

How do water table drawdown, duration of drainage and warming influence greenhouse gas emissions from drained peatlands of the Zoige Plateau?

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Abstract

As an important soil carbon pool in Qinghai-Tibet Plateau (QTP), alpine peatland are extremely sensitive to global change. Duration of drainage and water table drawdown accelerate peatland degradation due to the soil changed from anaerobic condition to aerobic condition, which may even worsen under climate warming. Hence, the objective of our research was to evaluate the effect of drainage on microbial characteristics, greenhouse gas (GHG) emissions and their influencing factors, and further analyze whether the the variability of GHG emissions increases with warming. The results showed that the influence of water table drawdown on microbial communities were greater than that of duration of drainage. Both the fungal and prokaryotic community compositions varied with water table gradient, and soil microbiota may served as a biomarker to analyze the differences in GHG emissions among three different water table treatments. Intriguingly, the GHG emission decreased with the increase of drainage age, while water table drawdown decreased the emissions of CO₂ and CH₄, and increased the emission of N₂O. In addition, high temperature increased CO₂ by 75% and N₂O by 42%, but not significantly decreased the CH₄ emission rates. Structural equation modeling showed that microbe was the primary factor affecting GHG emissions from drained peatlands, especially prokaryotes. In all, this study indicate water table has a greater effect on GHG emissions than duration of drainage, and the variability of GHG emissions increases with warming.

INTRODUCTION

Peatland are an important global carbon pool that contain 1,055 Gt of soil carbon, and covering 3 % of the Earth's land surface (Nichols & Peteet, 2019). With higher carbon densities than other ecosystems, they release more GHG emissions (Danevčič, Mandić-Mulec, Stres, Stopar, & Hacin, 2010). In particular, peatlands were destabilized by natural and human factors in recent years, such as climate change, land-use change and other disturbances, and more carbon was emitted into the atmosphere (Chen et al., 2014; Ward, Bardgett, McNamara, Adamson, & Ostle, 2007).

Because of the special altitude, alpine peatland ecosystem have higher sensitivity to global change (Ise, Dunn, Wofsy, & Moorcroft, 2008). The peatlands in this area are in a low temperature and anoxia all year round, and climate warming have changed peatlands as a carbon sink to a carbon source (Dise & Phoenix, 2011). Warming-induced the acceleration of carbon and nitrogen (C and N) decomposition in peatland, which further exacerbating climate change (Wen et al., 2019). So far, the research on C and N cycling of peatland induced by climate warming has most focused on undisturbed peatlands (McPartland et al., 2019; Weedon et al., 2013). In addition, many researchers have explored the response of carbon and nitrogen cycling to water table fluctuation (Cao, Chen, Wu, Zhou, & Sun, 2018; de Vries et al., 2018; Rhymes et al., 2016; Zhang et

al., 2018). However, there are relatively few studies on the effects of climate warming on drained peatlands. A recent study found in the period 2020-2100, the impact of emissions from drained peatlands could be as high as 41% of the GHG emissions budget (Leifeld, Wüst-Galley, & Page, 2019). Drainage peatlands become hotspots for both CO₂ and N₂O emissions from soils, as well as a minor part of CH₄ source or even carbon sink (Saurich, Tiemeyer, Dettmann, & Don, 2019).

Zoige peatlands is one of the largest alpine peatlands in the world, covered about 4605 km² area, and store approximately 0.477 Pg of carbon (Chen et al., 2014). Similar to other peatlands (Hooijer et al., 2010; Urbanova & Barta, 2016), it is currently experiencing ubiquitous warming and intensified anthropogenic activities. Since the 1960s, nearly half of the Zoige peatland have drained due to pasture expansion (Dong, Hu, Yan, Wang, & Lu, 2010). Meanwhile, global warming had doubled the rate of warming on Tibetan Plateau over the past century (Qiu, 2007).

Anaerobic surface peat changes to aerobic with the soil drainage, which increased in C and N decomposition rate (Borken & Matzner, 2009). The magnitude of GHG emissions and microbial activity increase as soils become oxygenated (Chapuis-Lardy, Wrage, Metay, Chotte, & Bernoux, 2007; Oertel, Matschullat, Zurba, Zimmermann, & Erasmi, 2016). Many studies have found that drained peatlands can release a lot of dissolved organic carbon (DOC) (Fenner & Freeman, 2011; Liu et al., 2019) and CO₂ (Gatis et al., 2019). In addition, peatlands drainage significantly reduced the emission of CH₄ (Laine et al., 1996), but substantially increased N₂O fluxes (Martikainen, Nykänen, Crill, & Silvola, 1993). Drainage changes the biogeochemical and hydrological processes of peatlands and shifting peatland from a carbon sink to a source of GHG emissions (Norberg, Berglund, & Berglund, 2018; Tiemeyer et al., 2016). Many researches have shown that GHG emissions from soils increase with anthropogenic disturbance (Cai & Chang, 2020; Peng et al., 2013; Saurich et al., 2019). Global warming can accelerate the decomposition of recalcitrant organic matter and old aged carbon, which resulting in the C and N loss from these ecosystems (Craine, Fierer, & McLauchlan, 2010; Dillon, Wang, & Huey, 2010). However, how the GHG production and responses to temperature in drained peatland are still uncertain.

Soil microbes play a critical role in the processes involved in the cycling of C and N, and they are sensitive to environmental changes (Anthony, Crowther, Maynard, van den Hoogen, & Averill, 2020). It was found that microorganisms are very sensitive to the availability of water and oxygen in wetland ecosystems (Jaatinen, Fritze, Laine, & Laiho, 2007). Water table drawdown enhances the activities of extracellular enzyme (Wiedermann, Kane, Potvin, & Lilleskov, 2017), increases microbial biomass (Minick, Mitra, Li, Noormets, & King, 2019), and thus changes the GHG emissions resulting from microbial activities (Wang et al., 2017; Zhong et al., 2017). As well the vulnerability or resilience of microbial communities to water table drawdown is likely to depend on duration of drainage. In the longterm, microbial structure and function will change due to the shifts in the composition of vegetation, which caused by water table drawdown (Murphy, Laiho, & Moore, 2009), which will alter (Kwon, Haraguchi, & Kang, 2013).

Because of the limited data about C and N dynamics of alpine peatlands, and together with ubiquitous global change, it may be of great significance to study the C and N dynamics in Zoige peatlands. Drainage lead to rapid peatland degradation and carbon losses, and the emissions of GHG are likely to increase further with the climate warming. Therefore, we wanted to answer the following questions in this study: 1) Whether the degradation of peatland caused by drainage change the microbial community? 2) what is the effect of drainage on CHG emission rates in Zoige peatlands? 3) Whether warming further increase the GHG emissions from the drained peatlands? 4) What are the influencing factors of GHG emissions from drained peatlands?

MATERIALS AND METHODS

Site and soil sampling

Samples were collected from two sites with different drainage histories in the Ruokeba peatland demonstration area in Hongyuan County town (33°04' N, 102deg34' E; avg. 3472 m a.s.l., Figure 1). The mean annual temperature was 1.6degC, and the mean annual precipitation was 760 mm for the period 1961-2016 (Cao et

al., 2018). Zoige plateau has experienced significant climate change and human activities in the past 50 years, and temperature increased 0.4 degC per decade since 1970 (Yang et al., 2014). The plant communities in this area is over 70% and consists mostly of Grass, Sedge, Gentianaceae, Rosaceae, Ranunculaceae, Leguminosae and Forb.

The long-term drainage site (L; drainage age = 48 years) was used as a grazing pasture in the 1970s, and the ditch is now 0.3-0.5 m deep and 1-1.5m wide. The adjacent short-term drainage site (S; drainage age = 3 years) was drained in 2015 (duration of drainage = 3 years) to analysis the effect of drainage age on GHG emissions, and the ditch is now 0.3-0.5 m deep and 0.5-1.0 m wide.

In July 2018, we sampled a total of six plots that were spaced 2, 10, and 50 m from the drainage ditch in the short- and long-term drainage sites. 0-15 cm soil columns were randomly sampled in quadruplicate using an auger at each plot. We used a grid layout to monitor the water table in these sites and collected data at different distances from the two ditches between 2016 and 2018. During the growing season, average water table depths at the short-term site were -31.38 cm (S2), -18.50 cm (S10), and -8.13 cm (S50), while depths at the long-term site were -31.75 cm (L2), -10 cm (L10), and -6.13 cm (L50) (Figure S1). Based on these values, the L2 and S2 treatments were considered as the low water table treatments (L); L10 and S10, intermediate water table treatments (I); and L50 and S50, high water table treatments (H). The collected soil samples were kept at 4degC. Moist soils were sieved through a mesh (2 mm) to remove impurities and to further homogenize the samples before subdivision for analysis. The soil was separated into three sections: one section was for incubation experiment, one section was stored at 4degC to analyze the physicochemical properties and the last was frozen at -80degC for microbiological analysis.

Soil parameters and microbial community composition analysis

Soil parameters including soil water content (% SWC), pH, total carbon (TC), dissolved organic C (DOC), total dissolved nitrogen (TDN), total nitrogen (TN), soil ammonium N ($\text{NH}_4^+\text{-N}$), soil nitrate N ($\text{NO}_3^-\text{-N}$) and microbial biomass C and N (MBC and MBN) were examined in 24 samples (4 replicates x 3 plots x 2 sites) before incubation. Soil samples were dried for at least 12 h at 105degC to measure SWC; pH was measured using an acidity meter (Sartorius PB-10, Gottingen, Germany); TC and TN were determined using an elemental analyzer (Elementar, Langensfeld, Germany); Concentrations of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were extracted with 2M KCl as the extractant and measured using a continuous flow analyzer (San++, Skalar, Breda, Netherlands); DOC and TDN were measured using a TOC/TN analyzer (Multi N/C 2100, Analytik, Jena, Germany) based on a water extraction method (Pinsonneault et al., 2016); Chloroform fumigation extraction method were used to detect MBC and MBN (Vance et al., 1987). Aboveground plant biomass of each plots was detected on August 2018, and weighed after oven dring samples for 36 h at 65degC.

For microbial diversity, about 0.25 g of each sample soil was used for DNA extraction by PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). High-throughput sequencing was carried out on the Illumina MiSeq platform using the MiSeq V2 Reagent Kit (Illumina, Inc., San Diego, CA), after amplified by prokaryote and fungi primer pairs 515F/909R and ITS4/gITS7F (Baker et al., 2003; Ihrmark et al., 2012). The sequencing data was trimmed via QIIME pipeline (<http://qiime.org/tutorials/tutorial.html>). For detailed analysis procedures refered to Xue et al. (2016). Taxonomy was assigned using the Greengenes database for prokaryote and the Unites database for fungi. 1,266,722 and 1,298,041 assembled paired-end reads were identified in 24 samples through sequencing of 16S rRNA gene and ITS2 amplicons, respectively. Subsampling (17,150 for prokaryote and 18,170 for fungi, the lowest) was performed to calculate microbial diversity. The sequencing datas have been deposited in Sequence Read Archive (SRA) in NCBI under the accession numbers SRP255927 and SRP256039.

Soil incubation experiment and GHG measurements

The soil incubation experiment was conducted under aerobic condition with two temperatures (8degC and 18degC) and four replicates (2 temperatures x 4 replicates x 3 plots x 2 sites = 48). Peat was sieved by a 2 mm mesh sieve, and the remaining coarse roots and stones were carefully removed and discarded. The soil was stored at 8degC (Average temperature in growing season) in the dark for one week of pre-incubation

before the experiment. 20 g soil was puted in a 100 ml glass bottle, sealed with rubber stopper and flushed with CO₂-free air for 8 min to maintain aerobic environment. During the incubation period of 35 days, 5 ml headair was collected every 24 h for CO₂, CH₄ and N₂O concentration measurement. The GHG emissions from the soil of peatland were detected on day 1, 3, 5, 7, 14, 21, 28 and 35 using gas chromatography (Agilent 7890A, Agilent Co., USA). After each sampling, the headspace was flushed with CO₂-free air again to fully remove the accumulated GHG. The greenhouse gases emissions were calculated as (Liu et al., 2016):

$$F = \frac{\text{PPM} \cdot M_0}{22.4} \cdot \frac{T_0}{T} \cdot \frac{P}{P_0} \cdot \frac{V_0}{m} \cdot \frac{1}{d}$$

where F (μg.d⁻¹g⁻¹) is the rate of greenhouse gas emission; M₀: molar mass of CO₂, CH₄ and N₂O; T and P: temperature and atmosphere pressure in headspace of the bottle; T₀ and P₀: standard temperature and atmosphere pressure; V₀: the bottle capacity is 100×10⁻⁶ m³; m: the weight of the dry soil; d: the incubation time is 1 d. TDN and DOC were analyzed after 35-day incubation.

Data analysis

NMDS and PERMANOVA based on Bray-Curtis distance matrix were used to evaluate the overall structural alteration of prokaryote and fungi. Random forest analysis was performed to select the important features that may contribute to the differences in GHG emissions among three different water table treatments (Breiman, 2001). Cross-validation was used for feature selection. Functional profiles of prokaryotic taxa were annotated using FAPROTAX v.1.1 (Louca, Parfrey, & Doebeli, 2016) to predict the process of the carbon, hydrogen, nitrogen, phosphorus and sulfur cycle of environmental samples.

The temperature sensitivity of the GHG emission is defined as the variation of GHG emission response to 10°C temperature gradient. Varied DOC and TDN represented the changes of DOC and TDN concentrations in the incubation period. The difference of GHG emission, DOC and TDN concentration between two temperatures calculated by *t*-Test. Differences in soil microbial compositions, GHG emissions, Q₁₀, varied DOC and TDN concentrations based on duration of drainage and water table drawdown were assessed using multi-factor analysis of variance (ANOVA) in SPSS 21.0 (IBM, Armonk, NY, USA). Correlation analysis was performed to evaluate the impact of varied DOC and TDN concentration, soil properties and microbial characteristics on GHG emission rate using R 3.5.1. (R Development Core Team, 2018).

Direct and indirect contributions of water table, drainage age, soil properties and microbial characteristics to GHG emissions used by Structural equation modeling (SEM) (Grace, 2006). The SEM of differet factors affecting GHG emission was developed from a priori models based on literature, knowledge and correlation analysis data (Figure S2). The prokaryotic and fungal community dissimilarity were obtained by NMDS of the Bray-Curtis distance matrix, and the first axes (NMDS 1) were used in the subsequent SEM analysis. SEM analysis was performed by AMOS 25.0 software (AMOS IBM, USA) using the robust maximum likelihood evaluation method. The SEM fitness was evaluated by the indexes of a non-significant chi-square test (df > 5; *p* > 0.05), the root mean square error of approximation (RMSEA < 0.05) and the goodness of fit index (GFI) (Byrne, 2016).

SPSS 21.0 (IBM, Armonk, NY, USA), R 3.5.1. software (R Development Core Team, 2018) and GraphPad Prism 8.0.2 (GraphPad Software, San Diego, CA, USA) were used to all statistical analysis and charting. *p* < 0.05 was considered significant differences.

RESULTS

Microbial characteristics

3.1.1 Variation in the community structures of prokaryotes and fungi

The microbial diversities of soils with different water level in short- and long-term drainage sites were characterized through partial 16S rRNA and ITS2 region gene sequencing. A total of 1,266,722 and 1,298,041

highquality sequences were analyzed for prokaryote and fungi, respectively. The prokaryotic and fungal community structures of different treatments were evaluated according to β -diversity using NMDS analysis and PERMANOVA test (Figure 2a and 2b). We found that water table and drainage age have significant effects on prokaryotic structure (PERMANOVA, $p < 0.001$ and $p = 0.008$) and fungal (PERMANOVA, $p < 0.001$ and $p = 0.002$) communities in Zoige peatlands. Additionally, both the prokaryotic and fungal communities of low-water table treatments (LWT: L2 and S2) was significantly different from that in intermediate water table treatments (IWT: L10 and S10) and high water table treatments (HWT: L50 and S50) (Figure 2a and 2b, PERMANOVA, $p < 0.001$ for both), but the difference of prokaryotic and fungal communities between IWT and HWT were also significant ($p = 0.006$ and $p = 0.008$, respectively). The differences caused by water table were significantly greater than those associated with drainage age (Figure 2a and 2b), indicating that the influence of water table on microbial community structures was greater than that of drainage age.

3.1.2 Changes in dominant phyla of prokaryotes and fungi

The 12 most abundant prokaryotic phyla (relative abundance higher than 1%) and 6 fungal phyla ($> 0.1\%$) were selected to evaluate the effects of water table drawdown and drainage age on the most significant taxonomic shifts in the soil microbial community of degraded peatlands (Figure 2c and 2d, Table S1). We observed the relative abundances of all prokaryotic and fungal phyla were changed significantly with water table ($p < 0.05$ for all, Table S1). Remarkably, the relative abundances of Proteobacteria, Acidobacteri, Actinobacteria, Basidiomycota and Zygomycota significantly increased, whereas Chloroflexi, Bacteroidetes, Crenarchaeota and Ascomycota markedly decreased with the water table drawdown (Figure 2c and 2d). Compared with short-term drainage, Actinobacteria, Gemmatimonadetes and Nitrospirae showed more relative abundance in long-term drainage sites, while the higher relative abundances of Bacteroidetes, Crenarchaeota, Chytridiomycota and Glomeromycota were observed in the short-term drainage sites ($p < 0.05$ for all, Table S1).

3.1.3 Soil microbiota as biomarkers

We subsequently analyzed whether we could discriminate samples with different water table based upon the microbiota composition using a random-forest machine learning analysis (Zhang et al., 2019). We performed a ten-fold cross-validation to evaluate the importance of indicator prokaryotic classes. We detected 14 classes as biomarker taxa when the cross-validation error curve was lowest (Figure 3a). Among these, 8 classes had higher relative abundance in intermediate and high water table treatments (IWT and HWT), while 6 classes showed higher relative abundance in low-water table treatments (LWT; Figure 3b). This result demonstrates that soil microbial biomarker can be used as one of the important indexes to evaluate peatland degradation.

3.1.4 Functional annotation and distribution of prokaryotic community

FAPROTAX was further applied to evaluate the influence of water table on soil C and N processes (Figure 3c). A total of 69 functional pathways were obtained from 1688 OTUs. We found no significant difference in the relative abundances of functional pathway between the IWT and HWT, so we further analyzed the difference between the LWT and IWT and HWT treatments, and found that there were 42 functional pathways with significant differences (Figure 3c). The results showed that the low water table treatments had higher nitrate denitrification, nitrite denitrification, nitrate reduction and respiration, but had lower nitrite ammonification and nitrogen respiration. This imply that more NO_3^- were used for denitrification in LWT than IWT and HWT. In addition, we found the relative abundances of many carbon metabolism-related pathways, including methanogenesis, methanotrophy, fermentation, hydrocarbon degradation and etc., were significantly higher in IWT and HWT than in LWT.

GHG emission and its temperature sensitivity

CO_2 and N_2O emission rates began low, peaked at about day 21, and kept a relative subsequently during the 35-day incubation. In addition, we found that 10°C warming brought forward the peak of CO_2 and N_2O emissions by a week (Figure S3).

3.2.1 GHG emission variation with water table and drainage age

The average GHG emission rate and its response to warming changed significantly with water table and drainage age ($p < 0.01$ for all, Table S2). At 8 °C and 18°C, the average rates of CO₂, CH₄ and N₂O emissions from different water table treatments were significantly higher at short-term drainage sites than long-term drainage sites, respectively (Figure 4 and Table S2). At the same time, we also found that CO₂ and CH₄ emission rates were all significantly higher under IWT conditions than the other conditions at both two temperatures, while the N₂O emission rates were significantly higher under LWT conditions (Figure 4 and Table S2). Similar to the results of FAPROTAX analysis, the GHG emission decreased with the increase of drainage age, and water table drawdown reduced the CO₂ and CH₄ emission rates, but increased N₂O emission rates.

3.2.2 GHG emission variation with warming

Warming significantly increased the average rates of CO₂ and N₂O emissions of all treatments at short-term and long-term drainage sites, but slightly decreased the CH₄ emission rates, even not significantly (Figure 4). We found the average CO₂ emission rate at short-term drainage site was $36.34 \pm 19.21 \mu\text{g g}^{-1} \text{d}^{-1}$ at 8 °C and $63.27 \pm 31.18 \mu\text{g g}^{-1} \text{d}^{-1}$ at 18 °C, and significantly increased by 74.11% with ten degree warming, while the average CO₂ emission rate at long-term drainage site was $24.25 \pm 10.21 \mu\text{g g}^{-1} \text{d}^{-1}$ at 8 °C and $42.57 \pm 10.75 \mu\text{g g}^{-1} \text{d}^{-1}$ at 18 °C, which significantly increased by 75.55% with 10 °C warming. In addition, we also found warming significantly increased average CO₂ emission rate of LWT conditions by 91.14% from $19.46 \pm 6.13 \mu\text{g g}^{-1} \text{d}^{-1}$ of 8 °C to $37.78 \pm 8.66 \mu\text{g g}^{-1} \text{d}^{-1}$ of 18 °C, IWT conditions by 56.44% from $46.60 \pm 13.20 \mu\text{g g}^{-1} \text{d}^{-1}$ of 8 °C to $72.90 \pm 28.88 \mu\text{g g}^{-1} \text{d}^{-1}$ of 18 °C, and HWT conditions by 93.60% from $24.83 \pm 3.56 \mu\text{g g}^{-1} \text{d}^{-1}$ of 8 °C to $48.07 \pm 5.64 \mu\text{g g}^{-1} \text{d}^{-1}$ of 18 °C. The results of temperature sensitivity (Q_{10}) of soil respiration also further proved that the sensitivity of IWT conditions to temperature were less than the other conditions (Figure S4).

Variation of DOC and TDN concentration during incubation

Compared with the soil before incubation, the variations of DOC and TDN concentrations after incubation showed different patterns (Figure 5). While TDN concentration increased, DOC concentration decreased with the water table drawdown at both short-term and long-term drainage sites during incubation ($p < 0.001$ for all; Figure 5 and Table S3). The DOC concentration of different water table treatments at short-term drainage site were significantly higher than long-term drainage site, respectively ($p < 0.001$; Table S3). Warming decreased the DOC concentration of all treatments ($p < 0.05$ for all), but only significantly increased TDN concentration of LWT conditions ($p < 0.05$; Figure 5).

The influence factors ofGHG emissions

The average rates of GHG emissions during the incubation period was expressed in CO₂, CH₄ and N₂O. CO₂ and CH₄ were positively correlated with DOC concentration under 8 °C and 18 °C ($r = 0.555$, $r = 0.483$ for CO₂; $r = 0.725$, $r = 0.555$ for CH₄; $p < 0.05$ for all), and were negatively correlated with TDN ($r = -0.495$, $r = -0.505$ for CO₂; $r = -0.449$ for CH₄ at 8 °C; $p < 0.05$ for all; Figure 6a, 6c and 6b,6d). No linear relationship was found among N₂O and DOC, but N₂O were correlated positively with TDN under 8 °C ($r = 0.459$, $p < 0.05$; Figure 6e and 6f).

Spearman's correlation analysis were used to further evaluate microbial influences on the GHG emissions, DOC and TDN concentrations (Figure 7). An interesting result was found that the relationship between the dominant microbial phyla (11 most abundant prokaryotic phyla and 5 fungal phyla) and carbon and nitrogen mineralization showed opposite trends (Figure 7). Firmicutes, Chloroflexi, Chlorobi, Bacteroidetes and Crenarchaeota of prokaryotic phyla and Ascomycota, Chytridiomycota and Glomeromycota of fungal phyla showed a positive relationship with carbon mineralization (including CO₂, CH₄ and DOC), but a negative relationship with nitrogen mineralization (including N₂O and TDN). Proteobacteria, Acidobacteria, Planctomycetes and Gemmatimonadetes of prokaryotic phyla and Basidiomycota, Zygomycota of fungal phyla showed a negative relationship with carbon mineralization (including CO₂, CH₄ and DOC), but a positive relationship with nitrogen mineralization (including N₂O and TDN).

Finally, SEM was applied to access the direct and indirect effects of water table, drainage age, soil properties and soil prokaryotic and fungal communities on GHG emissions (Figure 8). Drainage can directly influenced CO₂ and N₂O emissions, with little or no directly effect on CH₄ (Figure 8). Water table showed a directly negative influence on N₂O, with little or no directly effect on CO₂ and CH₄. Drainage age were directly negative related to CO₂, with little or no directly effect on CH₄ and N₂O. Drainage can indirectly affected GHG emissions by directly influenced plant biomass, TC, TN, DON, SWC, NH₄⁺-N, microbial C:N and soil prokaryotic and fungal communities (Figure 8). Prokaryotic community showed a directly positive associated with CO₂, CH₄ and N₂O emissions (Figure 8). SEM suggested that prokaryotic community exhibited a larger impact on GHG emissions than fungal community (Figure 8).

DISCUSSION

1. Microbial characteristics varied in relation to duration of drainage and water table draw-down

The response of microbes to drainage is likely to depend on peatland type, the alteration of water table fluctuation, and the extent of spatiotemporal variation (Andersen, Chapman, & Artz, 2013; Krista Jaatinen et al., 2008; Minick et al., 2019; Peltoniemi, Fritze, & Laiho, 2009). Our study found that both water table and drainage age significantly affected the microbial community structure and compositions (Figure 2), which was consistent with many studies (Jaatinen et al., 2007; Urbanova & Barta, 2016). Drainage can directly lead to water table drawdown in peatlands, resulting in persistent aerobic conditions (Holden, Chapman, Lane, & Brookes, 2006), while with long-term drainage may further change the vegetation composition, thus affecting microbial composition and function (Miller, Benschoter, & Turetsky, 2015; Urbanova & Barta, 2016). Our results showed that water table drawdown significantly increased the relative abundances of Proteobacteria, Acidobacteria, Actinobacteria and Basidiomycota (Figure 2c and 2d). In oxic conditions, Members of Proteobacteria (Di Lonardo, De Boer, Klein Gunnewiek, Hannula, & Van der Wal, 2017), Acidobacteria (Dedysh, 2011), Actinobacteria (Goodfellow & Williams, 1983) and Basidiomycota (Ludley & Robinson, 2008) are considered to be the principal decomposers of soil organic matter, that can degrade recalcitrant organic materials (e.g. lignin, cellulose and humic materials) (Chen et al., 2018; Pankratov, Dedysh, & Zavarzin, 2006). So these microbes play an important role in GHG emissions, and this results consistent with previous research (Schimel & Gullledge, 1998). In addition, we also found long-term drainage significantly increased the abundance Actinobacteria of compared to short-term drainage. Relevant studies have found that Actinobacteria are more sensitive to long-term water table drawdown than short-term water table drawdown (Jaatinen et al., 2008; Peltoniemi et al., 2009).

Microbes are ubiquitous and mediate the macroscopic characteristics of the ecosystems (Thompson, Johansen, Dunbar, & Munsy, 2019). Because of the complexity of microbial communities make it necessary to explore functional relationships between specific microbes and ecosystem characteristics. Here, we have used machine learning techniques to find that specific microbial taxa could be used as one of the important indexes to evaluate peatland degradation. The relative abundance of 4 classes of the phylum Proteobacteria were significantly higher in the LWT compared to IWT and HWT (Figure 3b). As the members of Proteobacteria are involved in bacteriochlorophyll-dependent photosynthesis, they also considered to be the major decomposers of soil organic matter, and showed important role in nutritionally limited or arid environments (Ren et al., 2018). In addition, as an important member of Deltaproteobacteria, methanotroph can effectively oxidize methane in nature (Hanson & Hanson, 1996). In consistent with other studies (Cao et al., 2018; Siljanen, Saari, Bodrossy, & Martikainen, 2012; Zhong et al., 2020), we also found the relative abundance of Deltaproteobacteria increased with water table drawdown.

Influence of duration of drainage and water table on GHG emissions

The emissions of CO₂, CH₄ and N₂O were significantly different between short-term drainage sites and long-term drainage sites (Figure 4 and Table S2). The long-term drainage peatlands are less suitable for microbial use compared with short-term drainage peatlands because of the poor quality of organic matter and low decomposability due to drainage over many decades of grazing history (Andersen et al., 2013; Leifeld,

Steffens, & Galego-Sala, 2012; Urbanova & Barta, 2016). So far, few studies have examined the impact of duration of drainage on GHG emissions of peatland. Most researches have focused on the effect of drainage on GHG emissions in disturbed peatland compared to natural peatland (Cao et al., 2018; Maljanen, Hytönen, & Martikainen, 2001; Nieveen, Campbell, Schipper, & Blair, 2005; Zhou, Cui, Wang, & Li, 2017), or the effect of the water table drawdown on GHG emissions due to drainage (Chen, Borken, Stange, & Matzner, 2012; Hou et al., 2013; Laiho, Silvan, Cárcamo, & Vasander, 2001; Saurich et al., 2019; Wang, Siciliano, Helgason, & Bedard-Haughn, 2017). Kang et al. (2018) showed that N₂O flux was found to be inconsistent under drought conditions, which may be caused by SOC variations by drought. This is in accordance with our results, We found N₂O emission in long-term drained peatland was lower than that in short-term drained peatland (Figure 4). Huang, Zou, Zheng, Wang, and Xu (2004) found long-term drought conditions may induced the SOC to be recalcitrant, indicating a reduced supply of organic carbon for microbial activity. Therefore, nitrification and denitrification processes were probably inhibited to produce less N₂O under the long-term drought conditions.

Many researches have found that water table drawdown caused by drainage make peatlands into sources for CO₂ and N₂O, whereas CH₄ emission is known to decrease (Cao et al., 2018; Saurich et al., 2019; Tiemeyer et al., 2016). In contrast, Knorr, Glaser, and Blodau (2008) and Muhr, Höhle, Otieno, and Borken (2011) found the emissions of CO₂ from minerotrophic fen peatland had no change after water table drawdown. In accordance with other previous researches (Hou et al., 2013; Maljanen et al., 2001; Regina, Silvola, & Martikainen, 1999), we also found the N₂O emission increased with the water table drawdown. The nitrogen cycle of peatland soil is very sensitive to the fluctuation of water table (Pal, Stres, Danevčič, Leskovec, & Mandic-Mulec, 2010). It is well known that soil nitrate is reduced to N₂, NO and N₂O through microbial processes (Knowles, 1982). N₂ is the end product under anaerobic conditions, while N₂ generally replaced by N₂O at higher oxygen levels (Weil & Brady, 2017). The results of FAPROTAX also further supported our result, which we found had higher nitrous oxide denitrification, nitrate denitrification, nitrite denitrification, nitrate reduction and respiration, but had lower nitrite ammonification and nitrogen respiration (Figure 3c). In addition, we also found that multiple carbon metabolism-related pathways were significantly higher in IWT and HWT than those of LWT, which was partly supports the results of the carbon emissions (Figure 3c and Figure 4). Freeman, Lock, and Reynolds (1992) and Kwon et al. (2013) pointed out that water table drawdown changes anaerobic surface peat into aerobic, increasing the decomposition rates, microbial activity and aerobic respiration, and then increasing CO₂ emissions. However, our results showed that CO₂ emissions first increased and then decreased along the water table gradient. Similarly, Laiho (2006) showed that short-term water level drawdown increased CO₂ emissions, but the longterm changes of the water level drawdown caused by the drought decreased the CO₂ emissions of peatland. Hou et al. (2013) also found that water depth of 5 cm below surface increased the CO₂ emission of peatlands, but the continued water table drawdown was no significant influenced or even decreased the CO₂ emission. Swails et al. (2018) further proved that degradation of soil organic matter quality and nutrients associated with drainage may decrease substrate driven CO₂ production from peat decomposition. Therefore, water table drawdown increased the emissions of CO₂, but this impact maybe offset by long-term drought.

Influence of temperature on GHG emissions

Our study results consistent with previous studies, which found warming increased CO₂ (Laine, Makiranta, et al., 2019) and N₂O emissions (Cui et al., 2018; Duval & Radu, 2018), but have no significant impact on CH₄ emission (Johnson, Pypker, Hribljan, & Chimner, 2013; Pearson et al., 2015). As for the impact of temperature on CO₂, it is now generally accepted that warming can significantly increase CO₂ emissions in both drained and undrained peatlands (Hopple et al., 2020; Laine, Makiranta, et al., 2019; Salm, Kimmel, Uri, & Mander, 2009). However, warming appears to have a complex impact on the emission of CH₄ from peatlands (Yang et al., 2014). Turetsky et al. (2008) found a positive correlation between warming and CH₄ emissions, some reported a negative relationship (Eriksson, Öquist, & Nilsson, 2010; Peltoniemi et al., 2016), and while some other studies have showed no effect (Laine, Mehtatalo, Tolvanen, Froking, & Tuittila, 2019; Pearson et al., 2015). Recently, many studies have found that warming effect on CH₄ emissions varied with the fluctuation of water table (Laine, Makiranta, et al., 2019; Peltoniemi et al., 2016; Yang et al., 2014). Gill, Giasson,

Yu, and Finzi (2017) and Munir and Strack (2014) reported that warming increased the CH_4 emission in water-saturated conditions, while the opposite phenomenon has been found from drier hummocks. This is partly consistent with our research, we only found that warming increased CH_4 emission of HWT condition in short-term drained peatlands, although not significant. Peltoniemi et al. (2016) concluded that the effect of warming under different moisture conditions on the activity and community of microorganisms regulating the methane cycle are not directly.

Consistent with other ecosystems, for example alpine swamp meadow (Chen et al., 2017), high arctic tundra (Gong, Wu, Vogt, & Le, 2019) and subarctic tundra (Voigt, Lamprecht, et al., 2017), we found that warming increased N_2O emissions with different water table treatments in both short-term and long-term drained peatlands at seasonal frozen soil. Butterbach-Bahl et al. (2013) reported that denitrification and consequently N_2O emissions have high temperature sensitivity. The emission of N_2O is controlled by mineral nitrogen availability and influenced by microbial nitrification and denitrification processes (Bouwman, 1990). N mineralization from SOM can be accelerated by warming and leaching of nitrate and ammonium may occur (Bai et al., 2013). Thus, increased soil temperature promoted N_2O emissions via denitrification (Voigt, Marushchak, et al., 2017). In addition, we also found Q_{10} values for GHG emissions were all lowest in IWT conditions (Figure S4). This indicates that water table is also an important index affecting the temperature sensitivity of GHG.

The role of biogeochemical factors in GHG emissions

Many researches have showed that drainage affected the processes of the carbon (C) and nitrogen (N) mineralization of peatland, and thus changed its C and N sink and sources function (Chen et al., 2012; Chimner, Pypker, Hribljan, Moore, & Waddington, 2017; Laine, Makiranta, et al., 2019; Zhang et al., 2020). The fluctuation of water table can directly affect soil biogeochemical properties, including soil basic physical and chemical properties, soil substrate, microbial community and enzyme activity, which lead to the change of GHG emissions (de Vries et al., 2018; Mpamah, Taipale, Rissanen, Biasi, & Nykanen, 2017; Swails et al., 2018; Wen et al., 2019). The concentration of DOC and TDN are the balance between soil organic matter production and soil microbial consumption, and DOC and TDN will be further decomposed and discharged in the form of CHG (van den Berg, Shotbolt, & Ashmore, 2012). Therefore, DOC and TDN concentration in soil can reflect carbon and nitrogen loss (Boothroyd, Worrall, & Allott, 2015). The results of our study found DOC and TDN concentration were strongly correlated with CO_2 and CH_4 emissions, while no linear relationship was found between N_2O and DOC, N_2O was only correlated positively with TDN (Figure 6). This suggests that soil substrate availability is crucial in GHG emission from soil. We further analyzed the relationship between soil microorganisms and substrate availability and GHG emission. An interesting result was found that some microbial taxa were contribute significantly to carbon mineralization, and others contribute significantly to nitrogen mineralization (Figure 7). Soil microorganisms affect the mineralization of soil organic C and N by secreting extracellular enzymes (Chapman, Cadillo-Quiroz, Childers, Turetsky, & Waldrop, 2017; Schneckler et al., 2015). Abatenh, Gizaw, Tsegaye, and Gene (2018) reported that microbial processes have a central role in GHG emissions and specific functional microorganisms are responsible for the related biochemical processes, and possibly a rapid response to climate change. In addition, SEM was used to analyze the impact of environmental factors on the emission of CHG, and it was found that the prokaryotic microbial community had the greatest impact on GHG, which also further supported the important role of microorganisms in soil GHG emissions (Singh, Bardgett, Smith, & Reay, 2010).

CONCLUSION

The emissions of CO_2 , CH_4 and N_2O response to drainage is inconsistent. CO_2 and CH_4 emission rates first increased and then decreased along the water table drawdown gradient, while N_2O increased along the water table gradient. The emissions of CO_2 , CH_4 and N_2O from different water table treatments were significantly higher at short-term drainage sites than long-term drainage sites. The results of FAPROTAX analysis also supported this perspective. In addition, warming significantly increased the average rates of CO_2 and N_2O emissions of all treatments at short-term and long-term drainage sites, but not significantly decreased the CH_4 emission rates. The Q_{10} values of GHG emissions were lowest in IWT conditions compared

to other conditions. Microbial community composition was the primary factor affecting GHG emissions from peatlands, especially prokaryotes. Collectively, Our results further reveal the mechanism of climate change and human activities on the emissions of GHG in alpine peatland ecosystem, which can provide support for the sustainable management of alpine peatland in the future.

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DATA AVAILABILITY STATEMENT

The data used in this study can be obtained from the corresponding author on reasonable request.

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Table Captions

Table S1. The relative abundance of Prokaryote and fungi at phylum level under different water table treatments in short-term and long-term drainage peatlands.

Table S2. The average GHG emission rate and temperature sensitivity (Q_{10}) of three different water table treatments in short- and long-term drainage peatlands under 8 °C and 18 °C.

Table S3. Soil DOC and TDN concentration variations under different water table (WT) treatments in short-term and long-term drainage peatlands.

Table S4. Data on soil and plant properties in short-term and long-term drained peatlands.

Figure captions

Figure 1. Map of sampling site (Ruokeba) in Zoige Plateau peatland

Figure 2. The compositions and structures of prokaryotic (a,c) and fungal (b,d) in peatlands with different drainage age and water table levels. S: Short-term drainage sites, L: Long-term drainage sites, S2 and L2: low water table treatment (LWT), S10 and L10: intermediate water table treatment (IWT), S50 and L50: high water table treatment (HWT).

Figure 3. Microbial biomarkers and predicted functional profiles of prokaryote with different water table levels. (a) Top 14 prokaryotic families were identified by using random-forest classification of the relative abundance of prokaryote with different water table levels. (b) Heatmap of the relative abundance of biomarker families in the individual samples. (c) The differences prokaryotic function in the FaProTax database for different water table treatments. S: Short-term drainage site, L: Long-term drainage site, S2 and L2: low water table treatment (LWT), S10 and L10: intermediate water table treatment (IWT), S50 and L50: high water table treatment (HWT).

Figure 4. The average GHG emission rate during 35d incubation in short- and long-term drainage peatlands with three different water table treatments under 8 °C and 18 °C. (a) CO₂ emissions; (b) CH₄ emissions; (c) N₂O emissions. Significance level: * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$. S: Short-term drainage site, L: Long-term drainage site, S2 and L2: low water table treatment (LWT), S10 and L10: intermediate water table treatment (IWT), S50 and L50: high water table treatment (HWT).

Figure 5. Variation of DOC (a) and TDN (b) concentration of three different water table treatments in short- and long-term drainage peatlands under 8 °C and 18 °C. Significance level: * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$. S: Short-term drainage site, L: Long-term drainage site, S2 and L2:

low water table treatment (LWT), S10 and L10: intermediate water table treatment (IWT), S50 and L50: high water table treatment (HWT).

Figure 6. Relationship between the average GHG emission and DOC(a, c, e) and TDN concentration (b, d, f). Grey circle represents at 8 °C, and red circle represents at 18 °C.

Figure 7. Spearman's correlation analysis between the dominant microbial phyla and GHG emissions, DOC concentration and TDN concentration. Grey font indicates fungal phyla, and black font indicates prokaryotic phyla. Significance level: * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$.

Figure 8. The impacts of water table, drainage age, soil properties and soil prokaryotic and fungal communities on GHG emissions as estimated using the structural equation modeling. (a) CO₂ emissions; (b) CH₄ emissions; (c) N₂O emissions. Standardized path coefficients are listed beside each path (Red and blue arrows represent positive and negative relationships, black double arrows represent covariant correlation; Paths with insignificant coefficients are represented using gray lines; * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$). R² values indicate the strength of explanation by independent variables. The prokaryotic and fungal diversities are represented using Shannon indexes, and the prokaryotic and fungal communities are represented using NMDS of the Bray-Curtis distance matrix.

Figure S1. Water table data at different distances from short- and long-term drainage ditches in recent three growing seasons (2016-2018). (a) The fluctuation of water table depth (WTD); (b) Average water table depths. S: Short-term drainage peatlands, L: Long-term drainage peatlands, S2 and L2: low water table treatment (LWT), S10 and L10: intermediate water table treatment (IWT), S50 and L50: high water table treatment (HWT).

Figure S2. Variation of GHG emission rate of soil from three different water table treatments in short- and long-term drainage peatlands under 8 °C and 18 °C. (a) CO₂ emission rate at 8 °C; (b) CH₄ emission rate at 8 °C; (c) N₂O emission rate at 8 °C; (d) CO₂ emission rate at 18 °C; (e) CH₄ emission rate at 18 °C; (f) N₂O emission rate at 18 °C.

Figure S3. Temperature sensitivity (Q₁₀) value variations from three different water table treatments in short- and long-term drainage peatlands. (a) CO₂; (b) CH₄; (c) N₂O. Significance level: * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$. S: Short-term drainage site, L: Long-term drainage site, S2 and L2: low water table treatment (LWT), S10 and L10: intermediate water table treatment (IWT), S50 and L50: high water table treatment (HWT).

Figure S4. Spearman's correlation analysis between GHG emissions and soil properties, soil prokaryotic and fungal communities. Significance level: * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$.

Figure 1

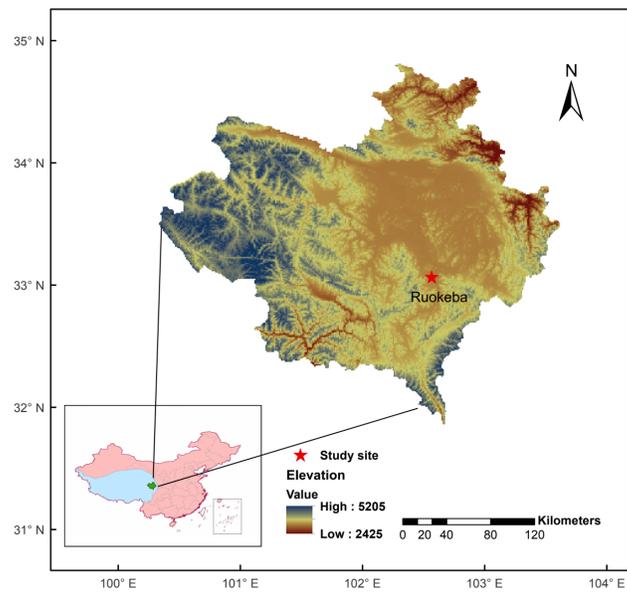


Figure 2

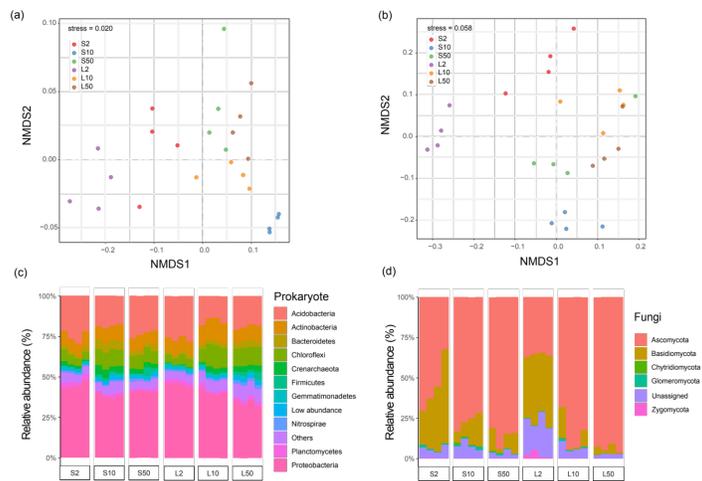


Figure 4

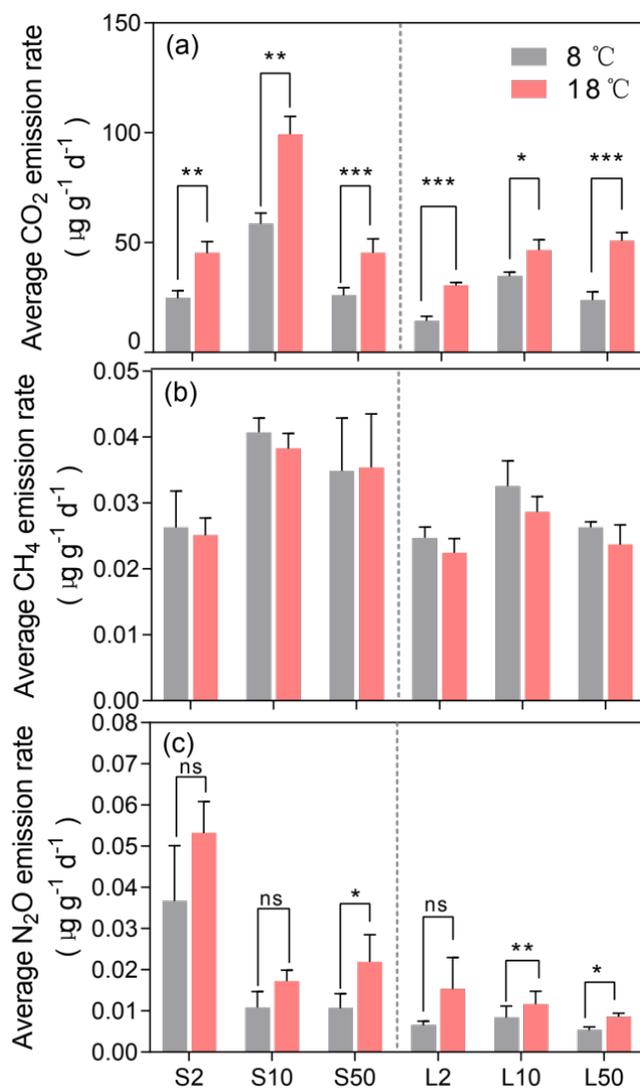


Figure 5

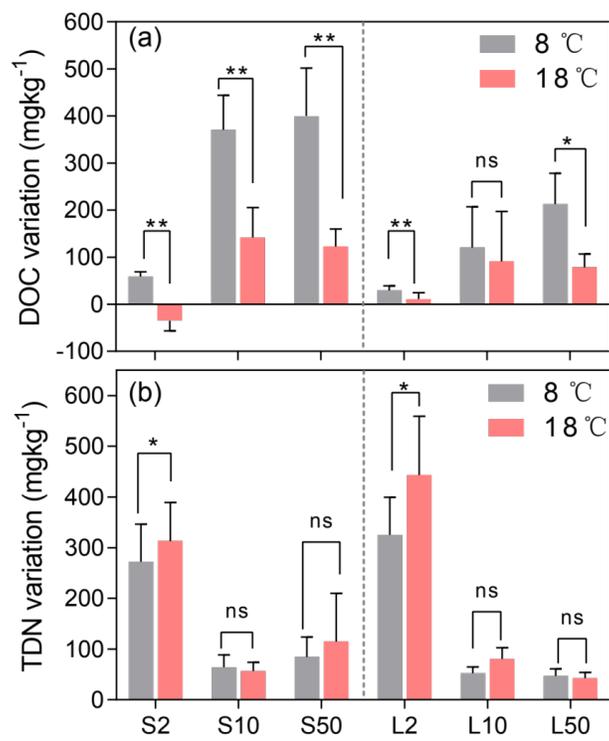


Figure 6

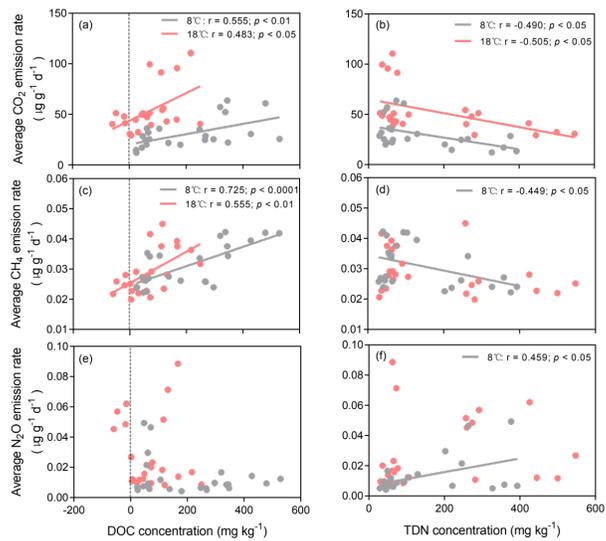


Figure 7

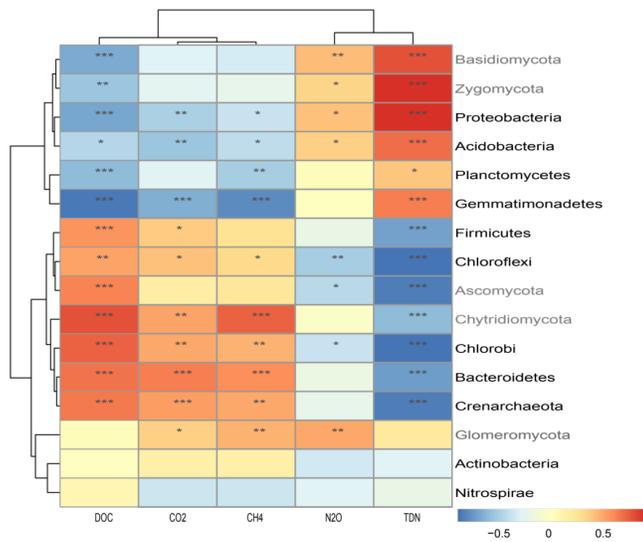


Figure 8

