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Conversion from natural wetlands to forestland and farmland alters the composition of soil fungal communities in Sanjiang Plain, Northeast China

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ABSTRACT

To understand the effect of human activities on fungal communities in wetland, forestland and farmland soils, in this study, we investigated the relationship between the composition of soil fungal communities and their perturbations in wetland in northeast China. The results showed that a total of 132 OTUs were identified from all three site types combined, while 72 were exclusively shared between farmland and pristine wetland, 60 between forestland and pristine wetland, and 305 between farmland and forestland. All sites also hosted unique fungal OTUs, with 397 OTUs unique to farmland, 388 unique to pristine wetland and 463 unique to forestland. The obtained sequences were affiliated to nine different phyla throughout the dataset. Sequence abundance showed that Ascomycota members were more frequently identified than Basidiomycota, in all soil samples. The dominant phyla were specific for habitat type with Ascomycota for wetland, Ascomycota and Zygomycota for farmland, and Ascomycota and Basidiomycota for forest land. The diversity of the fungal community was found highest in farmland, lower in forestland, and lowest in wetland. Canonical correlation analyses demonstrated that changes in land use significantly altered the fungal community composition of the soil. The β -diversity of the soil fungal community was most affected by soil pH, total carbon, nitrogen and phosphorus, as well as available nitrogen and available phosphorus in the soil. Cultivation can significantly enhance the fungal diversity. These findings highlight the importance of effectively managing the soil fungal community to maintain a naturally functioning soil ecosystem.

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Introduction

Sanjiang Plain, located in Northeastern China, originally contained vast areas of marsh wetland that naturally covered the original black soil. This soil has a high humus content and a relatively low number and variety of microorganisms, due to the special climatic conditions that apply to this geographical location. Therefore, the local ecological systems are fragile and can easily be destroyed, in particular since the environment is quite suitable for agricultural development [1,2]. It has been estimated that 84% of the wetland has been converted to farmland in the past 30 years [3]. Since the government implemented an active policy of turning farmland back to wetland or to forest, the region now displays areas with variable vegetation, of both agricultural farmland, wetland and forest. Agriculture is still being practiced, as it is required to feed the relatively high population in this region [3]. Therefore, three land types

(wetland, forestland and farmland) currently co-exist in Sanjiang Plain.

Intensive land use has locally severely lowered the water table, seriously affecting both organic and inorganic matter cycles of the wetland ecosystems and, in places, resulting in barren soil. This has obviously severely changed the community structure and composition of soil microbes [3–5]. These negative effects were reported by scientists who expressed their concerns, and eventually the subject got to the attention of the Chinese government. In recent years, this has resulted in intensive studies towards the impact of wetland cultivation [6,7], the treatment of wetland pollution [8], and wetland microbial participation in carbon and nitrogen cycles, which have become hot research topics [9,10]. It is now realized that soil microbes are highly affected by the soil's ecological environment, and ways are being explored to remediate this environment by specifically controlling soil microbes [1].

Bacteria are the most abundant microbes in soil, but fungi represent the second-most abundant microbial community. Fungi are widely distributed in the soil, where they are involved in decomposition of organic matter, mineralization processes, the natural cycling of chemical elements, and degradation of pollutants; therefore fungi represent important players in restoring a damaged ecological environment [11]. The fungal community structure and composition is affected by changes in soil nutrients and by other environmental changes, which in turn can directly affect soil functions [12]. Therefore, a detailed investigation is needed to classify and characterize the fungi of soils under different land use conditions. This can lead to a better understanding of the processes behind decomposition of organic matter, nitrogen fixation, effects on plant growth and the degradation of organic pesticides [13–15].

Traditional culture-dependent methods do not accurately reveal the community structure, function and diversity of fungi, because a large number of these cannot be cultivated. Molecular techniques have become an important tool to explore microbial diversity, the role of taxonomic groups and their relationship with the environment [16]. Non-cultured soil fungi can be identified by sequencing a fragment of their genomic DNA, and these sequences not only identify the fungal taxa but, by quantitative comparison, can also produce insights in relative abundances, resulting in a thorough understanding of soil fungal communities [17].

We have used next generation high-throughput DNA sequencing to assess the diversity of soil fungi and their relative abundance, as well as the relationship between soil fungi and soil environmental factors in the three different land use types of Sanjiang Plain. The generated data revealed the impact of land use changes on the fungal soil inhabitants. This research is of great practical significance to improve the utilization of microbial resources for local environmental management practices, and provides scientific insights into the protection and utilization of our wetlands.

Materials and methods

Site description and soil sampling

This study was conducted at the Sanjiang Wetland Experimental Station, owned by the Institute of Nature

and Ecology of Heilongjiang Academy of Sciences, China (47°35'N, 133°31'E). Three sites, representing wetland, forest and farmland, were selected for this study. The local climatic conditions can be summarized as follows: annual average temperature of 1.9 °C with a monthly range from −21.6 °C (January) to 21.5 °C (July); annual average precipitation of approximately 560 mm, 80% of which occurring between May and October.

Sampling was performed on 15 October 2016. Eight soil samples of approximately 1 kg were taken at 0–20 cm depth from each location and transported inside polyethylene bags in an ice-cooled container. In the laboratory, approximately 10 g soil was placed in a sterile 2 mL microcentrifuge tube and stored at 4 °C for Biolog analysis. The remaining part of the samples was air-dried to determine a number of physiochemical properties. These were measured as described before [18] and included the pH of the soil mixed with water (1:5 w/v); total organic carbon (TC), total nitrogen (TN) and total phosphorus (TP) content, as well as available nitrogen (AN) and available phosphorus (AP). The physicochemical properties of the soil samples from the three different types of land use are summarized in Table 1. Statistical analysis was performed by using SPSS 17.0 for Windows.

Soil DNA extraction and high-throughput sequencing

DNA was extracted from 0.5 g of each frozen soil sample as previously described using the MOBIO PowerSoil DNA Isolation Kit (USA) [18] and stored at −20 °C until use. The ITS1 region of fungal ITS rRNA was selected for PCR amplification and pyrosequencing [19]. High-throughput sequencing was performed by the Shanghai Majorbio Biotechnology Company, Shanghai, China. Barcoding was used to simultaneously sequence multiple samples. Sequence reads shorter than 150 bp were discarded, as were sequences with imprecise base calling, or reads starting with primer sequences that had two or more mismatches.

OTU-based analysis

The sequence reads were used to identify operational taxonomic units (OTU). Optimized gene sequences with gene lengths greater than 350 bp were selected,

Table 1. Physicochemical properties of soil from three different land use types.

Type	pH	Total carbon (g/kg)	Total nitrogen (g/kg)	Available nitrogen (mg/kg)	Total phosphorus (mg/kg)	Available phosphorus (mg/kg)
Wetland	5.47 ± 0.04 ^b	52.67 ± 1.34 ^a	4.29 ± 0.79 ^a	455.25 ± 29.58 ^a	6.36 ± 1.17 ^a	26.34 ± 1.82 ^a
Farmland	5.77 ± 0.06 ^b	25.60 ± 1.41 ^b	3.13 ± 0.63 ^b	197.61 ± 7.48 ^b	3.71 ± 0.72 ^b	26.65 ± 3.59 ^a
Forest	7.35 ± 0.05 ^a	25.13 ± 1.52 ^b	1.80 ± 0.32 ^c	143.75 ± 7.20 ^b	3.17 ± 0.51 ^b	32.71 ± 4.46 ^a

Statistical significance ($p < 0.05$) is indicated by identical superscript letters in the same column.

compared with the SILVA database and then clustered. Clustering analysis was performed using Mothur Software and the UniFrac statistical analysis tool was used to compare fungal community compositions [20]. Fungal functional groups were inferred by using FUNGuild.

Fungal community diversity and rarefaction curve

The species diversity and richness of the fungal communities under study was investigated by determination of Ace, Chao1, Shannon and Dice indices. Alpha-diversity was measured at significance levels of 97% (0.03). The estimates were calculated by employing the tools Aligner, Complete Linkage Clustering and Rarefaction of the RDP pyrosequencing pipeline. Randomly sampled reads were used to calculate a rarefaction curve [21].

Analysis on whole-sample similarity

Venn diagrams were constructed to visualize similarity in OTU content between samples [22]. The Jost algorithm was used to compare the differences in OTUs from the eight soil samples and to calculate the number of sequences from each OTU. A Canonical Correlation Analysis (CCA) was conducted by using R software. LEfSe was used to find indicator fungal groups specialized within the three types of samples [23].

Results and discussion

Analysis of different land use patterns by high throughput sequencing technology

The physicochemical properties of soil, combined with available water levels and gas phase, determine the survival of microorganisms. Changes in soil composition will significantly change the habitat. In the Sanjiang Plain wetland, changes in land use have caused considerable changes in the soil physical and chemical properties, with effects on the soil microbiota. After the conversion of wetlands to farmland, the top soil has become more susceptible to erosion, which in places could be so severe that the land has been left barren. Studies have indicated that the soil water retention improved after conversion from farmland to artificial forest, resulting in higher water tables [24,25]. The soil porosity of farmland is higher than that of forest soil, and also higher than that of wetland because of cultivation, while the bulk density is lower than that of the woodland and wetland.

After sequencing the ITS1 region of fungal ITS rRNA present in the obtained DNA, rarefaction curves were constructed showing the relationship between individuals and species for a randomly selected number of

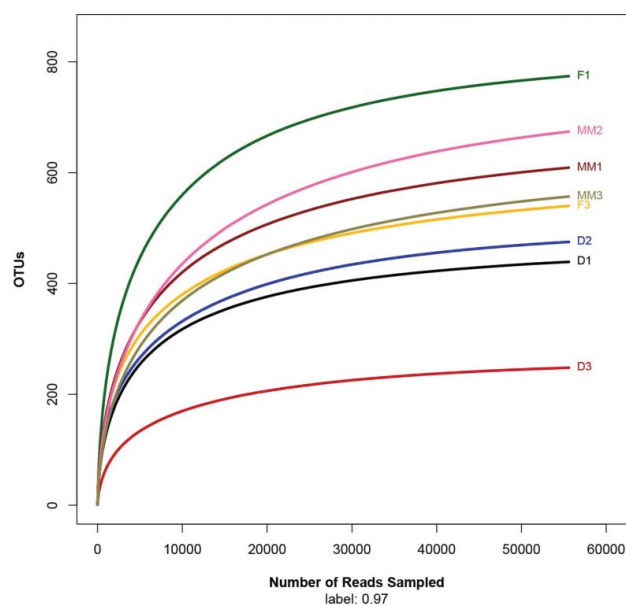


Figure 1. Rarefaction curves showing the extent of OTU detection at the different samples, with D: wetland; F: farmland; MM: forestland.

individual reads from all three sample types (Figure 1). This produced a relatively flat rarefaction curve, indicating that the sequencing data reasonably covered the existing variance, and that adding more sequencing data would only produce relatively few new OTUs.

The distribution of soil fungal community in different land use types

A Venn diagram was constructed to show the number of common and unique OTUs in the three samples (Figure 2). There were a total of 1817 different OTUs, of which 132 (7.3%) were encountered in all three land use types. Forest soil produced the largest number of OTUs (960 in total), accounting for 52.8% of the total OTUs obtained. Of those, 463 were unique to forestland, which is 48.2% of all forest soil OTUs and 25.5% of all obtained OTUs. Wetland soil produced only 652 OTUs (35.9% of the total) of which 388 were unique (equalling to 59.5% of wetland OTUs and 21.4% of the total OTUs). Farmland soil had produced 906 different OTUs, with 397 unique ones (43.8%, or 21.6% of the total). Thus, the total number of OTUs recovered from farmland and forest soil was significantly higher ($P < 0.05$) than that of wetland. The fractions of unique OTUs relative to the total fraction per soil type, or relative to the total OTUs recovered, did not significantly differ.

Figure 2 also illustrates how many OTUs were found in two out of three soil types. Farmland and forest soils had 437 OTUs (30.1% of the 1429 recovered OTUs from both land types), of which 305 (21.3%) were not found in

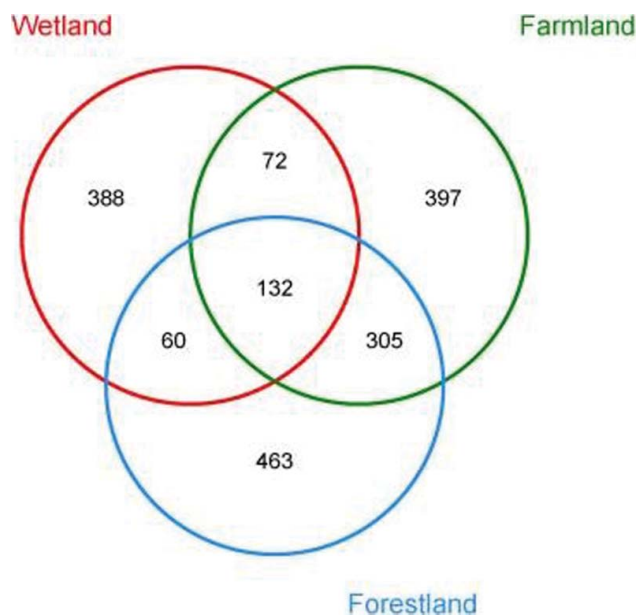


Figure 2. Venn diagram showing the numbers of shared and unique OTUs of fungal species obtained from soil of the different land use types.

wetland soil. These represent 16.8% of the total OTUs recovered. In contrast, only 60 OTUs were shared by forest and wetland soil but not found in farmland (3.3% of the total). The OTUs that were detected in wetland and farmland but not in forest soil represented 4.0% of the total. From these data it can be concluded that the distribution of fungal OTUs is most distinct between wetland and forest soil, while farmland soil more resembles forest than wetland soil in terms of numbers of recovered OTUs.

The α fungal diversity of different land use patterns

Calculating the microbial diversity index from obtained DNA sequences that have been attributed to OTUs is an effective method to evaluate the diversity of a microbial community. Exploring the diversity of soil microorganisms in different land use patterns is helpful to understand the structure and function of soil microbes, which reflects the health status of soil ecosystems in Sanjiang wetland. The α fungal diversity was used to analyze the fungal diversity in the soil of the three different land use types. Four different methods were used to calculate diversity indices. The results showed that the soil fungal

community diversity of wetland was lower compared with those of the other land use types (Table 2). The Ace diversity index was more distinctive, while the calculated Shannon and Simpson indices were not significantly different between the samples. Based on the results from Ace and Chao calculations, we conclude that farmland and forest land significantly increased the soil fungal community diversity compared to the original wetland. The qualitative and quantitative changes of soil microbial communities are sensitive indicators for monitoring the soil quality both for short- and long term changes [26].

Taxonomic composition of soil fungal communities in different soils

The taxonomic composition of the detected fungi is shown in Figure 3, with panel A showing the phyla found. In all three soil types, Ascomycota were more frequently identified than Basidiomycota, though the fraction of Ascomycota was lower in soil from farmland compared to the other two sample types. The wetland soils were richest in organic matters, with nearly double the amount of total carbon compared to the other two soil types (Table 1). Possibly because of this, wetland soil had a relatively high fraction of unclassified members. In contrast, the phylum Zygomycota was mainly found in soil from farmland, where Glomeromycota and Rozellomycota were also detected, while the Basidiomycota were highest in forest soil. Regarding the functional groups (guilds), the natural wetland and farmland soils were dominated by undefined saprotrophs, which were underrepresented in forest soil (Figure 3(b)). The latter was dominated by ectomycorrhizal fungi, which could be expected given the dominance of ectomycorrhizal trees (larch and birch) in the sampled forest. Fungi are of great ecological importance, and the fungal community composition of soil is affected by soil management [27] and nutrient status [28]. It was noted that the three wetland samples resulted in more variable distribution of fungal functional groups, compared to the limited variation within the farm and within the forest samples. In this study, we obtained a lower fungal diversity of wetland compared to farm- or forestland, which was consistent with previously described research [29]. The

Table 2. Fungal α -diversity indices of three different land use types.

Types	Ace	Chao	Shannon	Simpson
Wetland	407.51 \pm 73.80 ^a	405.17 \pm 74.25 ^a	3.34 \pm 0.46 ^a	0.10 \pm 0.03 ^a
Farmland	691.9700 \pm 112.61 ^b	696.52 \pm 110.52 ^b	4.20 \pm 0.29 ^a	0.07 \pm 0.02 ^a
Forest	666.09 \pm 35.37 ^{ab}	666.47 \pm 37.47 ^b	3.98 \pm 0.12 ^a	0.04 \pm 0.00 ^a

Statistical significance ($p < 0.05$) is indicated by identical superscript letters in the same column. Different superscripts represent lack of statistical significance.

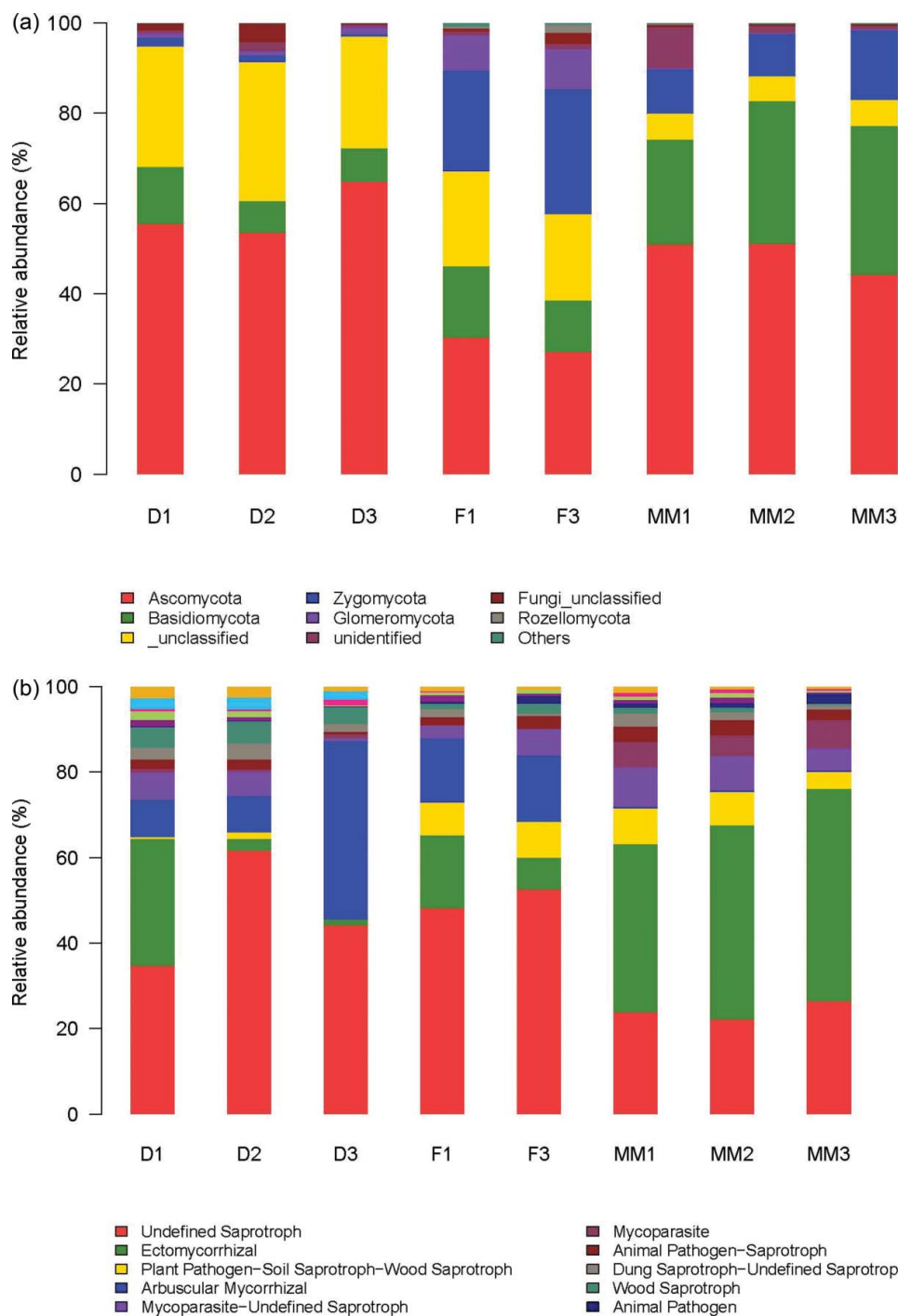


Figure 3. Variation in fungal community compositions across the soils from different land use types. (a) Taxonomic composition at the phylum level. (b) Compositions of fungal functional groups (guilds) inferred by FUNGuild. D1–D3 represent samples from wetland; F1 and F3 from farmland and MM1–MM3 from forest.

wetlands sampled here were most of the time flooded, resulting in decreased oxygen content. This most likely limits the growth of fungi, resulting in a more homogeneous community structure.

The diversity of soil fungi in farmland and forest was significantly higher than that of wetland, because the farmland was affected by frequent tillage, which resulted

in the fact that soil oxygen content was higher than that of wetland. In addition, the forest soil remained undisturbed once forest had been planted, which is beneficial for aggregates of microbiota that can fix organic carbon in soil [30]. This effect possibly increased the soil microbial biomass and maintained the microbial diversity [31], including that of fungi.

Variations in vegetation have major effects on soil microbial composition [32]. Studies have indicated that different plant species have different effects on soil microbial communities [33]. Likewise, plant roots have a significant effect on soil microbes [34] as do plant root exudates [35]. Plants form underground ecosystems with variable microbial components, depending on the plant species present [36]. Therefore, the relationships between microbes, vegetation and the environment need to be studied in order to understand processes and interactions at play to form local ecosystems and to predict trends in ecosystem changes. The results of the present study show that there were significant differences in soil fungal community structure and function when original wetland was converted to farmland and forestland. This indicates the obvious importance of vegetation type and land use on the soil fungal community structure and function.

Fungal groups with statistical differences

Diversity was further investigated by linear discriminate analysis (LDA). Figure 4 shows a cladogram of lineages with LDA scores 3 or higher. This mostly grouped the clades for soil type, with the exception of the wetland

clade, which also contained members obtained from farmland and 2 members from forest soil. A total of 635 fungal groups were distinct to at least one soil using the default logarithmic score LDA value of 2 (Figure 5).

The LDA scores were plotted for indicator fungal groups using a cutoff value of 3 (Figure 5). Using this cutoff, there were only 4 groups of fungi enriched in wetland, namely Ascomycota and Leotiomycetes, as well as unassigned fungi and unidentified fungi, all of which had an LDA value higher than 4 (Figure 5).

There were 13 fungal lineages enriched in the farmland passing the cutoff. Of those, the Pezizales, Pezizomycetes, Hypocreales, Tremellomycetes and Chytridiales produced LDA values higher than 4.5 in farmland. There were also 13 phyla enriched in forest soil: in particular the Mortierellales, Incertae sedis and Zygomycota phyla were enriched in this soil type, producing LDA values higher than 5 (Figure 5).

The relationships of fungal diversity and soil physical and chemical properties

The OTU (97%) composition of soil fungi was lastly analyzed by Canonical Correlation Analysis (CCA), testing the effect of various parameters including the

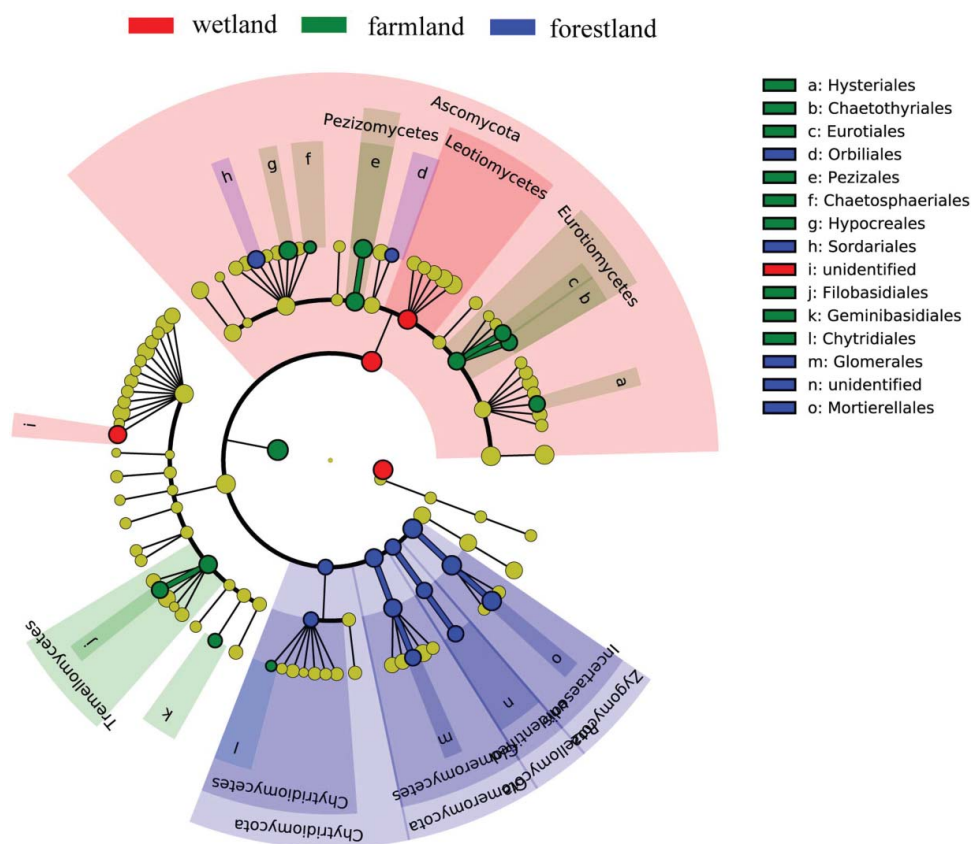


Figure 4. Cladogram indicating the phylogenetic distribution of microbial lineages associated with the three land use types.

Note: Lineages with LDA 3 or higher determined by LEfSe are displayed. Differences are represented in the colour of the most abundant class (red indicating wetland, green farmland, purple forest).

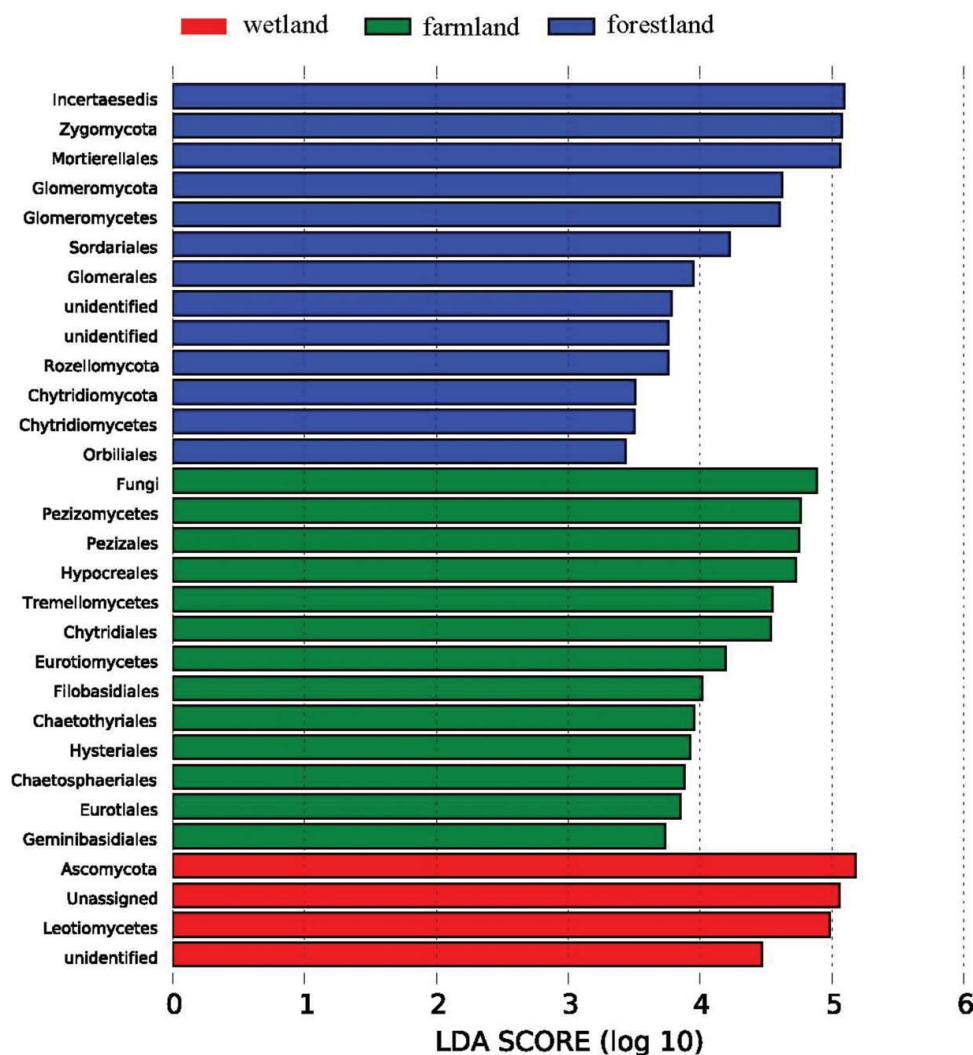


Figure 5. Indicator fungal groups within the three land use types plotted for LDA values.
Note: Only phyla with LDA values higher than 3 are shown.

physicochemical properties of the soils, which produced a contribution rate of the two axes of 81.77% (Figure 6). For the first ordinal axis, the fungi from forestland and farmland soils were distributed in the positive direction while those from original wetland were distributed in the negative direction, indicating that the first two land types were the main influencing factors of the first sorting axis. The level of available phosphorus (AP) and the soil pH are also positively correlated with the first ordinal axis, while TP, TC, AN and TN are negatively correlated with the first ordinal axis. That indicates that pH, AN, TN, TP and TC had the most significant effect ($P < 0.05$) on soil fungal community structure.

Environmental changes provide the specific conditions for fungal survival or limitation of growth, thus selecting particular fungal community structures most suited to the local conditions [37]. Our data showed how nine identified fungal phyla are affected in the three studied habitats of Sanjiang Plain. The variation of fungal

composition indicated that changes in land use destroyed the original wetland soil fungal community. New habitat conditions were formed with altered flora, resulting in the increase and/or decrease of specific populations, which thus changes the fungal community diversity [38].

Different habitats typically contain multiple high and low relatively abundant fungal species [39]. In our case, the relative abundance of the Ascomycota, Leotiomycetes and Unassigned fungi in wetland soil was significantly higher than that in forest and farmland soil, while the relative abundance of the Basidiomycota was significantly higher in forest soil, and Rozellomycota, Zygomycota and Glomeromycota were higher in farmland. The CCA analysis showed that the factors, i.e. pH, organic matter, phosphorus, available nitrogen and total nitrogen, had significant effects on fungal community structure (Figure 6). The high diversity of fungi in farmland soil is remarkable. Such insights play an important role

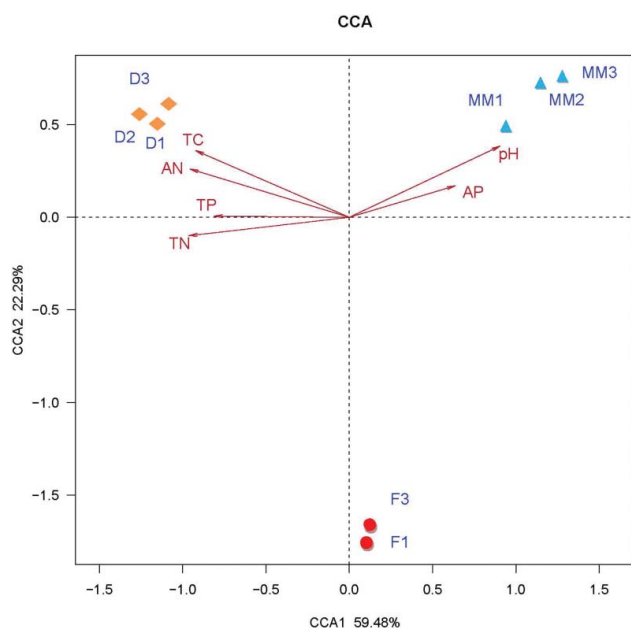


Figure 6. CCA of soil fungal community and environmental factors, showing the effect of soil type as well as soil pH, total C, P and N concentrations, and available nitrogen (AN) and phosphorus (AP) levels.

to regulate the soil ecosystem balance and promote sustainable farmland practices [40].

High-throughput sequencing technology provides a very effective method to analyze soil fungal communities and functions [28]. Our findings corroborate previous observations, namely that changed land from wetland to farm and forest land increased the soil fungal diversity (3.34–3.44) [41]. Soil carbon, total nitrogen and pH can improve the soil microbial diversity by supplying nutrients and this seemed to be particularly the case in farmland due to fertilization; hence, soil nutrient conditions are a key factor to control the soil microbial community diversity.

The process of changing from wetland to farmland and then to forest can indirectly affect the soil fungal community structure by changing the soil hydrothermal conditions, soil structure and soil nutrient conditions [42]. Changes in soil fungal community diversity are a direct manifestation of adaptation to land use changed, which can accelerate the decomposition of soil organic matter and also promote plant uptake of soil nutrients [43]. Changes in land use patterns affected the soil physical and chemical properties (organic carbon, total nitrogen, available phosphorus and phosphorus decreased) but the soil microbial diversity increased, inferring that a decrease in carbon and nitrogen can improve the soil diversity. This result seems to contradict the observation that the contents of TC, TN, AN and TP significantly

decreased from wetland to forestland. The explanation may be that the original wetland soil was extremely rich in organic matter as a result of long-term flooding. Although the soil nutrient content is very high, it is present in a form that cannot be used by the majority of soil fungi. As the land use changed, these nutrients were converted to other forms which provided favourable conditions for the utilization of carbon and nitrogen for soil fungi. Therefore, the content of carbon and nitrogen is not a key limiting factor of soil fungal diversity and is not a suitable parameter. We studied the effects of six environmental factors on soil fungal community diversity, but some important factors such as soil temperature and soil oxygen content were not included, so that their impact remains to be studied.

Conclusions

The results from this study demonstrated how the fungal community responds to land use activities of original wetland soils converted into forest and agricultural land, through the effects on various soil factors, not only those related to soil environments. The differential responses of the fungal communities to specific abiotic soil factors can help to reveal what drives the population changes in Sanjiang plain soils recently converted for cultivation. This can help open the possibilities to explore fungal communities as bioindicators for Sanjiang plain soil management effects in the wide Sanjiang plain area, North-east of China.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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