Variations in the diversity of soil microbial community and structure under various categories of degradation wetland in Sanjiang Plain, northeastern China

Abstract

Sanjiang Plain is the largest area of freshwater wetland in China. Due to agricultural development, a large volume of groundwater in this area has been extracted over the last few decades, resulting in wetland degradation. In order to provide information for the development and protection of wetland ecosystem, investigations examining processes of wetland degradation are important. The aim of this work is to assess the impacts of wetland degradation on the communities of soil microbial community under four different types of degradation wetland including swamp meadow (SW), meadow wetland (MW), paddy farmland (PF), and cropland (CL) in Sanjiang Plain. Using both 16S and ITS rRNA gene amplicon sequencing to evaluate the fungal and bacterial diversity and composition. The dominant fungal phyla and bacterial were Ascomycota and Proteobacteria in this study, respectively. In addition, wetland degradation remarkably augmented the partial affluence of Chloroflexi and Gemmatimonadetes, but the partial affluence of Proteobacteria and Verrucomicrobia significantly diminished. Bacterial Shannon index of SW was lower than those in other sites. While, fungal diversity had no significant differences under different types of degradation wetland. Along with the wetland degradation, such differential reactions of the dominant phyla microbial and diversity were notably coordinated with TP, TK, AK, and SOM, which were the most essential criteria influencing the soil microbial communities. Generally, these outcomes suggested that wetland degradation could result in variations in soil microbial community composition structure. These changes could be used as an early warning signal for the degradation wetland in Sanjiang Plain.

KEYWORDS

wetland degradation, bacterial community, fungal community, soil properties, high-throughput sequencing

1 INTRODUCTION

In general, Wetlands are defined as transitional areas between aquatic ecosystems and land, playing an important role in maintaining biodiversity and ecosystem functions of natural resources (An et al. 2019; Gutknecht et al. 2006b). Recently, 2006, An, Liu et al. 2019). global climate change and human interference have resulted in serious threats to wetland ecosystem stability, resulting in different degrees of destruction, such as serious degradation or a large reduction in area (Khaledian et al. 2017). (Khaledian, Kiani et al. 2017). In the process of wetland degradation, the types and quantities of plants have changed; aboveground plant communities have degraded, litter input has been reduced and mineralization rates of organic matter has increased (Ding et al. 2017; Li et al. 2016). 2016, Ding, Su et al. 2017).

Soil microbes are one of the most active fractions in the soil and play an important role in wetland soil ecosystems. Soil bacteria are essential in ecological processes, such as regulating soil structure, nutrient circulation pollutant removal and soil formation, providing feedback to the whole ecosystem function (Van der Heijden et al. 2015; DeLaune et al. 2008). In particular, soil bacteria play an important role in material transformation and energy flow in wetland ecosystems, restricting differentiation and succession of wetland types (Ding et al. 2017). Environmental observations indicate that the diversity of soil bacterial is mainly influenced through the soil variety, vegetation, pH, latitude, humidity, nutrient effectiveness, and temperature (Bárcenas-Moreno et al. 2009; Fierer & Jackson 2006; Hu et al. 2014; Lauber et al. 2009). According to the aforementioned criteria, soil species has a potent impact on the diversity of soil bacteria as well as composition (Lundberg et al. 2012). Based on the last investigations, it was found that the structure and abundance of the microbial communities in a soil are very sensitive to environmental changes (Argiroff et al. 2016; Arroyo et al. 2014; Moche et al. 2015; Wu et al. 2015; Zhou et al. 2018). Wetland degradation could result in large-scale and durable modifications in the structure of soil and microbial performances (Wen Y et al. 2019). The impact of changes in moisture status, vegetation type and soil nutrient content in a wetland can therefore be used as a predictor of wetland degradation (Urakawa & Bernhard 2017; Wu et al. 2016). Changes in soil nutrient conditions caused by wetland degradation in Sanjiang Plain might lead to modifications within the structure and composition of the microbial assemblies, resulting in ecosystem alternations which could be

used as early warning signals for soil degradation. It is therefore important to examine changes in wetland soil microbial communities and their role in wetland degradation for managing wetlands and evaluating their health status.

Sanjiang Plain is the largest and most concentrated area of marsh in China, having a high level of sensitivity to global climate change and human interference. This area has been affected by increasing population growth and agricultural activities under the influence of human activities and economic development since the 1950s when land reclamation was initiated, resulting in a reverse succession from meadow wetland to degraded meadow. From the ending years of the last century, the area of wetlands in this region has decreased sharply, and the area of meadow and cultivated land has increased. Although a series of wetland restoration policies were initiated such as reverting cultivated land to wetland, resulting in an improvement of the wetland area, ecosystems are still degraded due to low vegetation coverage, declining biodiversity and soil erosion.

In order to further understand the impact of wetland degradation processes in Sanjiang Plain, the microbial community composition and distribution in different styles of degradation wetland were analyzed, including swamp meadow (SW), meadow wetland (MW), paddy farmland (PF) and cropland (CL). The following hypotheses were examined in this study: (i) elucidate how microbial community structure (for both bacteria and fungi) shift during different types of degradation wetlands; (ii) the fungi variety and soil bacteria exhibited various dynamic patterns within the different degradation types of wetlands; and (iii) determine which factors are closely attributed to the modifications in the structure of
microbial assembly.

The overall aim of the current research is to determine the change of soil microbial and soil features in Sanjiang Plain during wetland degradation. Understanding the change characteristics of soil microbial communities under degradation processes will represent a scientific data for the control of wetland degradation and the improvement of wetland productivity.

2 MATERIALS AND METHODS

2.1 Site information

The investigation area was undertaken within the ecological positioning research station (47°35'N, 133°31'E), located in the Institute of Natural and Ecological Research of Heilongjiang Academy of Sciences in the research area. This area is located in a temperate humid climate zone, characterized by temperate monsoon climate features. The study area has an altitude range of 55-65 m and an average temperature of 1.9 °C. Average minimum and maximum temperatures occur in January (-20.4 °C) and July (21.6 °C), respectively. The Average of annual precipitation is 566 mm, with more than 60 % of precipitation occurring in July and August. Prior to the selection of the plot, we thoroughly evaluated the soil and vegetation to certify the comparability among selected plots (Yang et al. 2018). We also investigated the history through literatures and local residents (Wei et al. 2019). The last researches illuminated that the natural succession path of wetland degradation in our study area was to meadow wetland and farmland (Sun et al. 2019). Currently, a series of plots located in the positioning research station were selected included swamp meadow (SW), meadow wetland (MW), paddy field (PF) and cropland (CL). Soil texture in the four degradation statuses are swamp peat soil, meadow swamp soil, paddy soil and corn soil, respectively. SW is dominated by *Carex pseudoconica* and *Calamagrostis angustifolia*, while MW is dominated by *C. angustifolia*. PF and CL were taken from the respective surrounding farmlands that had been planted with rice and corn.

2.2 Sample collection

Three soil cores per degradation status, situated at least 50 m apart, were collected using a soil drill with a diameter of 8 cm in May 2019. In all plots, five specimens were uniformly piled up at a depth of 0–10 cm, with a soil auger and blended to create a composite specimen of bulk soil, which resulted in a total of 12 specimens. Roots and other plant tissue residues were eliminated before blending; specimens were kept at -20 °C in an ice box before being transported to the laboratory. Samples were then divided into two fractions: one fraction was kept at 4 °C for investigation of soil physical and chemical properties; the other fraction was stored at -20 °C and used for molecular biological analysis.

2.3 The determination of soil properties

Soil organic matter (SOM, g kg^{-1}) was calculated by utilizing the potassium chromate-external heating approach (Lu. 1999). Moisture content (MC) was ascertained *via* drying in the soil ambient for 48 h at 105 °C until a constant weight was recorded (Li et al. 2015). Soil pH was assessed in a 1:2.5 soil-water suspension by implementing a pH meter (ST2100, Ohrus, Jiangsu, China). Total nitrogen (TN g kg^{-1}) was evaluated using the Kjeldahl nitrogen determination approach (8420, FOSS Analytical Corporation, Denmark) (Rayment et al. 1992); Total phosphorus (TP g kg^{-1}) was measured using the H_2SO_4-$HClO_4$ solution and measured by a spectrophotometer (7200, UNICO, Wisconsin, USA) (Adeloju et al. 1984). Total K (TK g kg^{-1}) was measured *via* Na_2CO_3 extraction and determined with an atomic absorption spectrometer (IRIS Advantage-ER, Thermo Jarrell Ash Corporation) (Jackson. 1958). Available nitrogen (AN g kg^{-1}) was extracted by utilizing KCl and measured calorimetrically in the extracts of soil (8420, FOSS Analytical Corporation, Denmark) (Bao. 2000); Available phosphorus (AP g kg^{-1}) was evaluated through NaHCO3 Extraction-Mo-Sb colorimetry (Cary60, Aglilent Technologies Inc.) (Qing et al. 2018); Available K (AK g kg^{-1}) was assessed *via* flame photometry (IRIS Advantage-ER, Thermo Jarrell Ash Corporation) (Mehlich. 1984).

2.4 Soil DNA extraction and amplification sequencing

The samples of DNA were extracted from 0.5 g of each sample with the Kit of FastDNA SPIN for Soil (MP Biomedicals, Santa Ana, California), conforming to the instruction manufacturer. The region of 16S rRNA V3-V4 was reinforced for each specimen by utilizing primer sets of 338Fand 806R (Xu et al. 2016), the Internal Transcribed spacer (ITS) primers region of gene (ITS1F-ITS2F) (Caban et al. 2018; Nottingham et al. 2018). The PCR components contained 25 μl of 5 μl of 5× Q5 buffer of reaction, 5 μl of 5× Q5 High-Fidelity GC buffer, 0.25 μl of Q5 High-Fidelity DNA Polymerase (5U/μl), 1 μl (10 uM) of each Ahead and Reverse primer, 2 μl (2.5 mM) of dNTPs, 2 μl of DNA Template, and 8.75 μl of ddH_2O. The cycle of thermal performance was comprised of elemental denaturation for 2 min at 98 °C, succeeded *via* 25 cycles comprised of denaturation for 15 s at 98 °C, annealing for 30 s at 55 °C, and extension for 30 s at 72 °C, with an ultimate extension of 5 min at 72 °C.

The purification of PCR amplicons was carried out with Agencourt AMPure Beads (Beckman Coulter, Indianapolis, IN) and measured by utilizing a PicoGreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). Following the step of individual quantification, amplicons were pooled in even amounts, and pair-end 2×300 bp sequencing was applied through the platform of Illlumina MiSeq. The sequences data in a raw form was operated in QIIME 2 2019.4 (Bolyen et al. 2018). In brief, the sequence data in a raw form were demultiplexed utilizing the demux plugin succeeded through primers cutting with cutadapt plugin (Martin M. 2011). Furthermore, sequences were quality filtered, denoised, merged and chimera eliminated by utilizing the DADA2 plugin (Callahan et al. 2016). Non-singleton amplicon sequence variants (ASVs) were aligned with mafft (Katoh et al. 2002) and used to construct a phylogeny with fasttree 2 (Price et al. 2010). Raw sequence data were then submitted to the NCBI Sequence Read Archive (https://www.ncbi.nlm.nih.gov/sra/) with the accession number: PRJNA661140.

2.5 Statistical analyses

The physiochemical characteristics of soil as well as the diversity of soil microbial community were measured for differences among degraded wetlands by utilizing one-way Analysis of variance (ANOVA) in SPSS 20.0 (IBM SPSS Inc., USA). The relevance between dominant microbial and physiochemical features were investigated by implementing Spearman's rank correlation and visualized using R (v3.2.0) and also the package of "corrplot". Principal coordinate analysis (PCoA) was performed in line with a Bray–Curtis distance matrix in R software using the "ape" package. QIIME 2 computer program was utilized to carry out the unweighted paired group arithmetic (UPGMA) clustering analysis to study the resemblance of the communities of soil microbial and visualized by implementing Mega7 program. Heatmap illustration of the partial affluence of microbial OTUs among specimens was constructed applying R. Soil physicochemical properties and also microbial total affluence and variety were compared by implementing LSD experiments. Redundancy analysis (RDA) was performed using CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA) to observe the impact of soil physiochemical properties on dominant microbial communities. The selection principle of the RDA or CCA model was conforming to DCA (Detrended Correspondence Analysis) utilizing R, and the magnitude of the variables of explanatory was

measured against 499 Monte Carlo permutations. The contribution of all environmental criteria to the fungal and bacterial community was appraised through Variance Partitioning Analysis (VPA) by utilizing R with the package of "vegan".

3 RESULTS

3.1 Soil features under various types of degradation wetland

The nutrient conditions and moisture content, including 9 soil features, exhibited considerable differences among SW, MW, PF and CL. Moisture content in site SW was highest with 58%. Compared to MW and PF, CL could dramatically increase moisture content (P<0.01). It was slightly acidic in Sanjiang Plain, the increase pH values in farmland (PF and CL). In terms of SOM, TN, TP, AN and AP, all of them were the highest in SW, followed by MW, PF and CL. Further, MW is able to diminish TK and AK concentrations compared to SW, PF and CL (Figure 1).

3.2 Changes in soil microbial community distribution and composition

Eventually, a set of 11 fungal phyla and 40 bacterial phyla were achieved across all specimens. Composition results of the bacterial community at the level of phylum (relative abundance >1%; Fig. 2a) indicate that the most dominant phylum within the assembly of soil bacterial was Proteobacteria, succeeded *via* Acidobacteria, Actinobacteria, Chloroflexi, Gemmatimonadetes, Bacteroidete, Verrucomicrobia, Rokubacteria, Planctomycetes and Nitrospirae, covering 49.57, 42.08, 26.14 and 32.77% in SW, MW, PF and CL, respectively. Any statistically remarkable changes of Actinobacteria, Bacteroidete and Planctomycetes were found among treatments. SW hold the highest relative abundances of Proteobacteria and Verrucomicrobia with 49.57, 8.40%, respectively. Ascomycota, Basidiomycota and Mortierellomycota were found as the predominant gungal phyla, covering 67.66, 21.94, 3.36% in SW, MW, PF and CL, respectively (relative abundance >1%; Fig. 2b). No substantial changes were observed in Mortierellomycota among four positions. SW hold the highest relatively abundances of Ascomycota with 88.99%, while the lowest Basidiomycota with 0.77% (Figure 2b).

A number of 964 soil bacterial and 439 fungal genera were represented in all specimens, among which, 14 bacterial genera (*Subgroup_6*, *Pelomonas*, *RB41*, *Sphingomonas*, *KD4-96*, *Rokubacteriales*, *Candidatus_Udaeobacter*, *Gemmatimonas*, *MND*1, *TRA3-20*, *Subgroup_2*, *Nitrospira*, *Haliangium*, *Bryobacter*) (Figure S1) and 16 fungal genara (*Russula, Plectosphaerella, Tausonia, Hydnum, Mortierella, Humicola, Acremonium, Acaulium, Cortinarius, Tetracladium, Fusarium, Nectria, Cladorrhinum, Staphylotrichum, Lecanicillium, Elaphomyces*) more than 1%. Differences in relative abundance for the first 50 bacteria and fungi genera in all soil samples were analyzed using thermographic analysis (Figure S1). In different types of degradation wetland, the distribution of bacterial communities also significantly differed. The most representative bacteria were *Subgroup_6* and *Pelomonas* having average values of 1.38%, 6.78%, 15.18% and 1.53, and 13.89%, 13.70%, 0.00% and 0.10% for SW, MM, PF and CL, respectively. While, the representative fungi were *Humicola* with 12.39, 0.12, 0.19 and 0.08% in four sites. Our results indicate that significant differences were presented in the distribution and partial affluence of soil bacteria and fungi within various types of degradation wetland.

The outcomes of the plots of clustering heatmap related to the soil fungi and bacteria at level the of genus illustrated that composition of soil microbial community exhibited noticeably diverse and can be separated into two clusters, containing SW and MW, PF plus CL. Whilst the structure of soil fungal community was clustered into two groups, containing MW and SW, PF plus CL, denoting that the composition of soil microbial community from PF and CL displayed greater correspondence than those of MW and SW (Figure S2).

Biomarker with a statistically significant difference was further sought from different treatments and classification levels using Line Discriminant Analysis (LDA) Effect Size (LEfSe). LDA of 100 bacterial branches in different types of degradation wetland recorded obvious differences under the threshold >4.0. Biomarker was affiliated to Gemmatimonadetes, Latescibacteria, Nitrospirae, Proteobacteria, Rokubacteria, Verrucomicrobia, Acidobacteria at the phylum level (Figure 3a). In addition, the plot of cladogram founded on LEfSe with the threshold of 4.0 indicated that Biomarker was affiliated to Ascomycota and Basidiomycota at the phylum level (Figure 3b).

Modifications in soil bacterial community richness and diversity

The fungal and bacterial abundance tended to increase with degradation in the different types of degradation wetlands (Figure 4). The bacterial Shannon diversity index results in different types of degradation wetlands significantly differed (P<0.05) but Chao1 index showed no significant differences among different treatments. Using Alpha diversity analysis indicators, the Shannon index of SW was significantly lower than that of MW, PF and CL (Figure 4a). Regarding the fungal community, with no significant differences among four treatments (Figure 4b). According to the PCoA, we found that both the fungal and bacterial communities showed significant differences among the four degradation wetlands in bray-curtis distance (Figure 5a), suggesting that PF and CL were more similar to each other in bacteria composition than they were to SW and MW. For fungi, SW site was distant from MW, PF and CL (Figure 5b). Similar results were also recorded in the UPGMA-based cluster map (Figure S3)

Correlation between the diversity of microbial community soil properties is given in Table 1. pH value of the Soil had a notable positive effect on the diversity of soil bacterial community (P<0.05), and the index of Shannon related to the soil bacteria considerably decreased with an increase in SOM, TN, TP, AN and AP (P<0.01). By contrast, as the values of TK and AK increased, the Shannon index showed a downward trend. At the same time, AN had a negative impact on the soil fungal Chao 1 index (P<0.05).

Correlations between soil characteristics and soil bacterial communities

Redundancy analysis (RDA) indicates that the soil microbial classification unit has different responses to soil properties in phylum level (Figure 6). For bacterial communities, the first two main components explained 73.28% of total variation (Figure 6a); the first RDA axis had a higher variation value (50.39%) and the second axis had a lower variation value (22.89%). The contribution of soil properties to bacterial community variation was analyzed using variance partition analysis (VPA), results of which indicated that the TP value could explain the high variability of 41.6%, while TK, AK and SOM content could explain the low variability of 22.4%, 7.20% and 7.00%, respectively (Figure 7a). Concerning the communities of fungal, the first and second RDA axis respectively defined 61.81% and 22.37% of the total variation (Figure 6b). VPA showed that TK value could explain the high variability of 38.6% (Figure 7b).

Additionally, the relationship between the affluence of the dominant bacteria and environmental variables at the phylum stage (Table 2) was also examined. Proteobacteria had a positive effect on MC, SOM, TN, TP, AN and AP (P<0.05), although had a negative impact on pH (P<0.05); pH had a significant positive effect on Actinobacteria and Bacteroidetes (P<0.01). Chloroflexi (P<0.05). The partial affluence of Gemmatimonadetes and Bacteroidetes was negatively corresponded with SOM, TN, TP, AN and AP (P<0.01). Chloroflexi and Nitrospirae was considerably negative corresponded with MC and TK (P<0.05). TK had positive association with Ascomycota (P<0.05), however, AK exhibited negative relevance with the partial affluence of Basidiomycota (P<0.05). Fungal and bacterial communities from various types of degradation wetlands displayed clustering patterns, showing notable changes in the composition of microbial community among SW, MW, PF and CL.

4 Discussion

4.1 The response of soil characteristics to different wetland degradation levels

The varying degrees of degradation in Sanjiang Plain wetland provide a model for assessing degradation processes which simultaneously affect the physiochemical characteristics of the soil, as well as the soil bacterial community. Soil nutrients, important factors that affect the structure and growth of plant communities in wetland ecosystems, are reduced with wetland degradation (Zhang et al. 2019); wetland degradation also has a significant impact on physicochemical properties. In our study, SW recorded higher values for MC, the results are in accordance with previous findings (Xu et al. 2017), indicating more favorable soil nutrient conditions in undisturbed areas in Sanjiang Plain (Figure 1). In particular, SOM、TN、TP、AN and AP significantly decreased with wetland degradation, providing effective indicators for assessing wetland degradation. Compared with the other three degradation stages, soil physicochemical indices of natural wetland soil were higher due to soil degradation inhibiting plant growth by affecting nutrient circulation, thus hindering the development and stability of wetland communities. As the main feature of the wetland (Tian

1998), MC plays an important role in wetland restoration. Our research indicate that soil moisture content decreased with wetland degradation, a change associated to aggravation of wetland degradation, which is in a good agreement with the outcomes of a research in Sanjiang Plain (Wei et al. 2019). Here, wetland plant species indispensable for formation of swamp soil are replaced through the vegetation of meadow and the ventilation and water permeability of the wetland soil are reduced, resulting in a weakening of the soil water conservation function (Xu et al. 2017). Most nutrient elements also exchange with soil moisture content, ventilation conditions and redox potentials also shift; thus, the community structure and composition of soil microbial also changed accordingly (Ma et al. 2018). Our analyses of soil properties indicated that soils were slightly acidicin in Sanjiang Wetland (Yun et al. 2015), this is similar to our results. Soil pH was the main driving parameter for the development of the soil bacteria community, both on tiny and large scales (Rousk et al. 2010). Similarity to previous findings (Wu et al. 2017), our results indicated that pH decreased with wetland degradation. Synchronous changes of SOM, TN, TP, AN and AP with wetland degradation were observed in this study, Moges et al (2008) had also made similar trends under soil degradation. SOM of natural wetland is higher than that of the degraded wetland, probably because MC of the wetland changes the aerobic/anaerobic media of the soil, reducing the process of mineralization of organic matter, and thus limiting the decomposition of the SOM in different degradation stages of the wetland (Houghton et al. 1999). Previous studies have shown that a close relationship exists between SOM and other soil nutrients (Ahc et al. 2009). As the aggravation of degradation degree, significant SOM loss due to the erosion, lack of root C input, decomposition rate of organic substance in soil increases (Arroyo et al. 2014). High moisture content in natural wetlands forms an aerobic/anaerobic environment which limits the nitrification of bacteria, improves the fixation of N and enables the accumulation of N in the soil (Krause et al. 2013). Despite the use of nitrogen fertilizer in PF and CL, but the accumulation of N is a biological procedure containing a group of complex reactions between microorganisms and plants rather than simple accumulation (Binkley, 2005). In SW site, TP and AP were higher than those in MW, PF and CL, the same outcomes also realized in other researchers (Ducey et al. 2015). In our study TK and AK results indicated the highest value in SW, followed by PF and CL, and lowest in MW site. wetland degradation in this study. This suggest that SOM, TN, TP, AN and AP could be impacted with alike soil environmental modifications (Wang et al. 2002), therefore might be the cause N, P demonstrated closed relation to SOM in the present investigation. Potassium in wetland soil is mainly derived from the accumulation of available nutrients, depending on the accumulation of wetland plant absorption and plant residue death (Olde Venterink et al. 2002). In constrast, the increase TK and AK in PF and CL could be mostly ascribed to the nutrient load from K fertilization through the agricultural agronomy, these results correspond to the report of Lu et al. (2019). Briefly, our outcomes showed that wetland degradation affects soil nutrient circumstances in Sanjiang plain.

4.2 The response of soil microbial communities to different types of degradation wetland

The communities of soil microbial perform a vital task in the circulation of material and energy flow of the soil system, directly or indirectly affecting the healthy development of the wetland ecosystem (Falkowski & Jelen 2013). The diversity index of the soil bacterial community showed that the Shannon index in SW was significantly lower than those in other degraded wetlands. In addition, the diversity of soil fungal community (Chao1 and Shannon index) had no significant differences among four sites (Figure 4). Our observations might be due to their hydrologic environment, which the dry site might had consistently higher diversity (Ahn et al. 2009). Identical to the achieved data, the community of soil bacterial enhanced markly within degradation wetland (Zhang et al. 2008, Lu et al. 2019). Peralta et al. (2013) recorded a lower Shannon index in undegraded wetland that may be related to the acidic nature of the soil. Although, the last investigation had realized that a higher diversity of bacterial communities was detected on undegraded wetland in comparison with degraded sites (Zhou et al. 2018). The contradictions in the results of these researches could be occurred through the sort of degradation time as well as dominant vegetation. According to the aforementioned discussions, the diversity of soil microbial community could be an essential indicator in the procedure of ecological soil degradation. In addition, results from PCoA and cluster studies indicate that the clearly difference in the composition of fungal communities and soil bacterial among various sites and the distances in physiological properties between PF and CL were partially near (Figure 5). Meanwhile, the clustering plots of heatmap related to the fungi and bacterial exhibited the identical patterns (Figure S2), that is alike to the last studies (Gu et al. 2018). However, we further found that the communities of soil fungal and bacterial separated along the water gradient, which is similar to the study of Poyang Lake (Chen et al. 2019) and proved our hypothesis to some content.

Dominant bacterial groups at the phylum level included Proteobacteria, Acidobacteria, Actinobacteria, Chloroflexi, Gemmatimonadetes, etc. (Figure 2a), indicating that these soil bacterial communities have high adaptability and play an important role in these ecosystems. Similar results have also been recorded in other wetlands (Ahn et al. 2007; Gorra et al. 2007). In the

present research, Proteobacteria was the main phylum, that is widespread in various ecosystems and involved in many biogeochemical processes (Zhang & Xu 2008). This phylum is able to perform a major task in systemic development, ecological processes, and take part in the energy metabolism, in cluding the oxidation of organic/inorganic complexes as well as the acquisition of energy from light (Mukhopadhya et al. 2012). Proteobacteria can stimulate the increase of nutrition in the environment (Fierer et al. 2007). This factor also explains why Proteobacteria was more affluent in natural swamp soil, having greater organic substance contents (Röske et al. 2012). In the process of organic matter decomposition and nutrition cycling, Acidobacteria in degradation wetland was higher than in nature wetland (Eichorst et al. 2018), that is correspond to our results which indicate that the relative abundance of Acidobacteria and in PF, CL and MW was higher than that in SW. To the best of our knowledge, Acidobacteria also contain a large number of oligotrophs. In degraded wetland soil with low organic matter content, the relative abundance of Acidobacteria was relatively high (Peralta et al. 2013), possibly being beneficial for the growth of oligotrophs. These results indicated that microorganisms with nutritional degradation functions and high metabolic activities may successfully survive in degraded wetlands. In addition, the relative abundance of Chloroflexi and Gemmatimonadetes in SW is lower than that in other sites. Chloroflexi was found to survive on nutrient poor conditions. Previous work also documented Chloroflexi were less abundant under nutrient limitation (Hug et al. 2013) and last report has confirmed that Gemmatimonadetes possibly associated to the oligotrophic situations owing to the independence on nutrients (Zheng et al. 2016).

Literally, the composition and predominance of soil fungi varied among SW, MW, PF and CL. with different types of degradation wetlands. Ascomycota, Basidiomycota and Mortierellomycota were found as the predominant fungal phyla in four positions, which was in accordance with the findings discovered in Sanjiang plain (Wei et al. 2019) and in the degradation alpine meadow (Li et al. 2016). Ascomycota was known as the most abundant group in the fungal kingdom detected in soil all over the world (Al-Sadi et al. 2017). The phylum Basidiomycota is the second most affluent class which have ability to restrict mainly the decomposition of lignin (Floudas et al. 2012). In site SW, the partial affluence of Basidiomycota is the lowest compared with others. This could be ascribed to the fact that soil aeration improved and decomposed rapidly, which prompted amount of Basidiomycota proliferated (Heinemeyer et al. 2004). In terms of genus level species, the relative abundance of common genera in the wetland varied with degraded types, indicating that the soil bacteria and fungi with special functions could survive in wetland with different degradation types. Therefore, wetland degradation results in structure and composition modifications related to the communities of the soil microbial, which could be supported from PCoA results (Figure 5).

Overall, the distribution patterns of different bacteria and fungi groups reflect their ecological niche throughout the process of wetland degradation, and nutrition condition, moisture circumstances as well as other possible environmental parameters might contribute to partial abundance (Gu et al. 2018). These findings are important for the restoration and sustainable stability of wetlands. For a deeper comprehension of the micro-process mechanism of ecological progression, further analysis on functional genes needs to be undertaken.

4.3 Criteria influencing on soil bacterial communities under various categories of degradation wetland

It has been reported that soil physical and chemical properties are important driving factors of microbial communities (Leff et al. 2015; Song et al. 2020). With wetland degradation, the accumulation of soil MC, pH significantly changed (Figure 1), having a noticeable impact on soil microbial community diversity (Table 1). In addition, soil microbial community diversity also affected soil biogeochemical processes, the complexity of interactions, versatility and sustainability, thus affecting soil quality (Jansson & Hofmockel 2018; Wagg et al. 2014). Therefore, soil microbial diversity is an important factor in the maintenance of ecological function.

In the present investigation, soil bacterial diversity was considerably positively corresponded with pH (Table 1), similar to findings from previous investigations (Lauber et al. 2008). As an example, most researches proposed that pH was shown as the main indicator impacting the soil bacterial community (Hartman et al. 2008, Rousk et al. 2010). While no significant correlations were found in some research (Beales et al. 2004), this might be caused by the adaptability and sustainability of bacterial community to particular medium correlated with the Shannon and Chao 1 index, consistent with previously report (Yu et al. 2019; Lu et al. 2019;). Although soil organic matter is an important carbon source for soil bacteria, our findings indicate that Alpha diversity of soil bacteria was lowest in swamp wetlands with a higher organic matter content, a finding that is contrary to previous results (Yuan et al. 2016). This difference may be related to the accumulation of perennial water in the wetland swamp, poor soil aeration resulting from a high moisture content, and limited growth and propagation of aerobic bacterial, thus affecting the variety of soil bacterial assemblies. It should be stated that the large number of investigations have demonstrated the correspondences between soil

parameters and the diversity of fungal community, including AK (Guan et al. 2020), P content (Burke et al. 2019) and MC (Yu et al., 2019). But no similar results were found in our research.

The communities of soil microbial are impacted *via* the interaction of herb species and soil characteristics, and environmental factors perform an essential task in the composition of structure formation of soil bacterial communities (Freedman & Zak 2015). Results from our investigation indicate that the structure of a community of soil microbial was impacted *via* the variety of environmental criteria rather than single criterion (Zong & Shi 2020). Based on the VPA results, our results illustrated that TP, TK, AK and SOM were found to be driving factors of soil bacterial communities (Figure 7a). Additional research indicated that change in bacterial communities corresponds to a change in relative abundance of major groups (Zeng et al. 2017) and soil nutrients contribute to the selection and development of soil bacterial assemblies (Carey et al. 2015; Peralta et al. 2013). However, these findings are contrary to previous studies recording pH to be the best predictor of bacterial communities (Fierer & Jackson 2006), which was not consistent with present study. At the phylum level, Proteobacteria is the most important bacterial group in wetland ecosystems (An et al. 2019), which was completely consistent with our study and the 2019). correlation between soil microbial assemblies and soil features in different soil systems are different. Results from our study also recorded a negative correlation between Proteobacteria and pH (Table 2) , but positively corresponded with the partial affluence of Acidobacteria, similar to last results (Yu et al. 2019; Yin et al. 2020). Soil pH is the key soil physical and chemical property that affects the partial affluence of Acidobacteria (Lammel et al. 2018). Bacteroidetes affected strongly by C mineralization in terrestrial habitats (Fierer et al. 2007), thus, the partial abundance of Bacteroidetes are positively related with SOM in our study (Table 2). In contrast, we made an outcome that he partial abundance of Actinobacteria decreased with TN. Previous study found that Actinobacteria are considered as oligotrophs and tend to be associated with limited conditions (Fierer et al. 2007), which was consistent present study. Collectively, these results suggest that undegradation wetland in comparison with the degradation wetland ameliorates the levels of soil nutrient, consequently influencing on the classes of functional bacterial.

Regarding the fungal communities, RDA results suggest that TK was the predominant decisive parameters (Figure 6b), which was not completely similar with the last investigations (Lauber et al. 2008, Wei et al. 2019). The spearman studies illuminated that the relative abundance of Basidiomycota exhibited a more potent negatively correlation with TK and AK, while played notably positively impacts on Ascomycota (Table 2), these were not in accordance with previous studies (Ding et al. 2018). It is widely recognized that the climatic factors (MAP and MAT) could be the predominant aspects impacting the fungal communities (Ren et al. 2017), these contradictions might be due to the differences in the experimental sites, sampling times and climatic conditions. Concertedly, the obtained results propose that wetland degradation has significant impacts on bacterial community whilst negligible impacts on fungal community composition, soil nutrient condition exhibit essential shifts in the diversity and structure of fungal and bacterial community in this study.

5 Conclusions

Generally, the present research concentrated on the distribution pattern of the soil fungal and bacterial community under various types of degraded wetland in Sanjiang Plain and improve our knowledge of soil microbial diversity in alpine wetlands. Wetland degradation could reduce soil nutrients. SW harbored the lowest soil bacterial Shannon index. The dominant fungal and bacteria phyla were Proteobacteria as well as Ascomycota in our study positions. In particular, wetland degradation could significantly increase the partial affluences of Proteobacteria and Verrucomicrobia, whilst reduce the partial affluences of Chloroflexi and Gemmatimonadetes. Additionally, wetland degradation had significantly negative total influences on the relative abundance of Ascomycota, while positive effect on the relative abundance of Basidiomycota. Furthermore, wetland degradation directly or indirectly modified the soil medium, leading in considerable alternations in soil features, which drive changes in microbial community. TP, TK, AK and SOM were the most essential criteria influencing on the communities of bacterial soil, while TK was the dominant factor of soil fungal communities. Overall, our finding indicates that the collaborative development of relevance between the community of soil microbial and conditions, which results in the variation in soil microbial community in the process of wetland degradation in Sanjiang Plain.

ACKNOWLEDGMENTS

We would first like to thank referees for valuable comments on the manuscript. This work was funded by Outstanding youth fund of Heilongjiang academy of sciences (CXJQ2020ZR01, CXJQ2020ZR02). We really thank Melissa Dawes for language editing for this paper and also thank MogoEdit (www.mogoedit.com) for its linguistic assistance during the preparation of this manuscript.

DATA AVAILABILITY STATEMENT

All data included in this study are available upon request by contact with the corresponding author.

REFERENCES

Adeloju, S., Bond, A., & Briggs, M. (1984). Critical evaluation of some wet digestion methods for the stripping voltammetric determination of selenium in biological materials. Analytical Chemistry, *56*, 2397-2401. https://doi.org/10.1021/ac00277a031

Ahn, C., Gillevet, P., & Sikaroodi, M. (2007). Molecular characterization of microbial communities in treatment microcosm wetlands as influenced by macrophytes and phosphorus loading. Ecological Indicators, *7*, 852-863. https://doi.org/10.1016/j.ecolind.2006.10.004

Ahn, C., & Peralta, R. (2009). Soil bacterial community structure and physicochemical properties in mitigation wetlands created in the piedmont region of virginia (USA). Ecological Engineering, *35*, 1036-1042. https://doi.org/10.1016/j.ecoleng.2009.03.005

Al-Sadi, A., Al-Khatri, B., Nasehi, A., Al-Shihi, M., Al-Mahmooli, I., & Maharachchikumbura, S. (2017). High fungal diversity and dominance by ascomycota in dam reservoir soils of arid climates. International Journal of Agriculture and Biology, *19*. https://doi.org/10.17957/IJAB/15.0328

Argiroff, W., Zak, D., Lanser, C., & Wiley, M. (2016). Microbial community functional potential and composition are shaped by hydrologic connectivity in riverine floodplain soils. Microbial Ecology, *73*. https://doi.org/10.1007/s00248-016-0883-9

Arroyo, P., Sáenz de Miera, L. E., & Ansola, G. (2015). Influence of environmental variables on the structure and composition of soil bacterial communities in natural and constructed wetlands. Science of the Total Environment, *506-507C*, 380-390. https://doi.org/10.1016/j.scitotenv.2014.11.039

Bao, S. D. (2000). *Soil and agricultural chemistry analysis*. Beijing, China: China Agriculture Press.

Bárcenas-Moreno, G., Gómez-Brandón, M., Rousk, J., & BÅÅTh, E. (2009). Adaptation of soil microbial communities to temperature: Comparison of fungi and bacteria in a laboratory experiment. Global Change Biology, *15*, 2950-2957. https://doi.org/10.1111/j.1365-2486.2009.01882.x

Beales, N. (2004). Adaptation of microorganisms to cold temperatures, weak acid preservatives, low ph, and osmotic stress: A review. Comprehensive Reviews in Food Science and Food Safety, *3*, 1-20. https://doi.org/10.1111/j.1541-4337.2004.tb00057.x

Binkley, D. (2005). *How nitrogen-fixing trees change soil carbon.* Paper presented at the Tree Species Effects on Soils: Implications for Global Change, Dordrecht.

Bolyen, E., Rideout, J. R., Dillon, M., Bokulich, N., Abnet, C., Al-Ghalith, G., . . . Chase, J. (2018). Qiime 2: Reproducible, interactive, scalable, and extensible microbiome data science. Nature Biotechnology, *37*, 852-857. https://doi.org/10.7287/peerj.preprints.27295

Burke, D., Carrino-Kyker, S., & Burns, J. (2019). Is it climate or chemistry? Soil fungal communities respond to soil nutrients in a multi-year high-resolution analysis. Ecosphere, *10*. https://doi.org/10.1002/ecs2.2896

Caban, J., Kuppusamy, S., Kim, J., Yoon, Y., Kim, S., & Lee, S. S. (2018). Green manure amendment enhances microbial activity and diversity in antibiotic-contaminated soil. Applied Soil Ecology, *129*. https://doi.org/10.1016/j.apsoil.2018.04.013

Callahan, B., McMurdie, P., Rosen, M., Han, A., Johnson, A. J., & Holmes, S. (2016). Dada2: High-resolution sample inference from illumina amplicon data. Nature Methods, *13*. https://doi.org/10.1038/nmeth.3869

Carey, C., Beman, M., Eviner, V., Malmstrom, C., & Hart, S. (2015). Soil microbial community structure is unaltered by plant invasion, vegetation clipping, and nitrogen fertilization in experimental semi-arid grasslands. Frontiers in Microbiology, *6*, 466. https://doi.org/10.3389/fmicb.2015.00466

Chen, M., He, S., Li, J., Hu, W., Ma, Y., Wu, L., & Gang, G. (2019). Co-occurrence patterns between bacterial and fungal communities in response to a vegetation gradient in a freshwater wetland. Canadian Journal of Microbiology, *65*, 1-16. https://doi.org/10.1139/cjm-2019-0147

Ding, H., Ali, A., & Cheng, Z. (2018). Dynamics of a soil fungal community in a three-year green garlic/cucumber crop rotation system in northwest china. Sustainability, *10*, 1391. https://doi.org/10.3390/su10051391

Ding, L.-J., Su, J. Q., Li, H., Zhu, Y., & Cao, Z.-H. (2017). Bacterial succession along a long-term chronosequence of paddy soil in the yangtze river delta, china. Soil Biology and Biochemistry, *104*. https://doi.org/10.1016/j.soilbio.2016.10.013

Ducey, T., Miller, J., Lang, M., Szogi, A. A., Hunt, P. G., Fenstermacher, D., . . . McCarty, G. (2015). Soil physicochemical conditions, denitrification rates, and abundance in north carolina coastal plain restored wetlands. Journal of Environment Quality, *44*, 1011. https://doi.org/10.2134/jeq2014.09.0403

Eichorst, S. A., Trojan, D., Roux, S., Herbold, C., & Woebken, D. J. E. M. (2018). Genomic insights into the acidobacteria reveal strategies for their success in terrestrial environments. Environmental Microbiology, *20*. https://doi.org/10.1111/1462-2920.14043

Falkowski, P., & Jelen, B. (2015). Microbial genomes that drive earth's biogeochemical cycles. Encyclopedia of Metagenomics, 384-390. https://doi.org/10.1007/978-1-4899-7475-4_800

Fierer, N., Bradford, M. A., & Jackson, R. B. (2007). Toward an ecological classification of soil bacteria. Ecology, *88*, 1354-1364. https://doi.org/10.1890/05-1839

Fierer, N., & Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the United States of America, *103*, 626-631. https://doi.org/10.1073/pnas.0507535103

Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R., Henrissat, B., . . . Hibbett, D. (2012). The paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science, *336*, 1715-1719. https://doi.org/10.1126/science.1221748

Freedman, Z., & Zak, D. (2015). Soil bacterial communities are shaped by temporal and environmental filtering: Evidence from a long-term chronosequence. Environmental Microbiology, *17*. https://doi.org/10.1111/1462-2920.12762

Gorra, R., Coci, M., Ambrosoli, R., & Laanbroek, H. J. (2007). Effects of substratum on the diversity and stability of ammonia-oxidizing communities in a constructed wetland used for wastewater treatment. Journal of Applied Microbiology, *103*, 1442-1452. https://doi.org/10.1111/j.1365-2672.2007.03357.x

Gu, Y., Bai, Y., Xiang, Q., Yu, X., Zhao, K., Zhang, X., . . . Chen, Q. (2018). Degradation shaped bacterial and archaeal communities with predictable taxa and their association patterns in zoige wetland at tibet plateau. Scientific Reports, *8*. https://doi.org/10.1038/s41598-018-21874-0

Guan, B., Zhang, H., Wang, X., Yang, S., Chen, M., Hou, A., . . . Han, G. (2020). Salt is a main factor shaping community composition of arbuscular mycorrhizal fungi along a vegetation successional series in the yellow river delta. Catena, *185*, 104318. https://doi.org/10.1016/j.catena.2019.104318

Gutknecht, J. L. M., Goodman, R. M., & Balser, T. C. (2006). Linking soil process and microbial ecology in freshwater wetland ecosystems. Plant and Soil, *289*, 17-34. https://doi.org/10.1007/s11104-006-9105-4

Heinemeyer, A., Ridgway, K., Edwards, E., Benham, D. G., Young, J. P., & Fitter, A. H. (2004). Impact of soil warming and shading on colonization and community structure of arbuscular mycorrhizal fungi in roots of a native grassland community. Global Change Biology, *10*, 52-64. https://doi.org/10.1111/j.1365-2486.2003.00713.x

Houghton, R., Hackler, J., & Lawrence, K. (1999). The U.S. Carbon budget: Contributions from land-use change. Science, *285*, 574-578. https://doi.org/10.1126/science.285.5427.574

Hu, Y., Xiang, D., Veresoglou, S., Chen, F., Chen, Y.-L., Hao, Z., . . . Chen, B. (2014). Soil organic carbon and soil structure are driving microbial abundance and community composition across the arid and semi-arid grasslands in northern china. Soil Biology and Biochemistry, *77*, 51–57. https://doi.org/10.1016/j.soilbio.2014.06.014

Huang, C., Bai, J., Shao, H., Gao, H., Xiao, R., Huang, L., & Liu, P. (2012). Changes in soil properties before and after wetland

degradation in the yellow river delta, china. Clean – Soil Air Water, *40*, 1125-1130. https://doi.org/10.1002/clen.201200030

Hug, L., Castelle, C., Wrighton, K., Thomas, B., Sharon, I., Frischkorn, K., . . . Banfield, J. (2013). Community genomic analyses constrain the distribution of metabolic traits across the chloroflexi phylum and indicate roles in sediment carbon cycling. Microbiome, *1*, 22. https://doi.org/10.1186/2049-2618-1-22

Jackson, M. (1958). *Soil chemical analysis* (Vol. 46). New York: Prentice-Hall.

Jansson, J., & Hofmockel, K. (2018). The soil microbiome-from metagenomics to metaphenomics. Current Opinion in Microbiology, *43*, 162-168. https://doi.org/10.1016/j.mib.2018.01.013

Katoh, K., Misawa, K., Kuma, K.-i., & Miyata, T. (2002). Mafft: A novel method for rapid multiple sequence alignment based on fast fourier transform. Nucleic aAcids Research, *30*, 3059-3066. https://doi.org/10.1093/nar/gkf436

Khaledian, Y., Kiani, F., Ebrahimi, S., Brevik, E., & Aitkenhead-Peterson, J. (2017). Assessment and monitoring of soil degradation during land use change using multivariate analysis. Land Degradation and Development, *28*, 128-141. https://doi.org/10.1002/ldr.2541

Krause, S., Meima-Franke, M., Hefting, M., & Bodelier, P. (2013). Spatial patterns of methanotrophic communities along a hydrological gradient in a riparian wetland. FEMS Microbiology Ecology, *86*. https://doi.org/10.1111/1574-6941.12091

Lammel, D., Barth, G., Ovaskainen, O., Cruz, L., Zanatta, J., Ryo, M., . . . Pedrosa, F. (2018). Direct and indirect effects of a ph gradient bring insights into the mechanisms driving prokaryotic community structures. Microbiome, *6*. https://doi.org/10.1186/s40168-018-0482-8

Lauber, C., Hamady, M., Knight, R., & Fierer, N. (2009). Pyrosequencing-based assessment of soil ph as a predictor of soil bacterial community structure at the continental scale. Applied and Environmental Microbiology, *75*, 5111-5120. https://doi.org/10.1128/AEM.00335-09

Lauber, C. L., Strickland, M. S., Bradford, M. A., & Fierer, N. (2008). The influence of soil properties on the structure of bacterial and fungal communities across land-use types. Soil Biology and Biochemistry, *40*, 2407-2415. https://doi.org/10.1016/j.soilbio.2008.05.021

Leff, J. W., Jones, S. E., Prober, S. M., Barberán, A., Borer, E. T., Firn, J. L., . . . Fierer, N. (2015). Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. Proceedings of the National Academy of Sciences of the United States of America, *112*, 10967-10972. https://doi.org/10.1073/pnas.1508382112

Li, X., Hou, L., Liu, M., Zheng, Y., Yin, G., Lin, X., . . . Hu, X. (2015). Evidence of nitrogen loss from anaerobic ammonium oxidation coupled with ferric iron reduction in an intertidal wetland. Environmental Science and Technology, *49*. https://doi.org/10.1021/acs.est.5b03419

Li, Y., Wang, S., Jiang, L., Zhang, L., Cui, S., Meng, F., . . . Zhou, Y. (2016). Changes of soil microbial community under different degraded gradients of alpine meadow. Agriculture, Ecosystems and Environment, *222*, 213-222. https://doi.org/10.1016/j.agee.2016.02.020

Li, Z., & Xu, Z. (2008). Assessing bacterial diversity in soil. Journal of Soils and Sediments, *8*, 379-388. https://doi.org/10.1007/s11368-008-0043-z

Lu, M., Ren, Y., Wang, S., Tian, K., Sun, X., & Peng, S. (2019). Contribution of soil variables to bacterial community composition following land use change in napahai plateau wetlands. Journal of Environmental Management, *246*, 77-84. https://doi.org/10.1016/j.jenvman.2019.05.149

Lu, R., 1999. *Soil Agricultural Chemistry Analysis Method*. Beijing, China: China Agriculture Press.

Lundberg, D., Lebeis, S., Herrera Paredes, S., Yourstone, S., Gehring, J., Malfatti, S., . . . Dangl, J. (2012). Defining the core arabidopsis thaliana root microbiome. Nature, *488*, 86-90. https://doi.org/10.1038/nature11237

Ma, Y., Li, J., Wu, J., Kong, Z., Feinstein, L. M., Ding, X., . . . Wu, L. (2018). Bacterial and fungal community composition and functional activity associated with lake wetland water level gradients. Scientific Reports, *8*, 760. https://doi.org/10.1038/s41598-018-19153-z

Martin, M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. Embnet Journal, *17*. https://doi.org/10.14806/ej.17.1.200

Mehlich, A. (1984). Mehlich 3 soil test extractant: A modification of mehlich 2 extractant. Communications in Soil Science and Plant

Analysis, *15*, 1409-1416. https://doi.org/10.1080/00103628409367568

Moche, M., Gutknecht, J., Schulz, E., Langer, U., & Rinklebe, J. (2015). Monthly dynamics of microbial community structure and their controlling factors in three floodplain soils. Soil Biology and Biochemistry, *90*, 169-178. https://doi.org/10.1016/j.soilbio.2015.07.006

Moges, A., & Holden, N. (2008). Soil fertility in relation to slope position and agricultural land use: A case study of umbulo catchment in southern ethiopia. Environmental Management, *42*, 753-763. https://doi.org/10.1007/s00267-008-9157-8

Morgan N, P. (2009). Fasttree: Computing large minimum evolution trees with profiles instead of a distance matrix. Molecular Biology and Evolution, *7*. https://doi.org/10.1093/molbev/msp077

Mukhopadhya, I., Hansen, R., El-Omar, E. M., & Hold, G. L. (2012). Ibd—what role do proteobacteria play? Nature Reviews Gastroenterology and Hepatology, *9*, 219-230. https://doi.org/10.1038/nrgastro.2012.14

Nan, X., Tan, G., Wang, H., & Gai, X. (2016). Effect of biochar additions to soil on nitrogen leaching, microbial biomass and bacterial community structure. European Journal of Soil Biology, *74*, 1-8. https://doi.org/10.1016/j.ejsobi.2016.02.004

Nottingham, A., Fierer, N., Turner, B., Whitaker, J., Ostle, N., McNamara, N., . . . Meir, P. (2018). Microbes follow humboldt: Temperature drives plant and soil microbial diversity patterns from the amazon to the andes. Ecology, *99*. https://doi.org/10.1002/ecy.2482

Olde Venterink, H., Pieterse, N., Belgers, J. D. M., Wassen, M., & Ruiter. (2002). N, p, and k budgets along nutrient availability and productivity gradients in wetlands. Ecological Applications, *12*. https://doi.org/10.1890/1051-0761

Peralta, R. M., Ahn, C., & Gillevet, P. M. (2013). Characterization of soil bacterial community structure and physicochemical properties in created and natural wetlands. Science of the Total Environment, *443*, 725-732. https://doi.org/10.1016/j.scitotenv.2012.11.052

Rayment, G., & Higginson, F. (1992). *The australian handbook of soil and water chemical methods* (Vol. 63): Inkata Press Pty Ltd.

Reddy, K. R., & Delaune, R. (2008). Biogeochemistry of wetlands: Science and applications. Soil Science Society of America Journal, *73*, 1-781. https://doi.org/10.2136/sssaj2008.0013br

Ren, C., Zhang, W., Zhong, Z., Han, X., Yang, G., Yongzhong, F., & Ren, G. (2018). Differential responses of soil microbial biomass, diversity, and compositions to altitudinal gradients depend on plant and soil characteristics. Science of the Total Environment, *610*, 611-750. https://doi.org/10.1016/j.scitotenv.2017.08.110

Röske, K., Sachse, R., Scheerer, C., & Röske, I. (2012). Microbial diversity and composition of the sediment in the drinking water reservoir saidenbach (saxonia, germany). Systematic and Applied Microbiology, *35*, 35-44. https://doi.org/10.1016/j.syapm.2011.09.002

Rousk, J., Brookes, P., & Bååth, E. (2010). The microbial plfa composition as affected by ph in an arable soil. Soil Biology and Biochemistry, *42*, 516-520. https://doi.org/10.1016/j.soilbio.2009.11.026

Song, S., Zhang, C., Gao, Y., Zhu, X., Wang, R., Wang, M., . . . Wu, D. (2020). Responses of wetland soil bacterial community and edaphic factors to two-year experimental warming and spartina alterniflora invasion in chongming island. Journal of Cleaner Production, *250*. https://doi.org/10.1016/j.jclepro.2019.119502

Sun, Y., Li, X., Liu, J., Yao, Q., Jin, J., Liu, X., & Wang, G. (2019). Comparative analysis of bacterial community compositions between sediment and water in different types of wetlands of northeast china. Journal of Soils and Sediments, *19*, 3083-3097. https://doi.org/10.1007/s11368-019-02301-x

Tian, G. (1998). Effect of soil degradation on leaf decomposition and nutrient release under humid tropical conditions1. Soil Science, *163*, 897-906. https://doi.org/10.1097/00010694-199811000-00007

Urakawa, H., & Bernhard, A. E. (2017). Wetland management using microbial indicators. Ecological Engineering, *108*, 456-476. https://doi.org/https://doi.org/10.1016/j.ecoleng.2017.07.022

Van der Heijden, M., Bruin, S., Luckerhoff, L., Logtestijn, R., & Schlaeppi, K. (2015). A widespread plant-fungal-bacterial symbiosis promotes plant biodiversity, plant nutrition and seedling recruitment. The ISME Journal, *10*. https://doi.org/10.1038/ismej.2015.120

Wagg, C., Bender, S., Widmer, F., & Van der Heijden, M. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the United States of America, *111*.

https://doi.org/10.1073/pnas.1320054111

Wang, G., Ju, Q., Cheng, G., & Yuanmin, L. (2002). Soil organic carbon pool of grassland soils on the qinghai-tibetan plateau and its global implication. Science of the Total Environment, *291*, 207-217. https://doi.org/10.1016/S0048-9697(01)01100-7

Wang, Q., Wang, C., Yu, W., Turak, A., Chen, D., Huang, Y., . . . Huang, Z. (2018). Effects of nitrogen and phosphorus inputs on soil bacterial abundance, diversity, and community composition in chinese fir plantations. Frontiers in Microbiology, *9*, 1543. https://doi.org/10.3389/fmicb.2018.01543

Wardle, D., Bardgett, R., Klironomos, J., Setälä, H., Putten, W., & Wall, D. (2004). Ecological linkages between aboveground and belowground biota. Science, *304*, 1629-1633. https://doi.org/10.1126/science.1094875

Wei, J., Gao, J., Wang, N., Liu, Y., Wang, Y., Bai, Z., . . . Zhuang, G. (2019). Differences in soil microbial response to anthropogenic disturbances in sanjiang and momoge wetlands, china. FEMS Microbiology ecology, *95*. https://doi.org/10.1093/femsec/fiz110

Wen, Y., Zang, H., Freeman, B., Musarika, S., Evans, C. D., Chadwick, D. R., & Jones, D. L. (2019). Microbial utilization of low molecular weight organic carbon substrates in cultivated peats in response to warming and soil degradation. Soil Biology and Biochemistry, *139*, 107629. https://doi.org/10.1016/j.soilbio.2019.107629

Wu, H., Zeng, G., Liang, J., Guo, S., Dai, J., Lu, L., . . . He, X. (2015). Effect of early dry season induced by the three gorges dam on the soil microbial biomass and bacterial community structure in the dongting lake wetland. Ecological Indicators, *53*, 129-136. https://doi.org/10.1016/j.ecolind.2015.01.041

Wu, L., Nie, Y., Yang, Z., & Zhang, J. (2016). Responses of soil inhabiting nitrogen-cycling microbial communities to wetland degradation on the zoige plateau, china. Journal of Mountain Science, *13*, 2192-2204. https://doi.org/10.1007/s11629-016-4004-5

Wu, P., Zhang, H., Cui, L., Wickings, K., Fu, S., & Wang, C. (2017). Impacts of alpine wetland degradation on the composition, diversity and trophic structure of soil nematodes on the qinghai-tibetan plateau. Scientific Reports, *7*. https://doi.org/10.1038/s41598-017-00805-5

Xu, S., Zhang, B., Ma, L., Hou, A., Tian, L., Li, X., & Tian, C. (2017). Effects of marsh cultivation and restoration on soil microbial communities in the sanjiang plain, northeastern china. European Journal of Soil Biology, *82*, 81-87. https://doi.org/10.1016/j.ejsobi.2017.08.010

Yang, L., Sui, X., Liu, Y., Wang, J., Wu, Y., Zhang, T., & Ni, H. (2018). Abundance and diversity of arbuscular mycorrhizal fungi in calamanrostis angustifolia wetlands of the sanjiang plain, china. International Journal of Agriculture and Biology, *20*, 1424-1432. https://doi.org/10.17957/IJAB/15.0686

Yin, Y., & Yan, Z. (2020). Variations of soil bacterial diversity and metabolic function with tidal flat elevation gradient in an artificial mangrove wetland. SCIENCE OF THE TOTAL ENVIRONMENT, *718*, 137385. https://doi.org/10.1016/j.scitotenv.2020.137385

Yu, C., Han, F., & Fu, G. (2019). Effects of 7 years experimental warming on soil bacterial and fungal community structure in the northern tibet alpine meadow at three elevations. Science of the Total Environment, *655*, 814-822. https://doi.org/10.1016/j.scitotenv.2018.11.309

Yuan, X., Knelman, J., Gasarch, E., Wang, D., Nemergut, D., & Seastedt, T. (2016). Plant community and soil chemistry responses to long-term nitrogen inputs drive changes in alpine bacterial communities. Ecology, *97*, 1543-1554. https://doi.org/10.1890/15-1160.1

Yun, J., Zhang, H., Deng, Y., & Wang, Y. (2014). Aerobic methanotroph diversity in sanjiang wetland, northeast china. Microbial Ecology, *69*. https://doi.org/10.1007/s00248-014-0506-2

Zeng, Q., An, S., & Liu, Y. (2017). Soil bacterial community response to vegetation succession after fencing in the grassland of china. Science of the Total Environment, *609*, 2-10. https://doi.org/10.1016/j.scitotenv.2017.07.102

Zhang, D., Qi, Q., Tong, S., Wang, X., An, Y., Zhang, M., . . . Nutrition, P. (2019). Soil degradation effects on plant diversity and nutrient in tussock meadow wetlands. Journal of Soil Science and Plant Nutrition. https://doi.org/10.1007/s42729-019-00052-9

Zheng, J., Chen, J., Pan, G.-X., Liu, X., Zhang, X., Li, L., . . . Jinwei, Z. (2016). Biochar decreased microbial metabolic quotient and shifted community composition four years after a single incorporation in a slightly acid rice paddy from southwest china.

Science of the Total Environment, *571*, 206-217. https://doi.org/10.1016/j.scitotenv.2016.07.135

Zhou, H., Zhang, D., Jiang, Z., Sun, P., Xiao, H., Wu, Y., & Chen, J. (2018). Changes in the soil microbial communities of alpine steppe at qinghai-tibetan plateau under different degradation levels. Science of the Total Environment, *651*. https://doi.org/10.1016/j.scitotenv.2018.09.336

Zong, N., & Shi, P. (2020). Soil properties rather than plant production strongly impact soil bacterial community diversity along a desertification gradient on the tibetan plateau. Grassland Science. https://doi.org/10.1111/grs.12269

Table 1 Correlation analyses between the diversity of fungal and soil bacterial community and soil characteristics.

Kingdom	Variables	Chao1	Shannon
Bacteria	MC	-0.38	-0.32
	pH	0.30	.839**
	SOM	-.622*	-.650*
	TN	-.601*	-.608*
	TP	-.580*	-.629*
	TK	-0.38	0.24
	AN	-.622*	-.622*
	AP	-.699*	-.629*
	AK	-0.39	0.38
Fungi	MC	-0.11	-0.13
	pH	0.47	-0.04
	SOM	-0.56	0.04
	TN	-0.52	0.07
	TP	-0.15	0.32
	TK	-0.07	0.05
	AN	-.587*	-0.01
	AP	-0.50	0.07
	AK	0.02	0.30

MC, Moisture Content; SOM, Soil Organic Matter; TN, Total Nitrogen; TP, Total Phosphorus; TK, Total Kalium; AN, Available Nitrogen; AP, Available Phosphorus; AK, Available Kalium. *correlation significant at 0.05 level. **correlation significant at 0.01 level (two-tailed).

Table 2 Spearman's rank correlation between the partial affluence of predominant bacteria and fungi classes and soil characteristics.

Kingdom	Phylum	MC	pH	SOM	TN	TP	TK	AN	AP	AK
Bacteria	Proteobacteria	0.55*	-0.73**	0.65*	0.60*	0.67*	-0.04	0.57	0.60*	-0.20
	Acidobacteria	-0.72**	0.43	-0.57	-0.45	-0.58*	-0.27	-0.45	-0.50	-0.11
	Actinobacteria	-0.26	0.38	-0.69*	-0.75**	-0.54	-0.52	-0.58*	-0.69*	-0.57
	Chloroflexi	0.15	0.35	0.10	0.03	-0.08	0.61*	0.05	0.03	0.69*
	Gemmatimonadetes	-0.14	0.84**	-0.66*	-0.68*	-0.59*	0.25	-0.66*	-0.70*	0.26
	Bacteroidetes	-0.09	0.75**	-0.82**	-0.83**	-0.73**	-0.03	-0.83**	-0.81**	-0.13

	Verrucomicrobia	-0.46	-0.29	-0.18	-0.17	-0.15	-0.75**	-0.14	-0.22	-0.75**
	Rokubacteria	0.51	0.21	0.37	0.38	0.23	0.94**	0.24	0.28	0.89**
	Planctomycetes	-0.03	-0.22	0.35	0.37	0.39	-0.02	0.39	0.48	0.22
	Nitrospirae	0.41	0.15	0.40	0.40	0.27	0.87**	0.30	0.35	0.91**
Fungi	Ascomycota	0.36	0.38	0.06	0.03	0.06	0.70*	-0.04	0.13	0.73**
	Basidiomycota	-0.50	-0.22	-0.28	-0.30	-0.27	-0.82**	-0.22	-0.31	-0.86**
	Mortierellomycota	-0.04	0.41	-0.39	-0.38	-0.25	0.05	-0.38	-0.49	0.08

MC, Moisture Content; SOM, Soil Organic Matter; TN, Total Nitrogen; TP, Total Phosphorus; TK, Total Kalium; AN, Available Nitrogen; AP, Available Phosphorus; AK, Available Kalium. *correlation significant at 0.05 level. **correlation significant at 0.01 level (two-tailed).