

CONVERSION OF WETLANDS TO FARMLAND AND FORESTS REDUCES SOIL MICROBIAL FUNCTIONAL DIVERSITY AND CARBON USE INTENSITY

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(Received 2nd Jun 2022; accepted 2nd Sep 2022)

Abstract. Changes in land use types typically lead to changes in soil ecosystem functions, and soil microorganisms can sensitively reflect soil quality and the evolution of different ecosystem functions. To characterize the impact of land use changes on the microbial function of wetlands, our study assessed three typical land use types (wetland, farmland, and forest land) in the Sanjiang Plain, and Biolog microplate technology was used to study the changes in the use intensity and functional diversity of different soil microbial carbon sources, as well as their relationship with soil physicochemical properties. Our findings indicated that the physical and chemical properties of soil changed significantly in different land use types ($P < 0.05$). The functional diversity and carbon source metabolism of wetland soil were significantly higher than those of farmland and forest. Furthermore, the utilization intensity of compound carbon sources was significantly higher than that of forests and farmland, whereas amino acids, esters, alcohols, amines, and acid carbon sources did not change significantly. Soil water content, total phosphorus, organic carbon, available phosphorus, and other physical and chemical factors affected soil microbial function in different land use types. This study provides key insights into the mechanisms through which land use changes affect soil microbial functions in the Sanjiang Plain, and it also serves as a theoretical basis for the protection and sustainable utilization of wetlands in the future.

Keywords: *Sanjiang Plain, reclamation, functional diversity, soil physicochemical, carbon source utilization efficiency*

Introduction

Soil microorganisms are an important part of soil ecosystems and have important roles in organic matter decomposition, nutrient cycling, promotion or inhibition of plant growth, and various soil physical processes (Sui et al., 2022). Studies have shown that several microbial activity indicators such as soil microbial biomass, respiration intensity, and changes in microbial community structure and functional diversity can sensitively reflect soil quality and health status. Therefore, these biological indicators are indispensable for soil environmental quality evaluation (Weng et al., 2022).

Changes in land use patterns affect the cycle and supply of soil nutrients, directly causing changes in soil texture and subsurface microbial community structure (Sui et al., 2019; Turley et al., 2020), which in turn leads to changes in soil microbial diversity. In recent years, Biolog Eco microplates have been used to study microbial diversity in a variety of media including sediments (Lopes et al., 2016) and activated sludge (Paixão

et al., 2007). This method can be used to quickly characterize environmental samples and has therefore been applied in many fields. Deng et al. (2018) employed this technology to study the impact of different land use patterns on the diversity of soil microbial communities in the mountainous areas of Liaodong. Zhu et al. (2018) also found that cultivated land exhibited the lowest soil microbial metabolic activity among different land uses, whereas grasslands exhibited the strongest soil microbial metabolic activity and therefore, the highest microbial biomass carbon, followed by forest lands. Moreover, among six types of carbon sources, carbohydrates, amino acids, and carboxylic acids exhibited the highest relative utilization rates. Qin et al. (2017) reported that forest land can retain more soil nutrients, in addition to possessing higher bacterial and fungal diversity. Current research on soil microbial diversity has largely focused on natural soils such as forest land and grassland, and changes in land use patterns are known to significantly affect soil microbial activity and functional groups. However, very few studies have assessed the functional diversity of wetland soils, especially under different land use patterns.

The Sanjiang Plain Wetland is the largest concentration of freshwater wetlands in China and this ecosystem is highly biodiverse. The wetland ecosystem in the Sanjiang Plain is essential for the process of protecting regional biological resource diversity and maintaining the integrity of ecosystem functions (Sui et al., 2021). Therefore, this study employed Biolog microplate technology to study the changes in soil microbial functional diversity and carbon source utilization capacity under different land use patterns in the Sanjiang Plain. Moreover, the correlation between the soil carbon source metabolic diversity of microorganisms and environmental factors was also discussed. Understanding the functions of wetland ecosystems in the Sanjiang Plain provides a theoretical basis for the protection and sustainable utilization of wetland ecosystems in the future.

Materials and methods

Research area

The study site is located in the Sanjiang Plain in Heilongjiang Province (133°37'–133°45'E, 47°43'–47°52'N) and has an average elevation of 5.14–51.5 m. The site belongs to the mid-temperate continental monsoon climate zone and is mostly dry in spring. The region is windy, hot, and rainy in summer and cold with moderate snowing in winter, with an average annual temperature of 2.3 °C. The average precipitation is 454 mm. The freezing period begins in early November and the thawing period is in early May. The three land use methods selected in this area were the following: (1) Pristine wetlands, with an area of approximately 500 hm², the vegetation is mainly composed of *Deyeuxia angustifolia*, *Stellaria radians*, *Anemone dichotoma* and *Thalictrum simplex*. (2) Farmlands, which were transformed via swamp wetland reclamation 10 years ago, with an area of approximately 500 hm²; corn is the main crop in this area. (3) Forest, with an area of approximately 500 hm². This large artificial pure forest was planted in wetland soil 20 years ago.

Sample collection

In October 2021, three standard 10 m × 10 m plots were selected from the original wetland, farmland, and forest sample plots. Within each sampling plot, Fifteen to 20 soil

samples (0–20 cm) were obtained. After the top layer (0–20 cm) of soil samples was evenly mixed, the gravel and rhizomes in the samples were removed and then sieved through a 2 mm sieve. A portion of the sample was placed in a 15 mL centrifuge tube, stored in liquid nitrogen, transferred to the laboratory and stored at -80 °C for DNA extraction and microbiological analysis. The rest of the soil samples were divided into two parts in the laboratory, one was kept at 4 °C, and the other was air-dried for the determination of soil physicochemical properties.

Determination of physical and chemical properties of soil samples

Determination of soil moisture content: 0.01 g of fresh soil samples were accurately weighed and placed in an aluminum dish, after which they were maintained at 10 ± 2 °C. The samples were then dried in a constant temperature drying chamber for 8 h, then weighed again to determine the moisture content. pH: soil pH was measured with a pH meter at a water-soil ratio of 2.5:1. Soil organic matter: soil organic carbon content was measured with a Vario TOC instrument produced by Elementar, Germany. Total nitrogen: 0.25 g of soil sample was accurately weighed and passed through a 0.149 mm sieve. Next, 2 g of accelerator mixed with zinc sulfate and copper sulfate and 5 mL of concentrated H₂SO₄ were added for digestion.

Biolog-Eco microplate test

The Biolog-Eco microplate culture method was used to detect the carbon metabolism capacity of the wetland soil microbial community. A portion of the soil sample was activated at 25 °C for 1 d, after which 10 g of the activated fresh soil was placed in a 200 mL conical flask. Next, 90 mL of 0.85% sterile NaCl solution was added to the flask, after which the flask was mixed and sealed. Afterward, the samples were placed in a shaker for 0.5 h at 200 r•min⁻¹. Then, the soil suspension diluted to 10⁻³ was inoculated into the microplate with a pipette. Each experiment was repeated three times, and the microplate was continuously cultured at 25 °C for 168 h. During the culture, the absorbance value at a wavelength of 590 nm was recorded every 24 h.

Data analysis

Average well color development (AWCD) was calculated as follows:

$$AWCD = \sum(C_i - R)/31 \quad (\text{Eq.1})$$

In the formula, C_i is the absorbance value of the carbon sources at 590 nm; R is the absorbance value of the control well; the carbon source well with C_i-R < 0 is denoted as 0 in the calculation.

Soil microbial diversity index calculation:

$$\text{Shannon index: } H = P_i \ln P_i \quad (\text{Eq.2})$$

$$\text{Simpson index: } D = 1 - (\sum P_i)^2 \quad (\text{Eq.3})$$

$$\text{Margalef index: } D = (P_i - 1)/\ln P_i \quad (\text{Eq.4})$$

In the formula, P_i is the ratio of the difference between the absorbance values of the i -th carbon source well and the control well (n_i) to the sum of the relative absorbance values of all wells.

Data analysis was performed using Excel 2010. The SPSS 25.0 software was used for one-way analysis of variance (ANOVA) and Duncan tests at a 0.05 significance level. One-way ANOVA was conducted to identify variations in soil physicochemical parameters, soil microbial α -diversity, and the microbial utilization of different carbon sources in different land use types, after which Duncan tests were conducted. Scatter plots with trend lines were generated in Excel 2010 and SigmaPlot 10.0 was used to draw histograms. Analysis of soil microbial alpha diversity, redundancy analysis (RDA), and principal coordinates analysis (PCoA) were conducted in R (version 3.3.2) using the ‘vegan’ package (R Core Team, 2022). Permutational multivariate analysis of variance (PERMANOVA) between all habitats and each land use type were performed in R software (version 3.3.2) using the “vegan” package (R Core Team, 2022).

Results

Changes in soil physical and chemical properties under different land use patterns

Table A1 (see Appendix) summarizes the physical and chemical properties of the soil in the three land use modes. There were significant differences in soil pH, moisture content (MC), soil organic carbon (SOC), total nitrogen (TN), total phosphor (TP), available phosphor (AP), and available nitrogen (AN) among different land use types ($P < 0.05$). Overall, the soil SOC, TN, TP, AP, MC and AN of the original wetland were the highest. The pH values of the different soil types exhibited the following descending order: forest > farmland > wetland. MC exhibited the following order: wetland > forest > farmland.

Soil microbial alpha diversity of the wetland in Sanjiang Plain

To further determine the effect of different land uses on soil microbial functional diversity, the AWCD value at 168 h of cultivation was selected for α diversity analysis. As indicated in Table 1, all indices except for the Margalef richness index showed significant differences. Particularly, the Shannon, Simpson, and AWCD indices were the highest in the original wetlands and the lowest in the farmland. This indicated that the functional diversity of soil microorganisms decreased significantly after the wetlands were converted into farmland.

Table 1. α -Diversity of soils with different land use types

Land use type	Shannon	Simpson	Margalef	AWCD
Wetland	3.4 ± 0.03a	0.96 ± 0.00a	9.8 ± 0.46a	1.14 ± 0.08a
Farmland	3.3 ± 0.03b	0.96 ± 0.00b	12.0 ± 1.76a	0.88 ± 0.02b
Forest	3.3 ± 0.03a	0.96 ± 0.00ab	12.0 ± 0.83a	0.89 ± 0.06b

The values represent the mean ± standard deviation ($n = 3$); different lowercase letters indicate significant differences among different treatments based on Duncan tests ($P < 0.05$)

The relationship between soil microbial functional diversity indices and soil physicochemical properties in Sanjiang Plain is shown in Table 2. Except for MC and

TN, the environmental factors pH, AN, AP, TP, and SOC were all correlated with AWCD, the Shannon index, the Simpson index, and the Margalef index. AWCD was positively correlated with AN and TP but negatively correlated with pH. The Margalef index was correlated with AN and negatively correlated with TP. The Shannon index was positively correlated with AP and SOC. The Simpson index was positively correlated with AN, AP, and SOC.

Table 2. Correlation between soil environmental factors and soil microbial functional diversity in different land use types

	pH	AN	AP	TP	TN	SOC	MC
Simpson	-0.54	0.67*	0.81**	0.45	0.32	0.89**	0.41
Shannon	-0.41	0.54	0.78*	0.32	0.14	0.87**	0.52
Margalef	0.59	-0.72*	-0.62	-0.77*	-0.55	-0.58	-0.08
AWCD	-0.69*	0.82**	0.64	0.81**	0.62	0.64	0.04

* $P < 0.05$; ** $P < 0.01$

Carbon source metabolic activity of soil microorganisms in different land use types

The AWCD reflects the overall ability of the microbial community to utilize a single carbon source in the Biolog-ECO plate and is an important indicator of the functional diversity of the microbial community (Song et al., 2019). As shown in *Figure 1*, the soil microbial community AWCD increased with cultivation time in all of the examined land use types. The AWCD values of the soils of all plots remained low from 0 to 48 h. After 48 h, the AWCD values of the original wetland soil microorganisms increased rapidly, but the increase rate of the forest and farmland soils was slow. This indicated that the utilization of carbon sources by soil microbes began after 48 h. In general, the AWCD values of 31 carbon sources under different land use patterns exhibited the following trend: wetland > forest > farmland. It is also worth noting that there was no significant difference in AWCD values between forest and farmland ($P > 0.05$). However, both of them were significantly different from the original wetland ($P < 0.05$).

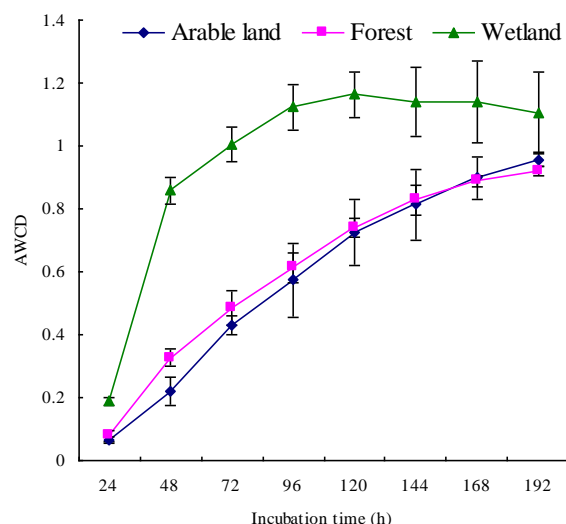


Figure 1. AWCD of the soil microbial community in different land use types of the Sanjiang plain. The data and error bar were expressed as the mean \pm standard deviation

There are 31 carbon sources in the Biolog-ECO board, which can be divided into six categories, namely 7 carbohydrates, 6 amino acids, 4 esters, 3 alcohols, 3 amines, and 8 organic acids. *Figure 2* illustrates the utilization of different carbon sources by soil microorganisms under different land use patterns in the Sanjiang Plain. Overall, only the carbohydrate carbon sources showed significant differences ($P < 0.05$) under different land use patterns, whereas the other five types of carbon sources did not show significant differences. However, the utilization intensity of all 6 types of carbon sources reached a maximum in wetland soil. This indicated that the wetland soil microorganisms had the highest utilization activity of the six types of carbon sources.

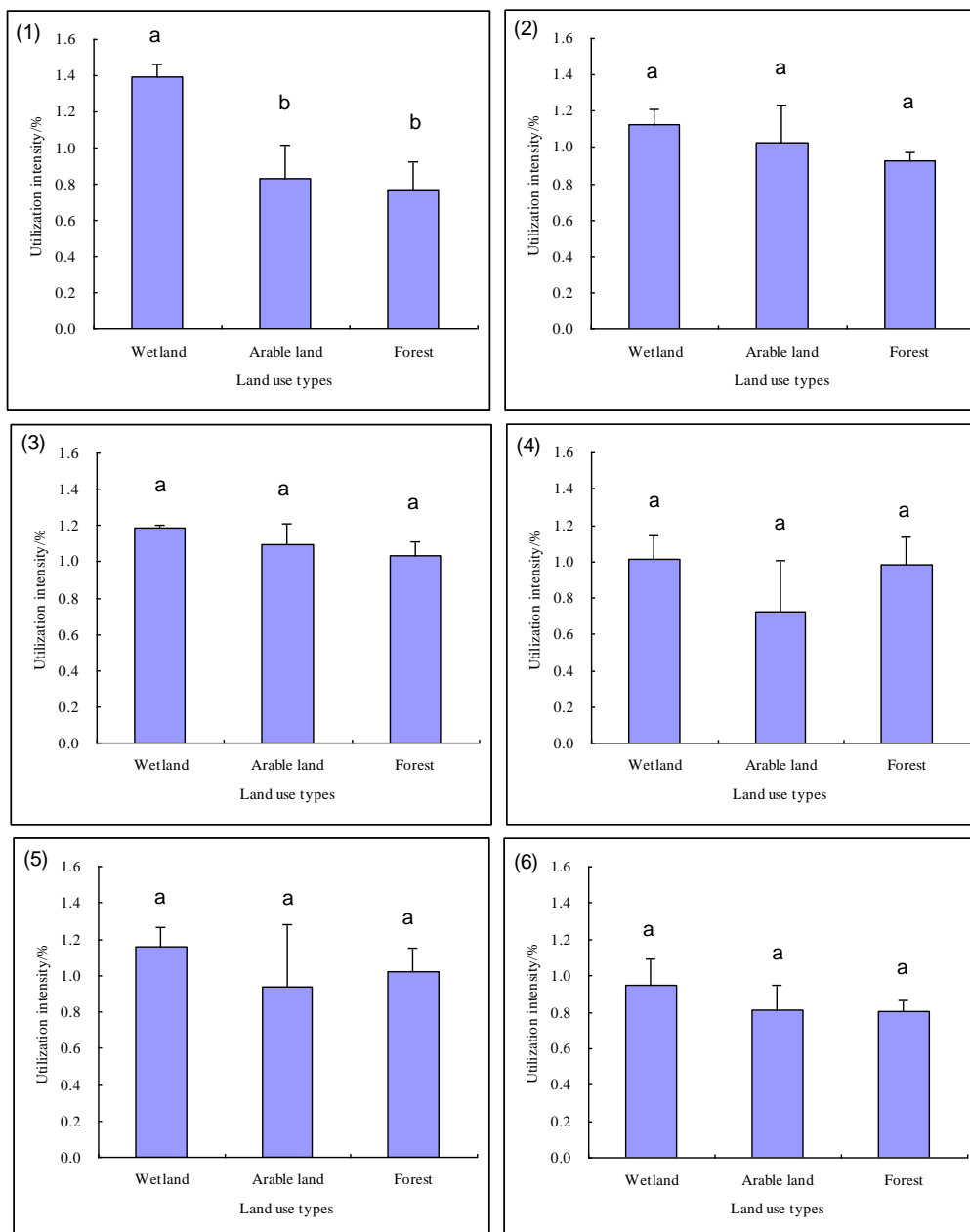


Figure 2. Changes in the microbial utilization of different carbon sources in different land use types. Different lowercase letters indicate significant differences among different nitrogen treatments based on Duncan tests ($P < 0.05$). (1): carbohydrates; (2): amino acids; (3): alcohols; (4): esters, (5): amines; (6): organic acids

As illustrated in *Figure 3*, there were significant differences in the metabolic activities of 31 carbon sources in soil microbial communities under three different land use methods. Wetland soil microorganisms mainly used α -cyclodextrin, α -D-lactose, glycogen, 4-hydroxy benzoic acid, and D-xylose. Farmland soil microorganisms mainly used L-asparagine, D-galactonic acid- γ -lactone, γ -hydroxybutyric acid, D-cellobiose, and L-serine. Forest soil microorganisms mainly used L-asparagine, D-mannitol, phenylethyl-amine, D-galacturonic acid, and L-serine. The PCoA results showed that the variance contribution rates of Pco1 and Pco2 were 45% and 17%, respectively (see *Fig. 4*). Overall, there were significant differences in the soil microbial community functions between wetlands, farmland, and forests (*Figure 4; Table A2*).

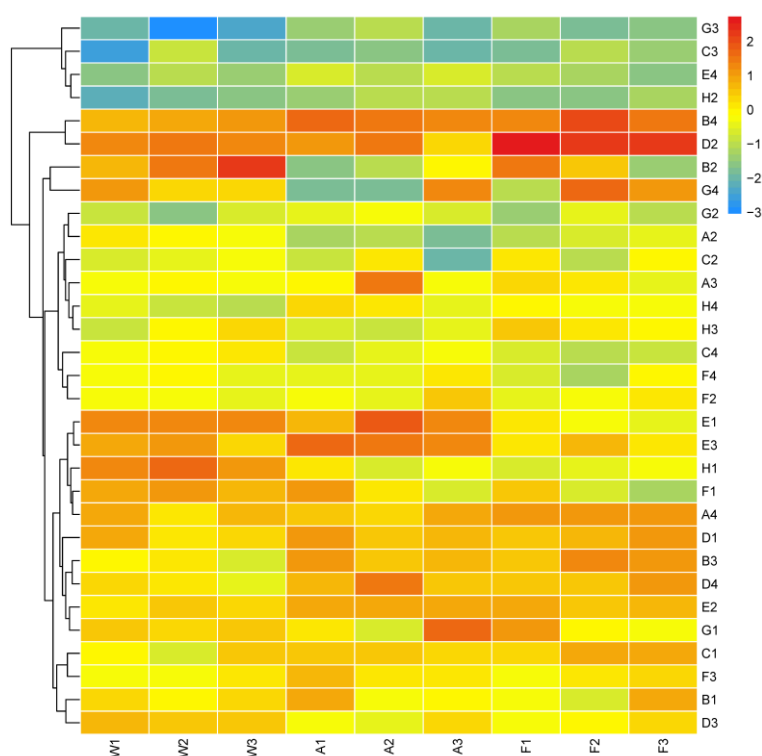


Figure 3. Metabolic activity heat map of soil microbial community in different land use types in the Sanjiang Plain. W(1-3): wetland, A(1-3): farmland, F(1-3): forest. G3- α -ketobutyric acid; C3-2-hydroxy benzoic acid; E4-L-threonine; H2-D, L- α -glycerol phosphate; B4-L-asparagine; D2-D-mannitol; B2-D-xylose; G4-phenylethyl-amine; G2- α -D-glucose-1-phosphate; A2- β -methyl-D-glucoside; C2-i-erythritol; A3-D-galactonic acid- γ -lactone; H4-putrescine; H3-D-malic acid; C4-L-phenylalanine; F4-glycyl-L-glutamic acid; F2-D-glucosaminic acid; E1- α -cyclodextrin; E3- γ -hydroxybutyric acid; H1- α -D-lactose; F1-Glycogen; A4-L-arginine; D1-tween 80; B3-D-galacturonic acid; D4-L-serine; E2-N-acetyl-d-glucosamine; G1-D-cellobiose; C1-tween 40; F3-itaconic acid; B1-pyruvic acid methyl ester; D3-4-hydroxy benzoic acid

Relationship between soil microbial carbon utilization activity and soil physicochemical properties

Redundancy analysis (RDA) was performed on the AWCD values of soil microbial communities in the Sanjiang Plain wetland cultivated for 168 h under different land use patterns (*Figure 5*). The first two RDA axes explained 48.29% and 17.98% of the

variance, respectively. The soil microbial community exhibited obvious spatial differences in carbon source utilization under different land use patterns. Particularly, changes in land utilization patterns had an impact on the ability of wetland soil microbes to utilize different carbon sources. Additionally, the RDA results demonstrated that MC, TP, SOC, and AP were among the soil environmental factors that had the greatest impact on soil microbial function. Among them, forests were significantly positively correlated with MC, pH, SOC, and AP, whereas wetlands were positively correlated with TN, TP, AN, AP, and SOC, and farmland was positively correlated with pH, TN, AN, and TP.

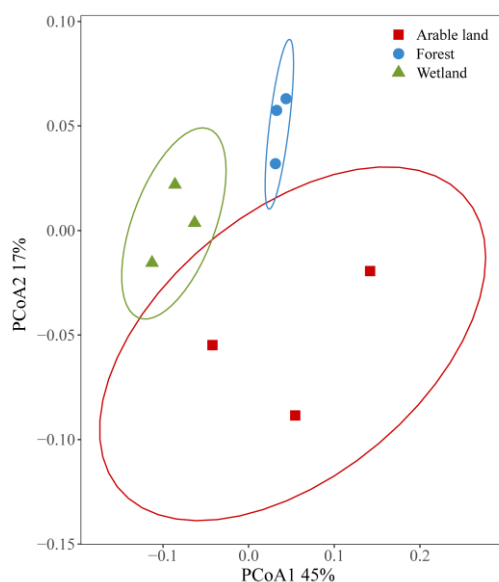


Figure 4. PCoA of soil carbon source metabolism of the different land use types

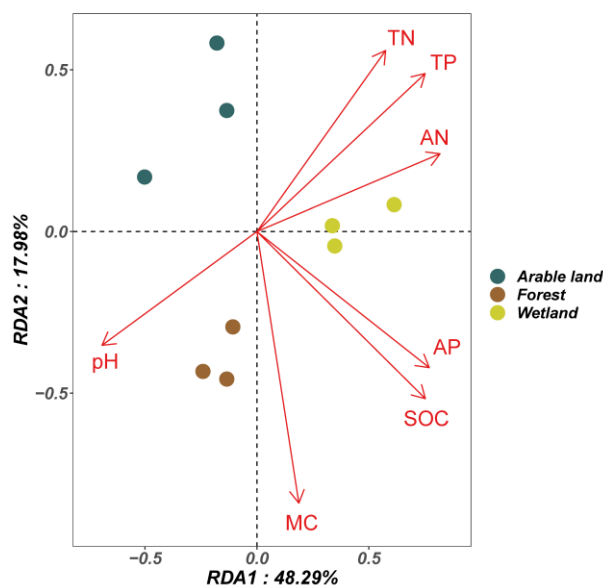


Figure 5. Redundancy analysis of soil carbon sources and soil physicochemical properties of the different land use types

Discussion

Effects of land use patterns on soil microbial functional diversity

Different land use patterns significantly affected the functional diversity of soil microbial communities. The AWCD of the original wetland was significantly higher than that of the farmland and forest (*Table 1*). This indicated that the soil microbial carbon source utilization ability decreased after the transformation of the original wetland. Moreover, the results of the Shannon index study also showed that the soil microbial functional diversity of the original wetland was significantly higher than that of the forests and farmland. In other words, the diversity and ability of soil microbes to utilize carbon sources decreased once the wetlands were converted into forests and farmlands. This may be due to the stability of the original wetland soil ecosystem. When wetlands are converted into farmlands and forests, the soil microbial structure changes due to the disturbance of aboveground vegetation and human activities (Sui et al., 2019; Guo et al., 2021). Jia et al. (2020) also found that after the original wasteland was converted into cultivated land, the microbial carbon source utilization rate decreased.

Land use can directly change the physicochemical properties and structure of soil, thereby affecting the soil microbial community and playing an important role in shaping its diversity (Burton et al., 2010). In a previous study that assessed the functional diversity of soil microorganisms in different land use types in the Sanjiang Plain, the authors found that there were significant differences in the soil microbial alpha functional diversity in the different land types, and the diversities of the original wetland and forest were significantly higher than those of farmlands. In primitive wetlands and forest ecosystems, the soil environment is conducive to the reproduction and growth of microorganisms due to the high diversity of aboveground vegetation, which results in high functional diversity. Therefore, the diversity of soil microbial species decreases and harmful microorganisms increase in farmland ecosystems, and the functional diversity of farmland soil microorganisms will be significantly lower than that in wetlands and forests. Zhang et al. (2015) compared the soil microbial functional diversity of primitive wetlands and paddy fields, and the results were consistent with this study, suggesting that microbial metabolic diversity is related to carbon input. Moreover, this study also found that soil microbial Shannon diversity was positively correlated with organic carbon utilization. Therefore, the soil microbial Shannon diversity of farmland soil was lower due to low carbon input and agricultural disturbances.

Effects of land use patterns on soil microbial carbon source metabolism

This study found that there were significant differences in soil carbohydrate carbon sources when the original wetland was converted into forest and farmland, and the utilization intensity of carbohydrate carbon sources in wetland soil microorganisms was significantly higher than that in forest and farmland soils. However, no significant differences were observed in the utilization of amino acids, esters, alcohols, amines, and organic acids. There is currently no consensus regarding the utilization patterns of different types of carbon sources by soil microorganisms. This may be because microbial communities are highly sensitive to soil environmental changes and stresses, resulting in changes in microbial carbon utilization patterns related to changes in environmental parameters (Kumar et al., 2017). Moreover, different carbon source types

have different functional groups (e.g., carbohydrates: R-C = O; amino acids: -NH₂ and -COOH; carboxylic acids: -COOH; phenolic compounds: -OH; amines: -NH₂; polymers: monomers). Carbohydrate carbon sources are the most widely used carbon sources by soil microorganisms, and decreases in carbohydrate utilization may be related to a decrease in the overall diversity of soil microorganisms. Sui et al. (2019) studied soil microbial diversity in different succession stages in the Sanjiang Plain and found that wetland soil microbial diversity was significantly higher than that of forests. Therefore, this may explain why carbohydrate utilization in wetland soil was higher than that in forest and farmland. However, our findings indicated that although the differences in the utilization of amino acids, esters, alcohols, amines, and organic acids were not significant, the utilization intensity of these carbon sources by wetland soil microorganisms was still higher than in forests and farmlands. This may be because the forest and farmland in this study had not been transformed from wetlands for a long time, and the original microbial composition in the soil may not have changed significantly. Therefore, the utilization of other carbon source types by soil microorganisms has not changed significantly. However, Wang et al. (2017) studied the metabolic intensity of soil microbial carbon sources in the Xiaoyezhang wetlands, larch plantations, and soybean fields in the Sanjiang Plain, and found that the utilization of all types of carbon sources were significantly different.

Currently, there are many methodological difficulties and obstacles in the determination of soil microbial functional diversity. On the one hand, the Biolog analysis method can only reflect the functional diversity of microorganisms from the perspective of metabolic characteristics, but cannot reflect the diversity of specific species. Only the culturable microorganisms that can utilize the carbon source on the plate can be reflected. Furthermore, after the mixed culture is added into the wells of the Biolog microplate, synergistic effects or countermeasure effects will cause the final color in the microplate to not necessarily represent the simple sum of the colors produced by various microorganisms alone. Therefore, a combination of techniques is needed to comprehensively characterize changes in soil microbial function. High-throughput sequencing technology has proven to be a very powerful tool in microbial ecology research. Therefore, this technology must also be implemented in ecology studies to fully and accurately reflect the functional diversity of soil microorganisms. This approach would provide important insights into the factors that shape the structure of microbial communities and the response of microorganisms to environmental changes. In turn, this would improve our understanding of the dynamics of natural or managed ecosystems.

Conclusion

Our findings demonstrated that changes in the land use types in the Sanjiang Plain resulted in significant variations in soil microbial functional diversity and carbohydrate utilization. The α -diversity of wetland soil microorganisms was significantly higher than that of forest and farmland soils. Moreover, the utilization of different carbon sources by wetland soil microorganisms was also higher than that of forest and farmland microbes. The differences in soil microbial functional diversity, carbon source utilization capacity, and microbial functional diversity of carbon source utilization under different land use patterns were related to soil physicochemical factors. Soil MC, TP, SOC, and AP are the most important environmental factors affecting soil microbial

function. Collectively, our findings revealed the impact of soil microbial functions on wetland ecosystems and provide a theoretical basis for the future management and sustainable utilization of wetland ecosystems.

Acknowledgements. This study was supported by the “Touyan” Innovation Team Program of Heilongjiang Province, China (Grant Number: [2019] No. 5).

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APPENDIX

Table A1. *Physicochemical properties of soils with different land use practices*

Land use types	pH	MC (%)	SOC (g/kg)	TN (g/kg)	TP (g/kg)	AP (mg/kg)	AN (mg/kg)
Wetland	4.5 ± 0.13c	43.5 ± 2.79a	55.4 ± 0.97a	4.2 ± 0.22a	7.0 ± 0.55a	47.5 ± 1.70a	365.9 ± 19.11a
Farmland	5.5 ± 0.13b	18.2 ± 0.70c	27.3 ± 2.15c	3.3 ± 0.09b	5.1 ± 0.40b	28.7 ± 0.63c	194.6 ± 5.52b
Forest	6.1 ± 0.21a	28.5 ± 4.76c	45.1 ± 1.52b	1.8 ± 0.21c	3.5 ± 0.51c	38.7 ± 1.39b	141.0 ± 11.13c

MC, soil moisture content; SOM, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; AN, available nitrogen. The values represent the mean ± standard deviation (n = 3), different lowercase letters indicate significant differences among different treatments (P < 0.05)

Table A2. *Permanova analysis of soil microbial community functions comparing two types along different land use types in Sanjiang Plain, northeastern China*

Land use types	R ²	P
Habitat	0.48	< 0.05
Wetland versus farmland	0.45	< 0.05
Farmland versus forest	0.65	< 0.05
Forest versus wetland	0.58	< 0.05