

# IMPACT OF WETLAND CONVERSION INTO FORESTS AND ARABLE LAND ON SOIL MICROBIAL COMMUNITY STRUCTURE AND DIVERSITY IN THE SANJIANG PLAIN, NORTHEASTERN CHINA

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**Abstract.** Changes in land use patterns lead to changes in soil ecosystem functions, and soil microorganisms can sensitively reflect the evolution of soil quality and different ecosystem functions. Here, three typical land use patterns (wetland, arable land, and forest) in the Sanjiang Plain of northeastern China were selected to study the effect of land use changes on the microbial community structure of wetlands. High-throughput sequencing technology based on bacterial 16S rRNA genes was used to study the community structure of soil bacteria in three land use patterns and to explore the relationship between soil bacterial community and environmental factors. Our findings indicated that the dominant bacterial phyla in soils of different land use patterns were Proteobacteria, Acidobacteria, and Actinobacteria. However, the land use patterns significantly changed the composition and abundance of soil bacterial genera. Combined with the soil bacterial alpha diversity index, the soil bacterial  $\alpha$  diversity in wetlands was higher than that in forests and farmlands. Soil bacterial beta diversity varied significantly among land use patterns. The redundancy analysis results showed that soil moisture content was the main factor affecting the bacterial community structure of wetland soils, whereas pH, soil organic carbon, and total nitrogen were the main factors affecting the soil bacterial community structure in forests, and total phosphorus and available phosphorus were the main factors affecting the soil bacterial community structure in arable land.

**Keywords:** *alpine wetlands, reclamation, high-throughput sequencing, bacterial communities, soil physicochemistry*

## Introduction

Soil microbial communities are a central component of the soil biogeochemical cycle, and are involved in regulating ecosystem processes at all scales (Huang et al., 2019). These communities are the driving force for the transformation and cycling of soil organic matter and crucial nutrients such as C and N (Zhang et al., 2022), and are therefore important biological indicators of soil health (Sui et al., 2022). Soil microbial community diversity is influenced by several factors such as soil organic carbon, soil pH, C/N ratio, and nutrient bioavailability (Deng et al., 2020), all of which are regulated by land use patterns (Sui et al., 2019). Different land use patterns have been associated with unique vegetation types and species structure (Li et al., 2013), soil structure (Acín-Carrera et al., 2013), soil water characteristics (Zucco et al., 2014), soil respiration (Sheng et al., 2010),

soil nutrient fertility characteristics (Liu et al., 2010), soil enzyme activity (Tischer et al., 2015), soil microbial biomass, and soil microbial community (Van Leeuwen et al., 2017). Land use not only affects nutrient levels in soil but also nutrient cycling by affecting water, heat, and other environmental conditions, thus affecting the transformation and flow of soil nutrients. In turn, this can directly or indirectly affect the number, composition, and activity of soil microorganisms, resulting in changes in the structure and function of soil microbial communities. Moreover, the diversity of soil microbial communities can also reflect changes in vegetation. The rational use of land plays an important role in improving soil structure and promoting regional ecological restoration. In addition, land use change is an important factor affecting soil properties (Birkhofer et al., 2012). Previous studies have demonstrated that different vegetation (Sui et al., 2021) and management measures (Sánchez-Moreno et al., 2006) can significantly modify soil properties among different land use modes. For example, in the process of land use change, soil aggregates with larger particle sizes are more likely to be lost (Li et al., 2014). Other studies have reported that anthropogenic disturbances such as tillage and fertilizer application led to soil compaction and slabbing, and relatively high powder and clay particle contents resulted in the continuous refinement of large soil particles (Ren et al., 2014). Lv et al. (2011) reported that incorporating more plants into a landscape (i.e., by planting) results in higher levels of litter, which promoted the formation of the root system aggregates and enhanced soil erosion resistance. At the same time, the species diversity increased, the soil physical properties improved, the soil layer thickened, and the bulk density decreased. With the accumulation of a large amount of litter on the surface, soil organic matter accumulated, total nitrogen, available nitrogen, and available potassium increased, and soil fertility exhibited an obvious upward trend (Liu et al., 2005). Tillage and harvesting and utilization of surface vegetation not only accelerates the decomposition and loss of soil organic matter, but also intensifies soil disturbances, soil and water loss, and the loss of other nutrients in the soil, particularly the bioavailable fraction of these nutrients (Zhao et al., 2012). Zhao et al. (2011) found that different land use modes have a significant impact on the contents of soil organic matter, total nitrogen, available phosphorus, and available potassium. Among various land use modes, the average contents of total nitrogen and organic matter in cultivated soil are generally considered low or very low. Most previous studies have focused on the impact of land use changes on soil properties in the study area, whereas the impact of land use-driven soil property changes on microbial community structure and function remains unclear.

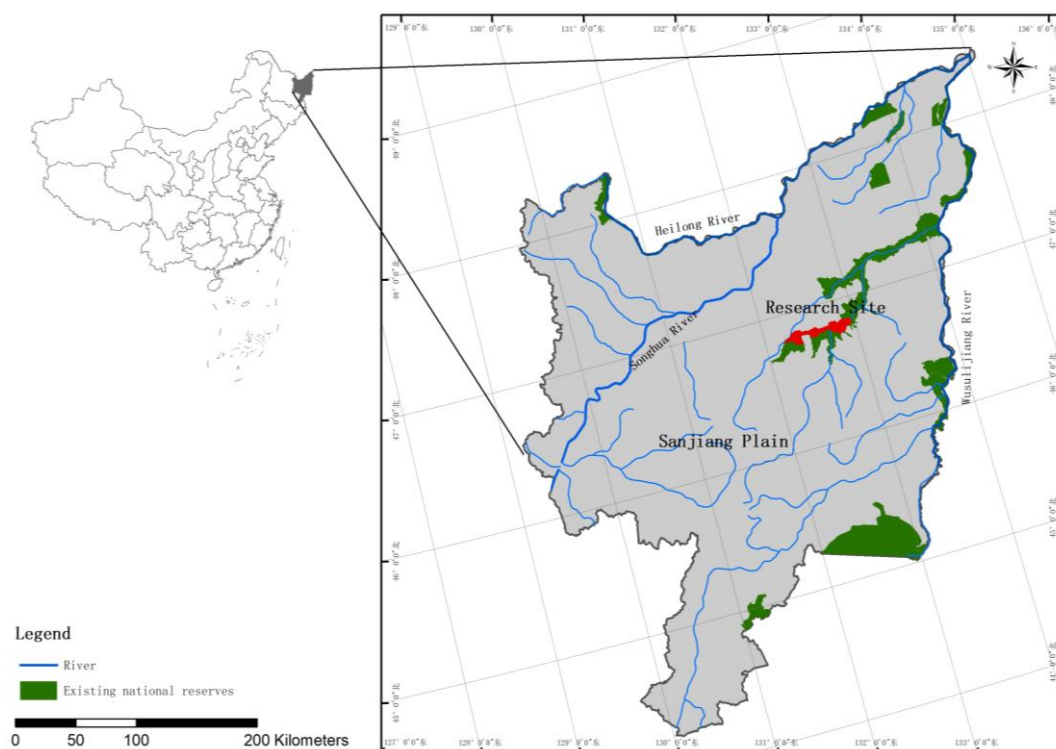
The Sanjiang Plain wetland is among the most important freshwater wetland distribution areas in Northeast China, and is also the primary terrestrial environment dominated by black soil (Sui et al., 2021). Due to the particular climatic conditions and geographical location of the study area, its soil is characterized by high humus content and low abundance and diversity of microorganisms (Weng et al., 2022). Therefore, this ecosystem is extremely fragile despite being uniquely suitable for agricultural development. Many studies have characterized the effects of land use changes on community structure and soil physicochemical properties in the wetlands of the Sanjiang Plain (Wu et al., 2010; Xu et al., 2017; Sui et al., 2019). However, the effects of these parameters on the soil microbial community structure have remained largely unexplored. Therefore, our study characterized the effect of land use on soil physicochemical properties and soil microbial functional diversity in typical swampy meadow wetlands, artificial larch forests, and cornfields in the Sanjiang Plain. Moreover, we analyzed the mechanisms of different land use practices on soil microbial

community structural characteristics in the Sanjiang Plain, and clarified the main environmental factors affecting soil microbial community differentiation. Collectively, our findings provide a scientific basis for the preservation and enhancement of soil fertility and the conservation of soil microbial diversity, as well as for the ecological reconstruction and rational use of land resources in the study region.

## Materials and methods

### *Overview of the study sample site*

The study area belongs to the ecological transition zone between the Xiaoxinganling Mountains and the Sanjiang Plain, and is located in the Sanhuanpao and Naolihe Nature Reserve of Heilongjiang Province, downstream of the Songhua River in northeastern of China ( $46^{\circ} 57' 55'' \sim 47^{\circ} 14' 7''\text{N}$ ,  $130^{\circ} 24' 51'' \sim 130^{\circ} 57' 38''\text{E}$ ) (Fig. 1). The region exhibits a temperate continental monsoon climate, with an altitude of 65–81 m, an average annual rainfall of 548 mm, an average annual evaporation of 1,155 mm, and an average annual frost-free period of approximately 130 d. The average temperature for five months of the year is below  $0^{\circ}\text{C}$ , with the average annual temperature being  $2.1^{\circ}\text{C}$ . The highest temperature occurs in July, with an average temperature of  $21.2^{\circ}\text{C}$ , and the lowest temperature occurs in January, with an average temperature of  $-19.4^{\circ}\text{C}$ . The freezing and thawing period is from mid-October to mid-May of the following year, with a freezing period of 150 d and a wetland freeze depth of 80 to 125 mm. The vegetation in the reserve is dominated by wet herbaceous and shrub vegetation, with intermittent planted forests. The main vegetation includes *Salix siuzevii*, *Salix sungkianica*, *Salix viminalis*, *Carex lehmanii*, *Acorus calamus* and *Deyeuxia angustifolia*, among others. The characteristics of three land use types were shown in Table 1.



**Figure 1.** The location of this research site

**Table 1.** Characteristics of the three land use types in the Sanjiang plain

Land use type	Primary vegetation species	Position
Wetland	<i>Deyeuxia angustifolia</i> , <i>Stellaria radicans</i> , <i>Anemone dichotoma</i> , <i>Lathyrus quinquenervius</i> , <i>Carex appendiculata</i>	132°21'11"E, 46°51'4"N
Forest	Pure <i>Populus simonii</i> , planted in 2010, the average height was about 12 m, the diameter at breast height was about 15 cm, and the average density was 1600 stems ha <sup>-1</sup>	132°19'15"E, 46°45'7"N
Arable land	The maize plantation was fertilized with 370 kg ha <sup>-1</sup> y <sup>-1</sup> of fertilizer (N:P:K) each year in the end of May	132°32'91"E, 46°83'91"N

### Sample collection

In June 2019, three standard 50 m × 50 m plots were selected from three different land use sample plots, including a pristine wetland, agricultural land, and forest land (Fig. 2), respectively, and soil samples were taken from a 0 to 20 cm depth using a five-point mixed sampling method. After each layer of soil samples were thoroughly mixed, the debris and rhizomes were removed from the samples and passed through a 2 mm sieve, after which a portion of the samples was placed in a 15 mL centrifuge tube, stored in liquid nitrogen, transferred to the laboratory, and stored in a refrigerator at -80 °C refrigerator for DNA extraction and for microbiological analysis. The rest of the soil samples were divided into two parts in the laboratory, one was kept in a refrigerator at 4 °C whereas the other was naturally air-dried for the determination of soil physical and chemical properties.

### Determination of physical and chemical properties

For the determination of soil moisture content, the retrieved fresh soil sample was immediately placed in an aluminum box and weighed on a scale accurate to 0.01 g. The sample was then baked at constant temperature in a drying oven preheated to 10 °C ± 2 °C for 8 h, after which moisture content was calculated. Soil pH was determined using an acidity meter with a water to soil ratio of 2.5:1. Soil organic carbon content was determined using a Vario TOC meter (Elementar, Germany). For the analysis of total nitrogen, 0.25 g of soil sample was passed through a 0.149 mm sieve, followed by the addition of 2 g of accelerant mixed with zinc sulfate and copper sulfate and 5 mL of concentrated H<sub>2</sub>SO<sub>4</sub> for decoction. The sample was then fixed and filtered after decoction, and total nitrogen determination was conducted with a continuous flow analyzer (Auto Analyzer 3-AA3, SEAL Company, Germany). Total phosphorus was determined via sulfuric acid/perchloric acid dissolution molybdenum antimony anti colorimetry. Fast-acting phosphorus was determined using 0.5 mol·L<sup>-1</sup> sodium bicarbonate leaching - molybdenum antimony anti-colorimetric.

### DNA extraction and high-throughput sequencing

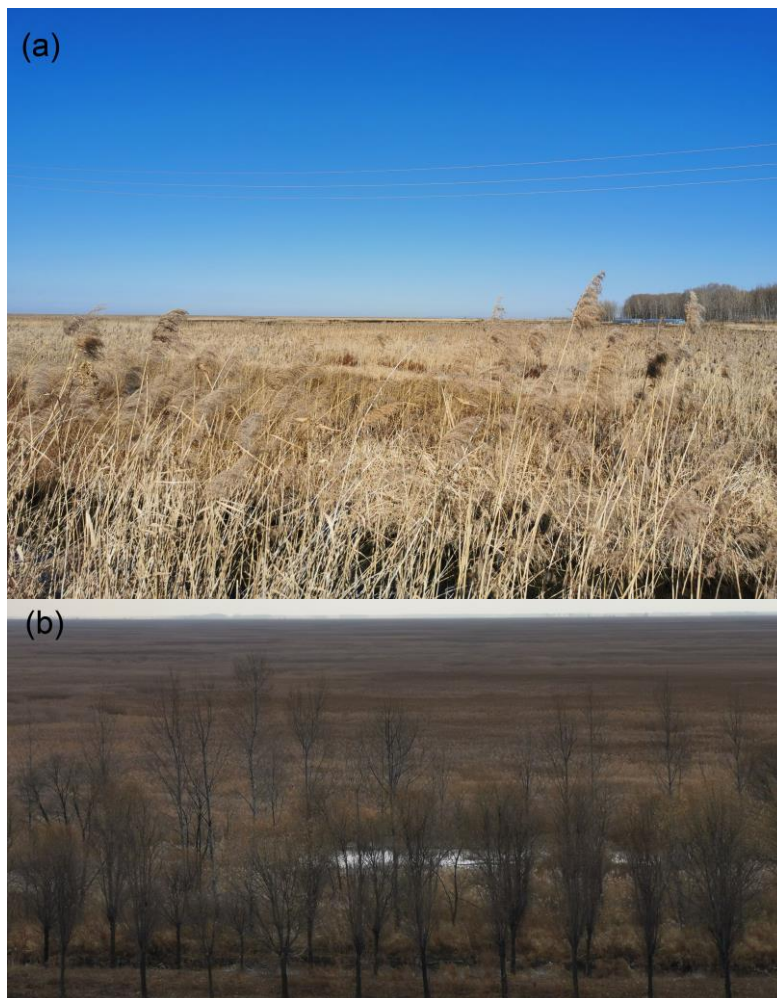
Genomic DNA was extracted from fresh soil samples (n = 18; 0.5 g each) using the power soil DNA extraction kit according to the manufacturer's instructions. PCR was performed on a Geneamp 9700 PCR system (Applied Biosystems, CA, USA). The extracted genomic DNA was detected by 1% agarose gel electrophoresis (CHEF-DR II, Bio-red, Beijing, China). The 338F (5'-ACTCCTACGGGAGGCAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') universal primers were used for bacterial 16S

rRNA gene amplification. The amplified products were detected by 2% agarose gel electrophoresis, recovered from the gel using the AxyPrep DNA gel extraction kit, washed with tris HCl, and verified by 2% agarose gel electrophoresis. The PCR products were quantified using a QuantiFluor™-ST fluorometer, after which the concentration of the samples was adjusted as needed for sequencing. Sequencing was performed by Beijing Biomaker Technology Co., Ltd. (Beijing, China) using an Illumina HiSeq sequencer.

### ***16S rRNA gene sequence analysis***

The original fastq sequence files were quality filtered using Trimmomatic and then spliced by FLASH using the following criteria: (i) sequences less than 50 bp and with an average quality score less than 20 were eliminated; (ii) 2 nucleotide mismatches were allowed and fragments containing ambiguous bases were removed; (iii) sequences with overlapping lengths of more than 10 bp were merged according to their overlapping sequences.

Using UPARSE (version 7.1, <http://drive5.com/uparse/>), operational taxonomic units (OTUs) were assigned with a 97% similarity threshold and chimeric sequences were identified and removed using UCHIME. All 16S rRNA gene sequences were classified using the RDP classification algorithm (<http://rdp.cme.msu.edu/>) against the Silva (SSU123) 16S rRNA database.





**Figure 2.** The habitats of three land use types: (a) wetland; (b) forest; (c) arable land

### **Data analysis**

For alpha diversity analysis, community richness parameters (Chao1 and ACE indices) and community diversity parameters (Shannon-Wiener indices) were calculated using Mothur version v.1.39.1 (Schloss et al., 2009). Beta diversity was calculated using R v3.3.2 (R Development Core Team, 2017) using “Vegan” package and redundancy analysis (RDA) was conducted based on OTU levels using R v3.3.2 (R Development Core Team, 2017) using “Microeco” package. One-way ANOVA was used to analyze the effects of different site types on soil properties and microbial diversity, and Duncan’s test was used to test the significance of the differences between site types for each indicator ( $\alpha = 0.05$  and  $0.01$ ). The results for all samples were reported as mean  $\pm$  standard deviation (SD). A P-value  $< 0.05$  was deemed statistically significant.

### **Results**

#### ***Effect of different land uses on soil physicochemical properties***

Table 2 summarizes the physicochemical properties of the soils of the three land uses. The pH of all three samples was acidic. The arable land exhibited the lowest pH value, followed by the forest soil, with wetland soil exhibiting the highest pH. Compared with arable soil (13.48% soil moisture content) and forest soil (13.19% soil moisture content), the wetland soil (13.66% soil moisture content) had a higher water content ( $P < 0.05$ ). Except the soil available phosphorus ( $P > 0.05$ ), the soil organic matter, total nitrogen and total phosphorus were significantly different between three land use types ( $P < 0.05$ ). Soil organic matter, total nitrogen and total phosphorus in wetland were higher than that in forest and arable land.

#### ***OTU of soil bacteria from different land use types***

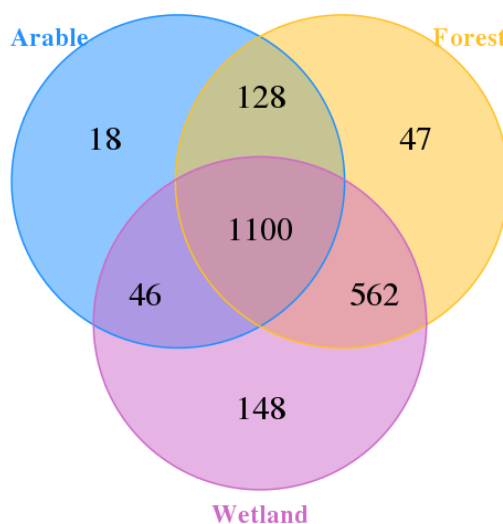
A total of 2049 soil bacterial OTU sequences were identified in the three land use types, of which 1100 soil bacterial OTU sequences were shared among all three land

use types (Fig. 3). The highest number of total OTUs was observed in the wetland soil (1856, accounting for 90.58% of the total), followed by forest soil (1837, accounting for 89.65% of the total), and finally arable soil (1292, accounting for 63.06% of the total). Therefore, pristine wetland and forest soils exhibited the highest number of bacterial OTUs, and the number of OTUs specific to wetland soils was the highest (148).

**Table 2.** Physicochemical properties of soils with different land use practices

Land use type	pH	SMC (%)	SOM (g/kg)	TN (g/kg)	TP (g/kg)	AP (mg/kg)
Wetland	5.45 ± 0.16b	73.66 ± 0.27a	52.27 ± 0.51a	4.29 ± 2.77a	6.42 ± 0.89a	28.84 ± 1.74a
Forest	5.85 ± 0.07a	23.19 ± 0.52b	34.01 ± 0.51b	1.13 ± 2.03c	4.23 ± 0.52b	25.45 ± 2.15a
Arable land	4.87 ± 0.11b	15.48 ± 0.82c	23.06 ± 0.08c	3.14 ± 1.11b	3.71 ± 0.14b	23.74 ± 1.23a

SMC, soil moisture content; SOM, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus



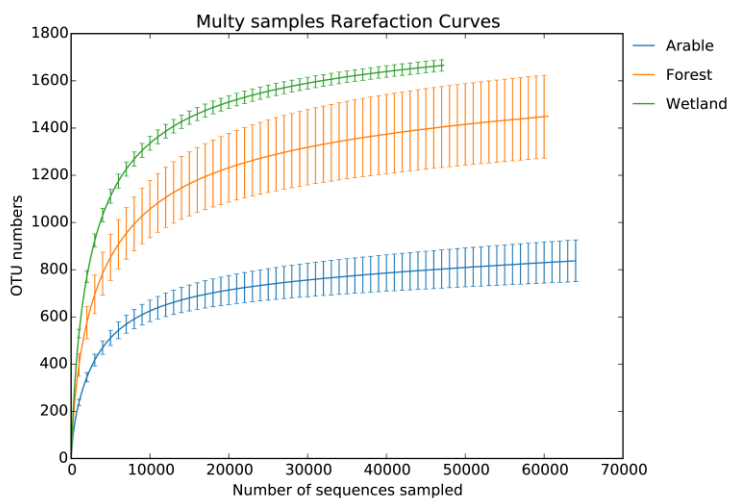
**Figure 3.** Venn diagram of bacterial community structure for different land use practices

For rarefaction curve analysis, a certain number of individuals were randomly selected from the sample, the number of species represented by these individuals was then counted, and the curve was constructed based on the number of individuals and species. As illustrated in Figure 4, the rarefaction curves of nine soil samples tended to be flat, indicating that the sequencing data provided an accurate representation of the samples (i.e., more sequencing data would only produce a small amount of new OTUs). Furthermore, the number of soil bacterial OTUs in different land use patterns exhibited the following descending order: wetland > forest > arable land.

### **Differences in soil microbial alpha and beta diversity under different land use patterns**

The  $\alpha$ -diversity indices of bacteria in soil samples from three land use types are shown in Figure 5. ACE, Chao1, and Shannon indices showed a consistent pattern: wetland > forest > arable land. The differences in soil ACE, Chao1, and Shannon

indices between wetlands and forests were not significant (*Fig. 5*, Duncan test,  $P > 0.05$ ). There were significant differences in the soil ACE, Chao1, and Shannon indices between wetland and arable land (*Fig. 5*, Duncan test,  $P < 0.01$ ). Moreover, there were significant differences in soil ACE, Chao1, and Shannon indices between forest and arable land (*Fig. 5*, Duncan test,  $P < 0.05$ ).



**Figure 4.** Bacterial rarefaction curves of different land use modes

The beta diversity of bacterial communities in different land use modes was measured by PCoA based on the Bray-Curtis distance. As illustrated in *Figure 5*, there were significant differences in bacterial community structure among different land use modes (PERMANOVA:  $r = 0.68$ ,  $P < 0.01$ ). The difference within the samples was not significant, with the main differences occurring only between different samples (*Fig. 6*). These findings indicated that long-term land use change can significantly affect the bacterial community structure of the soil.

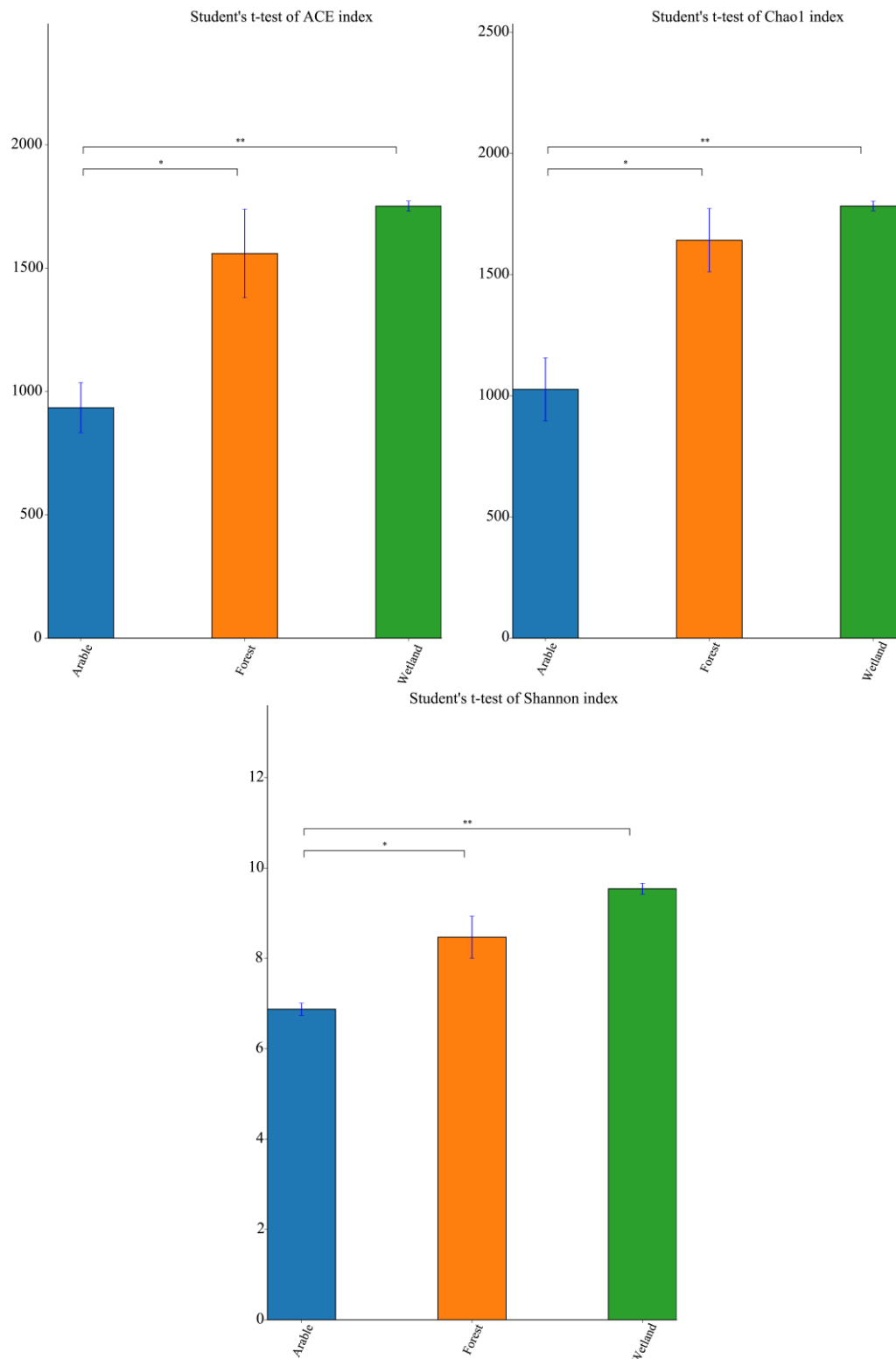
#### ***Analysis of soil bacterial community structure in different land use modes***

From the perspective of the overall bacterial community structure, all OTUs belonged to 33 bacterial phyla. If a given sequence could not be classified as a known phylum, the phyla were uniformly classified as “others.” Based on the relative abundance of all phyla levels of the three land types (*Fig. 7a*), the dominant phyla in the sample are Proteobacteria, Acidobacteria, and Actinobacteria. The relative abundances of Proteobacteria, Acidobacteria, and Actinomycetes in wetland soil were 37%, 18%, and 11%, respectively. The relative abundance of the dominant Proteobacteria in forest soil was 39%, Acidobacteria was 17%, and Actinobacteria was 14%. The relative abundance of dominant bacteria in Arable land soil was 67%, Acidobacteria was 5%, and Actinobacteria was 6%.

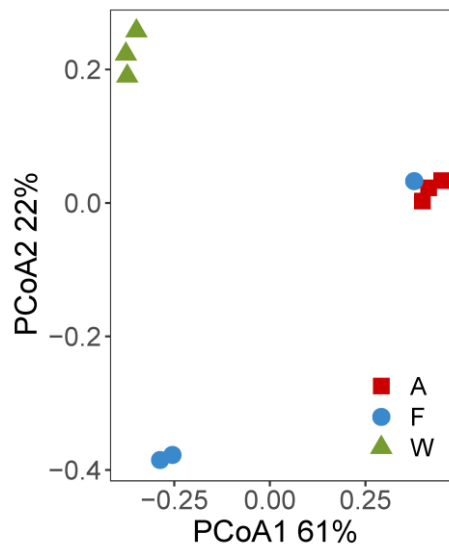
In terms of relative abundance at the genus level (*Fig. 7b*), the composition of soil bacterial genera was not the same under different land use practices. As seen in *Figure 6b*, the major genera of soil bacteria in arable land were *Cupriavidus*, *Reyranelia*, *Aquabacterium*, and *Azohydromonas*; the major genera of soil bacteria in forest soil were *Bradyrhizobium*, *RB41*, *Rhizobacter*, *Novosphingobium*, and *Sphingomonasc*; the major genera of soil bacteria in wetland were *RB41*,



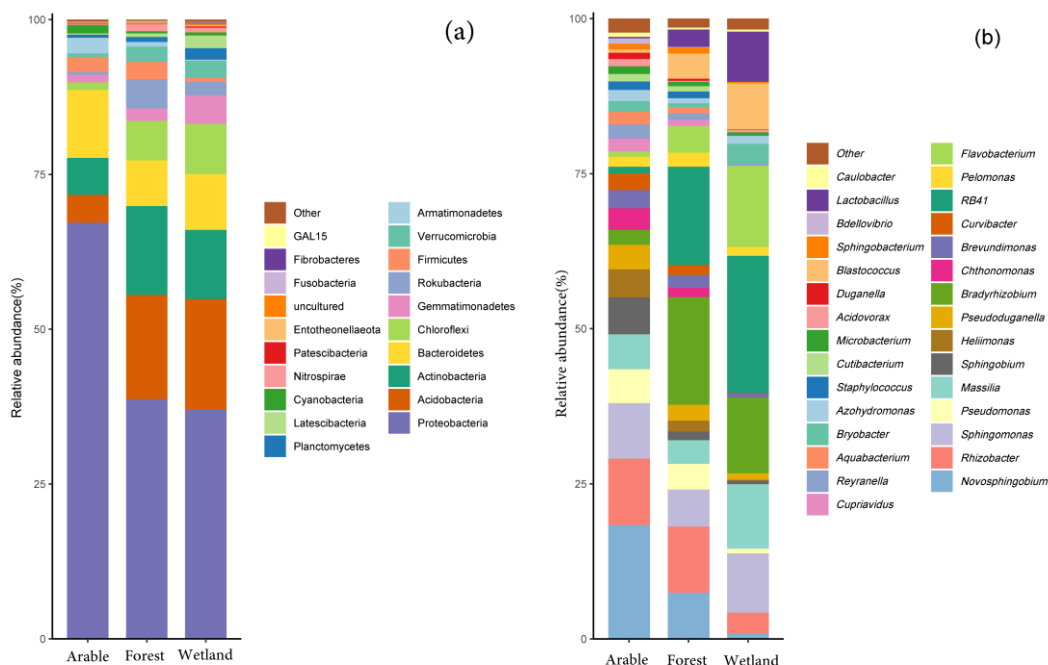
*Flavobacterium*, *Bradyrhizobium*, *Massilia*, and *Sphingomonas*. Therefore, we concluded that different land use practices significantly affect the composition of the main genera of soil bacteria.



**Figure 5.** Alpha diversity of soil bacteria in different land use modes. \* and \*\* indicated the one way-ANOVA, Duncan's test at 0.05 and 0.01 level, respectively



**Figure 6.** PCoA diagram of soil bacterial community under different land use modes. A, arable land; F, forest; W, wetland

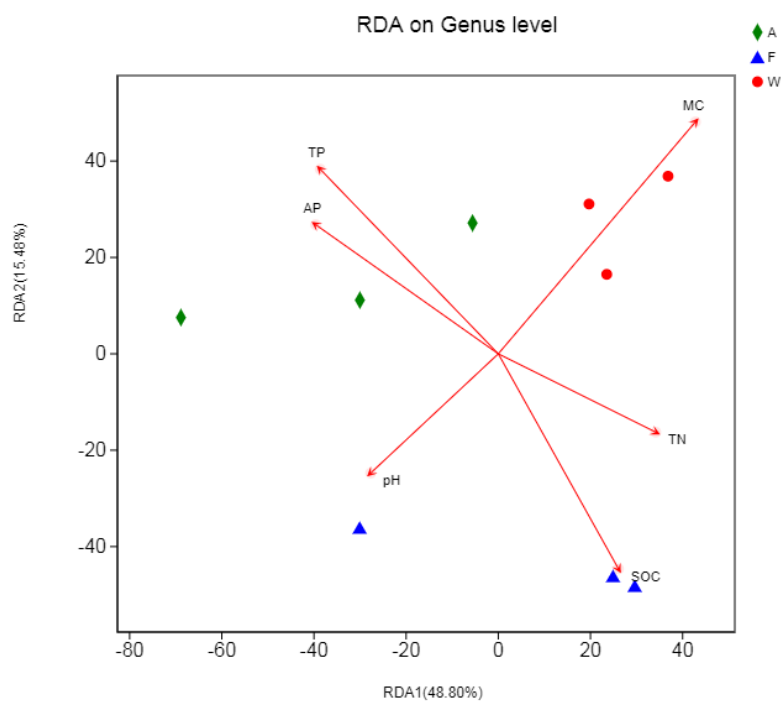


**Figure 7.** Structural composition of bacterial communities in different land use practices. Phylum level (a); genus level (b); abundances less than 1% were combined into the category “other”

### Redundancy analysis of soil bacterial communities and physicochemical properties for different land use practices

Figure 8 shows the RDA of the soil physicochemical properties in relation to the community composition of bacteria at the genus level. RDA1 explained 81.31% of all variation, RDA2 explained 7.37% of all information, and the first two axes could

explain 88.68% of the information. Longer rays of pH and TN indicated that they had a greater influence on bacterial community composition, whereas the shorter rays of SOC, AP, and TP values indicated that they had a smaller influence on bacterial community composition.



**Figure 8.** RDA of soil bacterial community structure and soil physicochemical properties. A: Arable; F: Forest; W: Wetland. MC, soil moisture content; SOM, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus

## Discussion

Changes in the diversity of soil microbial communities can reflect the quality and health of soil ecosystems (Hermans et al., 2020; García-Orenes et al., 2013). The disturbance of natural ecosystems by human activities is the most important direct driver that alters ecosystem service functions. Therefore, studying bacterial community structure and diversity in areas impacted by human activities can provide insights into the structural differences in soil bacterial communities under different land uses (Rampelotto et al., 2013; Cheng et al., 2021). In this study, the soil bacterial ACE, Chao1, and Shannon indices all exhibited the same descending pattern: wetland > forest > arable land. The differences in diversity indices between wetlands and forests were not significant, whereas the differences with farmland soil were significant. This may be due to the high nutrient content of the original wetland soil coupled with the stable ecosystem, which provided a suitable habitat for bacteria. Once reclaimed into agricultural land, the application of chemical fertilizers and tillage resulted in the destruction of the stable soil ecosystem, making it difficult for the original soil bacterial microorganisms to survive, thus reducing microbial diversity. This is consistent with the findings of Zhang et al. (2020), who reported a significant decrease in soil bacterial diversity after the reclamation of wetlands into agricultural

fields. Lynn et al. (2017) also found that the soil bacterial diversity of original wetland was higher than other land use types because the land use disturbed the ecological stability and thus decreased the soil bacteria diversity. Suleiman et al. (2013) also proved that the bacterial diversity in soil decreased from pristine forest and grassland resulted from the deforestation. However, Xu et al. (2016) found that reclamation could significantly increase the soil bacterial diversity index in swampy wetlands, and concluded that reclamation increased the abundance of soil aerobic bacteria as a result of increased aeration of agricultural soils after reclamation. The moderate storm disturbances believed that disturbance had a positive effect on microbial communities by increasing their production and both their community and diversity (Galand et al., 2016). Barba et al. (2019) also proved that disturbance increased the soil microbial diversity. However, we believe that the reason for the inconsistency with the moderate disturbance hypothesis may be that the vegetation diversity on the original wetland was higher (see *Table 1*). After changing to artificial forest and maize, the vegetation on the ground became simple (see *Table 1*), and resulted the composition of litter simple, this directly affected soil microbial nutrient sources, leading to a decrease in soil bacterial diversity. Addition, we also believe that different tillage intensity, tillage treatment, and tillage time will affect soil bacterial diversity. Therefore, additional studies are required to assess the long-term effects of different land use practices on soil bacterial diversity.

Currently, the mechanisms of soil bacterial community generation and maintenance are not fully understood. However, differences in soil bacterial community components can explain the effects of environmental changes on in situ soil bacterial community reconstruction (Xun et al., 2015). The significant differences in soil bacterial  $\beta$ -diversity among different land use practices (*Fig. 5*) indicate that changes in land use practices have modified the structure of soil bacterial communities. This may be because there were significant changes in soil nutrient cycling due to changes in the original aboveground vegetation when the original swampy wetlands were transformed into forests and agricultural lands, as bacteria are closely associated with the diversity of the aboveground vegetation (Sui et al., 2021). Although short-term changes may not be obvious, the input of litter caused by the changes in aboveground vegetation after long-term land change and the long-term changes in plant root exudates and biomass ultimately affect the soil bacterial community structure, which is consistent with the findings of Xu et al. (2021).

We found that the main factors affecting soil bacterial community structure of three land use types were different, among which soil moisture content was the main environmental factor affecting wetland soil bacterial community structure, while available phosphorus and total phosphorus were the main environmental factors affecting farmland soil bacterial community structure, and soil pH, soil organic carbon and total nitrogen were the main environmental factors affecting forest soil bacteria. This may be because the wetland environment was mainly dominated environmental factor (e.g. high water level), especially the original wetland soil has high water content, which may be the main factor affecting the soil bacterial structure. However, due to the application of phosphorus fertilizer, the phosphorus content of the farmland changed, which may be the main reason affecting the farmland soil bacterial community. The above-ground vegetation in forest was mainly affected litter input and the litter contained a large amount of organic carbon and total nitrogen. Many studies showed that wetland soil microbiome were affected by soil water content (Clairmont et al., 2019; Choi et al., 2022), which was consistent with the results of this study. However,

Clairmont et al. (2019) also found that soil microbial community structure was not only affected by soil water content, but also the composition of aboveground vegetation also played an important role. However, since this study did not study the root soil microbial structure, hence, it is necessary to carry out research on the changes of root microorganisms and their driving factors in the future. Soil phosphorus was the main nutrient factor affecting soil microbial structure (Turley et al., 2020). When the phosphorus element in the soil increases, the microbial groups related to the phosphorus element content in the soil microorganisms would change, which lead to the change of the soil microbial community structure. pH, organic carbon and total nitrogen were the main physicochemical factors affecting soil microorganisms (Plassart et al., 2019). Studies have shown that soil pH, organic carbon and nitrogen significantly affected the structure of soil bacterial community in soil forests (Praeg et al., 2020). This is consistent with these results, but the factors affecting soil bacterial structure are complex, and different aboveground vegetation compositions and disturbance intensity will affect soil bacterial community structure, so further research is still needed.

Changes in land use mode did not affect the main phyla of the soil bacterial communities (Fig. 7a). The dominant phyla in the three land soils were Proteobacteria, Acidobacteria, and Actinobacteria. According to Wang et al. (2019), different land use modes have an important impact on the bacterial community structure of wetland soil, with Proteobacteria, Acidobacteria, and Actinobacteria being the dominant bacteria in the wetland soil environment. Ogola et al. (2021) also found that Proteobacteria, Acidobacteria, and Actinobacteria play an important role in different soil bacterial communities. Therefore, changes in land use mode will not affect the main dominant flora of soil bacteria, but may still have a significant impact at the genus level. In other words, although the main components of the community did not change at the phylum level, significant effects were observed at the genus level because different land use modes are affected by different soil physical and chemical factors. In this study, the major genera of soil bacteria in arable land were *Cupriavidus*, *Reyranelia*, *Aquabacterium*, and *Azohydromonas*; the major genera of soil bacteria in forest soil were *Bradyrhizobium*, *RB41*, *Rhizobacter*, *Novosphingobium*, and *Sphingomonas*; the major genera of soil bacteria in wetland were *RB41*, *Flavobacterium*, *Bradyrhizobium*, *Massilia*, and *Sphingomonas*. Specifically, our findings indicated that wetland soil bacteria are mainly affected by soil water content, whereas forest soil bacteria are affected by soil organic carbon and total nitrogen, and arable land soil bacteria is most significantly affected by soil total phosphorus and available phosphorus (Fig. 8). This suggested that different bacterial species respond differently to habitat changes. This is consistent with other research findings (Ormeño-Orrillo et al., 2012; De Meyer et al. 2018) indicating that when the habitat changes, the microbial niche will be differentiated, which will lead to the change of species composition (Hartmann et al., 2017). This would explain why different dominant genera of soil bacteria were observed under different land use modes, which is consistent with the findings of Xu et al. (2016) and Sui et al. (2019).

## Conclusion

Changing the land use patterns of primitive swamp wetlands in Sanjiang Plain has led to significant changes in soil physical and chemical properties, in addition to causing significant differences in soil bacterial community diversity among different land use types. Different land use habitats have their own distinct dominant flora. The

variations in wetland soil bacterial communities are mainly caused by soil water content. Pristine marsh wetland habitats are a key factor in maintaining high levels of bacterial alpha diversity. The dominant phylum of soil bacteria in each land use type habitat remained stable. However, the bacterial community structure at the genus level was significantly influenced by the physicochemical properties of the soil in each land use type. Collectively, our findings demonstrate that long-term land use changes can significantly change the bacterial community composition and diversity of soil.

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