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Distribution of bacterial communities across plateau freshwater lake and upslope soils

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ABSTRACT

Microorganisms are involved in a variety of biogeochemical processes in natural environments. The differences between bacterial communities in freshwaters and upslope soils remain unclear. The present study investigated the bacterial distribution in a plateau freshwater lake, Erhai Lake (southwestern China), and its upslope soils. Illumina MiSeq sequencing illustrated high bacterial diversity in lake sediments and soils. Sediment and soil bacterial communities were mainly composed of Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi and Planctomycetes. However, a distinctive difference in bacterial community structure was found between soil and sediment ecosystems. Water content, nitrogen and pH affected the distribution of the bacterial community across Erhai Lake and its upslope soils. Moreover, the soil bacterial community might also be shaped by plant types. This work could provide some new insights into plateau aquatic and terrestrial microbial ecology.

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Introduction

Freshwater sediments harbor a huge diversity of microorganisms, which are involved in a variety of biogeochemical processes (Cheng et al., 2014; Liu et al., 2014a; Zhang et al., 2015). A shift in the sediment bacterial community can significantly affect its function of transforming organic and inorganic elements (Song et al., 2012). Numerous previous studies have been carried out to investigate the bacterial community structures of freshwater lake sediments and their influential factors (Haller et al., 2011; Kadnikov et al., 2012; Liu et al., 2009; Song et al., 2012). Compared to plain lakes, plateau lakes have relatively poor water exchange capacity and are more sensitive to environmental disturbance (Zhang

et al., 2015). Although the bacterial community in some high-altitude lakes, mainly located in the Qinghai-Tibet Plateau (China), has been well explored (Dong et al., 2006; Jiang et al., 2007; Liu et al., 2013; Xiong et al., 2012), little information exists on the sediment bacterial community in plateau freshwater lakes (Bai et al., 2012; Zhang et al., 2015).

Soil microorganisms play crucial roles in the formation of soil structure, decomposition of organic matter, cycling of primary elements, and stimulation of plant health and growth (Dey et al., 2012; Han et al., 2007; Stroobants et al., 2014). Soil bacterial community structure can be shaped by a variety of factors, such as soil type (Garbeva et al., 2008; Liliensiek et al., 2012), plant type (Garbeva et al., 2008; Liliensiek et al., 2012), herbicide and fertilizer application (Aira et al., 2010; Liliensiek

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et al., 2012; Wan et al., 2014; Zhou et al., 2013), rotation (Chen et al., 2012), land use (Yu et al., 2013), temperature (Zhang et al., 2014a), and soil moisture (Zhang et al., 2013, 2014b). Moreover, the structure of the soil bacterial community has been extensively investigated in the Loess Plateau (China) and Qinghai–Tibet Plateau (Huang et al., 2011; Ollivier et al., 2014; Zhang et al., 2013, 2014a,b). In contrast, little is known about the soil bacterial community in other plateaus. In addition, the difference between the microbial communities in aquatic ecosystems and upslope soils remains poorly understood.

Erhai Lake, the second largest freshwater lake in the Yunnan Plateau (southwest China), is located in the subtropical monsoon climate zone with a mean annual temperature of 15.1 °C and a mean annual precipitation of 1000–1200 mm. This plateau lake has a surface area of 251 km², an average water depth of 10.5 m, and a hydrologic residence time of approximately 2.75 years (Liu et al., 2014b). It is experiencing a transition from oligo-mesotrophic to eutrophic status due to environmental pollution and improper management of water resources (Yu et al., 2014). So far, information on the bacterial communities in sediments of Erhai Lake and upslope soils is still lacking. In addition, progress in high-throughput sequencing technologies can contribute to the extensive and systematic investigation of microbial communities in aquatic and terrestrial ecosystems. The recently developed Illumina MiSeq sequencing system can provide more detailed information on the diversity and structure of microbial communities with greater throughput but lower cost (Zhang et al., 2015). Illumina MiSeq sequencing has found increasing application in characterizing bacterial communities in sediment and soil ecosystems (Jiang et al., 2013; Kim et al., 2014; Sun et al., 2015; Wang et al., 2015; Yang et al., 2015a; Zhang et al., 2014c, 2015). Therefore, the objective of the present study was to investigate the distribution of bacterial communities in Erhai Lake and upslope soils using Illumina MiSeq sequencing.

1. Materials and methods

1.1. Site description and sampling

Five lake sediment samples (E1–E5) and ten upslope soil samples (N1–N5 and S1–S5) were collected in triplicate in June 2014 (Fig. S1). Sediment samples (0–5 cm depth) were selected according to water depth, from the northern (E1), central (E2–E4), and southern (E5) areas of the lake, and were collected using a core sampler. Soil cores (3 cm in diameter; 0–5 cm depth) were obtained from the bare lake riparian zone (S1 and N1), rice field (S2 and N2), maize field (S3 and N3), grassland (S4 and N4), and tree-vegetated mountain field (S5 and N5), respectively. Fine roots and visible organic debris (<2 mm) in soil samples were removed. These soil and sediment samples were kept on ice and immediately transported back to the laboratory for further analysis. Sediment/soil organic matter (OM), total nitrogen (TN), nitrate nitrogen (NO₃-N), ammonium nitrogen (NH₄-N), total phosphorus (TP), and pH were determined according to the literature (Yang et al., 2015b). Water content was measured using a DH836 moisture meter (Jiashi Electric Scientific Technology, Inc., Shanghai, China).

The geographic and physicochemical parameters of the sediment and soil samples are illustrated in detail in Table S1.

1.2. Molecular analyses

Total genomic DNA of soil and sediment samples was extracted using a Powersoil DNA extraction kit (Mo Bio Laboratories, Carlsbad, CA, USA), and was amplified using primer set 515 F (5'-GTGCCAGCMGCCGCGG-3')/R907 (5'-CCGTCGAATTCMTTTRA GTTT-3') under the following conditions: 95 °C for 2 min; 27 cycles of 95 °C for 30 sec, 55 °C for 30 sec, followed by 72 °C for 45 sec, with a final extension 72 °C for 10 min (Wang et al., 2015). Polymerase chain reaction (PCR) products from each triplicate sediment (or soil) sample were mixed in equal amounts for Illumina MiSeq sequencing. The reads obtained from the Illumina MiSeq platform in this study were deposited in the NCBI short-read archive under accession numbers SRR1646954 and SRR1656825–SRR1656838. The raw reads were merged using FLASH (V1.2.7, <http://ccb.jhu.edu/software/FLASH/>), and quality filtering was conducted following the standard protocol (Caporaso et al., 2011). Chimeric reads were removed using UCHIME (Edgar et al., 2011). The UPARSE pipeline was used to assign the operational taxonomic units (OTUs), using 97% similarity as a cutoff, and then generate the bacterial community Shannon diversity index and rarefaction curve for each sample (Edgar, 2013). For community comparison, OTU-based beta diversity was calculated using the Bray–Curtis algorithm with QIIME (<http://qiime.org/index.html>) and then used for unweighted pair group method with arithmetic mean (UPGMA) clustering. The taxonomic identities of selected sequences were determined using the Ribosomal Database Project (RDP) classifier (Wang et al., 2007).

1.3. Statistical analyses

Pearson's correlation analysis using SPSS 20.0 software was used to identify the relationship between the bacterial community and environmental factors (organic matter (OM), total nitrogen (TN), ratio of OM to TN (C/N), NH₄-N, NO₃-N, total phosphorus (TP), and water content). Canonical correspondence analysis (CCA) of OTU composition and the environmental factors were also performed using CANOCO 4.5. The absolute abundance in each OTU (defined at 50 sequence cutoff) and the seven determined environmental factors were used as species input and environmental input, respectively (Zhang et al., 2015). The significance tests of Monte Carlo permutations were performed to select the suitable models of the microorganism–environment relationships.

2. Results

2.1. Bacterial community diversity and structure

In this study, the number of the retrieved valid Illumina reads from each soil or sediment sample was normalized to 4400 for the comparison of bacterial richness and community diversity. Using a 97% sequence identity cutoff, the number of OTUs ranged between 486 and 1028 (Table 1). All the studied soil and sediment samples showed high bacterial diversity (Shannon

Table 1 – Community richness and diversity indices for bacterial communities in each soil or sediment sample.

Sample	OTUs ^a	Shannon index ^a
E1	951	5.7
E2	967	5.65
E3	1028	5.73
E4	989	5.73
E5	814	5.87
N1	795	5.5
N2	891	5.86
N3	873	5.89
N4	486	5.4
N5	653	4.87
S1	846	5.86
S2	979	6
S3	660	5.4
S4	711	5.51
S5	583	5.11

OTUs: operational taxonomic units.

^a Tags are normalized to 4400.

index = 4.87–6). Moreover, these results also illustrated a remarkable variation in bacterial richness and diversity among these studied samples.

Microorganisms assigned to unclassified bacteria existed with a much higher proportion in lake sediment samples (5.9%–14.4%) than in soil samples (0%–1.5%) (Fig. 1). A total of 19 major bacterial phyla (with relative abundance no less than 1% in at least one sample) were found in sediments of Erhai Lake and upslope soils, including Proteobacteria, Acidobacteria, Actinobacteria, Armatimonadetes, Bacteroidetes, Candidate division OP3, Candidate division OP8, Candidate division WS3, Chlorobi, Chloroflexi, Cyanobacteria, Deferribacteres, Firmicutes, Gemmatimonadetes, Nitrospirae, Planctomycetes, Spirochaetae, TA06 and Verrucomicrobia. Proteobacteria was the largest bacterial phylum in all soil and sediment samples. However, soils (29.6%–38.2%) had relatively higher proportions of Proteobacteria than lake sediments (15.6%–24.3%). Much higher proportions of class Alphaproteobacteria were also

found in soils (8.1%–18.9%) than lake sediments (1.5%–2.8%) (Fig. 2). In contrast, class Deltaproteobacteria showed higher proportions in lake sediments (10.6%–12.8%) than in soils (2.7%–10.2%). Moreover, riparian and rice soils had relatively higher betaproteobacterial and deltaproteobacterial but lower alphaproteobacterial proportions, compared to other soils. Therefore, a remarkable variation in the proteobacterial proportion and community structure occurred in lake sediment and soil samples.

Acidobacteria, Bacteroidetes, Chloroflexi, and Planctomycetes were also the dominant bacterial groups in soils and lake sediments. Acidobacteria showed much higher proportions in soils (11.3%–19.6%) than lake sediments (7.6%–9.3%). Bacteroidetes also tended to show dominance in soils (6.1%–15.1%) over lake sediments (3.4%–6.4%). However, a much higher proportion of Chloroflexi was found in lake sediments (11.1%–13.9%) than upslope soils (3.1%–9.3%). Compared to lake sediments, the Planctomycetes proportion experienced a large variation in soils (5%–12%). Moreover, Actinobacteria illustrated a high abundance in dry soils from maize fields, grasslands, and mountain fields (8.4%–17.9%), but a much lower abundance in wet soils (riparian and rice soils) and lake sediments (1.3%–7.3%). The candidate bacterial phyla (OP3, OP8, and TA06) showed relatively higher proportions in lake sediments ($\geq 1.5\%$), compared to upslope soils ($\leq 0.6\%$). The Spirochaetae proportion was also higher in lake sediments (2.3%–3.2%) than soils (0%–1.3%).

The result of OTU-based UPGMA clustering illustrated that sediment samples were grouped together, but they were distantly separated from soil samples (Fig. 3). This further confirmed the profound difference in bacterial community structure between soil and sediment ecosystems. Wet soils (riparian and rice soils) were clustered, but they were distantly separated from dry soils (maize soils, grassland soils, and mountain soils), indicating the distinctive difference in bacterial community structure between wet and dry soils. A remarkable difference was also observed between riparian and rice soils. In addition, dry soils formed two different groups. One group contained S3, N3 and S4, while another group included S5, N5 and N4. This result indicated that the two grassland soils

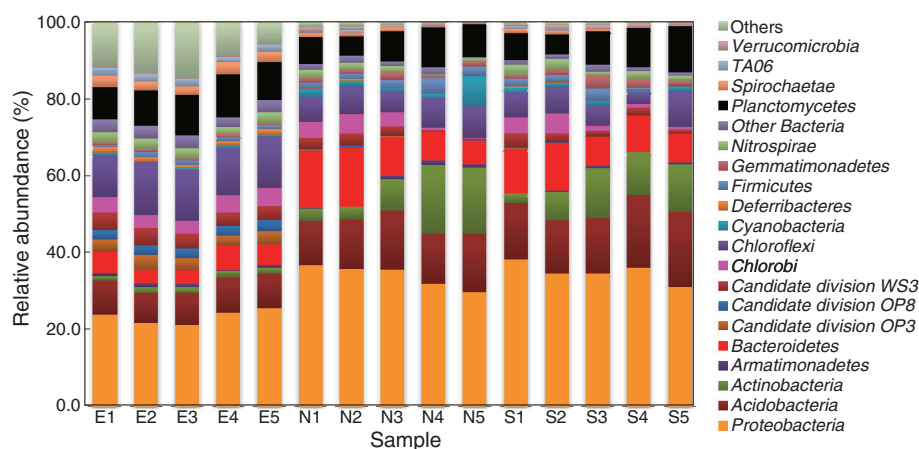


Fig. 1 – Comparison of the quantitative contribution of the sequences affiliated with different bacterial phyla to the total number of sequences from the soil or sediment samples. Sequences not classified to any known phylum are included as unclassified bacteria. For each soil or sediment sample, the bacterial phyla with the largest proportion less than 1% are included as others.

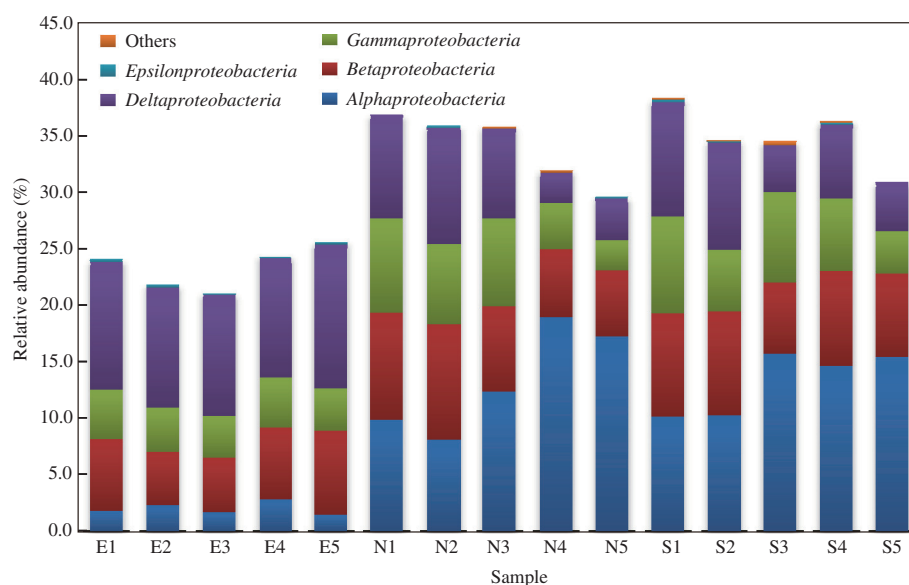


Fig. 2 – Comparison of the quantitative contribution of the sequences affiliated with different proteobacterial classes to the total number of sequences from the soil or sediment samples. Sequences not classified to any known proteobacterial class are included as others.

differed greatly in bacterial community structure, while the two maize soils and two mountain soils each shared similar bacterial community structures. Therefore, these results suggested that both water content and plant type could shape the soil bacterial community.

2.2. Influential factors on bacterial community

The number of OTUs had highly significant positive correlations with pH and water content ($P < 0.01$) (Table 2). Shannon diversity was negatively correlated with C/N and nitrate nitrogen ($P < 0.05$), but positively with water content ($P < 0.01$). Therefore, water content could be a key determinant of bacterial richness and diversity in the sediments of freshwater Erhai Lake and upslope soils.

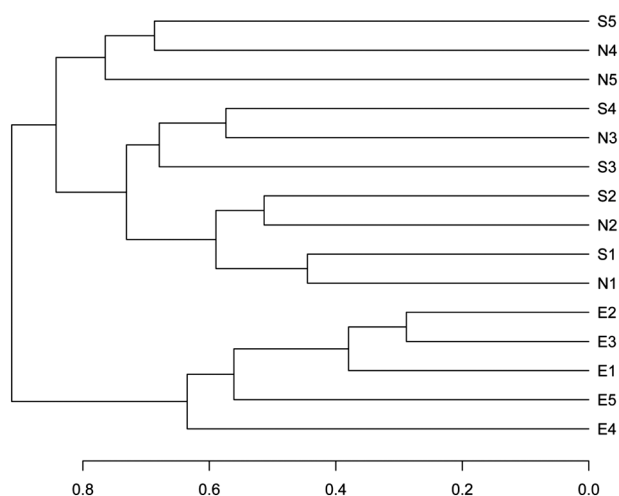


Fig. 3 – Unweighted pair group method with arithmetic mean clustering of soil and lake sediment samples.

Ammonia nitrogen, pH and water content exhibited significant negative correlations with the alphaproteobacterial proportion ($P < 0.05$ or 0.01), while they were positively correlated with the proportions of Epsilonproteobacteria, Candidate division OP3, Candidate division OP8, Candidate division WS3, Chloroflexi, Deferribacteres and TA06 ($P < 0.05$ or 0.01). Deltaproteobacteria, Chlorobi, Nitrospirae and Spirochaetae were positively affected by pH and water content ($P < 0.05$ or 0.01), while these two environmental factors negatively influenced the distribution of Actinobacteria assemblages ($P < 0.01$). Bacteroidetes exhibited a significant negative correlation with ammonia nitrogen ($P < 0.05$), while Cyanobacteria was regulated by C/N and nitrate nitrogen ($P < 0.05$). Moreover, Gemmatimonadetes was positively correlated with TP ($P < 0.05$), but negatively with water content ($P < 0.01$). The distribution of Verrucomicrobia assemblages was governed by ammonia nitrogen, TP, pH, and water content ($P < 0.05$ or 0.01). Therefore, ammonia nitrogen, pH, and water content might be the key drivers for the distribution of the bacterial community across Erhai Lake and upslope soils.

The environmental factors in the first two CCA axes respectively explained 22 and 15.7% of the total variance in bacterial composition (Fig. 4). Only water content ($P = 0.0010$, $F = 3.509$, 999 Monte Carlo permutations) and nitrate nitrogen ($P = 0.0030$, $F = 2.762$, 999 Monte Carlo permutations) significantly contributed to the bacterial assemblage–environment relationship.

3. Discussion

3.1. Bacterial community diversity in plateau soil and freshwater lake sediment

There have been a number of studies on soil bacterial community diversity in the Loess Plateau and Qinghai–Tibet

Table 2 – Statistical analysis of physicochemical properties with OTU number, Shannon diversity and relative abundance of bacterial phyla and proteobacterial classes.

Parameter	OM	TN	C/N	NO ₃ -N	NH ₃ -N	TP	pH	Water content
OTU number	−0.23	0.09	−0.37	−0.17	0.36	−0.43	0.65**	0.85**
Shannon diversity	0.07	0.39	−0.62*	−0.61*	0.13	−0.49	0.30	0.67**
Alphaproteobacteria	−0.04	−0.10	0.23	0.20	−0.56*	0.38	−0.71*	−0.94**
Betaproteobacteria	0.12	0.36	−0.34	−0.29	−0.51	−0.04	−0.03	−0.07
Gammaproteobacteria	−0.05	0.11	−0.43	−0.41	−0.43	0.26	−0.10	−0.18
Deltaproteobacteria	0.06	0.19	−0.35	−0.28	0.41	−0.43	0.70**	0.90**
Epsilonproteobacteria	−0.17	−0.29	−0.01	0.18	0.52*	−0.30	0.74**	0.68**
Acidobacteria	−0.06	0.07	−0.01	0.07	−0.54*	0.14	−0.44	−0.82**
Actinobacteria	0.02	−0.13	0.41	0.34	−0.39	0.37	−0.73**	−0.88**
Armatimonadetes	0.16	0.01	0.21	0.19	0.46	−0.07	−0.15	0.06
Bacteroidetes	0.05	0.30	−0.27	−0.25	−0.59*	0.11	−0.18	−0.16
Candidate division OP3	0.07	−0.09	0.01	−0.06	0.77**	−0.28	0.52*	0.75**
Candidate division OP8	0.08	−0.03	−0.01	−0.05	0.64*	−0.34	0.61*	0.84**
Candidate division WS3	−0.01	0.10	−0.36	−0.27	0.52*	−0.31	0.68**	0.9**
Chlorobi	0.02	0.28	−0.44	−0.37	0.12	−0.45	0.59*	0.82**
Chloroflexi	0.15	−0.01	0.14	0.02	0.66**	−0.35	0.54*	0.69**
Cyanobacteria	−0.07	−0.36	0.73**	0.86**	−0.27	0.34	0.04	−0.41
Deferribacteres	0.15	0.05	−0.06	−0.04	0.54*	−0.30	0.66**	0.84**
Firmicutes	0.06	−0.19	0.26	0.05	−0.21	0.37	−0.46	−0.34
Gemmatimonadetes	−0.05	−0.05	0.06	0.04	−0.30	0.55*	−0.49	−0.66**
Nitrospirae	−0.18	0.07	−0.50	−0.27	0.42	−0.41	0.65**	0.78**
Planctomycetes	0.06	−0.22	0.18	−0.07	0.24	−0.11	−0.16	−0.23
Spirochaetae	0.01	−0.01	−0.13	−0.13	0.48	−0.40	0.70**	0.90**
TA06	−0.05	−0.02	−0.17	−0.05	0.60*	−0.33	0.63*	0.84**
Verrucomicrobia	0.04	0.08	0.10	−0.05	−0.57*	0.52*	−0.72**	−0.64**

OM: organic matter; TN: total nitrogen; NO₃-N: nitrate nitrogen; NH₄-N: ammonium nitrogen; C/N: ratio of OM to TN; TP: total phosphorus; OTU: operational taxonomic unit.

* Correlation is significant at the 0.05 level.

** Correlation is significant at the 0.01 level.

Plateau, using either low-throughput biology techniques (e.g., terminal restriction fragment length polymorphism (T-RFLP) analysis, clone library analysis, and phospholipid fatty acids (PLFA)) (Huang et al., 2011; Ollivier et al., 2014; Xiao et al., 2013; Yuan et al., 2014; Zhang et al., 2014a), or high-throughput pyrosequencing techniques (Zhang et al., 2013, 2014b, 2014d). In contrast, the soil bacterial community diversity in the Yunnan Plateau remains unknown. In this study, the obtained soil bacterial OTU number and Shannon diversity using Illumina MiSeq sequencing were usually greater than 550

and 5, respectively, suggesting high diversity of bacteria in various soils. This was in agreement with the results of pyrosequencing of soil microbes in the Qinghai-Tibet Plateau (Zhang et al., 2013, 2014b, 2014d). In addition, high sediment bacterial diversity was also found in each of the five sediment samples from Erhai Lake. This coincided with the results of previous investigations on sediment bacterial diversity in other freshwater lakes in the Yunnan Plateau (Bai et al., 2012; Zhang et al., 2015). So far, no report has been available on the influential factors regulating bacterial community diversity across freshwater lakes and upslope soil. In this study, soil/sediment bacterial Shannon diversity was negatively affected by C/N ratio and nitrate nitrogen, but positively by water content. Our previous study also revealed that nitrate nitrogen negatively influenced lake sediment bacterial diversity in the Yunnan Plateau (Zhang et al., 2015). Moreover, soil bacterial diversity in the Tibet Plateau was found to be positively correlated with soil moisture, but negatively with C/N ratio (Zhang et al., 2013, 2014d).

3.2. Links between bacterial communities of lake sediment and upslope soil

So far, the differences between bacterial communities in freshwater sediments and upslope soils remain unclear. In this study, a sharp difference in bacterial composition was found between sediments of Erhai Lake and upslope soils. Lake sediment and soil ecosystems differed greatly in the

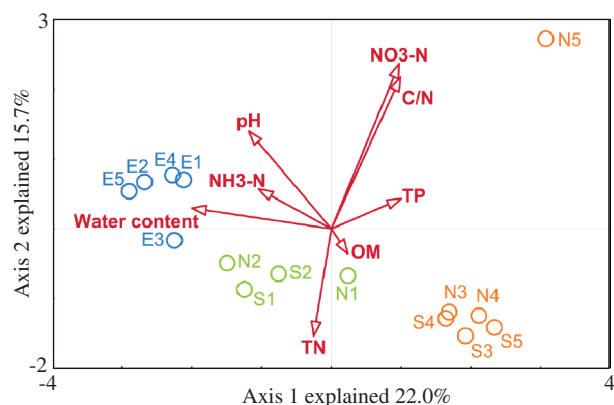


Fig. 4 – Canonical correspondence analysis ordination plot for the first two principal dimensions.

proportion of unclassified bacteria, Proteobacteria, Acidobacteria, Bacteroidetes, Chloroflexi, Spirochaetae, and candidate bacterial phyla (OP3, OP8 and TA06). OTU-based UPGMA clustering also confirmed the profound differences in bacterial community structure between soil and sediment ecosystems. Different habitats may select for specific bacterial taxa. Water content could be a key contributor to the differences in bacterial community structure between soil and sediment ecosystems.

3.3. Bacterial community structure in plateau soil and freshwater lake sediment

The variations in soil bacterial community structure in the Loess Plateau (China) and Qinghai–Tibet Plateau have been well documented (Huang et al., 2011; Ollivier et al., 2014; Xiao et al., 2013; Yuan et al., 2014; Zhang et al., 2013, 2014a, 2014b, 2014d). Our previous study found a variation in the structures of ammonia- and methane-oxidizing microorganisms in soils with different plant types adjacent to Erhai Lake (Yang et al., 2014a). However, the differences in the soil total bacterial community in the Yunnan Plateau remain unclear. In this study, OTU-based UPGMA clustering showed remarkable differences in bacterial community structure between wet and dry soils. Wet and dry soils also showed large variations in the proportions of Alphaproteobacteria, Betaproteobacteria, Deltaproteobacteria, Actinobacteria, Bacteroidetes, Chlorobi, Planctomycetes, Spirochaetae, and candidate bacterial phyla (OP8, WS3 and TA06). Therefore, water content could be a key determinant of soil bacterial community structure. Previous studies also reported the strong effect of moisture on soil bacterial community structure (Zhang et al., 2013, 2014b, 2014d). Moreover, soil bacterial community structure could be shaped by plant type (Garbeva et al., 2008; Liliensiek et al., 2012). In this study, with the exception of grassland soils, soils with the same plant type also tended to have closer bacterial community structures. The variation of water content in the two studied grassland soils might partly account for their different bacterial community structures.

Organisms from phylum Proteobacteria have been linked to numerous biogeochemical functions (Cheng et al., 2014; Liao et al., 2013; Liu et al., 2014a; Wang et al., 2014; Yang et al., 2014b). The predominance of Proteobacteria assemblages has been usually found in freshwater lake sediment (Haller et al., 2011; Song et al., 2012; Tang et al., 2010). Two recent studies using high-throughput sequencing also revealed the predominance of proteobacterial organisms in sediments of Dianchi Lake and thirteen other freshwater lakes in the Yunnan Plateau (Bai et al., 2012; Zhang et al., 2015). However, the relative abundance of proteobacterial assemblage in sediments of Erhai Lake (15.6%–24.3%) was much lower than that in other freshwater lakes (35.8%–83.6%) in the Yunnan Plateau (Bai et al., 2012; Zhang et al., 2015). Proteobacteria was found to be one of the most important phylum groups in plateau soils (Chen et al., 2014; Guan et al., 2013; Yuan et al., 2014; Zhang et al., 2013, 2014b,d). In this study, Proteobacteria was identified as the largest bacterial group in each soil. In addition, the proteobacterial community in plateau freshwater lake sediment might be affected by organic matter, temperature, and nitrate nitrogen (Bai et al., 2012; Zhang et al., 2015), while it might be regulated by water content and C/N ratio in

plateau soil (Zhang et al., 2013, 2014d). In contrast, water content as well as ammonia nitrogen and pH were found to be the important drivers for the proteobacterial community across Erhai Lake and upslope soils.

Acidobacteria organisms are ubiquitous in the environment, but relatively little is known about their diversity and function (Rawat et al., 2012). Acidic conditions can favor the high abundance of Acidobacteria species (Lauber et al., 2009; Rousk et al., 2010). Acidobacteria were found to be a minor component of the bacterial community in plateau freshwater lake sediment (Bai et al., 2012; Zhang et al., 2015), while their dominance was commonly found in plateau soils (Chen et al., 2014; Guan et al., 2013; Yuan et al., 2014; Zhang et al., 2013, 2014b,d). So far, the environmental factors regulating the distribution of the Acidobacteria community in plateau freshwater lake and soil remains unclear. In this study, dominance of Acidobacteria assemblages was found in low pH lake sediments and upslope soils, and their distribution was influenced by ammonia nitrogen and water content.

Actinobacteria organisms play an important ecological role in recycling substances in natural ecosystems and are able to degrade a variety of environmental chemicals (Fuentes et al., 2014; Polti et al., 2014; Zhou et al., 2013). Actinobacteria were usually rare species in freshwater lake sediment ecosystems (Haller et al., 2011; Song et al., 2012). The low proportion of Actinobacteria assemblages was also found in sediments of Dianchi Lake and many other freshwater lakes in the Yunnan Plateau (Bai et al., 2012; Zhang et al., 2015). Actinobacteria could be a minor component in plateau soils (Chen et al., 2014; Guan et al., 2013; Yuan et al., 2014), while other studies showed its dominance (Zhang et al., 2013, 2014d). So far, the driver for the distribution of Actinobacteria in natural ecosystems is still unclear. In this study, the dominance of Actinobacteria was found in dry soils, rather than wet soils and lake sediments. Water content as well as pH affected the distribution of Actinobacteria assemblages across Erhai Lake and upslope soils. Actinobacteria members can tolerate drought through spore formation (Gao and Gupta, 2005), which might account for their dominance in dry soils.

Bacteroidetes species are known for degrading high molecular weight compounds in natural environments (Fernández-Gómez et al., 2013; Liu et al., 2009). Previous studies showed the dominance of Bacteroidetes in sediments of Dianchi Lake, Jianhu Lake and Tianchi Lake, but appeared to be rare species in many other freshwater lakes in the Yunnan Plateau (Bai et al., 2012; Zhang et al., 2015). Moreover, microorganisms from the phylum Bacteroidetes usually showed high abundance in plateau soils (Chen et al., 2014; Guan et al., 2013; Zhang et al., 2013, 2014b, 2014d). However, so far, the links between Bacteroidetes in natural ecosystems and environmental factors are still unclear. In this study, Bacteroidetes showed dominance in plateau soils and became less abundant in lake sediments. Ammonia nitrogen was found to be a key driver for the distribution of Bacteroidetes assemblages across Erhai Lake and upslope soils. In contrast, a previous study revealed that TP, rather than ammonia nitrogen, was an important driver for the distribution of Bacteroidetes organisms in freshwater lake sediment (Song et al., 2012).

Chloroflexi species are ubiquitous in natural environments and have usually been linked to dechlorination of chlorinated

organic chemicals (Yan et al., 2009; Zanaroli et al., 2012). The dominance of Chloroflexi organisms was detected in sediments of many freshwater lakes in the Yunnan Plateau (Bai et al., 2012; Zhang et al., 2015). Nitrate nitrogen was found to be an important determinant of Chloroflexi assemblages in plateau lake sediments (Zhang et al., 2015). In contrast, Chloroflexi commonly appeared to be a minor bacterial group in plateau soils (Chen et al., 2014; Guan et al., 2013; Yuan et al., 2014; Zhang et al., 2013, 2014b, 2014d). In this study, Chloroflexi organisms showed dominance in lake sediments and were also abundant in soils. The distribution of Chloroflexi assemblages across Erhai Lake and upslope soils could be affected by ammonia nitrogen, pH and water content. Moreover, Planctomycetes is also a ubiquitous bacterial phylum, but its role in natural ecosystems is still uncertain. Previous studies showed its low abundance in both plateau freshwater lake sediments (Bai et al., 2012; Zhang et al., 2015) and plateau soils (Chen et al., 2014; Guan et al., 2013; Yuan et al., 2014; Zhang et al., 2013, 2014b, 2014d). In this study, high abundance of Planctomycetes was detected in both lake sediments and soils. However, further work is still needed to elucidate the environmental factors governing the distribution of the Planctomycetes community across Erhai Lake and upslope soils.

4. Conclusions

Sediments of freshwater Erhai Lake and upslope soils harbored high diversity of bacteria. Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, and Planctomycetes were the largest bacterial phyla. A profound difference of bacterial community structure occurred between soil and sediment ecosystems. Water content was the most important driver for the distribution of the bacterial community across Erhai Lake and upslope soils.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jes.2015.08.012>.

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