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 as the soils are no longer protected by anaerobic condition, which may worsen under climate warming. Hence, the purpose of our study 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 reduced the CO_2 and CH_4 emission rates, and increased N_2O emission rates. In addition, high temperature increased CO_2 by 75% and N_2O by 42%, but not significantly decreased the CH_4 emission rates. Structural equation modeling showed that microbe was the primary factor affecting GHG emissions from drained peatlands, especially prokaryotes. Overall, our results indicate that water table has a greater impact 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 play an important role in GHG emissions (Danevčič, Mandic-Mulec, Stres, Stopar, & Hacin, 2010). In particular, peatlands were destabilized by natural and hunman 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).

Becase 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 acceleration of carbon and nitrogen decomposition of peat, leading to positive feedback and exacerbating climate change (Wen et al., 2019). So far, the research on carbon and nitrogen cycling

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of peatland caused by climate warming has most focused on undisturbed peatlands (Clark et al., 2009; McPartland et al., 2019; Ward 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, comparatively little study has been done on the effect of climate warming on drained peatlands. A recent study found in the period 2020–2100, the impact of emissions from drained peatlands could account for 12- 41% of the remaining GHG emissions budget for keeping global warming below +1.5 to +2 °C (Leifeld, Wüst-Galley, & Page, 2019). Drainage peatlands become hotspots for both CO_2 and N_2O emissions from soils, as well as minor sources or even small sinks of CH_4(Saurich, Tiemeyer, Dettmann, & Don, 2019).

Zoige peatlands, covered about 4605 km^2 area, regard as one of the largest alpine peatlands in the world, 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 41 % of the area of 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 leading to an increase in carbon and nitrogen 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 CO_2 (Gatis et al., 2019; von Arnold, Nilsson, Hånell, Weslien, & Klemedtsson, 2005). In addition, peatlands drainage have resulted in significant reductions in CH_4 emissions (Laine et al., 1996), but substantially increased N_2O fluxes (Martikainen, Nykänen, Crill, & Silvola, 1993). Drainage changes the biogeochemical and hydrological processes of peatlands and turns the peatlands from a natural carbon sink to a hotspots of GHG emissions from soils (Norberg, Berglund, & Berglund, 2018; Tiemeyer et al., 2016). The variability of GHG emissions increases with anthropogenic disturbance were proved by many researches (Cai & Chang, 2020; Peng et al., 2013; Saurich et al., 2019). Global warming can accelerate the decomposition rate of recalcitrant organic carbon with complex structures 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 microbe plays 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). In addition, 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 climate change and human activities disturbances on the Plateau, so researches on the C and N dynamics of Zoige peatlands may be of great importance. 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

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Site description and soil sampling

Soil 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 climate is cold and continental, the mean annual temperature for the period 1961-2016 was 1.6degC, and the mean annual precipitation was 760 mm (Cao et al., 2018). During the past 50 years, the Zoige plateau has experienced significant climate change and human activities, and temperature increased 0.4 degC per decade since 1970 (Yang et al., 2014). Peat in this area have a depth of 0.3-5 m; an average pH of 5.77; TC of 22%; TN of 1.78%. 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 test the influence 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). Soil samples were transported to the laboratory in ice bags 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.

Soilparameters and microbial commum.ity 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 (NH_4^+-N), soil nitrate N (NO_3^--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. SWC was calculated by oven drying soil samples for at least 12 h at 105degC; The pH was measured using an acidity meter (Sartorius PB-10, Gottingen,, Germany); TC and TN were measured using an elemental analyzer (Elementar, Langenselbold, Germany); Concentrations of NH_4^+-N and NO_3^--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); and MBC and MBN were detected using the chloroform fumigation extraction method (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 performed 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), at the Environmental Genome Platform of the Chengdu Institute of Biology, Chinese Academy of Sciences. The sequencing data was trimed 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 alpha and

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beta-diversity. The sequencing datas were deposit in Sequence Read Archive 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 remaining roots and stones were carefully removed. 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 that was tightly sealed with a rubber stopper and flushed with CO_2-free air for 8 min to keep an aerobic environment. All bottles were kept sealed during the incubation period and 5 ml headspace gas was collected every 24 h for CO_2, CH_4 and N_2O concentration measurement during the 35-day incubation period. The greenhouse gases emissions from the peatland soil were measured on day 1, 3, 5, 7, 14, 21, 28 and 35. The concentration of gases were measured by gas chromatography (Agilent 7890A, Agilent Co., USA). After each sampling, the headspace was flushed with CO_2-free air again to remove the accumulated greenhouse gases. The greenhouse gases emissions were calculated as (Liu et al., 2016):

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

where F ($\mu g.d^{-1}g^{-1}$) is the rate of greenhouse gas eemission; M_0: the molar mass of CO_2, CH_4 and N_2O; T and P: the temperature and atmosphere pressure in the top space of the bottle; T_0 and P_0: the absolute temperature and atmosphere pressure under standard conditions; V_0: the bottle capacity is $100 \times 10^{-6} m^3$; 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

The overall structural alteration of prokaryote and fungi were evaluated using Non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis distance matrices. 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). For selecting appropriate features, cross-validation was used by the rfcv() function. Functional annotations of prokaryotic taxa (FAPROTAX) were carried out using FAPROTAX v.1.1 (Louca, Parfrey, & Doebeli, 2016) to perdict the process of the carbon, hydrogen, nitrogen, phosphorus and sulfur cycle of environmental samples.

The temperature sensitivity (Q_{10}) of the GHG emission is calculated as the ratio of GHG emission at temperature T + 10 (°C) relative to that at temperature T (°C). Varied DOC and TDN were the variation of DOC and TDN concentration during 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, Q_{10}, 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 effect 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).

Structural equation modeling (SEM) was used to access the direct and indirect contributions of water table, drainage age, soil properties and microbial characteristics to GHG emissions (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 sofeware (AMOS IBM, USA) using the robust

maximum likelihood evaluation method. The SEM fitness was evaluted 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 statistically significant.

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 significantly affected the structure of prokaryotic (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) significantly differed from community structures of 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). The relative abundances of the Actinobacteria, Gemmatimonadetes and Nitrospirae were significantly higher in long-term drainage sites compared to short-term drainage, 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 carried out ten-fold cross-validation to access the importance of indicator prokaryotic classes. The cross-validation error curve was lowest when the 14 most relevant classes were used. So, we defined these 14 classes as biomarker taxa (Figure 3a). Among theses, 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

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FAPROTAX analysis was further used to evaluate the effect of water table on soil C and N processes (Figure 3c). A total of 69 functional pathways were obtained from 1688 OTUs. We found that there was no significant difference of the relative abundances of functional pathway between the IWT and HWT, so we further analyzed the difference between the low water table treatments and the intermediate and high water table 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 the intermediate and high water table treatments than in the low water table treatments.

GHG emission and itstemperature 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).

3.2.1GHG emission variation with water table and drainage age

The average GHG emission rate and its response to warming varied significantly with water table and drainage age ($p < 0.01$ for all, Table S2). At 8 °C and 18°C, the average rates of CO_2, CH_4 and N_2O 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 CO_2 and CH_4 emission rates were all significantly higher under IWT conditions than the other conditions at both two temperatures, while the N_2O 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 CO_2 and CH_4 emission rates, but increased N_2O emission rates.

3.2.2 GHG emission variation with warming

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 slightly decreased the CH_4 emission rates, even not significantly (Figure 4). We found the average CO_2 emission rate at short-term drainage site was 36.34 ± 19.21 µg g^{-1} d^{-1} at 8 °C and 63.27 ± 31.18 µg g^{-1} d^{-1} at 18 °C, and significantly increased by 74.11% with 10 °C warming, while the average CO_2 emission rate at long-term drainage site was 24.25 ± 10.21 µg g^{-1} d^{-1} at 8 °C and 42.57 ± 10.75 µg g^{-1} d^{-1} at 18 °C, which significantly increased by 75.55% with 10 °C warming. In addition, we also found warming significantly increased average CO_2emission rate of LWT conditions by 91.14% from 19.46 ± 6.13 µg g^{-1} d^{-1} of 8 °C to 37.78 ± 8.66 µg g^{-1} d^{-1} of 18 °C, IWT conditions by 56.44% from 46.60 ± 13.20 µg g^{-1} d^{-1} of 8 °C to 72.90 ± 28.88 µg g^{-1} d^{-1} of 18 °C, and HWT conditions by 93.60% from 24.83 ± 3.56 µg g^{-1}d^{-1} of 8 °C to 48.07 ± 5.64 µg g^{-1}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 those in original soil, 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 CHG emissions over 35-day incubation was expressed in CO_2, CH_4 and N_2O. CO_2 and CH_4 were positively correlated with DOC concentration under 8 °C and 18 °C conditions (r = 0.555, r = 0.483 for CO_2; r = 0.725, r = 0.555 for CH_4; $p < 0.05$ for all), and were negatively correlated with TDN (r = -0.495, r = -0.505 for CO_2; r =-0.449 for CH_4 at 8 °C; $p < 0.05$ for all; Figure 6a, 6c and 6b,6d). No linear relationship was found among N_2O and DOC, but N_2O 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 explore 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 CO_2, CH_4 and DOC), but a negative relationship with nitrogen mineralization (including N_2O and TDN). Proteobacteria, Acidobacteria, Planctomycetes and Gemmatimonadetes of prokaryotic phyla and Basidiomycota, Zygomycota of fungal phyla showed a negative relationship with carbon mineralization (including CO_2, CH_4 and DOC), but a positive relationship with nitrogen mineralization (including N_2O and TDN).

Finally, Structural equation modeling (SEM) was used 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 CO_2 and N_2O emissions, with little or no directly effect on CH_4 (Figure 8). Water table showed a directly negative influence on N_2O, with little or no directly effect on CO_2 and CH_4. Drainage age were directly negative related to CO_2, with little or no directly effect on CH_4 and N_2O. Drainage can indirectly affected GHG emissions by directly influenced plant biomass, TC, TN, DON, SWC, NH_4^+-N, microbial C:N and soil prokaryotic and fungal communities (Figure 8). Prokaryotic community showed a directly positive associated with CO_2, CH_4 and N_2O emissions (Figure 8). SEM suggested that prokaryotic community exhibited a larger impact on GHG emissions than fungal community (Figure 8).

DISCUSSION

Microbial characteristics varied in relation toduration ofdrainage and water table drawdown

The response of the microbial communities to drainage is likely to depend on peatland type, the alteration of water table fluction, and the extent of the change in time and space (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, Benscoter, & 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 & Gulledge, 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, & Munsky, 2019). However, due to the complexity of microbial communities, it is necessary

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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 have been shown to play a key role in nutritionally limited or arid environments (Ren et al., 2018). In addition, as an important member of Deltaproteobacteria, methanotroph plays an important role in the oxidation of 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 fluxes of CO_2, CH_4 and N_2O 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 due to 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, there are few studies have examined the effects of duration of drainage on GHG emissions of peatland. Most researches have focused on the impact 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 N_2O 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 N_2O 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 N_2O under the long-term drought conditions.

Many researches have found that water table drawdown caused by drainage turn peatlands into sources and hotspots for CO_2 and N_2O, whereas CH_4emission 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 CO_2 from minerotrophic fen peatland had no change after water table drawdown. In consistent with the results of previous researches (Hou et al., 2013; Maljanen et al., 2001; Regina, Silvola, & Martikainen, 1999), we also found the N_2O 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 N_2, NO and N_2O through microbial processes (Knowles, 1982). N_2 is the end product under anaerobic conditions, while N_2 generally replaced by N_2O 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 CO_2 emissions. However, our results showed that CO_2 emissions first increased and then decreased along the water table gradient. Similarly, Laiho (2006) showed that the short-term water level drawdown increased the CO_2effluxes, but the longterm changes of the water level drawdown induced by the drought caused the reduced CO_2 emission in peatlands soils. Hou et al. (2013) also found that water depth of 5 cm below the ground surface increased soil CO_2 emission of peatlands, but the continued water table drawdown was no significant influenced or even decreased the

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CO_2 emission. Swails et al. (2018) further proved that degradation of soil organic matter quality and nutrients associated with drainage may decrease substrate driven CO_2 production from peat decomposition. Therefore, water table drawdown was expected to increase the CO_2 emissions, but this effect maybe offset by long-term drought.

Influence of temperature on GHG emissions

Our study results consistent with previous studies, which found warming increased CO_2 (Laine, Makiranta, et al., 2019) and N_2O 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 effect of temperature on CO_2, it is now generally accepted that warming can significantly increase CO_2emissions 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 methane emissions from peatlands (Yang et al., 2014). Turetsky et al. (2008) found a positive relationship between warming and CH_4 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, Frolking, & Tuittila, 2019; Pearson et al., 2015). Recenly, many studies have found that warming effect on CH4 emissions varied with the fluction 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 emisssion 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 conditionin 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.

Consisitent with other ecosystems, for example alpine swamp meadow (Chen et al., 2017), high arctic tundra (Lamb et al., 2011) 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, Baggs, Dannenmann, Kiese, and Zechmeister-Boltenstern (2013) reported that denitrification and consequently N_2O emissions have high temperature sensitivity. The emission of N_2O is controlled by of mineral nitrogen availability and influenced by microbial processes of nitrification and denitrification (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 fluction 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 play a key role in the cycle of soil nutrients and elements, and affect the mineralization of soil organic C and N by secreting extracellular enzymes(Chapman, Cadillo-Quiroz, Childers, Turetsky, & Waldrop, 2017; Schnecker et al., 2015). Abatenh, Gizaw, Tsegaye, and Genene (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 response of CO_2, CH_4 and N_2O emissions 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 emission rates 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 emisssions 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 of this study are available 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 - Zoige Plateau, locates at the northeast of Qinghai-Tibet Plateau.

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 differen water table levels. (a) The 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 differeces 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) CO_2 emissions; (b) CH_4 emissions; (c) N_2O 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 soil 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 rate and DOC concentration(a, c, e) and TDN concentration (b, d, f). Grey circle indicates at 8 °C, and red circle indicates at 18 °C.

Figure 7. Spearman's correlation analysis between the dominant microbial phyla and GHG emissions, DOCconcentration 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) CO_2 emissions; (b) CH_4 emissions; (c) N_2O emissions. Standardized path coefficients are listed beside each path (Red and blue arrows indicate 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 ***$p < 0.001$). R^2 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).
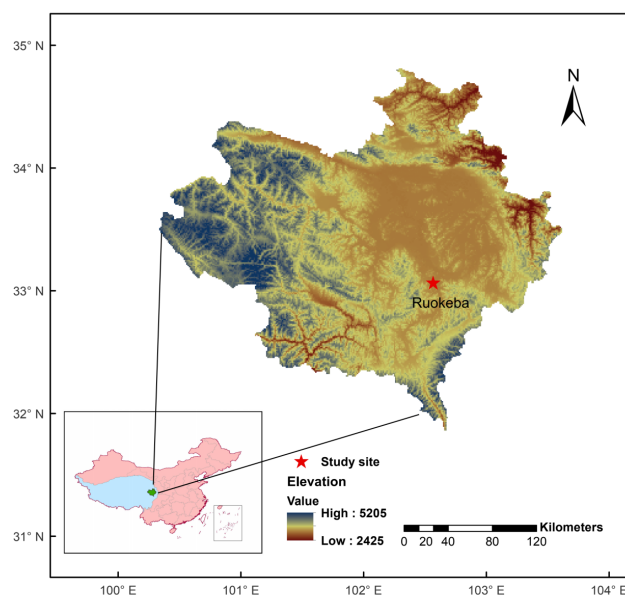
Figure S2. Variation of GHG emission rate of soil from three different water table treatments in short- and long-term drainage peatlands under 8 °C and 18 °C. (a) CO_2 emission rate at 8°C; (b) $CH\sout_4$ emission rate at 8°C; (c) N_2O emission rate at 8°C; (d) CO_2 emission rate at 18°C; (e) CH_4 emission rate at 18°C; (f) N_2O emission rate at 18°C.

Figure S3. Temperature sensitivity (Q_{10}) value variations from three different water table

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treatments in short- and long-term drainage peatlands. (a) CO_2; (b) CH_4; (c) N_2O. 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 ***$p < 0.001$.
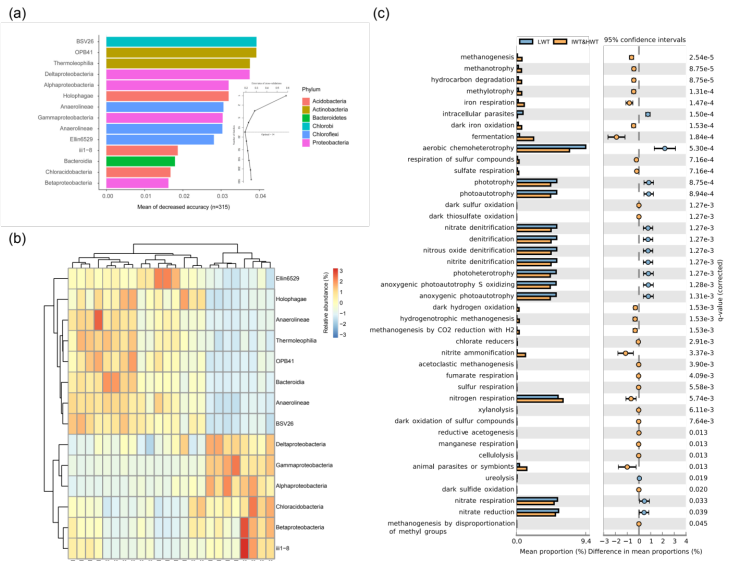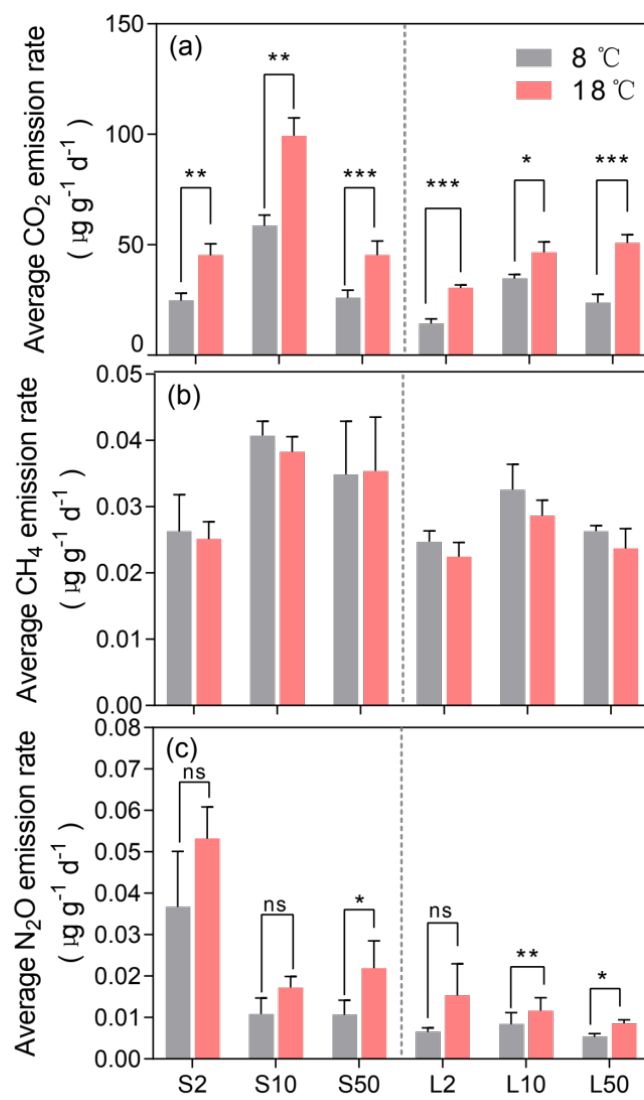
Figure 1

Figure 2

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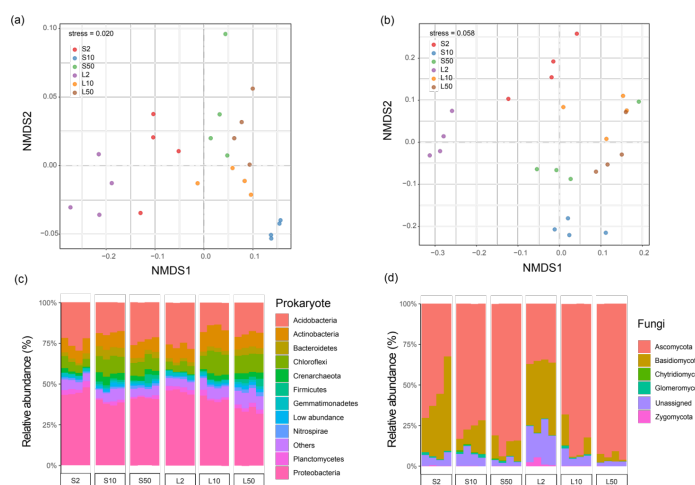
Figure 3

Figure 4

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Figure 6

Figure 7

Figure 8

(a) χ2=16.164, df=19, *P* = 0.646, RMSEA< 0.001 (b) χ2=4.385, df=7, *P* = 0.735, RMSEA< 0.001 (c) χ2=4.671, df=7, *P* = 0.700, RMSEA< 0.001