

EFFECTS OF LAND USE CHANGE ON THE STRUCTURE AND FUNCTION OF SOIL FUNGAL COMMUNITY IN SANJIANG PLAIN WETLAND

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Abstract. This study analyzed the impact of land use changes on the structure and function of soil fungal communities in the Sanjiang Plain wetland. Soil samples were collected from natural wetlands, paddy fields, and restored wetlands in the Sanjiang Plain, after which the internal transcribed spacer (ITS) of soil fungi was sequenced by Miseq technology. Our results demonstrated that the reclamation of wetlands into paddy fields can significantly reduce the α diversity index of soil fungi ($P < 0.05$), whereas the restoration of wetlands can significantly increase the soil fungus Chao1 index ($P < 0.05$). A total of 16 phyla were identified in three types of land use soil, among which Ascomycota, Basidiomycota, Mortierellomycota, and Rozellomycota were the most dominant (relative abundance $> 1\%$). Mycorrhizal fungi and parasitic fungi are the main functional groups of fungi in natural wetlands and restored wetlands, whereas saprophytes were the main functional groups of paddy fields. Soil pH, total carbon, organic carbon, total nitrogen, and total phosphorus are the main factors affecting the diversity of soil fungal communities. Therefore, our findings indicated that resource development in natural wetlands increases potential ecological risks and reduces ecosystem stability.

Keywords: soil pH, soil microbial structure, diversity, Miseq

Introduction

Wetlands are an important natural resource and are among the three most important ecosystems on Earth. Specifically, wetlands play irreplaceable ecological roles such as soil conservation, water purification, and hydrological adjustment (Sui et al., 2021). In recent years, the ecological impacts of wetland land use changes have garnered increasing attention from the scientific community worldwide. Many studies have demonstrated that land use changes can alter the environmental conditions of wetlands and have an important impact on the quality and stability of the ecosystem (Huang et al., 2013; Wang et al., 2017). Overexploitation and excessive utilization of resources and environmental pollution are the main reasons for the loss of biodiversity and functional degradation of wetlands along rivers (Kang et al., 2018). Therefore, coordinating the relationship between wetland resource development and ecological protection has become a key measure to ensure the healthy development of ecosystems and sustainable resource utilization (Hou et al., 2021). Fungi are among the main groups of microorganisms in soil. These microorganisms not only break down recalcitrant substances such as lignin and cellulose derived from plant decomposition but also form tight symbiotic relationships with plants to promote plant metabolism and nutrient absorption, in addition to playing an important role in the accumulation, transformation, and material cycle of soil nutrients (Tedersoo et al., 2014; Yong et al., 2017). At the same time, the spatial distribution

pattern of soil fungi has significant habitat-dependent characteristics, and changes in environmental conditions can thus affect the structure and function of soil microbial communities (Tedersoo et al., 2014). Therefore, the diversity of soil fungal communities is considered to be one of the most important indicators for evaluating the health and stability of ecosystems and is often used to predict changes in soil nutrient conditions and environmental quality (Wei et al., 2017; Rodriguez et al., 2019; Adamo et al., 2021).

The Sanjiang Plain encompasses several wetlands and is an important food production base in China. Therefore, this region is not only ecologically relevant but is also instrumental in ensuring national food security (Wang et al., 2013). Human activities such as reclamation, river sand excavation, and dam construction have changed the types of land use, thus leading to black soil degradation, wetland shrinkage, and biodiversity reduction, and seriously threatening the health and safety of wetland ecosystems (Dang et al., 2020). Therefore, improving habitat quality, biodiversity, and sustainability are key strategies to restore degraded wetland ecosystems (Zhang et al., 2021). Soil fungi are a crucial component of underground biodiversity and thus have an important role in shaping the overall biodiversity and functions of ecosystems. Higher levels of soil fungal community diversity are generally linked to more stable ecosystems (van der Wal et al., 2006; Sun et al., 2019). At the same time, the diversity of soil fungi is affected by natural or anthropogenic factors such as pH value, soil physical and chemical properties, as well as vegetation and land use patterns, and can interact with plants and soil to affect the ecological processes of wetland soil (Puangsombat et al., 2010; Deng et al., 2019). Therefore, characterizing the soil fungal community diversity and its influencing factors in different land use types in the Sanjiang Plain wetland would be conducive to the protection and restoration of this area. However, most studies on the impact of land use on wetlands have focused on the soil nutrients and the temporal and spatial distribution of physical and chemical properties, whereas the structure and function of soil fungal communities in inland river wetlands in northern China have remained largely uncharacterized.

Additionally, very few studies have assessed the status of black soil degradation in the region. Due to the unique geographical characteristics and cold climate of the study location, the soil microbial richness is low and the humus content is high. Further, the soil fungal community structure and its influencing factors are highly complex in this region due to the co-existence of both natural and anthropogenic disturbances (Dai et al., 2020). Therefore, this study sought to elucidate the impact of different land use types on the soil environment of the Sanjiang Plain wetland and evaluate the natural restoration potential of the degraded wetland ecosystem. To this end, the soil fungal community in the Sanjiang Plain wetland was examined using high-throughput sequencing technology and biological information to explore the impact of land use changes on the composition and function of the soil fungus community in the Sanjiang Plain wetland. Additionally, this study analyzed the interaction between the soil fungal community diversity and environmental factors to serve as a scientific basis for the improvement of wetland resource management strategies in the Sanjiang Plain.

Materials and Methods

Research area

This study was conducted in a region of the Heilongjiang Honghe National Nature Reserve (N46°57' 55"–47°14'7", E130°24'51"–130°57'38") located northeast of the

Sanjiang Plain (Figure A1). The area north of the Lahong River and south of the Nongjiang River has a temperate continental monsoon climate, with an altitude of 65–81 m, annual rainfall of 548 mm, and annual evaporation of 1,155 mm. From mid-October through the freezing and thawing season and until mid-May of the following year, the average temperature for 5 months is below 0 °C, the annual average temperature is 2.1 °C, and the frost-free period lasts approximately 130 days. The main vegetation types include wet shrubs and herbaceous plants (e.g., *Deyeuxia angustifolia*, *Carex lehmannii*, and *Phragmites communis*) (Wang et al., 2013), with small areas of farmland and island-like plantations distributed throughout the study region.

Soil collection

In October 2017, three land use types [natural wetland (NW), restoration wetland (RW), and paddy field (PF)] were selected for research in the Honghe Nature Reserve, accounting for a total of nine plots (Figure A2). The latitudes and longitudes of three land use types were 47°44'42''N and 133°35'02''E for natural wetland, 48°15'27''N and 138°30'08''E for restoration wetland and 49°50'32''N and 128°25'07''E for paddy field. Among them, the main vegetation types of the natural wetlands were *D. angustifolia* and *Carex sphaerocephala* (*C. lehmannii*). Further, the restoration of wetlands consisted of leveling abandoned farmlands and artificially transplanting *Carex angustifolia* and *Carex sphaerocarpa*. The paddy fields had been in operation since the beginning of wasteland cultivation in 2010. All plots exhibited small slopes that is between 0.5° ~ 2° and consistent slope on north directions.

Soil samples were collected from each plot in October 2017. Three 10 m × 10 m plots were randomly established in each plot, and soil drills were used to collect surface soil (0–20 cm) samples. The soil samples taken from five points in the same plot were fully mixed, after which the soil samples from each spot were passed through a 2 mm soil sieve and divided into two equal parts (approximately 500 g each), then stored in a cooler with dry ice. Half of each sample was used to extract the genomic DNA of the soil fungi, whereas the other half was used to test the physical and chemical properties of the soil.

Determination of soil physical and chemical indices

The gravimetric method was used to determine soil moisture content (MC); a pH analyzer (HQ30d; Hach Company, United States) was used to determine the pH value of soil; an automatic carbon and nitrogen analyzer (ElementarVarioMaxCN, German Elementar) was used to detect the total soil nitrogen (TN) and organic carbon; and total phosphorus (TP) in the soil was determined via alkali fusion-molybdenum antimony spectrophotometry.

Extraction of soil fungal DNA and PCR amplification

A DNA extraction kit (power soil 12888 Extraction Kit) was used to extract the total soil DNA, and a universal primer pair (ITS1F/ITS2) was used to amplify the internal transcribed spacer (ITS) rRNA gene of soil fungi via PCR. Each reaction was conducted using TransStart Fastpfu DNA polymerase in 20 µL reaction volumes: 10 µL of PCR mix buffer, 1.0 µL of 5 µmol L⁻¹ upstream primer (ITS1), 1.0 µL of 5 µmol L⁻¹ downstream primer, 15 ng of DNA template, and enough double distilled water to reach a 20 µL volume. The following were the PCR reaction parameters: 30 cycles of 95 °C for 5 min; 95 °C for 60 s, 55 °C for 60 s, 72 °C for 60 s; 72 °C for 10 min. The PCR products were

recovered using the AxyPrep DNA gel recovery kit, and the Illumina MiSeq sequencing platform was used to construct a library and conduct high-throughput sequencing.

Bioinformatics and statistical analyses

The QIIME software (version 1.17; <http://qiime.org>) (Caporaso et al., 2010) was used to analyze the sequencing data and divide different operational taxonomic units (OTU) according to a 97% similarity threshold, the USEARCH software (version 7.1) was used to remove chimeric sequences (Edgar, 2010). The RDP (Ribosomal Database Project) Bayesian classification algorithm was used to perform taxonomic analysis on the OTU representative sequences according to a confidence threshold of 0.7 and the resulting sequences were compared with those in the Unite 8.0 its_fungi database. Soil alpha-diversities diversity indices (Ace, Chao1, Shannon, Simpson) were performed by R software (version 3.0, vegan package) based on OTU level. Principal coordinate analysis (PCoA) and was performed by R software (vegan package) based on Bray-Curtis. Permutational multivariate analysis of variance (PERMANOVA) was used to identify soil fungal community characteristics with significant differences and performed by R software (version 3.0, vegan package) based on genus level. The Cladogram of soil fungal communities were performed based on LAD score = 2.5 by R software (version 3.0, vegan package). The Redundancy analysis (RDA) of the soil fungal community and environmental factors were performed by R software (version 3.0, vegan package) based on OTU level. The Funguild micro-ecological tools were then used to predict and analyze soil fungal functions according to nutritional methods. Pearson correlation between soil physicochemical properties and soil fungal α -diversity indexes used IBM SPSS Statistics 17.0 software at 0.05 and 0.01 levels. Significant differences between groups were identified via one-way analysis of variance (ANOVA) coupled with Duncan's multiple comparison and permutation test using the IBM SPSS Statistics 17.0 software.

Results

Differences in soil physical and chemical properties in different land use types

Changes in land use types have had a significant impact on the physical and chemical properties of wetlands in the Sanjiang Plain (*Table 1*). Our findings indicated that the soil pH of the restored wetland and paddy field was significantly higher than that of the natural wetland ($P < 0.05$). The soil pH of the restored wetland was the highest (6.81), whereas that of the natural wetland was the lowest (5.57).

Table 1. Comparison of soil physicochemical properties in different land use types of the Sanjiang wetland

Land use types	pH	MC (%)	SOC (g/kg)	TN (g/kg)	TP (mg/kg)
NW	5.57±0.05c	40.20±3.15b	45.83±8.12a	6.20±0.51a	31.56±3.20a
RW	6.81±0.04a	25.35±2.46c	10.45±2.31c	1.51±0.12c	18.42±2.82c
PF	5.82±0.03b	52.45±3.20a	25.38±5.64b	3.25±0.20b	24.68±1.65b

Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF). MC: moisture content; SOC: soil organic carbon; TN: total nitrogen; TP: total phosphors

The soil water content of the paddy fields was the highest (52.45%), followed by natural wetlands (40.20%), and finally the restored wetlands (25.35%). From a soil nutrient content perspective, the natural wetlands had the highest soil organic carbon, total nitrogen, and total phosphorus content, followed by paddy fields, and finally the restored wetlands. Among these different soil conditions, organic carbon ranged from 10.45 to 45.83 g/kg, total nitrogen ranged from 1.51 to 6.20 g/kg, and total phosphorus ranged from 18.42 to 31.56 g/kg (*Table 1*).

DNA sequencing analysis of soil fungi in each plot

A total of 537,138 pruning sequences were detected in nine soil samples, with an average sequence number of 50,214. The number of soil fungi OTUs in all plots was 1,349. The number of soil fungi OTUs in each type of plot exhibited the following descending order: PF > NW > RW (*Figure 1*). Among them, the number of soil fungi OTUs unique to natural wetlands was 326, accounting for 24.1% of the total OTU number. The number of unique soil fungi OTUs in the restored wetland was the lowest, accounting for only 16.4% of the total OTU number. In contrast, paddy soil exhibited the highest number of unique soil fungus OTUs, accounting for 44.8% of the total OTU data. The number of OTUs shared by all types of plots was 36, accounting for approximately 2.6% of the total OTUs.

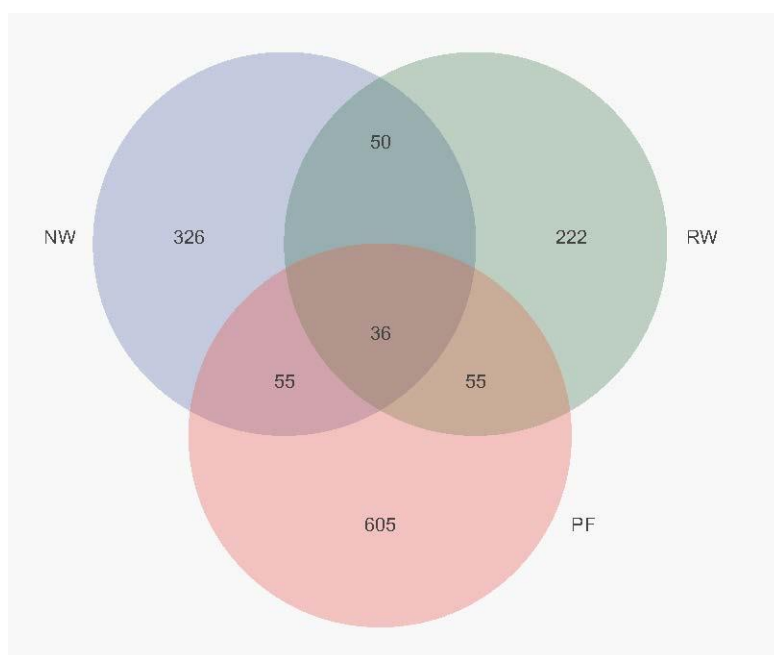


Figure 1. Comparison of the number of OTUs in different land use types. Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

Comparison of soil fungal communities in different types of plots and analysis of indicator species

Taxonomic analysis of OTU at the phylum level (*Figure 2*) indicated that the soil fungi of all soil samples belonged to 16 known fungi phyla. Among them, Basidiomycota, Ascomycota, Mortierellomycota, and Glomeromycota were the main fungal phyla (relative abundance > 1%).

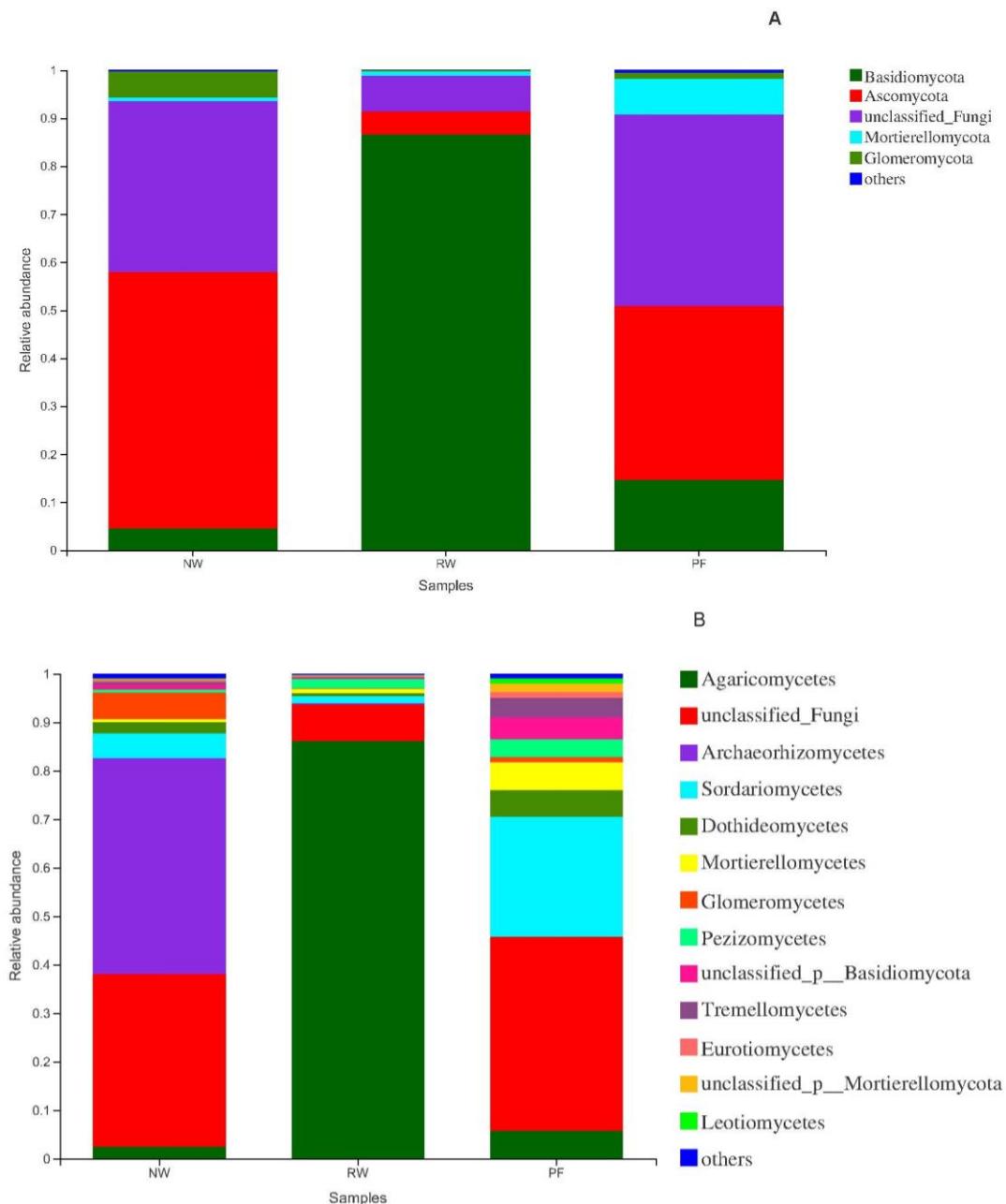


Figure 2. Composition of the horizontal community structure of soil fungus phyla and classes under different land use types. Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

The results of the principal coordinate analysis of the beta diversity distance matrix (Figure 3) indicated that the differences in soil fungi under different land use conditions were mainly attributed to the different land use methods, whereas the internal differences were not significant. The differences between groups determined using PERMANOVA (Figure 2) indicated that there were significant differences in the soil fungal community structure in natural wetlands, restored wetlands, and paddy fields ($P < 0.05$).

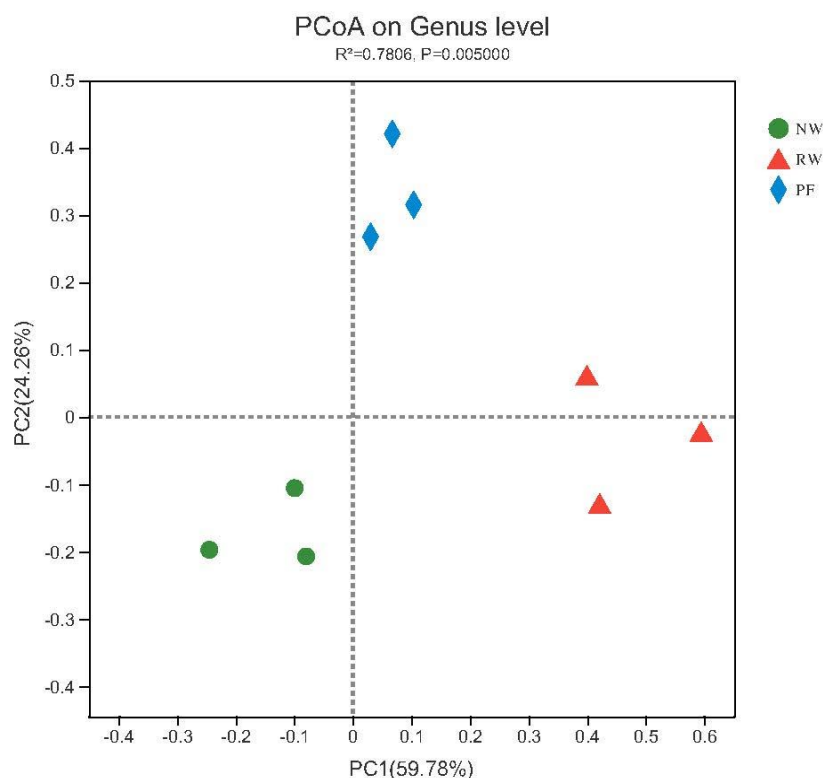


Figure 3. Principal coordinates analysis (PCoA) of soil fungal communities in different land use types. Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

The analysis of the different characteristics of soil fungi of different land use types at each classification level (*Figure 4*) indicated that the dominant soil fungus groups in natural wetlands were Lentitheciaceae, Epicoccum, and Archaeorhizomycetes; the dominant soil fungus groups in rice fields were Ascobolaceae, Pseudombrophila, Dothideomycetes, Serophoma, Ophiosphaerella, Ascobolus, Trichophaeopsis, Mycosphaerellaceae, Setophoma, and Didymella; the dominant soil fungus groups in the restored wetland were Agaricales, Cortinariaceae, Cortinarius, Hebeloma, Inocybaceae, and Inocybe.

Analysis of the relationship between soil physical and chemical properties and soil fungal diversity

By comparing the α diversity of fungal communities in soil samples from different land use types (*Table 2*), the Ace index, Chao1 index, Shannon-Wiener index, and Sobs index of natural wetlands, restored wetlands, and paddy fields were significantly different ($P < 0.05$). Among them, the natural wetland soil fungus Chao1 index was the highest (405.2), whereas the paddy soil fungus Chao1 index was the lowest (165.2); the natural wetland soil fungus Ace index was the highest (425.2) and the paddy soil fungus Chao1 index was the lowest (170.3); the natural wetland soil fungus Shannon-Wiener index was the highest (4.15) and the paddy soil fungus Shannon-Wiener index was the lowest (2.29); the natural wetland soil fungus Sobs index was the highest (359.7), whereas the paddy soil fungus Sobs index was the lowest (151.3).

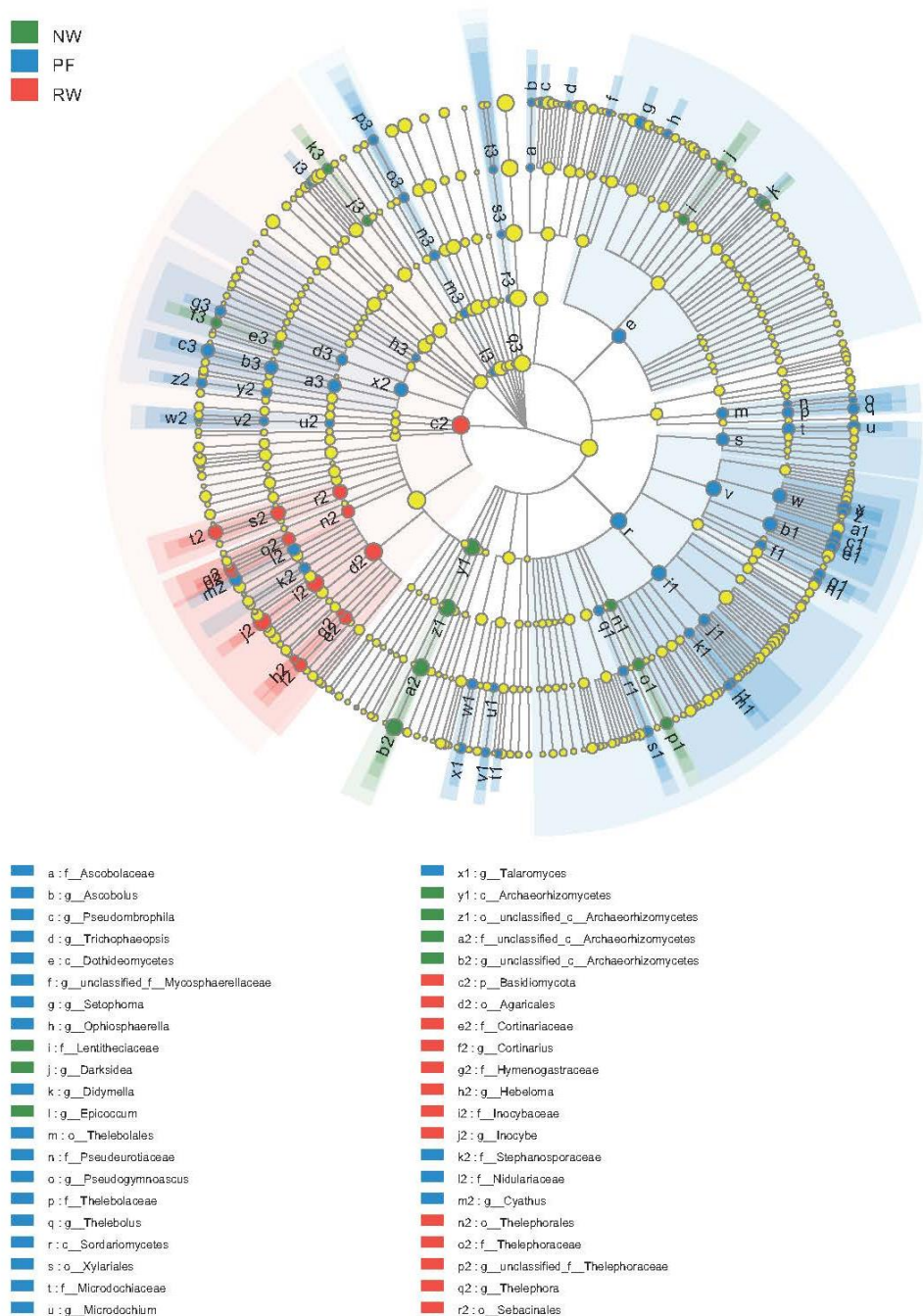


Figure 4. Cladogram of soil fungal communities for the different land use types (LAD score = 2.5). Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

Table 2. Comparison of α diversity index of soil fungi in different land use types

Land use types	Chao1	Ace	Shannon-Wiener	Sobs
NW	405.2±102.79a	425.2±51.72a	4.15±0.44a	359.7±74.01a
RW	221.1±27.70b	220.9±27.26b	3.45±0.76a	202.7±23.02b
PF	165.2±55.79b	170.3±55.27b	2.29±0.40b	151.3±52.54b

Mean±SD (n=3); different lowercase letters indicate significant differences between different land use types ($P<0.05$). Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

The analysis of the correlation between soil physical and chemical properties and soil fungus α diversity (Table 3) indicated that the Ace, Chao1, and Sobs indices were significantly and negatively correlated with soil carbon to nitrogen ratio ($P < 0.05$). Further, there was a significant negative correlation between the Shannon-Wiener index and soil pH ($P < 0.05$), as well as a significant positive correlation between organic carbon, total nitrogen, and the Shannon-Wiener index ($P < 0.01$).

Table 3. Correlation coefficients between the soil physicochemical properties and soil fungal α -diversity indexes

α -diversity	pH	SOC	TN	C/N
Sobs	-0.372	-0.009	0.281	-0.828**
Ace	-0.337	-0.037	0.247	-0.819**
Chao1	-0.352	-0.022	0.262	-0.815**
Shannon-Wiener	-0.650*	0.849**	0.884**	-0.587

* $P < 0.05$; ** $P < 0.01$. Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF); MC: moisture content; SOC: soil organic carbon; TN: total nitrogen; TP: total phosphors; C/N: soil organic carbon/total nitrogen

Prediction of soil fungus functions in different land use type plots

Using the FUNGuild fungus prediction tool, soil fungus functions were predicted based on the fungal community and assuming similar environmental resources (Li et al., 2018). As shown in Figure 5, the detected soil fungi were classified as symbiotrophs based on the way these microorganisms absorb and utilize environmental resources. Among the three types of soil, 12 pathotroph- and saprotroph-specific functions were identified. Concretely, the restored wetland soils exhibited a higher incidence of arbuscular mycorrhizal, plant pathogen, endophyte-litter, animal pathogen-saprotroph, parasite-plant, ectomycorrhizal, wood saprotroph, and arbuscular mycorrhizal functions, whereas plant pathogen functions were more common in natural wetlands, and wood saprotroph and dung saprotroph had significant advantages in rice fields.

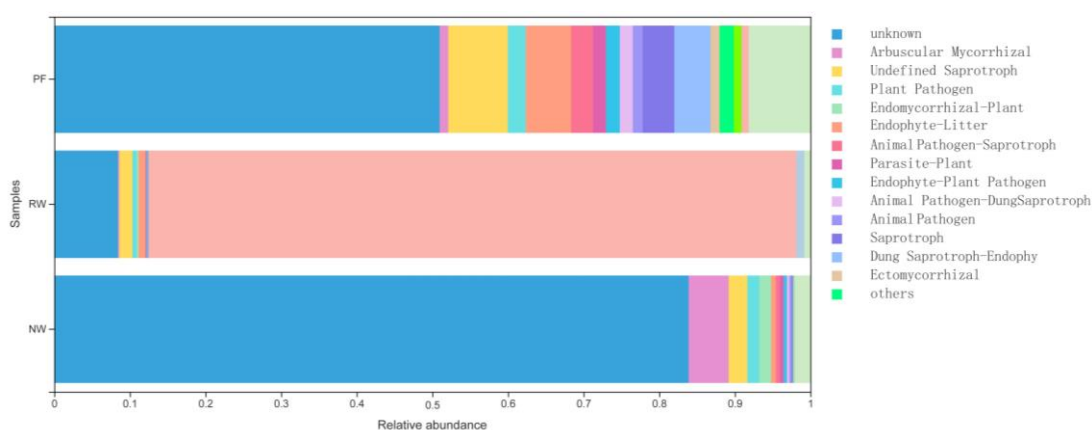


Figure 5. Variations in the composition of the soil fungal functional communities based on the OTU level in different land use types. Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

To analyze the key influencing factors that caused the changes in the soil fungus community structure of the Sanjiang Wetland, redundancy analysis (RDA) was carried out on the structure of the soil fungus community and the physical and chemical properties of the soil (Figure 6). The results indicated that the cumulative variation of the two axes reached 66.16%, which can explain nearly 70% of the soil fungal community change characteristics and their influencing factors. The results of the replacement test indicated that the soil MC ($r^2 = 0.875$, $P = 0.03$), total nitrogen (TN, $r^2 = 0.682$, $P = 0.02$), organic carbon (SOC, $r^2 = 0.542$, $P = 0.05$), C/N ($r^2 = 0.758$, $P = 0.03$), and pH ($r^2 = 0.542$, $P = 0.01$) were key environmental factors that shaped the structure of the fungal communities.

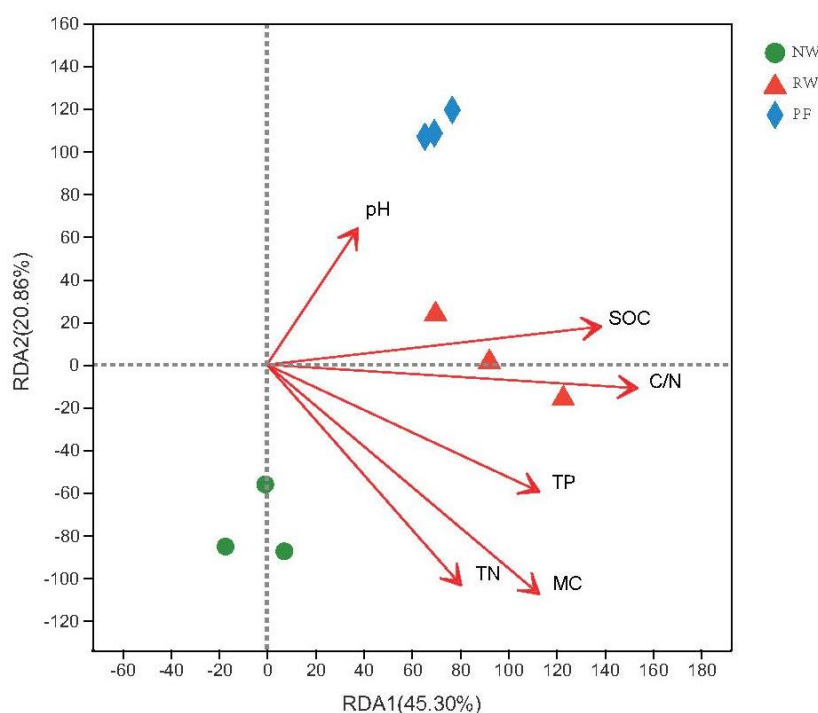


Figure 6. RDA of the soil fungal community and environmental factors in the Sanjiang plain wetland. Note: natural wetland (NW); restoration wetland (RW); and paddy field (PF)

Discussion

Comparison of soil fungal communities in wetlands of different utilization types

Environmental filtration, interspecies competition, and random diffusion mechanisms are among the most important factors to maintain the stability of soil fungal community structures (Li et al., 2018). In this study, we found that the soil fungal structure and diversity of natural wetland, restoration wetland and paddy field were significant changes in the Sanjiang Plain, particularly α diversity index of soil fungi decreasing from natural wetland to paddy field (Table 2). Our findings are consistent with the literature, indicating that land use types changed soil α diversity (Bossio et al., 2005; Sui et al., 2019;), because the condition of the soil environment in the paddy field was influenced by disturbances such as agricultural tillage, which resulted in a higher soil nutrient content than the wetland soils. Moreover, because of above-ground vegetation change, the abundance of litter inputs, the diversity of soil fungi in natural wetland was

also higher than that in the paddy field (Sheik et al., 2012). Wetland restoration did not significantly change the soil fungal community, as short-term wetland restoration did not change the composition of the original fungal community in the soil, and therefore the original fungal community remained in the restored wetland soil. Reclamation of wetlands into paddy fields caused significant changes in the soil fungal community structure, presumably because part of the original soil fungal community structure gradually changed under the influence of chemical fertilizers and pesticides, and therefore the relative abundance of the Basidiomycota in the paddy field was often significantly high.

The α diversity index is an important indicator for evaluating the diversity of soil fungus communities. The diversity of soil fungus communities in wetlands can serve as an indicator of ecosystem health (Sui et al., 2016). Our findings demonstrated that the diversity and richness of the soil fungus communities in restored wetlands and paddy fields were significantly lower than those in natural wetlands. As expected, the diversity of soil fungi in undisturbed natural wetlands is higher than that of converted farmlands at different succession stages. This may be because rice crop cultivation practices severely inhibited the diversity of soil fungi, after which the spread of exogenous fungi was insufficient. Wetland restoration greatly increased the Ace and Chao1 indices of the soil fungal community diversity, whereas the Shannon index did not increase significantly. This may be ascribed to the restoration of soil vegetation after a short-term restoration of the wetland. Further, the restoration of above-ground vegetation might have led to habitat improvements, thus promoting bacterial proliferation. The rapid increase in the number was due to the increase in the Chao1 index; however, the Shannon index did not increase significantly due to the heterogeneous and steady restoration of the wetland ecosystem.

Determining the influencing factors that drive soil fungal community diversity is essential to promote the balance and health of wetland ecosystems. In this study, different land use types changed the physical and chemical properties of surface vegetation and soil, as well as the diversity of soil fungal communities. Further, changes in land use affected material circulation and energy flow in the soil ecosystem (Xu et al., 2017). This study also demonstrated that the diversity of soil fungal communities is closely related to changes in soil pH, total nitrogen, organic carbon, and total phosphorus, which is consistent with the factors affecting soil fungal community diversity reported in a previous study (Anderson et al., 2010). The high soil water content in the Sanjiang Plain wetlands is a prerequisite for a high diversity of soil fungi, and soil pH and nutrient conditions are the key limiting factors for the development of healthy soil fungi communities in wetlands. Most soil fungi in the environment prefer a moist and weakly acidic soil environment, and the community diversity increases with lower soil pH. However, when the pH reaches a certain limit, the soil fungus community diversity begins to decrease. Good soil nutrient conditions can provide the material and energy requirements for fungal survival. However, reclamation in natural wetlands can significantly reduce the content of soil total carbon, total nitrogen, organic carbon, and total phosphorus. The reduction of soil nutrient content also hinders the growth of soil fungi. Further, the survival of the community reduces the diversity of soil fungal communities in wetlands. Additionally, the existing form and content of soil nutrients in the natural environment may affect the use of carbon and nitrogen by soil fungi, which also explains why different forms of carbon and nitrogen are the key limiting factors for the diversity of wetland soil fungi (Anderson et al., 2010).

Function analysis of wetland soil fungi of different utilization types

Higher abundances of soil fungi commonly translate to an increase in functional species, which can play a greater role in maintaining the stability of the structure and function of the ecosystem (Puangsombat et al., 2010). This study demonstrated that natural wetlands exhibited the highest diversity of fungal communities. Functional fungi such as ectomycorrhizal, moss parasitic fungi, lichen parasitic fungi, endophytic fungi, litter saprophytic fungi, and soil saprophytic fungi occupied a large proportion of the overall population, which is consistent with the fungal composition of natural wetlands. Further, the ecosystem exhibited stable structural and functional characteristics. Ectomycorrhizas mostly exist in forests and are aerobic fungi. The relatively high abundance of ectomycorrhizal fungi in natural wetlands may be due to drought conditions in the northern regions of China. The annual flooding duration in the Sanjiang Plain wetlands is very short, which provides several benefits. For example, these conditions promote the growth of oxygen fungi, and the relative abundance of animal and plant pathogenic fungi in natural wetlands is extremely low. This may be due to the elimination of lesser resistant species through natural selection, and therefore the remaining wetland vegetation has high resistance to animal and plant pathogenic fungi. Additionally, a stable interaction is formed between wetland plants and soil microorganisms, which can secrete metabolites and effectively inhibit pathogen invasion (Casper, 2006). The relative abundance of dung rot fungi in the restored wetlands was significantly higher than that of the other soil samples. This may be because wild animals often choose bare beaches as foraging grounds. Constructed wetlands often contain sand as a substrate, which slowly transforms into silt similar to natural wetlands. This results in a habitat type that is different from natural wetlands, thus serving as a large habitat and spawning ground for birds, frogs, and other animals. Fecal rot fungi are introduced by animal activities (Zhu et al., 2009). The relative abundance of animal and plant pathogenic fungi in rice fields was significantly higher than that of other habitats. This may be due to the imbalance of the soil-plant-microbial system interaction caused by human cultivation, fertilization, and pesticide use, as well as the loss of some fungal community components. These processes may introduce pathogenic microorganisms into rice paddy fields, which may be directly related to the occurrence of rice blast disease (Lumini et al., 2011). This study used Funguild microecological tools to classify fungal communities using similar environmental resources (Schmidt et al., 2019). As a result, many repeated classifications were identified, which is one of the shortcomings of this functional classification method.

Conclusions

Changes in wetland land use in the Sanjiang Plain can lead to a significant decrease in soil nutrient content and a gradual increase in soil pH, resulting in a continuous decrease in the diversity of soil fungal communities. As the habitat conditions continue to deteriorate, soil fungal communities tend to become less diverse, which increases the relative abundance of a few dominant fungal communities. The Sanjiang Plain wetland is naturally resilient, and therefore the diversity of fungal species can be quickly recovered. The relative abundance of plant pathogenic fungi in relatively closed farmland habitats was significantly higher than that in natural wetlands and restored wetland habitats, whereas the relative abundances of ectomycorrhizal fungi and parasitic fungi in natural wetlands were significantly higher than those in farmland and

restored wetlands. The underlying mechanisms related to soil fungal composition and function deterministic factors are multifaceted and provide a fruitful area for further investigation.

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APPENDIX

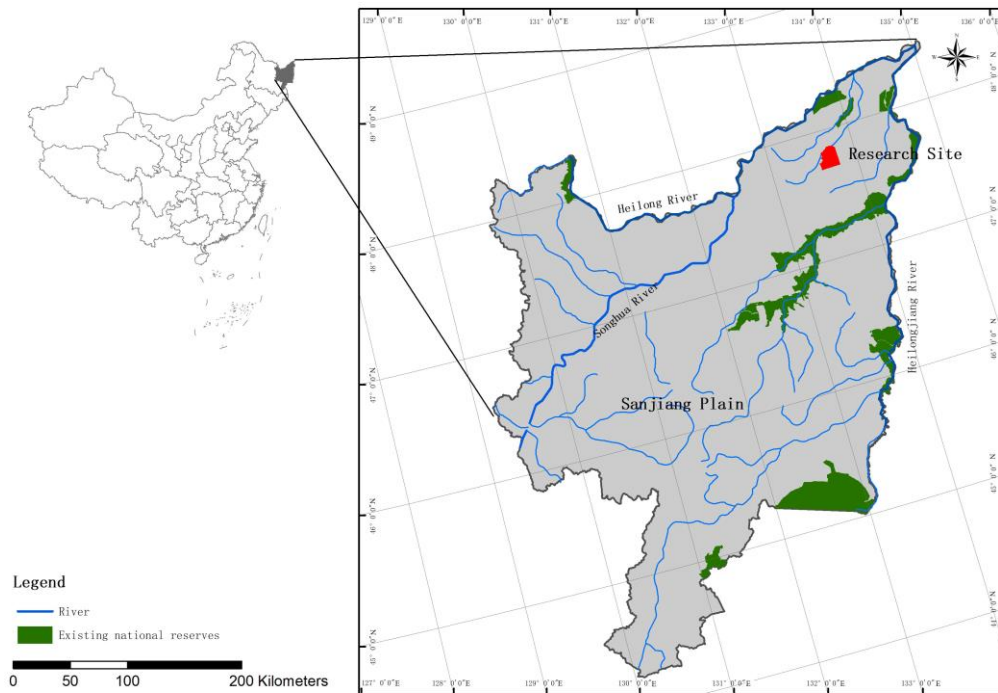


Figure A1. Location of sampling sites in the Sanjiang Plain

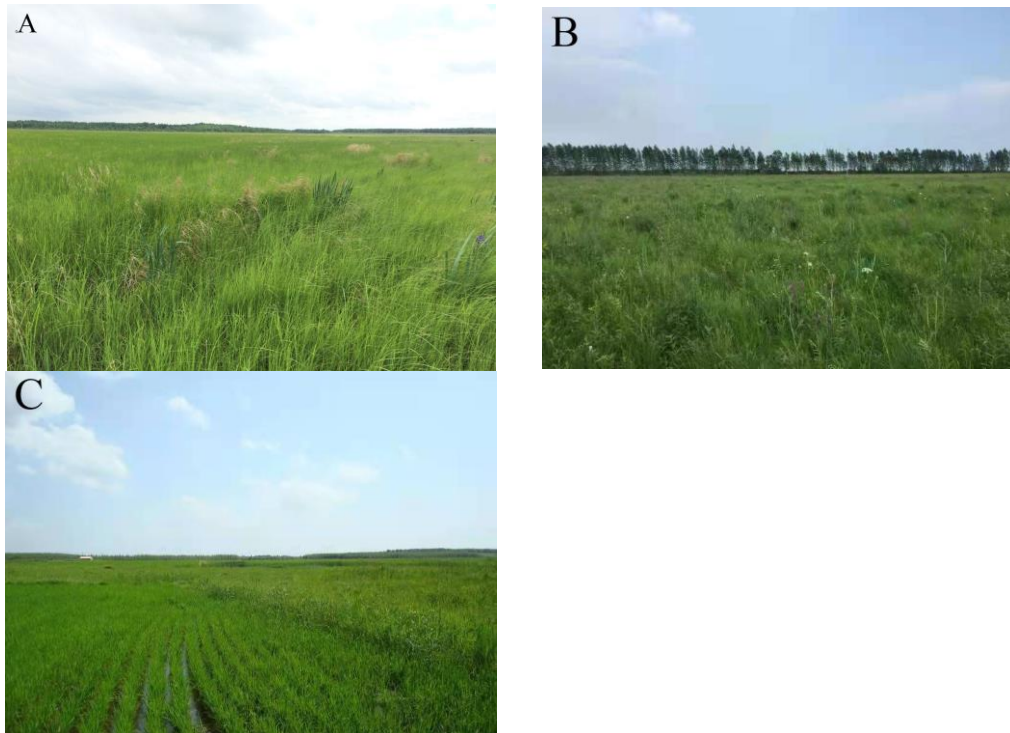


Figure A2. Habitats of three land use types: natural wetland (A), restoration wetland (B) and paddy field (C) in the Sanjiang Plain