Variations in bacterial and archaeal community structure and diversity along the soil profiles of a peatland in Southwest China

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Abstract

As bacteria and archaea are key components in the ecosystem, information on their dynamics in soil profiles is important for understanding the biogeochemical cycles in peatlands. However, little is known about the vertical distribution patterns of bacteria and archaea in the Bitahai peatland, or about their relationships with soil chemical properties. Here, bacterial and archaeal abundance, diversity, and composition of the Bitahai peatlands at 0-100 cm soil depths were analyzed by sequencing of 16S rRNA genes (Illumina, MiSeq). Soil pH, total C, N, and P concentrations and stoichiometric ratios were also estimated. The results revealed that total C and total N contents, as well as C:P and N:P ratios, significantly increased with increasing peatland soil depths, while total P decreased. The top three dominant phyla were Proteobacteria (39.64%), Acidobacteria (12.93%), and Chloroflexi (12.81%) in bacterial communities, and were Crenarchaeota (58.67%), Thaumarchaeota (14.34%), and Euryarchaeota (10.82%) in archaeal communities in the Bitahai peatland, respectively. The total relative abundance of methanogenic groups and ammonia-oxidizing microorganisms all significantly decreased with soil depth. Both bacterial and archaeal diversities were significantly affected by the soil depth. Soil C, N, and P concentrations and stoichiometric ratios markedly impacted the community structure and diversity in archaea, but not in bacteria. Therefore, these results highlighted that the microbial community structure and diversity depended on soil depth for the Bitahai peatlands, and the factors affecting bacteria and archaea in the Bitahai peatlands were different.

Keywords Soil stoichiometry · Wetland · Diversity · Community · MiSeq

Introduction

Peatlands cover only about 3% of the earth’s terrestrial surface but store nearly 30% of global soil carbon (Dise 2009). They are an important carbon sink because of their low rate of organic matter decomposition and high water table (Laiho 2006). The carbon accumulated in the northern, tropical, and southern peatlands was 547, 50, and 15 Gt C respectively (Yu et al. 2010). Carbon storage in peat soils is so high that carbon cycling in peatland ecosystems plays an important role in global carbon cycling. Microbial communities, as important decomposers, play a key role in the carbon cycle of peatlands.
and in overall ecosystem functioning. They not only directly control the turnover of organic carbon, but also improve nutrient mineralization and uptake (Andersen et al. 2013). Carbon and nitrogen cycling are inextricably linked, and several studies have confirmed the emission of greenhouse gas N₂O (Dinsmore et al. 2009; Saari et al. 2013), CH₄ (Godin et al. 2012), and CO₂ (Hoyt et al. 2019) from peatlands. Soil microbes are involved in the production of N₂O, CH₄, and CO₂ (Liu et al. 2020), therefore uncovering their vertical distribution patterns would improve our understanding of nitrogen and carbon cycling in peatlands.

Peatland soil microbial communities in the surface and subsurface layers (Cadillo-Quiroz et al. 2006; Seward et al. 2020) have been well studied; however, studies on communities in deeper peat layers are relatively lacking (Putkinen et al. 2009; Zhou et al. 2017). Currently, known peatland soil profiles are often meters deep, and deeper layer soil microbial communities might be specialized for their own conditions, and thus, may be distinct from communities in shallower, surface layers (Blume et al. 2002; Eilers et al. 2012; Tisitsko et al. 2014). Many types of functional microbes involved in the carbon and nitrogen cycles of anaerobic processes exist widely in peatlands, such as methanogenic archaea (Godin et al. 2012), methane anaerobic oxidizing bacteria (Zhu et al. 2012), ammonia-oxidizing microorganisms (Xu et al. 2019), and anaerobic ammonia-oxidizing bacteria (Liu et al. 2020a). Therefore, studying the vertical distributions of soil microbial groups across deep soil profiles may be important for understanding the underlying mechanisms of carbon and nitrogen cycling in peatlands.

Soil C, N, and P contents and stoichiometry vary with depth (Hu et al. 2019), thus, understanding how variations in physicochemical characteristics along with the soil profile shape microorganism communities is essential to understanding corresponding biogeochemical processes. Previous studies have revealed that soil microbial communities are determined by several abiotic factors (Andersen et al. 2013; Jeanbille et al. 2016), such as carbon, nitrogen, and phosphorus contents (Koranda et al. 2011; Li et al. 2014; Wang et al. 2020) and C: N: P stoichiometry (Ren et al. 2016; Shen et al. 2019). For peatland microbial communities, soil C:N ratio (Lin et al. 2014), pH, total organic carbon, total nitrogen, water table (Wang et al. 2019; Zhong et al. 2017), redox condition (Martinez et al. 2007), and carbon quality (Lamit et al. 2017) are factors that affect microbial communities. However, the factors controlling microbial communities and their functions across vertical samples (taken every 10 cm, to a depth of 100 cm) remain poorly understood. Likewise, there is little information available on how the magnitude of variation in bacteria, archaea, methanogens, and ammonia-oxidizing microorganisms within deeper soil profiles.

The Bitahai peat fen, located at the heart of the Hengduan Mountains, is a globally important wetland with high species diversity. Many studies have recognized that this wetland also plays an important role in the water storage, flood control, and water balance of the middle and lower reaches in the Yangtze River (Yin 2002; Yu et al. 2015). Thus, it is very important for the supply of regional ecosystem services and the construction of ecological security barriers. Studies on this wetland mainly focused on land-use changes (Wu et al. 2015), diversity (He et al. 2019; Shu et al. 2013; Zhou and Chen 2006), Phytophthora species (Hui et al. 2013), basic chromosome numbers of the genus Streptopus (Zhang and Gu 2005), and soil nutrients and nitrous oxide flux in the upper soil layers (Wang et al. 2017). However, microbial communities in the deep soil layer, which play an enormous role in driving the carbon and nitrogen cycles along with the soil profile, are missing. Studying the differences between bacterial and archaeal communities along with the peat profile and linking these to the changes in the soil properties of the Bitahai peatland is important. Thus, our hypothesis was that (1) bacterial and archaeal composition and diversity vary with soil depth, and (2) soil properties affect the bacterial and archaeal communities and diversity along with soil profiles in the Bitahai peatland.

Materials and methods

Site description and soil sampling

The study site was located in the Bitahai Nature Reserve (27°46′–27°57′N, 99°54′–100°09′E), Yunnan Province, Southwest China. The elevation of this region is 3512.9 m, and it has a cold and humid plateau climate with an annual average temperature of 5.4 °C. The hottest and coldest months are July and January, with average temperatures of 13.2 °C and -3.8 °C, respectively. The annual average precipitation is 617.6 mm and mostly falls between June to September. Fens are less acidic, often more nutrient-enriched and eutrophic, saturated with water and support sedges, grass, and trees, and bogs are characterized by sphagnum moss, acidic water, and low nutrient status (Chen et al. 2020). The Bitahai peat is saturated throughout the year, and the peat thickness is approximately 3 m deep. There is no sphagnum, and the most dominant species at this site are Carex lehmanii, Sanguisorba filiformis, Deschampsia cespitosa, and Sinocarum coloratum. The range of peat soil pH was 5.2–5.8. Thus, the Bitahai peatland is a fen. Our sampling sites were distributed among the typical peat environment of Bitahai. Three sampling plots were set in this fen during the 2017 growing season, and ten soil depths (0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, 50-60 cm, 60-70 cm, 70-80 cm, 80-90 cm, and 90-100 cm) were collected from each plot. Three replicate cores (ca., 100 g soil) were taken from each plot using a Russian peat corer (diameter 52 mm, Eijkelkamp, Giesbeek, Netherlands).
For each soil core, roots were carefully removed by hand, and soil was sieved through by a 2-mm sieve. A total of 30 soil samples were obtained and stored in sterilized and sealed polyethylene packages, transported on ice to the laboratory, and stored at -20 °C until processing.

Soil properties analysis

Soil pH was determined using a pH meter (Orion 868, USA) with a soil-to-water ratio of 1:2.5. Total carbon (TC) was measured using a Vario TOC instrument manufactured by Elementar Company. Total nitrogen (TN) and total phosphate (TP) were determined by the measurement of H2SO4 digestion with a continuous flow analytic system (SEAL Analytical AA3, Germany).

DNA extraction, PCR amplification, and MiSeq sequencing

Total soil DNA was extracted using the E.Z.N.A.™ Soil DNA kit (Omega Bio-tek, Inc., GA, USA) according to the manufacturer’s instructions and was collected in 50 μl of elution buffer. DNA concentration was determined using a NanoDrop One (Thermo Scientific, Wilmington). The 16S rRNA genes of the bacteria (515F: GTG CCA GCM GCC GCG GTAA and 926R: CCG YCA ATT YMT TTR AGT TT, V4–V5 regions) and archaea (Arch519F: CAG CCG CCG CGG TAA and Arch915R: GTG CTC CCC CGC CAA TTC CT, V4–V5 regions) were amplified in triplicate (Vissers et al. 2010; Walters et al. 2016). The primers were tagged with sequences to incorporate Illumina adapters with indexing barcodes. A 50-μl PCR mix consisted of 25 μl Taq-Mix, 2.5 μl of each primer, 5 μl template and 15 μl ddH2O. PCR was performed under the following conditions: a 3-min initial denaturation step at 94 °C followed by 30 thermal cycles of 30 s at 94 °C, 30 s at 50 °C/57 °C (annealing temperature 50 °C and 57 °C for 515F/926R and Arch519/Arch915R respectively), 40 s at 72 °C, and followed by a 10-min incubation at 72 °C. The DNA concentrations were quantified, and the amplicons from each sample were pooled at an equimolar concentration for sequencing on an Illumina MiSeq Sequencer (San Diego, CA, USA).

Processing of sequencing data

Raw sequence data were processed and analyzed using the QIIME pipeline (Caporaso et al. 2012). Briefly, sequencing reads with an average quality value ≤ Q20 were obtained, ambiguous nucleotides in barcodes and homopolymer reads longer than 8 bp and shorter than 150 bp were removed to improve sequence quality. Paired ends were joined with FLASH (Magoc and Salzberg 2011), whereas the chimeric sequences were detected and eliminated using the USEARCH function in QIIME (Caporaso et al. 2010). After quality control and chimeric sequence removal, a total of 886,894 bacterial 16S rRNA genes and 789,965 high-quality archaeal gene sequences were obtained for community analyses of the 30 soil samples. The number of sequences per sample ranged from 7,597 to 34,181, with an average of 29,563 sequences for bacteria, whereas the number of sequences ranged from 14,008 to 33,467 with an average of 26,332 sequences for archaea. All sequences were clustered into operational taxonomic units (OTUs) with a 97% identity threshold. Shannon’s diversity index, Simpson’s index, and the Ace and Chao1 estimators were generated for each sample based on the OTU table (Caporaso et al. 2010). The phylogenetic affiliation of each sequence was analyzed using the RDP Classifier (http://rdp.cme.msu.edu/classifier/class_help.jsp#copynumber) at a confidence level of 80%.

Statistical analysis

PCoA is a method to visualize the similarity and difference of microbial community composition in different environmental samples, and the first axis of PCoA represents the principal coordinate component that can explain the microbial data changes maximally. Principal coordinates analysis (PCoA) in Fast UniFrac was used to show the general differences in archaeal community structure among samples based on the relative abundances of the entire archaeal community data. Regression analysis was used to determine variations in soil properties, bacterial and archaeal diversity, and relative abundances of the dominant bacterial and archaeal communities along with the peatland vertical profile. Pearson correlation analysis was used to analyze relationships among the soil properties, scores of the first PCoA axis, and the diversity of bacteria and archaea. All statistical analyses were performed using IBM SPSS Statistics 20 (IBM, Armonk, New York, U.S.A), and the figures were created using Origin 9.0. Values were considered statistically significant at p<0.05.

Results

Vertical distribution of soil C, N, and P concentrations and stoichiometry

In this study, soil pH ranged from 5.47 to 5.60 and showed no significant changes along with the soil profile in the Bitahai peatland. With the exception of C: N (Fig. 1d), soil depth significantly influenced the C, N, and P concentrations as well as the C:P and N:P ratios (p<0.05). Soil C and N concentrations and C:P and N:P ratios significantly increased (Fig. 1a, b, e, f), but P concentration decreased (Fig. 1c) with increasing soil depth.
Vertical patterns of structure and diversity of bacterial and archaeal communities

The dominant phyla that accounted for more than 3% of the mean relative abundance across all sites and depths for overall bacterial communities were Proteobacteria (39.64%), Acidobacteria (12.93%), Chloroflexi (12.81%), Ignavibacteriae (4.54%), Planctomycetes (4.21%), Spirochaetae (3.67%), and Bacteroidetes (3.23%) (Fig. 2a). Crenarchaeota (mean relative abundance across all sites and depths of 58.67%), Thaumarchaeota (14.34%), and Euryarchaeota (10.82%) were the phyla detected in the archaeal communities (Fig. 2b).

The relative abundances of the dominant bacterial groups significantly changed with soil depth at the phylum and class levels ($p<0.05$). With increasing depth, the relative abundances of Proteobacteria (-36%) and Acidobacteria (-50%) significantly decreased, but Spirochaetae (+434%), Ignavibacteriae (+93%), Chloroflexi (+95%), and Planctomycetes (+184%) significantly increased (Figure S1 a, b, c, d, e, f, g). At the class level, the relative abundances of Betaproteobacteria (-71%), Alphaproteobacteria (-87%), and Acidobacteria (-93%) significantly decreased with the peatland depths, while that of Deltaproteobacteria (+9%) increased (Figure S2 a, b, c, d, e). The relative abundances of dominant archaea phyla also varied significantly with soil depth ($p<0.01$). As the depth increased, the relative abundance of Crenarchaeota (+63%) significantly increased (Figure S3 a), but those of Thaumarchaeota (-74%) and Euryarchaeota (-30%) significantly decreased (Figure S3 b, c).

Chao1, Ace, and Shannon values were all significantly higher in bacteria than in archaea ($p<0.001$) (Fig. 3). With increasing soil depth, the Chao1 and Ace values
of bacteria and archaea showed a significant increasing trend (Fig. 3a, b), and Shannon values of bacteria and archaea exhibited significant and non-linear variation trends (Fig. 3c). There was a significant increase in the Simpson values of archaea along with soil depth (Fig. 3d).
The shifts of methanogen and ammonia-oxidizing microorganisms with soil depths

Archaeal communities were analyzed at the order level, and the total relative abundance of the methanogenic groups (4.03-11.54%) was found to significantly decrease with soil depth ($R^2=0.13$, $p<0.001$) (Fig. 4). The mean relative abundances of the order Nitrospira (bacteria) and Nitrososphaerales (archaea) were 2.37% and 14.34%, respectively. The total relative abundance of ammonia-oxidizing microorganisms also significantly decreased with soil depth ($R^2=0.44$, $p<0.001$) (Fig. 5).

Relationships between bacterial, archaeal communities, and soil properties

The PCoA analysis showed that the first principal coordinate axis (PCoA1) explained 39.61% and 65.84% of the overall bacterial and archaeal communities in our study, respectively (Tables 1 and 2). For the bacterial community, Pearson correlation analysis showed that there was no significant relationship between soil properties and PCoA1, and only soil P correlated significantly and negatively with the Ace index (Table 1). For the archaeal community, PCoA1 was correlated significantly and positively with soil C, N, N:P, and C:P, and was significantly and negatively correlated with soil P. Both Chao1 and Ace indices of archaea were correlated significantly and positively with soil pH and negatively with C: N, while soil C, N, and N:P were correlated significantly and positively with archaeal Shannon diversity and negatively with Simpson diversity (Table 2).

Discussion

Vertical patterns of bacterial and archaeal communities along with soil depths

As predicted, this study showed that soil depth had a marked impact on bacterial and archaeal community structures. According to the 16S rRNA gene analysis, the dominant groups at the phylum level were Proteobacteria (39.64%), Acidobacteria (12.93%), and Chloroflexi (12.81%) for soil bacteria and were Crenarchaeota (58.67%), Thaumarchaeota (14.34%), and Euryarchaeota (10.82%) for soil archaea, respectively. This demonstrated that these groups play a key role in the Bitahai peatland. These findings are consistent with many other comprehensive studies on peatland soil bacterial and archaeal communities (Rooney-Varga et al. 2007; Seward et al. 2020; Sun et al. 2014).

Proteobacteria are involved in biogeochemical processes in various ecosystems, and are able to promote soil nutrient availability (Fierer et al. 2007). Specifically, a sharp decline of Proteobacteria was reflected in the reduction of the relative abundances of Alphaproteobacteria, Betaproteobacteria, and Deltaproteobacteria at the class level. The decrease in Betaproteobacteria could affect N cycles as a result of their members displaying metabolic diversity in nitrification (Prosser et al. 2014). Sulfate-reducing bacteria, belonging to the class Deltaproteobacteria, have been shown to mineralize organic carbon (Miyatake et al. 2009). Thus, the decreasing trend of the relative abundance of Deltaproteobacteria along with soil profiles may represent a decrease in organic carbon mineralization (Chen et al. 2019). Moreover, upper soil layers with low organic carbon content had a higher relative
abundance of Acidobacteria than the deeper soil layers. This was similar to a report of high proportions of Acidobacteria in degraded wetland soil with low organic matter content (Peralta et al. 2013). In addition, there was a significant increase in the abundance of Chloroflexi along with the soil profiles. It has been detected in a wide range of anaerobic habitats, and plays an important role in the degradation of complex polymeric organic compounds into low molecular weight substrates (Speirs et al. 2019). A previous study has also shown that Chloroflexi can survive in nutrient-deprived environments (Wu et al. 2021), and thus were relatively more abundant under limited nutrient conditions (Hug et al. 2013). Therefore, the significant vertical change of these predominant groups in soil microorganisms implies profound differences in the C and N cycles at different soil depths in the Bitahai peatland.

Furthermore, soil depth influenced the abundance of the functional microbial groups related to the pivotal processes of the C and N cycles (Figs. 4 and 5). Specifically, the total relative abundance of the methanogenic groups significantly decreased with soil depth (Fig. 4), which demonstrated that methane production in deeper layers is constrained. Methanotrophs play an important role in mitigating the release of the greenhouse gas methane (Liebner and Svenning 2013). Most methanotrophs belong to Proteobacteria, of which three families Methylococcaceae, Methylocystaceae, and Beijerinckiaceae are methanotrophs (Dworkin et al. 2006; Liebner et al. 2009). The decreasing trends of the above three families may thus indicate a reduction of aerobic methane oxidation in deeper soil (Table S1). The ammonia-oxidizing microorganisms included Nitrospirales (bacteria) and Nitrososphaerales (archaea) and their mean relative abundances also significantly decreased with soil depth (Fig. 5), indicating that a weak ammonia-oxidizing process may exist in deeper soil layers (Prosser et al. 2014). The significant vertical decline in the relative abundance of methanogenic, methanotrophs and ammonia-oxidizing microorganisms suggests that the deeper soil layers had a low intensity of methane production, oxidation, and nitrification processes in the Bitahai peatland.

In the present study, bacterial richness, evenness, and diversity were higher than those of archaea. This result was consistent with studies performed on peatlands (Basiliko et al. 2013), anaerobic sediments of a soda lake (Rojas et al. 2018), and a deep-sea mud volcano (Pachiadaki et al. 2011). Compared with some studies on Zoige peatlands (Zhong et al. 2017), both Chao1 and Ace values significantly increased with soil depth in the Bitahai peatlands. Our results further
showed that Shannon in bacteria and Simpson in archaea increased, while Shannon in archaea decreased with soil depth. The observed similar and obvious increasing vertical trends of diversity prokaryotic communities suggested that prokaryotic diversity also played a pivotal role in peatland functions in the deep soil layer. Based on the above results, therefore, our study found that soil depth significantly influenced the structure and diversity of bacteria and archaea in the Bitahai peatland, supporting our first hypothesis.

**Relationship between bacterial and archaeal communities and soil properties along with soil profiles**

Our study clearly showed that various soil depths exhibited distinct prokaryotic structures and diversity (Figs. 2 and 3). These vertical distribution patterns essentially reflect the variation in environmental factors with soil depth (e.g., physicochemical properties and oxygen limitations) (Lamit et al. 2017; Zhong et al. 2017). The relative abundances of aerobic and anaerobic microbes decreased and increased with soil depth, respectively (Figure S2). This indicated that in the Bitahai peatlands, the upper soil layers were dominated by aerobic processes, while deeper soil layers were dominated by anaerobic processes. These results were identical to those of a previous study of Zoige peatlands (Zhong et al. 2017). Such opposite trends of aerobic and anaerobic prokaryote along with soil profiles may be explained by changes in soil water content and oxygen limitations (Fierer et al. 2003). C:P and N:P in soil are generally negatively correlated with nutrient mineralization rate and availability (Hu et al. 2019; Ren et al. 2016; Shen et al. 2019). Higher C:P and N:P ratios in the deep soil layers (Fig. 1e, f) implied a relatively poor nutrient status. The abundance of Chloroflexi was positively correlated with soil N:P ratio, with increasing variation along with the soil profiles (Figure S1). These results possibly indicate a reversed trend in the vertical distribution of copiotrophic (i.e., Proteobacteria) and oligotrophic bacteria (i.e., Chloroflexi) along with the soil profiles. More precisely, in the deeper soil layers of the Bitahai peatlands, Proteobacteria could be depleted and Chloroflexi could be enriched (Figure S2 a, f).

Interestingly, bacterial diversity was not related to soil properties, except for soil P (Table 1). This result suggests that other underlying environmental factors, rather than soil properties, may drive bacterial diversity in the Bitahai peatland. Previous studies have shown that climatic factors, such as temperature, soil moisture (Stres et al. 2008), and water table (Zhong et al. 2017), can influence soil bacterial communities in the peatland ecosystem. Other studies have also highlighted that climatic factors have unexpectedly strong impacts on soil bacterial community composition and variation (Zheng et al. 2020). In the present study, Bitahai peatland is saturated throughout the year, making it very unlikely that the soil moisture or water table could be undetected drivers of microbial diversity. In light of the above, despite a lack of further measurement, it was reasonable to speculate that these unattended climatic factors may regulate the diversity of the bacterial community along the soil profile of the Bitahai peatland. In order to better understand the distribution of bacterial communities along this soil profile, it is necessary to further explore the drivers of bacterial communities along the soil depths in the Bitahai peatland. Furthermore, only soil P had a negative effect on the bacterial richness of Bitahai peatland. This means that natural and human activities that cause changes in soil phosphorus could affect bacterial richness in the future (Zheng et al. 2020).

Archaeal community structure was markedly impacted by soil C, N, and P concentrations and stoichiometric ratios along the peatland profile (Table 2). This is consistent with previous studies that have shown that soil C, N, and P (Bergkemper et al. 2016) and elemental stoichiometry (Shen et al. 2019) are drivers of microbial community structure. Our findings also showed that changes in soil physicochemical characteristics (e.g., pH, TC, TN, C: N, and N:P) with depth had significant positive or negative correlations with archaeal richness and diversity (Table 2). These results were similar to those of previous studies that documented that the changes in prokaryotic diversity were probably attributable to the differences in physicochemical properties (Pachiadaki et al. 2011; Wu et al.)

**Table 2** Relationships among the score of the first PCoA axis, diversity index and soil properties for archaea

|                | Archaea PCoA1 (65.84%) | Chao    | Ace     | Shannon | Simpson |
|----------------|------------------------|---------|---------|---------|---------|
| pH             | 0.054                  | 0.446*  | 0.451*  | 0.288   | 0.082   |
| Total N        | 0.471**                | 0.118   | 0.182   | -0.640**| 0.563** |
| Total P        | -0.400*                | -0.036  | -0.058  | 0.069   | -0.169  |
| Total N:P      | 0.676**                | 0.146   | 0.206   | -0.546**| 0.561** |
| Total C        | 0.404*                 | -0.178  | -0.115  | -0.599**| 0.426*  |
| Total C:N      | -0.200                 | -0.398* | -0.421* | 0.357   | -0.256  |
| Total C:P      | 0.406*                 | -0.199  | -0.168  | -0.213  | 0.257   |

* Correlation is significant at the 0.05 level; **. Correlation is significant at the 0.01 level
Conclusions

Soil depth can affect the relative abundance of C- and N-related microbes. With increasing soil depth, the relative abundance of methanotrophic bacteria, methanogenic groups, and ammonia-oxidizing microorganisms decreased. The higher abundances of such functional groups indicated that some key processes involving soil C and N cycles may be more active in the upper layers. Bacterial richness, evenness, and diversity were higher than those of archaea, but their vertical distribution patterns were consistent. Across soil profiles, C, N, and P concentrations and their stoichiometric ratios markedly impacted the community structure and diversity of archaea, but not for bacteria in the Bitahai peatland. Our results highlighted that the microbial community structure and diversity depended on soil depth, and the factors affecting bacteria and archaea were different in the Bitahai peatland.

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Authors’ contributions WL, DFF, and BH conceived and designed the study; MML and RS collected the data; ZAY and HC contributed field sampling; DFF performed the analysis; WL and BH wrote the paper.

Data availability All data generated or analyzed during the current study are included in this article and its supplementary information files.

Declarations

Ethical approval  Not applicable.

Consent to publish  Not applicable.

Conflict of interest  The authors declare no competing interests.

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