic forces, predominated the microbial community assembly in termite mounds. Deterministic processes exhibited a significantly weaker impact on bacteria (*NST* = 45.23%) than on fungi (*NST* = 33.72%), likely due to the wider habitat niche breadth and higher potential migration rate of bacteria. Random forest model further demonstrated that mean annual temperature was the most important predictor of both bacterial and fungal profiles in termite mounds. These findings improved our understanding of spatial patterns and processes of microbiome in termite mounds, which is critical to decipher the role of termite mounds associated microbes in regulating ecosystem multifunctionality.

Keywords: Community assembly; Biogeography; Ecological model; Biotic interaction; Termite mounds

Introduction

Unravelling the role of ecological processes and environmental factors in governing the assembly of microbial communities is a central goal in microbial ecology (Dumbrell et al., 2010; Stegen et al., 2013). Mounting evidence suggested that microbes can coexist in the environment with limiting resources and exhibit a significant biogeographic pattern (Nemergut et al., 2013; Zhou and Ning, 2017). Deterministic and stochastic processes, based on the niche-based and neutral theory, respectively, are commonly used to explain the assembly of species into communities (Dini-Andreote et al., 2015; Zhou and Ning, 2017). The fundamental premise of niche-based theories is that ecological traits differ among species within a community (e.g., different nutrition requirements), which allow them to occupy different niches and differentiate limited resources within the ecosystem (Leibold and McPeek, 2006; Mitchell et al., 2019). Neutral theories assume that all individuals are ecologically equivalent and have the same demographic rates (Chave, 2004), and dispersal limitation and stochasticity are the key processes that drive the community assembly (Hubbell, 2001). Growing evidence, after a long-standing debate, shows that deterministic and stochastic processes are not mutually exclusive, but rather act concurrently to regulate the community assembly (Dini-Andreote et al., 2015; Kim et al., 2018; Chen et al., 2019).

Currently, ecologists have had a good knowledge of how abiotic factors (e.g., pH, temperature) drive the diversity and distribution of bacterial and fungal communities in terrestrial ecosystems across regional to global scales (Tedersoo et al., 2014; Bahram et al., 2018; Delgado-Baquerizo et al., 2018). Recent studies reported that the global distribution of soil faunal communities including earthworms, nematodes, and invertebrates, is primarily driven by vegetation and climate across biomes (Bastida et al., 2019; Phillips et al., 2019; van den Hoogen et al., 2019). Termites are among the most abundant groups of insects on Earth, and play a vital role in the terrestrial ecosystem by consuming dead plants, woods and feces, driving nutrient cycling processes, and producing greenhouse gas methane (CH_4) (Lavelle et al., 2006; Nauer et al., 2018; Ashton et al., 2019). Some termites can create unique nest structures (also known as 'mounds') from soil, saliva and excreta, which substantially alter soil physicochemical properties, increase soil nutrient availability, and enhance plant growth (Pringle et al., 2010; Bonachela et al., 2015; Singh et al., 2019). Termite mounds, as an 'island of fertility', harbour a broad range of microorganisms that are essential to regulation of multiple ecosystem functions (Chiri et al., 2020). A recent study demonstrated that the methanotrophic bacteria dwelling in termite mound walls mitigated approximately half of termite produced CH_4 (Nauer et al., 2018). However, we still lack the knowledge of microbiomes and microbial assembly processes in ubiquitous termite mounds, which is essential to predict the role of termite mounds in regulating terrestrial ecosystem functions.

In this study, we conducted a large-scale investigation across >1500 km in northern Australia to explore the microbial assembly processes and drivers in regulating the composition of termite mound associated microbial communities (Figure S1). Our hypothesis is that, if stochastic process dominates the microbial assembly, chance events due to the restricted dispersal to nearby locations would probably produce more compositionally similar communities between termite mounds and its matrix soil. Owing to the differences in physiochemical properties between termite mounds and surrounding soils, if deterministic process dominates the microbial assembly, distinct microbial community compositions would be found between termite mounds and soil. Therefore, by comparing the microbial community assembly in termite mounds and surrounding soils, this study provides an ideal setting to improve our understanding of the mechanisms governing the microbial biogeographic pattern and the contribution of deterministic and stochastic processes to community assembly processes. The present study aimed to (1) quantify the relative importance of deterministic and stochastic processes in termite mound microbial assembly; (2) explore whether bacterial and fungal taxa assemble via similar or different community assembly mechanisms in termite mounds; and (3) identify the dominant driver in shaping the microbial communities in termite mounds.

Materials and Methods

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) (Figure S1). 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) were highly abundant and widely distributed in the sampling region. We established a 50 m × 50 m plot at each sampling location, and collected composite samples (0-5 cm) from 8~10 termite mound walls. A total of 134 termite mound samples were collected in this sampling campaign. All samples were sieved < 2 mm mesh and divided into two fractions. One fraction was frozen at -80 ºC for molecular analyses of bacterial and fungal communities, and the other was stored at 4 ºC for soil physicochemical analyses.

Climatic data collection

Climatic attributes, including mean annual precipitation (MAP) and temperature (MAT) of each sampling location, were obtained from the WorldClim database version 2 (http://www.worldclim.org/) based on the spatial geographical coordinates (Fick and Hijmans, 2017). We calculated the aridity index (AI, the ratio of precipitation and evapotranspiration) of each location using the Global Aridity Index and Potential Evapotranspiration in Climate Database v2 (https://cgiarcsi.community/). Extracted data were processed with the 'raster' and 'sp' packages in R (Pebesma and Bivand, 2005; Hijmans and van Etten, 2019).

Soil physicochemical analysis

Standard methods were used to characterize soil physicochemical properties (Rayment and Lyons, 2011). 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 MilliQ water and measured using a TOC analyzer (Shimadzu, Kyoto, Japan). Total carbon (TC) and nitrogen (TN) were measured using the Dumas combustion method on LECO FP628 analyzer (LECO Corp., MI, USA). Nitrate nitrogen (NO_3^--N) and ammonium-nitrogen (NH_4^+-N) were extracted with 2 M KCl solution and measured with a flow analyzer (Skalar Analytical B. V. Tinstraat, Breda, Netherland).

Characterization of microbial community structure

Total genomic DNA 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).

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™ PCR Detection System (Bio-Rad, Herculers, USA). 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). Raw sequences were filtered for quality control by Majorbio. Briefly, raw pair-end reads containing over three ambiguous nucleotides, reads with a low ($Q < 20$) average quality score, short reads (< 100 nt) and barcode were discarded to generate the high-quality sequences. The sequences were processed and analyzed using the Quantitative Insights Into Microbial Ecology 2 (Bolyen et al., 2019). Chimeric sequence was checked using the ‘USEARCH’ package with the UCHIME algorithm (Edgar et al., 2011). DADA2 pipeline was used to generate a feature table of amplicon sequence variants (ASVs) (Callahan et al., 2016). Singletons, chloroplast and mitochondrial sequences were discarded from the final dataset. 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 raw sequences data were uploaded to the NCBI Sequence Read Archive (SRA) data depository (PRJNA647630).

Statistical analysis

All statistical analyses were performed in the R platform (R Core Team, 2016). To estimate the relationships between the bacterial and fungal communities, we performed the Procrustes analysis and Mantel test with the ‘vegan’ package (Oksanen et al., 2017). The pairwise geographic distance between sampling sites was calculated using the ‘sp’ package (Pebesma and Bivand, 2005) based on the coordinates of each sampling site. The distance–decay rate of the microbial communities was calculated as the slopes of ordinary least-squares regressions between geographic distance and community similarity (1–dissimilarity of the Bray–Curtis matrices). We calculated Levins’ niche breadth index for both bacteria and fungi with the ‘niche.width’ function in ‘spaa’ package in R (Zhang et al., 2016). A neutral community model (NCM) was used to predict the potential importance of stochastic processes in community assembly by determining the relationships between the detection frequency of microbial taxa in a set of local communities and their relative abundance across the wider metacommunity (Sloan et al., 2006). NCM was constructed in R with the code provided by Burns et al. (2016). We further used the normalized stochasticity ratio (*NST*) to quantify the relative importance of deterministic and stochastic processes in community assembly with 50% as the boundary point between more deterministic ($NST < 50\%$) and more stochastic ($NST > 50\%$) assembly (Ning et al., 2019). Random forest model was performed to identify the important predictors of microbial assembly in termite mounds with the packages of 'randomForest' (Liaw. A and Wiener. M, 2002), 'rfPermute'(Archer, 2018) and 'A3'(Fortmann-Roe, 2015). Ordinary least-squares (OLS) regression model was used to determine the relationships between the abundance of the most important predictor and microbial profiles in termite mounds.

Results

Characterization of edaphic and climatic variables

Soil properties were as follows: soil pH ranged from 4.93 to 7.36 (with an average of 6.16), total carbon and total nitrogen ranged from 0.19-1.32% and 0.02-0.10%, respectively. Mean annual precipitation and temperature ranged from 254 to 583 mm and 21.36 to 26.54 ℃. Aridity index ranged from 0.08 to 0.21, with an average of 0.12. More detailed information about the soil properties and climatic variables in this study is provided in Table S1.

Microbial community compositions in termite mounds

After assembling and quality filtering, a total of 8,185,293 and 8,190,911 high quality sequences were obtained for bacteria and fungi, respectively. These sequences were clustered into 14,772 bacterial ASVs and 4,503 fungal ASVs. The bacterial community compositions were predominated by the bacterial phyla Actinobacteria and Proteobacteria, which together occupied over 80% of the total sequences. Ascomycota, a common fungal phylum, showed an extremely higher relative abundance in termite mounds, which accounted for over 96% of the total sequences (Figure 1a). Mantel test (R = 0.739, $P < 0.001$) together with Procrustes analysis (sum of squares $M^2 = 0.234$, $P < 0.001$, 9999 permutations) indicated that bacterial profiles were significantly correlated with the fungal communities (Figure 1b).

Distance-decay of community similarity in termite mounds

We estimated the distance decay relationship (DDR) for both bacteria and fungi in termite mounds. Although DDR was significant for both bacteria and fungi ($P < 0.001$), the fitness values were remarkably low ($R^2 < 0.1$), indicating a weak decay of microbial community similarity with geographic distance. In addition, the slope of distance-decay curves, based on the OLS regression model, was steeper for fungi (slope = -1.91) than that for bacteria (slope = -0.21) in termite mounds (Figure 2).

Microbial community assembly processes in termite mounds

We calculated the community-level habitat niche breadths (*Bcom*) to explore the relative importance of deterministic and stochastic processes in microbial community assembly (Figure 3). A significantly higher *Bcom* value was observed for bacteria than fungi in termite mounds ($P < 0.001$) (Figure 3a). In addition, we fitted the bacterial and fungal communities to the neutral community model. The goodness of fit was better for bacteria (65.42% of the variations explained) than fungi (32.85% of the variations explained) (Figure 4). Bacteria ($m = 0.0372$) exhibited a higher mitigation rate than fungi ($m = 0.0015$), indicating that bacterial taxa were less limited by dispersal. We further employed the normalized stochasticity ratio (*NST*) to quantify the role of deterministic and stochastic processes in microbial community assembly (Figure 3b). The *NST* value was below the 50% boundary point for both bacterial and fungal communities, suggesting that deterministic process played a more important role than stochasticity during the microbial assembly in termite mounds. Additionally, a significantly ($P < 0.001$) higher *NST* value was observed in bacterial communities with an average of 45.23% than that in fungal communities with an average of 33.72% (Figure 3b)

Multiple drivers accounting for the microbial assembly in termite mounds

Random forest modeling was employed to identify the most important predictors of microbial assembly in termite mounds, and OLS model was used to test the relationship between selected predictors and microbial community composition profiles. Our random forest modelling (ntree = 5000) explained 69.3% and 70.1% of the microbial assembly variance in bacteria and fungi, respectively (Figure 5a). Most edaphic properties e.g. soil pH (Bacteria, $P < 0.05$; Fungi, $P < 0.01$), NH_4^+ ($P < 0.05$), TN ($P < 0.05$) and C/N ($P < 0.05$) exhibited significant impacts on both bacterial and fungal community compositions in termite mounds. Climatic factors including MAT ($P < 0.01$), MAP ($P < 0.05$) and AI ($P < 0.05$) also significantly influenced the microbial compositions. Among all the factors, MAT was the most important driver in shaping both bacterial and fungal community compositions in termite mounds. OLS model further indicated that microbial profiles (as represented by nMDS1) were positively correlated with MAT for both bacteria ($R^2 = 0.449$, $P < 0.001$) and fungi ($R^2 = 0.491$, $P < 0.001$) (Figure 5b). Nevertheless, it should be noted that a large proportion of variation (71% for bacteria and 75% for fungi) remained unexplained in the variation partitioning (Figure S2).

Discussion

Temperature based deterministic selection dominates microbial community assembly in termite mounds

The biogeographic pattern of microbial communities has received little attention so far in ubiquitous termite mounds, a unique environment for microorganisms in terms of nutrient availability and soil properties. The present study improves our understanding of the spatial patterns of termite mound-associated microbial communities and sheds light into the underlying processes and mechanisms of microbial community assembly. A significant distance decay pattern for both bacterial and fungal communities was observed in termite mounds across large spatial scales. The fitness values ($R^2 < 0.1$) of the DDR were substantially lower than those reported in other natural soil ecosystems (Griffiths et al., 2011; Wang et al., 2017), suggesting that microbial communities in termite mounds exhibit less apparent spatial patterns across a large scale. According to Hubbell's neutral theory, community similarity was predicted to decrease with increasing spatial distance due to dispersal limitation (Hubbell, 2001). Nevertheless, it is difficult to disentangle the relative importance of deterministic and stochastic processes by solely analyzing DDR. The differences in environmental factors, such as pH, MAT, MAP and vegetation, also likely increase with increasing geographical distance and play a key role in structuring microbial communities across regional and global scales (Maestre et al., 2015; Delgado-Baquerizo et al., 2016). In this case, the environmental changes induced shifts in microbial community compositions can be attributed to the taxonomic niche differentiation i.e. the deterministic process (Bell, 2010). Based on the neutral community model, we observed a lower fitness value (R^2) and mitigation rate (*m*) compared with previous studies (Burns et al., 2016; Chen et al., 2019), in which stochastic processes were dominant in shaping microeukaryotic and zebrafish gut microbial community assembly. Thus, our results indicate that stochastic processes may play a less important role in termite mound microbial community assembly. This finding is supported by the *NST*, a general mathematical framework for quantitatively assessing the influences of stochastic and deterministic processes in microbial community assembly (Ning et al., 2019). The *NST* value below the boundary (50%) further provided evidence that the niche based deterministic selection dominates microbial community assembly in termite mounds.

In the present study, we found that both climatic and edaphic factors play an important role in microbial community compositions in termite mounds, which is consistent with the global topsoil microbial communities (Bahram et al., 2018). Moreover, the MAT could be the most important diver in shaping the termite mound microbial compositions as revealed by random forest and OLS models. However, some potential caveats in the interpretation of our findings should be considered. Regarding the biological interactions, trophic-level interactions, e.g. predation and mutualisms, are not considered in the present study, but they play a unique role in maintenance of species diversity (Chesson, 2000). In addition, the mitigation of termites may increase the termite-associated microbial dispersal and modify the relative importance of deterministic and stochastic processes in shaping the microbial community assembly in termite mounds. These limitations together with the undetermined environmental variables could explain why over 70% proportion of variation remains unexplained for both bacterial and fungal communities in the variation partitioning (Figure S2). Actually, it is impractical to address the effects of all potentially biotic and abiotic variables, especially for a broad-scale field survey and this is consistent with previous studies where 50% - 90% variation remains unexplained in exploring the drivers that shaping the soil microbial patterns (Wang et al., 2017; Jiao et al., 2019).

Differences in community assembly between bacteria and fungi

In the present study, we demonstrated that overall the niche-based deterministic processes determine the termite mound and matrix soil microbial community assembly. An interesting finding is that the *NST* value of bacteria is significantly higher than that of fungi (Figure 3b), suggesting that stochastic processes contribute more to bacterial communities than to fungal communities. This observation could be due to the size-plasticity hypothesis (body size effect) that smaller organisms (bacteria) are less environment filtered than larger organisms (Liu et al., 2015), and thus ecological determinism will increase with organism size (De Bie et al., 2012; Farjalla et al., 2012). We further quantified the community-level habitat niche breadth, and found that bacteria had a significant wider niche breadth than fungi. A previous study reported that organisms with wider niche breadths might have greater metabolic plasticity and be less influenced by deterministic processes (Pandit et al., 2009). In addition, we observed that the mitigation rate of bacterial communities was approximately 25 times higher than fungal communities based on the NCM (Figure 4), which is an important factor for stochastic processes and partially explains why the slope of the fungal distance-decay pattern was steeper than that of bacteria.

Other explanations could be related to differential responses of bacteria and fungi to environmental factors, which has been suggested as a main reason for the contrasting global biogeographic trends for bacteria and fungi (Bahram et al., 2018). For instance, we observed a significant positive relationship between bacterial alpha diversity and MAT (*P*

< 0.001), in contrast, no significant correlation was identified for fungal alpha diversity (P = 0.280) (Figure S3). Microbial dormancy is suggested to promote biodiversity within microbial communities by allowing competing organisms to partition resources across time (Chesson, 2000; Lennon and Jones, 2011). It has been suggested that less than 10% of bacterial cells in a given community are in an active stage at any time (Locey, 2010). Like some bacteria (e.g., *Bacillus subtilis*) (Leggett et al., 2012), fungi also have the ability to form dormant status (e.g. resistant spores). The difference in dormancy strategies between bacteria and fungi may affect the community niche breadth and assembly, which was supported by a previous study that protist communities are more responsive to species sorting than bacterial communities, because protists have a more limited tendency to enter dormancy (Wu et al., 2018).

Conclusions and implications

Our work provides novel evidence that microbial community assembly in termite mounds was governed to a great extent by temperature based deterministic selection, rather than by stochastic processes, which is the first step to predict the ecological activities and processes of termite mounds in the context of global changes. The difference in the stochasticity between bacteria and fungi may be attributed to the differences in habitat niche breadth, potential mitigation rate, responses to environmental variations and dormancy strategies, which highlight the importance of considering organism characteristics in differentiating the role of stochastic and deterministic assembly processes in microbial communities.

Conflict of interest

The authors declare that they have no competing interests

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Appendix A. Supplementary data

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Figure

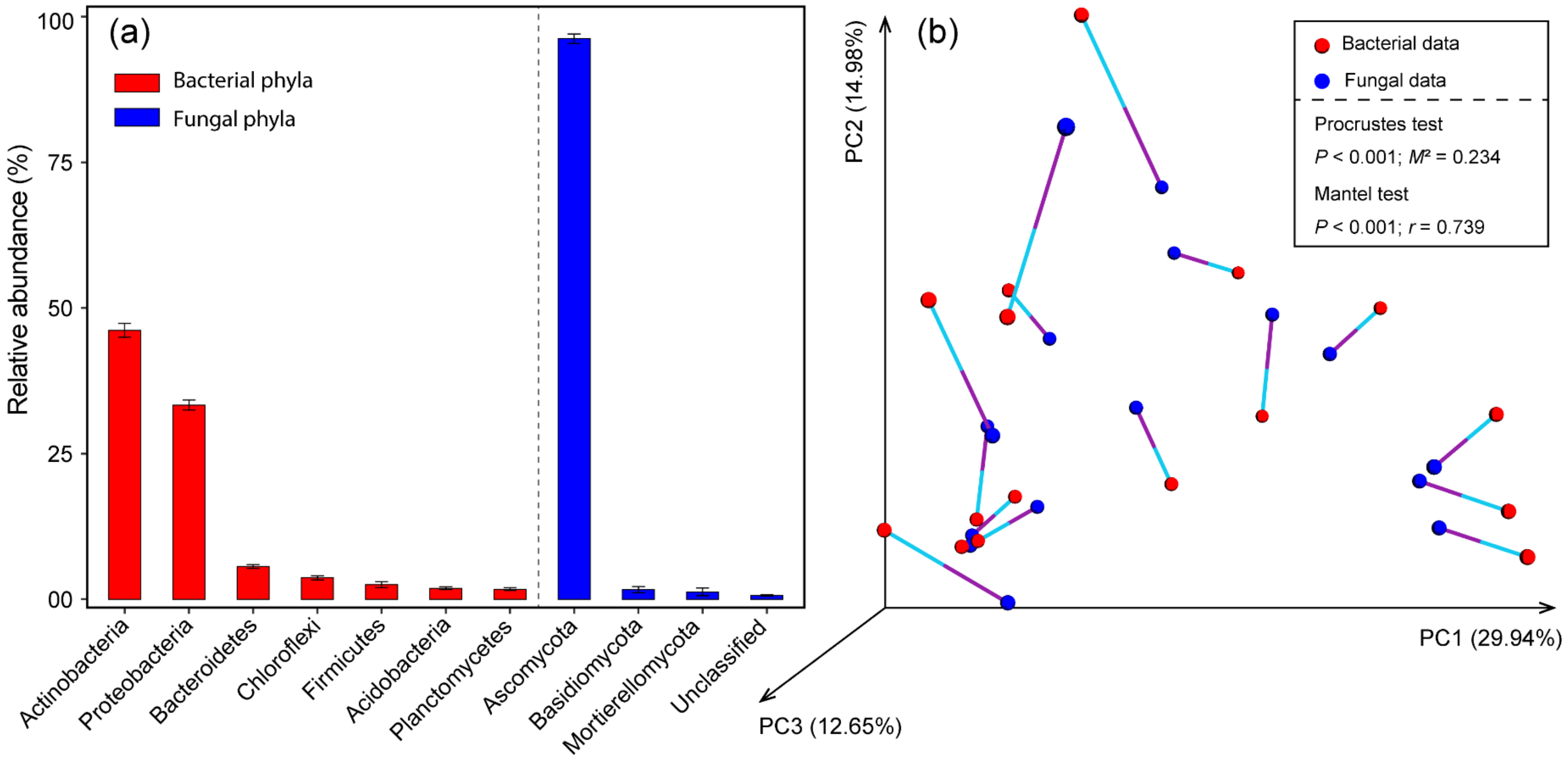

Figure 1 Distribution of bacterial and fungal phyla in termite mounds (a); Procrustes analysis (OTU-level) depicts significant correlations between bacterial and fungal compositions (b).

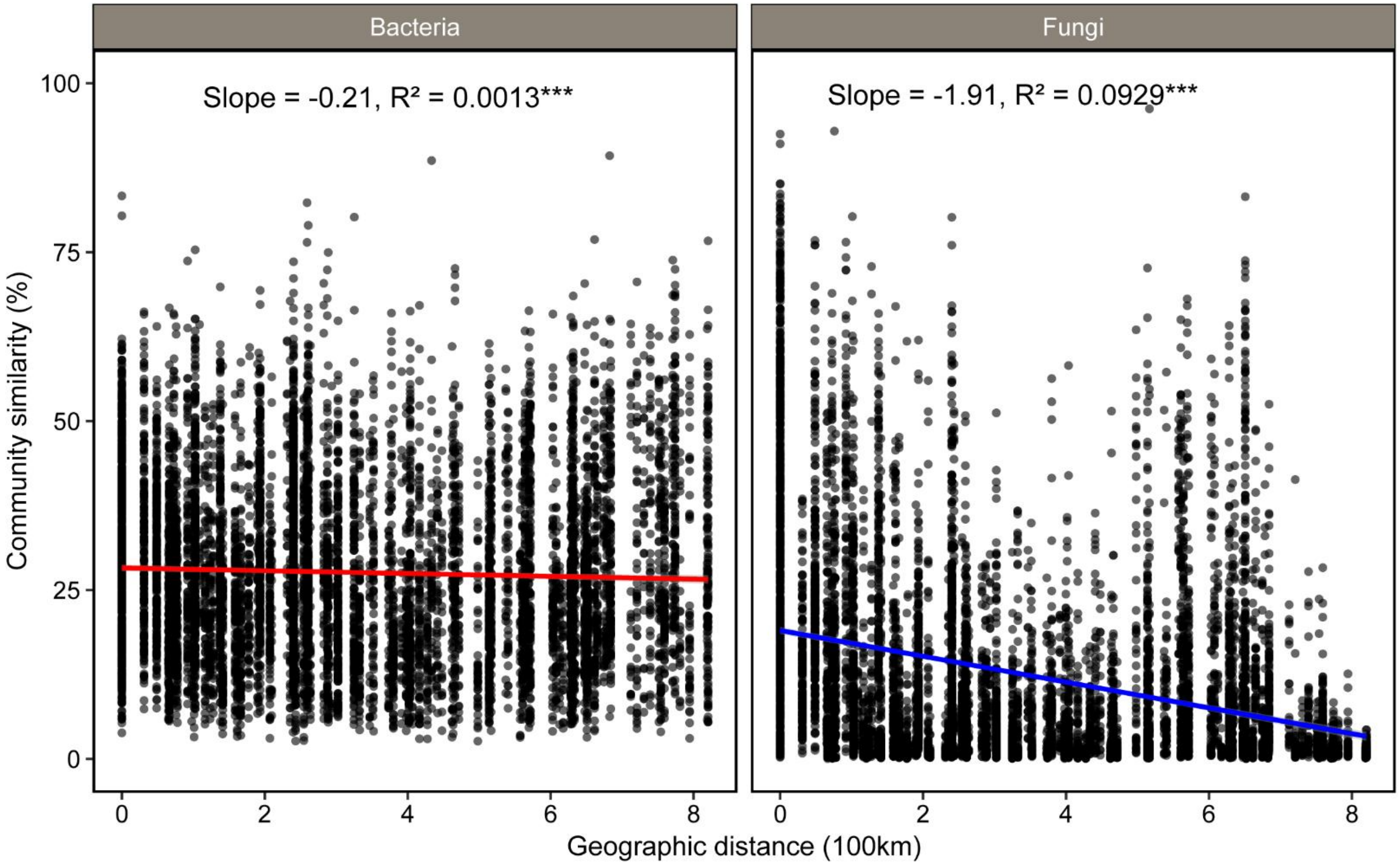

Figure 2 Distance-decay curves showing the relationships between the Bray–Curtis similarity of bacterial and fungal communities and geographic distances between sampling sites. Solid blue and red lines denote the ordinary least-squares linear regressions. The results are based on a 97% sequence similarity cut-off. Asterisks denote significant correlation (***$P < 0.001$).

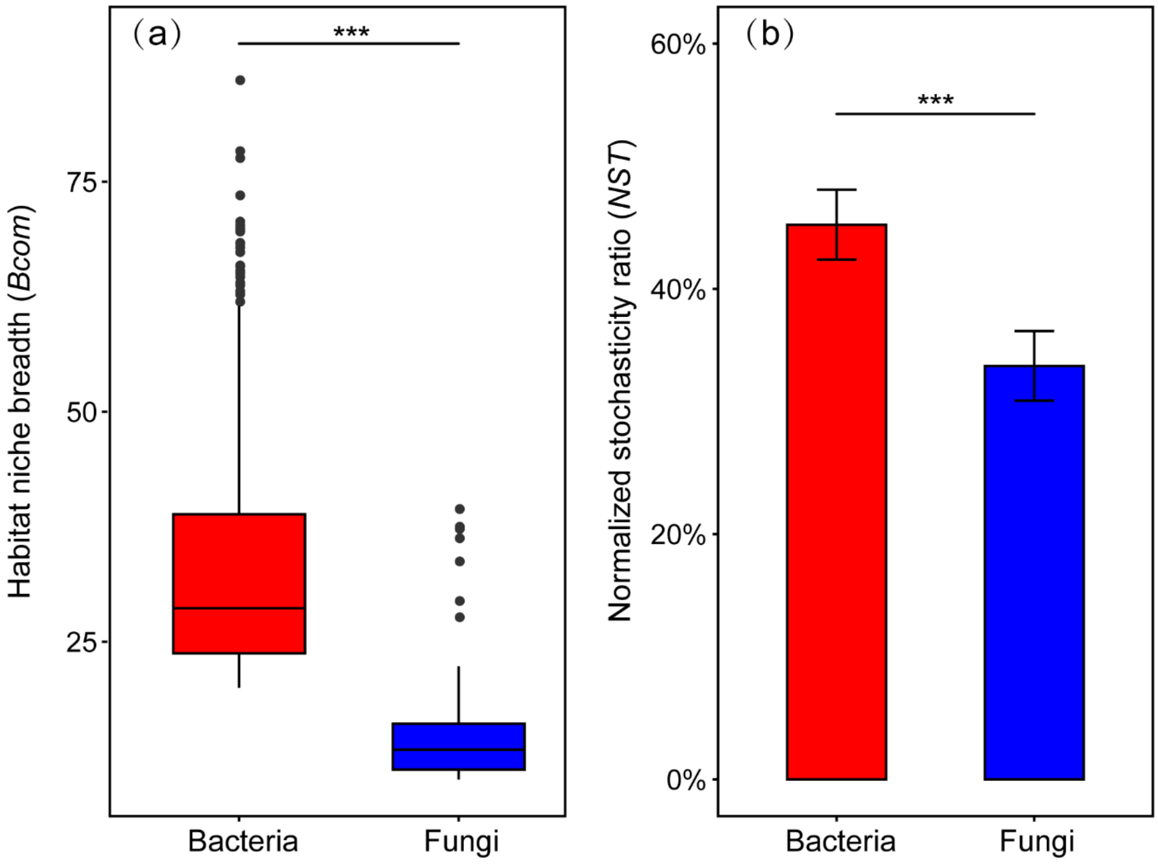

Figure 3 Boxplots showing the mean habitat niche breadth from all taxa for each sample (*Bcom*) in termite mounds (a). Barplots showing the comparison of normalized stochasticity ratio (*NST*) between bacterial and fungal communities in termite mounds (b). Asterisks denote significant differences (***$P < 0.001$).

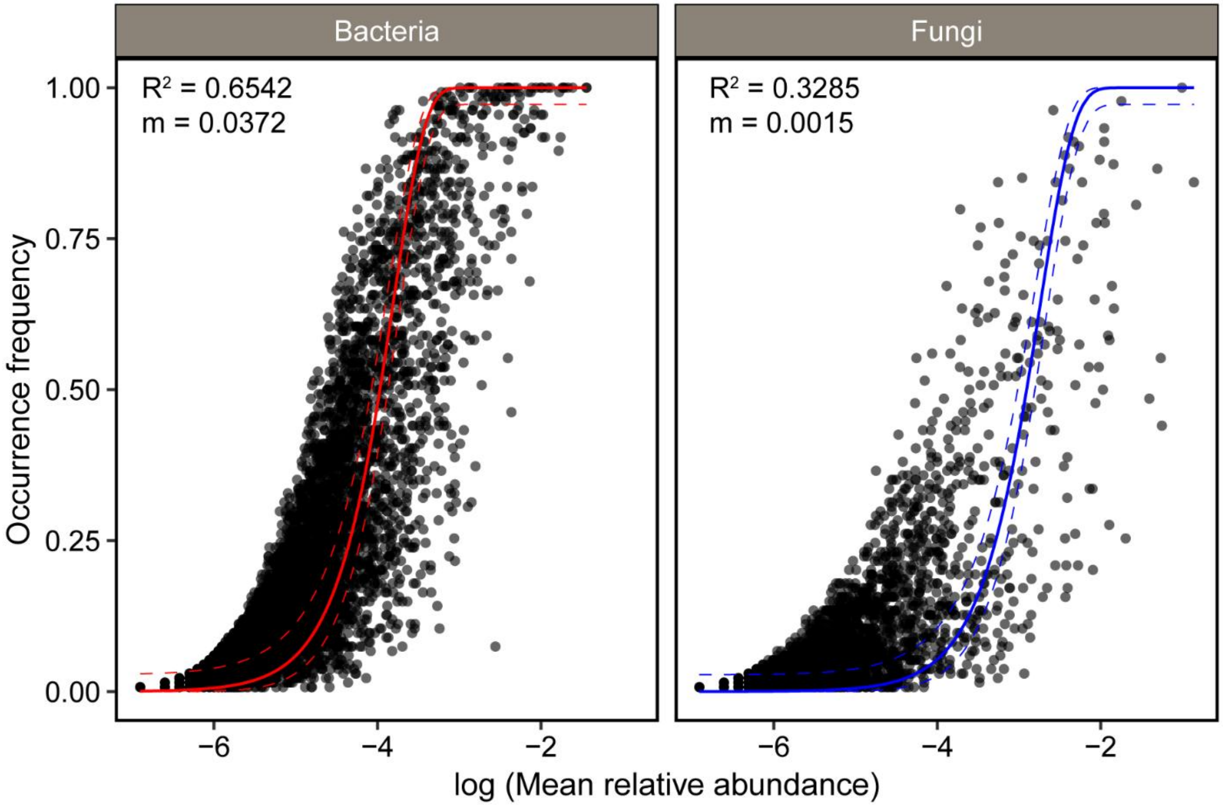

Figure 4 Fit of the neutral community model (NCM) showing the OTU predicted occurrence frequencies versus the relative abundance in termite mounds. The blue and red solid lines indicate the best fit to the Sloan's neutral model and the dashed lines represent 95% confidence intervals around the model prediction. R^2 and m values indicate the goodness of fit to the neutral model and the estimated migration rate, respectively.

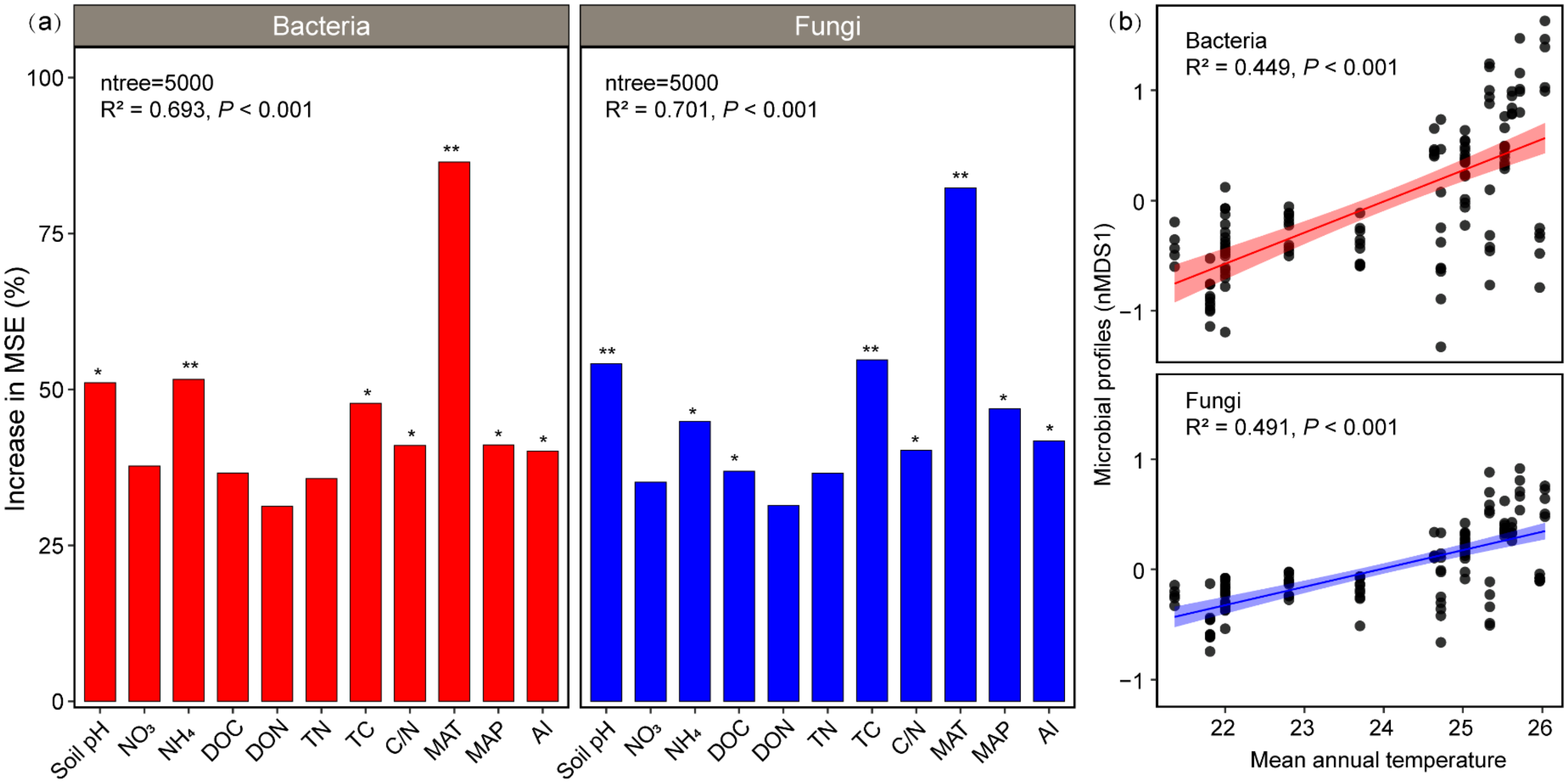

Figure 5 Random Forest modelling indicating the importance the predictors for microbial profiles (a); Ordinary least squares (OLS) regression analysis showing the relationships between the microbial profiles and mean annual temperature (b). NO_3: nitrate nitrogen, NH_4: ammonium-nitrogen, DOC: dissolved organic carbon, DON: dissolved organic nitrogen, TN: total nitrogen, TC: total carbon, C/N: ratio of total carbon and nitrogen, MAT: mean annual temperature, MAP: mean annual precipitation, AI: aridity index. *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

***Declaration of Interest Statement**

The authors declare no conflict of interest.