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Temporal and Spatial Variations of Microbial Carbon Utilization in Water Bodies from the Dajiuhu Peatland, Central China

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ABSTRACT: To investigate the microbial utilization of organic carbon in peatland ecosystem, water samples were collected from the Dajiuhu Peatland and nearby lakes, central China across the year of 2014. The acridine orange (AO) staining and Biolog Eco microplates were used to numerate microbial counts and determine the carbon utilization of microbial communities. Meanwhile, physicochemical characteristics were measured for subsequent analysis of the correlation between microbial carbon utilization and environmental factors. Results indicated that total microbial counts were between 10^6–10^7 cells/L. Microbial diversities and carbon utilization rates showed a similar pattern, highest in September and lowest in November. Microbial communities in the peat pore waters preferred to utilize N-bearing carbon sources such as amines and amino acids compared with microbial communities in lakes. The network analysis of microbial utilization of 31 carbon substrates clearly distinguished microbial communities from peat pore waters and those from lakes. Redundancy analysis (RDA) showed the total organic nitrogen content (P=0.03, F=2.5) and daily average temperature (P=0.034, F=2.4) significantly controlled microbial carbon utilization throughout the sampling period. Our report is the first one to address the temporal and spatial variations of carbon utilization of microbial communities which are closely related to the decomposition of organic matter in the Dajiuhu Peatland in context of climate warming.

KEY WORDS: carbon source, microbial carbon utilization, average temperature, Dajiuhu Peatland.

0 INTRODUCTION

Peatlands with massive deposits of organic carbon (approximately 30% of the terrestrial soil C) in peatlands act as important sinks of atmospheric carbon dioxide (CO_2) during the past millennia (Armstrong et al., 2015; Bon et al., 2014). However, peatlands could become a potential source for large CO_2 and methane (CH_4) emission to atmosphere or dissolved carbon (DC) to rivers in context of global warming or changes in land use (Brown et al., 2014; Moore et al., 2013).

Besides the climatic and anthropogenic impacts, microbial activities in peatlands can also contribute significantly to CH_4 production and oxidation, CO_2 fixation, organic matter degradation and transformation. Thus, any changes affecting microbial activities may impact on the carbon cycles in peatlands. For example, higher water saturation usually favors anaerobic processes for methane-emitting, and contributes to methanogenesis as indicated by enhanced *mcrA* gene abundance (Freitag et al., 2010). Besides methane, microbial mediated decomposition and sedimentation of organic carbon in soils are also linked with environmental conditions such as hydrologic condition, inorganic nutrient or climatic factor (Gougoulias et al., 2014). For example, increase in temperature can enhance microbial respiration and CO_2 release to atmosphere. In fact, microbial mediated carbon cycle is mainly controlled by microbial communities via their metabolism and carbon source utilization. Previous research also showed environmental variables such as temperature and soil property affected the contents and characteristics of dissolved carbon matters. It has been demonstrated that soil property significantly impacted microbial communities, and subsequently resulted in the varied consumptions and accumulations of dissolved organic carbon (Williams et al., 2010). Thus, understanding the correlation between microbial carbon source utilization and environmental factors will enhance our capability to decipher the microbial information recovered from environmental record and better manage the peatlands in the future. However, carbon utilization of microbial communities among different habitats with time and their correlation with environmental factors are still poorly understood to date.

Biolog microplates have been used to analyze the carbon utilization by different microbial communities from various environments, such as soils (Zhang et al., 2005; Busse et al.,

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2001), saline lakes (Litchfield and Gillevet, 2002), grasslands (Zhang et al., 2015; Grayston et al., 2004), sediments (Bushaw-Newton et al., 2012; Dahllöf et al., 2001), sludges (Huang et al., 2016; Gryta et al., 2014), and sea waters (Xie et al., 2007) which greatly enhance our understanding about microbial activities across different environments. In this study, to understand the variations of microbial carbon utilization and their correlations with environmental conditions, we measured the physicochemical parameters and conducted the analysis of microbial carbon source utilization in pore waters of the peatland and lakes closed to the peatland. The results will shed light on understanding carbon cycle in peatlands in modern processes and biogeochemical functions in sedimentary history.

1 MATERIALS AND METHODS

1.1 Site Description and Water Sampling

The Dajiuhu Peatland locates in the Shennongjia Forestry Region at the middle reaches of the Yangtze River, central China. Regional climate is dominated by the East Asian Monsoon, with a mean annual local rainfall of 1 560 mm and mean temperature of 7.2 ºC (Gong et al., 2015; Huang et al., 2010). The pore water samples were taken from peatland (P40, P46, P48, P52 and P53) and lake water samples were taken from lakes (L1, L4 and L5) closed to the peatland (Fig. 1) seasonally (in April, July, September and November across the year of 2014). Samples were collected with sterilized apparatus and stored immediately in 50 mL aseptic plastic corning centrifuge tubes. Samples were transported to the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, within 48 hours with a cooler and stored at 4 ºC for further studies.

1.2 Samples Analysis

1.2.1 Physicochemical analysis

The pH, oxidation reduction potential (ORP) and electrical conductivity (CON) of samples were measured *in situ* with a HQ40d Portable Meter (HACH, USA). The daily average temperature (AT), sunshine time (SH) and daily average precipitation (AP) were monitored via the meteorological station at the Dajiuhu Peatland. The total organic nitrogen (TON) content was analyzed with UV-6000PC Spectrophotometer (METASH, China) and DR2800 Portable Spectrophotometer (HACH, USA).

1.2.2 Microbial counts, diversities and carbon utilization of microbial communities

Cells in water samples were counted after stained with acridine orange (AO) (Kourtev et al., 2011; Francisco et al., 1973). An aliquot of 6 mL water sample and 2 mL AO (1 g/L) was mixed for 5 minutes, and subsequently filtered with 0.2 μm black polycarbonate films. Microbial counts were conducted with a fluorescent microscopy (Olympus Corporation, Japan) and 25 visual fields were randomly selected for counting with 30–50 bacteria per visual field.

Biolog Eco microplates were used to analyze the diversities and carbon utilization of microbial communities including carbon utilization rates and carbon preferences. The microplates were preheated to 25 ºC before use. An aliquot of 150 μL water sample was transferred into the microplate. The inoculated microplates were incubated at 25 ºC and tested with a Biolog MicroStation (BIO-TEK Instruments INC, USA) with 590 and 750 nm at 0, 24, 48, 72, 96, 120, 144, 168, and 192 h, respectively.

1.3 Data Analysis

1.3.1 Microbial counts

The microbial counts were calculated according the formula

$$B=\frac{N_a\times S}{S_f\times(1-0.02)\times V} \tag{1}$$

where B stands for microbial cell count (cells/L), N_a (cell) is the average cell count in the total field, S (mm^2) is the filtration area of the membrane, S_f (mm^2) is the microscope field area, V (L) represents the volume of filterable water.

1.3.2 Microbial carbon utilization rates

The average well color development (*AWCD*) stands for microbial carbon source utilization (Kong et al., 2013) and was calculated according to formula

$$AWCD=\sum(C_i-R)/31 \tag{2}$$

with R is optical absorbance of A1 which has no carbon substrate, C_i is the optical absorbance of other cells except A1.

1.3.3 Diversity indices

The Shannon Wiener index (H') is an index of microbial diversity based on uncertainty of community information and diversity of probability theory. The McIntosh diversity index (U) reflects the relative position of individual species on the multidimensional space of community structure level based on Euclidian distance. In this study, diversity indices were calculated via Eqs. (3), (4) and (5) after 72 hrs' incubation (Tian et al., 2015)

$$H'=-\sum p_i \ln p_i \tag{3}$$

$$U=(\sum n_i^2)^{0.5} \tag{4}$$

$$p_i=AWCD/\sum AWCD_i \tag{5}$$

where *AWCD* represents average well color development, p_i stands for proportion of individual *AWCD* to total *AWCD*, n_i is C_i–R.

1.3.4 Microbial carbon preferences

The microbial carbon preference analysis was based on the measurement after 72 hrs' incubation. The heatmap analysis of microbial carbon preferences among different samples was conducted with *R* heatmap3 package (Zhao et al., 2014). Correlation between carbon utilization of samples was analyzed by network analysis with Spearman rank correlation method (Barberán et al., 2012). A valid robust co-occurrence event is denoted when the rank correlation coefficient is >0.6 and statistical significance<0.01 (Xiang et al., 2017; Barberán et al., 2012). The network was characterized by network topology indices (diameter, average path length, modularity, number of the shortest path, average clustering coefficient) and network indices of individual node (degree, closeness centrality, between centrality). All those analyses were performed by *R* psych package and Gephi software (Bastian et al., 2009).

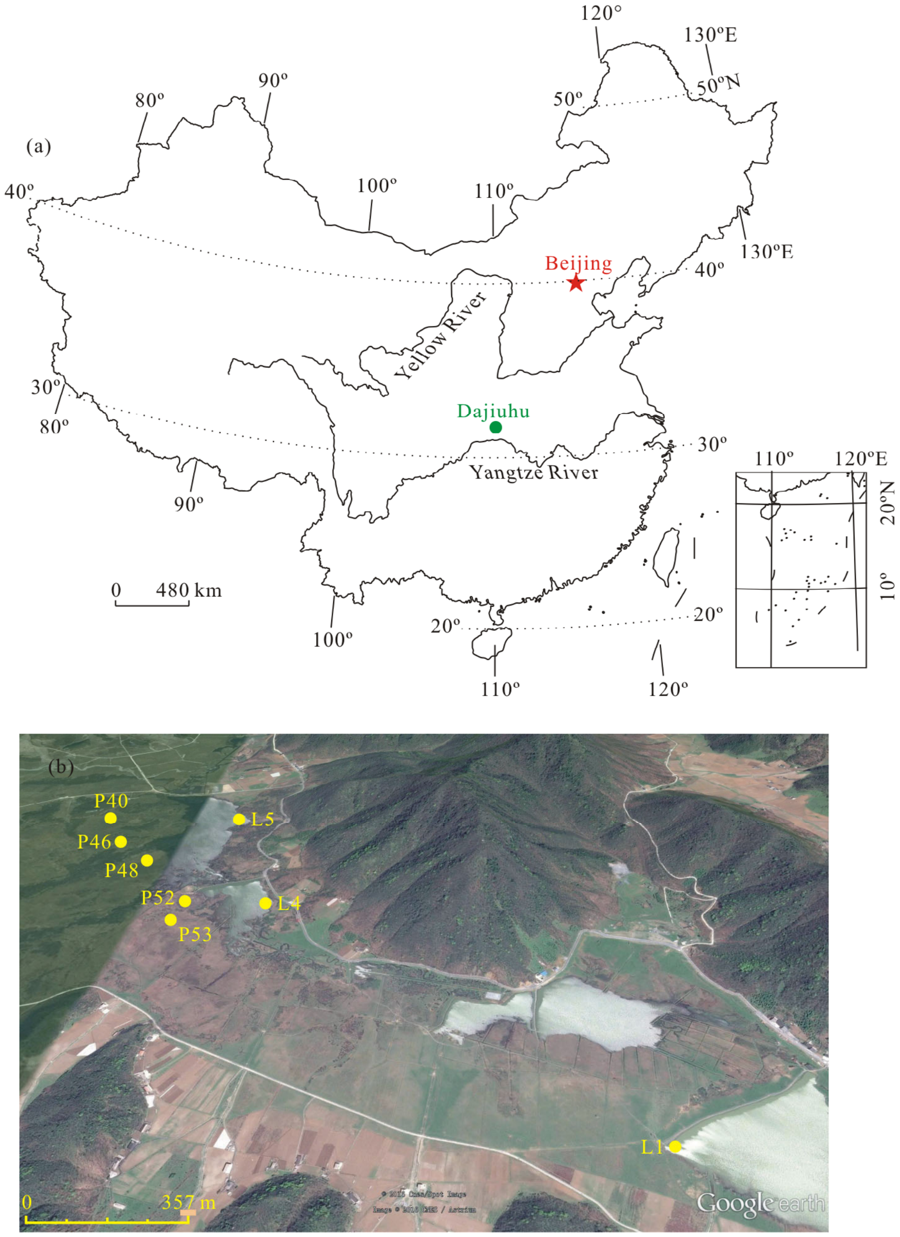

Figure 1. Location of the Dajiuhu Peatland (a) and sketch map of sampling sites (b). Background maps were from: http://www.sbsm.gov.cn/ and www.earthol.com.

1.3.5 Correlation between microbial metabolism and environmental conditions

The correlation between microbial metabolism and environmental conditions was performed via RDA analysis with Canoco for Windows 5.0. Statistical tests using Canoco were run using the Monte Carlo permutation procedure.

2 RESULTS

2.1 Microbial Counts and Diversities

Generally, average cell counts and diversities of microbial communities in pore waters (*B*: 1.09×10^7 cells/L, *H'*: 3.24±0.09, and *U*: 5.80±0.61) were slightly higher than those in lake waters (*B*: 7.86×10^6 cells/L, *H'*: 3.20±0.11, and *U*: 4.96±0.41) (Table 1). The microbial counts varied between 10^6–10^7 cells/L. Despite of the lowest microbial counts (peat waters: 4.63×10^6 cells/L and lake waters: 2.18×10^6 cells/L) in September, microbial diversities showed the highest values (peat waters *H'*/*U*: 3.33±0.04 and 6.35±0.99, lake waters *H'*/*U*: 3.33±0.02 and 5.46±0.12) (Table 1).

2.2 Dynamics Rates of Microbial Carbon Utilization

Relative higher *AWCD* values were observed in peat pore water samples (Fig. 2). Specifically among the pore water samples, the highest and lowest *AWCD* values (8.13 and 6.42) were seen in September and November respectively and values for April and July were 7.09 and 6.80. As for lake waters, *AWCD* values were 6.27, 6.63 and 7.00 in samples collected from April, July and September respectively, and value in November samples was the lowest (5.59).

2.3 Preferences of Microbial Carbon Utilization

Heatmap analysis of carbon utilization clearly distinguished microbial communities from peat pore waters and those from lakes (Fig. 3).

Table 1 Microbial counts and diversities in water samples from the Dajiuhu Peatland across the year of 2014

	Peat water				Lake water			
	Apr	Jul	Sep	Nov	Apr	Jul	Sep	Nov
B	8.59E+06	2.25E+07	4.63E+06	7.80E+06	1.53E+07	9.54E+06	2.18E+06	1.33E+07
H'	3.19±0.12	3.30±0.05	3.33±0.04	3.13±0.24	3.18±0.07	3.22±0.06	3.33±0.02	3.07±0.24
U	5.35±0.88	5.20±1.77	6.35±0.99	6.31±3.23	4.86±0.27	5.05±0.83	5.46±0.12	4.48±0.71

B. Cell count (cells/L), *H'*. Shannon Wiener index, *U*. McIntosh index.

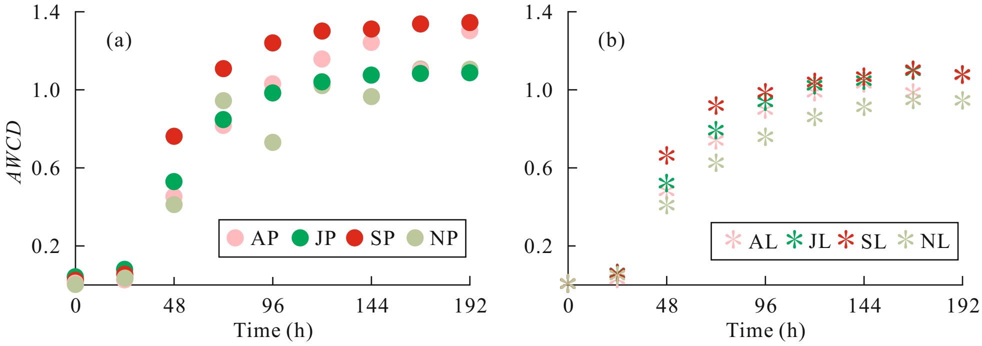

Figure 2. Dynamic characteristics of microbial carbon utilization in peat pore water (a) and lake water (b) samples from the Dajiuhu Peatland; AP, JP, SP and NP denoted for samples collected from the pore waters in Apr, Jul, Sep and Nov; AL, JL, SL and NL denoted samples collected from lakes in Apr, Jul, Sep and Nov.

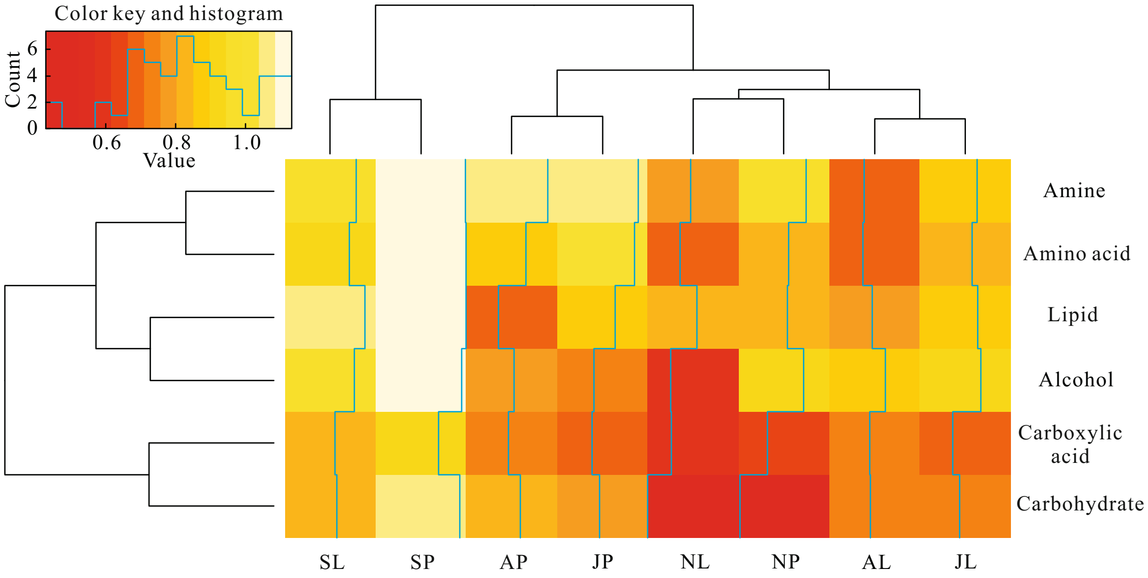

Figure 3. Preferable utilization of carbon substrates by microbial communities in peat pore water and lake water samples from the Dajiuhu Peatland. Abbreviation denoted the same as those in Fig. 2. The color key and histogram all represent utilization ratio of carbon substrates.

The microbial communities from pore waters preferred using N-bearing carbon sources such as amines and amino acids. Specifically amines were the most favorite carbon sources with an averaged value of 1.05 across whole year followed by amino acids (0.97). Microbial communities from pore waters showed moderate utilization of alcohols and lipids (0.88 and 0.87), but weak utilization of carboxylic acids and carbohydrates (0.76 and 0.78) (Fig. 3).

In contrast, lipids with an averaged value at 0.87 was preferred by microbial communities in lakes. Carbohydrates were the most un-favorite carbon source compared with others (Fig. 3). Furthermore, the microbial metabolism was weaker than those in pore waters and highly depended on carbon substrates.

2.4 Network Analysis of Carbon Utilization

We performed network analysis of the utilization of 31 carbon substrates by microbial communities in pore waters and lake waters. The metabolic network composed of 31 nodes and 166 edges in total, of which 20 nodes and 134 edges were related to peat pore water samples and 11 nodes and 103 edges were related to lake water samples (Fig. 4a).

Microbial communities can be divided into 3 modules according to their carbon utilization (Fig. 4b). Modules 1 and 2 were mainly associated with microbial communities from peat

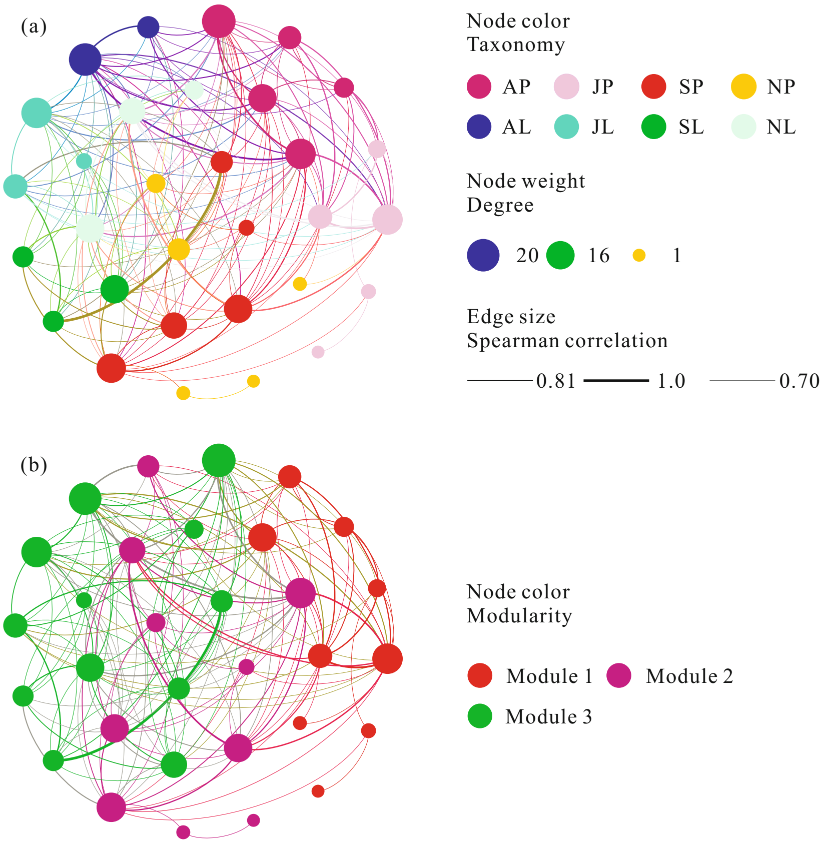

Figure 4. Network analysis of microbial carbon utilization in peat pore waters and lake waters nearby based on Spearman correlation in the Dajiuhu Peatland. Nodes represent metabolic characteristics of microbial communities of individual samples and the node weight is proportional to degree. Edges between nodes show significant ($P<0.01$) Spearman correlation. (a) Nodes were colored by the taxonomy and abbreviation denoted the same as in Fig. 2. (b) Same network as above, but the nodes were colored according to modularity.

pore waters, and module 3 was affiliated with microbial communities from lake waters.

2.5 Correlation between Environmental Factors and Microbial Carbon Utilization

The RDA analysis showed that total organic nitrogen (TON) content (Monte Carlo test, $P=0.03$, $F=2.5$) and daily average temperature (AT) (Monte Carlo test, $P=0.034$, $F=2.4$) were the main factors significantly controlling microbial metabolic variations throughout the year. The TON content, AT, SH (sunshine time), AP (average precipitation), pH, ORP (oxidation reduction potential) and CON (electrical conductivity) explained 8.0%, 8.6%, 7.0%, 5.7%, 3.3%, 3.4% and 1.7% of the variance of the microbial metabolism respectively. In total, 26% of the variance between microbial metabolism and environmental factors were explained by two axes (Fig. 5).

3 DISCUSSION

3.1 Temperature as an Important Factor Affecting the Temporal Variations of Microbial Activities

Temperature has been demonstrated to affect microbial activity and metabolism. For example it has been demonstrated that microbial growth and primary production are regulated by water temperature from polar waters to low-latitude oceans (Kirchman et al., 2009). Moreover, with increasing temperature in soils, microbial communities utilize more C and N substrates and produce more ATP by increasing microbial metabolic rates (Dijkstra et al., 2011). Temperature significantly controls the car-

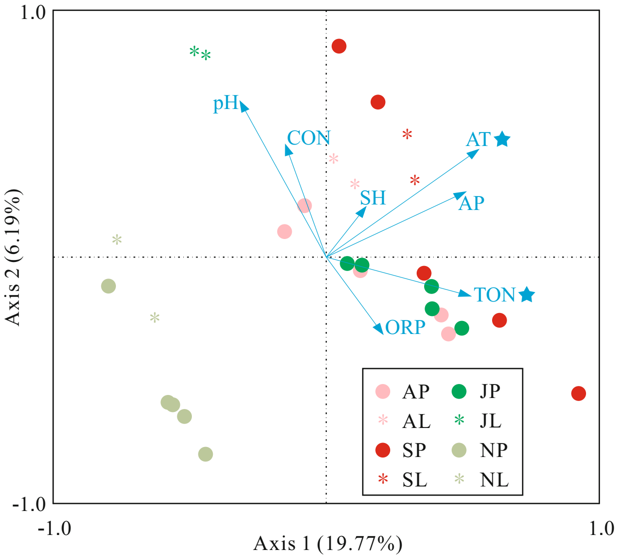

Figure 5. RDA analysis of microbial utilization of carbon substrates in water samples and the environmental factors in the Dajiuhu Peatland. TON: total organic nitrogen, AT: average temperature, SH: sunshine time, AP: average precipitation, ORP: oxidation reduction potential, and CON: electrical conductivity. Abbreviation denoted the same as in Fig. 2.

bon cycles, such as low temperature contributes to carbon sequestration, and high temperature promotes carbon release via enhancing microbial metabolic rates and geochemical actions (Sanz-Lázaro et al., 2011; Ridgwell et al., 2007; Davidson and Janssens, 2006). In the Dajiuhu Peatland, average temperature varies dramatically from month to month which generally matched well with microbial utilization rates of carbon substrates (Fig. 2). Increase of temperature usually enhances microbial utilization of carbon substrates by improving microbial respiration such as primary and secondary metabolism and metabolic enzyme activity (Brzostek and Finzi, 2011; Archer et al., 2004; Mikan et al., 2002). Therefore, under the control of temperature in the Dajiuhu Peatland, microbial carbon utilization showed seasonal variations across the whole year.

Of note we did not see high carbon utilization rates in July with high temperature, which might result from the strong UV radiation during this month. The strong ultraviolet radiation could inhibit bacterial growth and impair microbial primary and secondary metabolism by damaging DNA structure and functional proteins and enzymes (Conan et al., 2008; Hijnen et al., 2006; Häder and Sinha, 2005).

Besides daily average temperature, the sunshine time (SH) and average precipitation (AP) were also found to be the important environmental parameters influencing microbial carbon utilization across the whole year. In fact, the SH is a predominant variable which affects the carbon fixation of *Sphagnum* and their symbiotic Cyanobacteria via regulating photosynthesis (Xiang et al., 2014). The long light illumination time promotes photosynthesis activity of *Sphagnum* and their symbiotic Cyanobacteria, which subsequently result in more deposition of organic carbon in the peatland (Bengtsson et al., 2016; Loisel et al., 2012). Besides, the AP shows a strong impact on the variations of water levels in the peatland, and then regulates microbial communities, especially *mcrA* and *pmoA* genes (Juottonen et al., 2012). Compared with previous studies, we found those environmental factors such as SH and AP contributed to variations of microbial carbon utilization across the whole year though not as significant as that of daily average temperature.

3.2 TON Shaping the Spatial Variations of Carbon Utilization

The preferences of microbial carbon utilization are closely related to available carbon substrates in the environments where microorganisms live. For example, microbial communities in petroleum-contaminated soils and oil fields show high preference to utilize polycyclic aromatic hydrocarbons due to the high content of aromatic compounds in their living environments (Wong et al., 2002; Heitkamp and Cerniglia, 1988). High content of organic N-containing substrates in natural environments could influence microbial substrate preferences, stimulate microbial N-acquiring enzyme activity and contribute to more utilization of N-containing carbon substrates such as amino acid compounds and N-containing polysaccharides in different N-cycling conditions by microbial communities (Moorhead et al., 2012; Myers et al., 2001; Zak and Pregitzer, 1990). Generally, carbon utilization profiles of microbial communities are affected significantly by the compositions and relative abundances of total organic matters such as organic N-substrates and dissolved organic carbon (Berman and Bronk, 2003; Bending et al., 2000). In this study, network analysis clearly distinguished microbial communities into two major clusters (modules 1 and 2, module 3) according to their carbon utilization which corresponded to microbial communities from peat pore waters and lake waters respectively. Microbial communities into modules 1 and 2 preferred to N-containing carbon sources (amines and amino acids) and module 3 utilized more lipids. The total organic nitrogen significantly shaped the carbon utilization of microbial communities, and should be the main factor affecting carbon utilization pattern of microbial communities between pore waters and lake waters. In the peatland ecosystem, nitrogen is usually limited for plant and microbial growth. The dominant plants *Sphagnum* has been demonstrated to obtain nitrogen mainly via their symbiotic microbes such as *Methylobacterium*, *Beijerinckia*, *Burkholderia*, *Azorhizobium*, *Rhodoferax*, *Cupriavidus*, *Bradyrhizobium*, and even Cyanobacteria (Xiang et al., 2014; Bragina et al., 2013; Foster et al., 2011; Huang et al., 2010). The biomass of *Sphagnum* could serve as the important organic N-source of the peatland ecosystem which can be in turn decomposed by microorganisms and explain the preferences of N-bearing carbon substrates by microbial communities in the peat pore waters. Thus, we surmise that the preferences of N-carbon sources such as amines and amino acids by microbial communities in pore waters may result from the higher organic nitrogen contents in peat pore waters, especially organic N-containing substrates such as N-containing carbon sources. For the lake ecosystem, the total organic matters are low and lack of liable organic matters, which may result in the preferences for lipid utilization by the microbial communities.

Besides TON, other environmental parameters such as pH, electrical conductivity (CON) and oxidation reduction potential (ORP) may also impact the microbial carbon utilization. Generally, pH has an important impact on compositions and structures of microbial communities, and microbes show high enzyme activity and microbial metabolism under suitable pH conditions (Rousk et al., 2010; Louis et al., 2007). The CON and ORP also influence the microbial communities and metabolic characteristics (Zhao et al., 2008; Satoh et al., 2007). However, in the Dajiuhu Peatland, the impact of pH, CON and ORP on the carbon utilization of microbial communities between peat pore waters and lake waters was not as significant as that of TON.

4 CONCLUSIONS

By exploiting Biolog Eco plate and RDA analysis, we found that the diversities of microbial communities as well as microbial carbon utilization showed temporal and spatial variations in water samples in the Dajiuhu Peatland across the year of 2014. The temporal variations were significantly affected by temperature and the spatial difference was mainly controlled by the TON content. Particularly microbial diversities and carbon utilization rates were highest in September and lowest in November. Despite of similar temporal variation patterns in all the water samples investigated, microbial counts and carbon utilization rates in lake water samples were generally lower than those of microbial communities in pore waters. The network analysis of microbial utilization of 31 carbon substrates clearly distinguished microbial communities from peat pore waters and lake waters with different C-substrate preferences. Microbial communities in pore waters preferred N-bearing carbon substrates while those in lake waters preferred lipids as their carbon sources. Our results was the first one to describe the microbial counts, diversities and utilization of carbon sources in the Dajiuhu Peatland which will greatly enhance our understanding about the microbial mediated carbon and nitrogen cycles in water bodies in peatland ecosystem.

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