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# Phosphorus fractions affect fungal compositions and functions under land use conversions in saline-alkali soil in northeastern China

Juan Hu<sup>1,2</sup>, Yingxin Huang<sup>1,2\*</sup> and Daowei Zhou<sup>1,2</sup>

## Abstract

**Background** Little is known about the link between the fungal community and phosphorus fractions when land use is converted from cropland to grassland in saline-alkali soil in northeastern China. Therefore, in this study, the diversity, composition, and function of fungi, as well as phosphorus fractions including Olsen-P and inorganic phosphorus (Pi), were investigated under land use conversions from maize cropland (MC) to alfalfa (*Medicago sativa* L.) (AG), *Leymus chinensis* (LG), and natural restored grasslands (RG).

**Results** The results showed that the Pi fractions of Ca<sub>8</sub>-P, Fe-P, Ca<sub>2</sub>-P, and Ca<sub>10</sub>-P were closely related with Olsen-P. Significantly increased Olsen-P content was found in 0–10 cm soil layer in the AG treatment, relative to LG and RG treatments ( $P < 0.05$ ). The occluded P content in 0–10 cm and the Al-P content in 10–20 cm in the RG treatment were the highest. The RG treatment increased the Shannon index of fungi, as well as the abundances of phyla Mortierellomycota and phyla Glomeromycota. Higher abundance of genus *Mortierella* and lower abundance of genus *Cladosporium* were observed at RG treatment. Moreover, the RG treatment greatly reduced the abundance of plant pathogens and enhanced the abundances of mycorrhizal and ectomycorrhizal. The Olsen-P was positively correlated with the abundance of plant pathogen ( $P < 0.01$ ), and the Olsen-P, Ca<sub>2</sub>-P, and Fe-P were negatively correlated with both the abundances of mycorrhizal and ectomycorrhizal ( $P < 0.05$ ).

**Conclusion** Land use conversion from maize cropland to natural restored grassland could reduce plant pathogens and enhance useful fungi by decreasing the availability of phosphorus.

**Keywords** Land use conversion, Phosphorus fractions, Fungal community structure, Fungal functional groups, Saline-alkali soils

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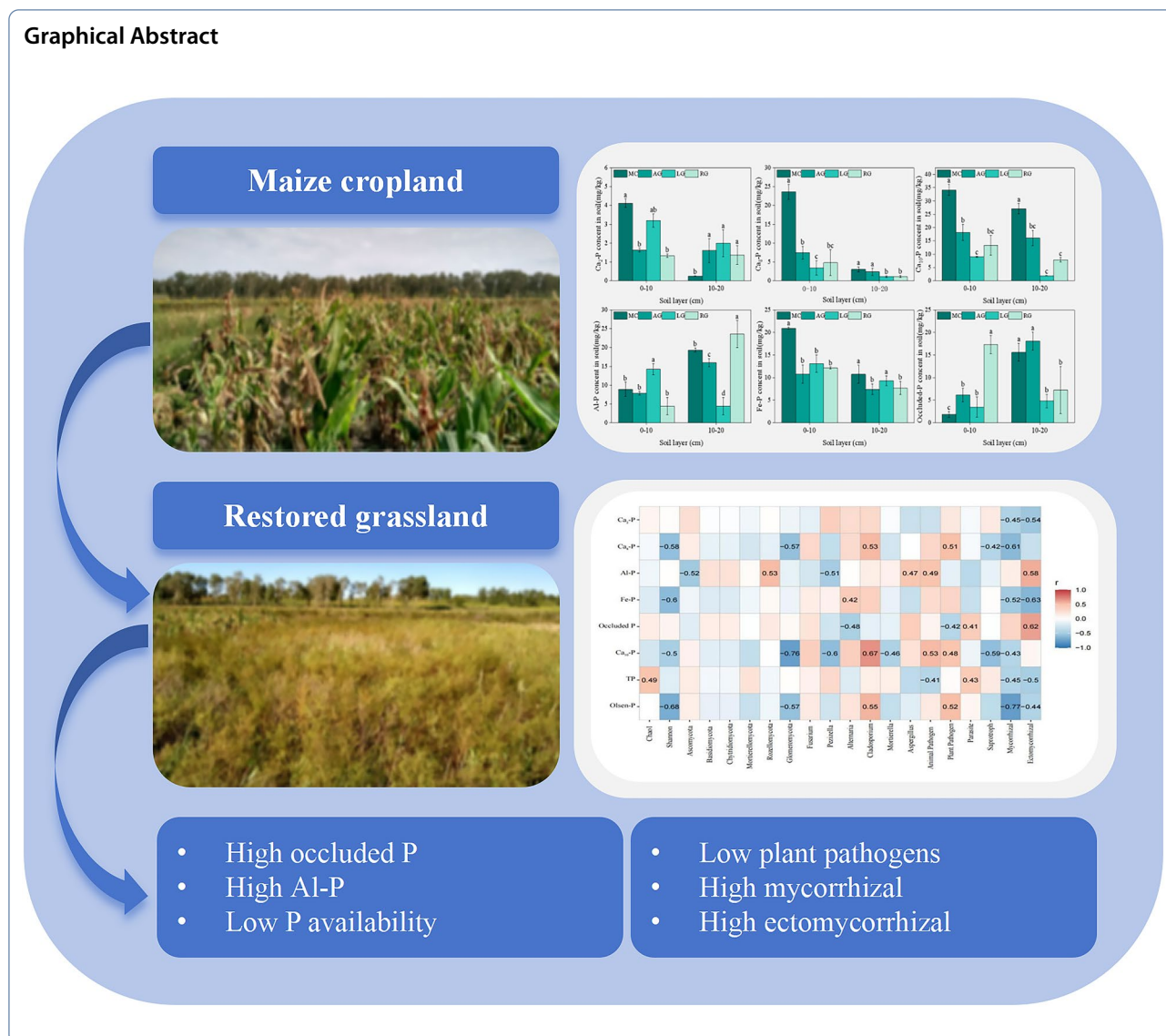
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Graphical Abstract



Introduction

Land use can be defined as the human employment of land cover types for certain purposes or functions [1]. It can change the original structure and function of soil ecosystems through different use patterns and intensities [2–4]. The Songnen Plain, located in the eastern part of northern China, is one of the three distribution areas of soda saline-alkali soils in the world [5]. The coexistence of agriculture and animal husbandry in this region leads to the multifarious land uses including croplands and grasslands [6]. In the past few decades, the cropland area increased by 7.50%, whereas the areas of woodland and grassland decreased by nearly 29% [7, 8]. However, the intensive cropland leads to a decline in soil quality and an increase in the degree of saline-alkali conditions [9–12]. Therefore, it is critical to alleviate this threat to

the sustainable development of agriculture and animal husbandry in this region [13]. Existing studies have shown that the conversion of farmland to grassland not only improves soil quality, but also increases soil nutrient content and improves soil productivity [14–16], owing to the reduction in human disturbance activity and the increased aboveground and underground biomass inputs into the soil [17, 18].

Soil phosphorus (P) derives from the weathering of parent material and is recycled by microorganisms and plants [19, 20]. Soil P can be divided into organic P (Po) and inorganic P (Pi), and the content of Po accounts for 30–50% of the total P. However, Po must be converted into Pi before it can be absorbed and utilized by plants and microorganisms. Soil Pi is the main component of total P with six fractions (Ca<sub>2</sub>-P, Ca<sub>8</sub>-P, Al-P, Fe-P,

occluded P, and  $\text{Ca}_{10}\text{-P}$ ). Based on the availability and solubility of each fraction, they can be separated through a sequential extraction procedure [21, 22]. The available P is mainly supplied by parent material and recycled by organic matter decomposition, which can directly regulate crop productivity [23–27]. The P is taken up from soil and transported to the leaves and stored in plant biomass or returned to the soil through the litter-fall. The quality and quantity of organic inputs through litter and root turnover change as plant type change, which causes the alterations of soil P fractions [19, 28]. Therefore, changes in P inputs and outputs can affect the chemically defined P pools in soils and their availability through land use conversions [29–36]. The saline-alkali soil is more sensitive to land use than other soils partly because that P is a limiting factor in arid ecosystems [37]. However, the effect of returning farmland to grassland on soil P fractions in saline-alkali soil is unclear.

Soil microbial community diversity and structure are sensitive indicators of soil health and quality, responding rapidly to land use conversions [38–40]. Fungi is widely distributed among all terrestrial ecosystems with high biodiversity and ecological importance [41–43]. Changes in land use conversions have resulted in great changes in plant diversity and litter inputs, and have significantly affected soil fungi. The soil fungi is sensitivity to nutrient contents in soil, exudation of allelochemicals, and presence/absence of host plants for mycorrhizal fungi [44–47]. Thus, we should further investigate the impact of land use conversion on soil fungal community structure and functional groups.

P is a major limiting element in microbial metabolism due to its low bioavailability [48, 49]. Recently, more attention has been paid to research the effect of P limitation on soil fungal community structure following the resource optimization theory [50]. In nutrient-impoverted soils, soil fungal community may be primarily driven by P availability, which can further restrict microbial community assembly [51, 52]. The alterations in soil P availability could shape fungal communities by influencing fungal enzyme activity and functional gene abundance [53]. Additionally, the relative abundance of dominant microbial taxa increased significantly with increasing soil P availability [54]. However, the study also reported that the decreasing soil P availability could limit microbial growth and community structure [51]. Studies have reported that land use can affect specific functional genes and the composition of the fungal community with P bioavailability in soils [55, 56]. The changes of soil P bioavailability in land use possibly affect the material exchange and energy flow between plants and between plant–soil fungi, which affect the soil fungi diversity [57–59]. However, knowledge of the linkage between P fractions

and the fungal community in saline-alkali soils remains scarce.

Therefore, we explored the responses of P fractions and fungal community structure to the conversions of cropland (maize cropland) to grasslands (alfalfa grassland, *Leymus chinensis* grassland, and natural restored grassland). The aims of the present study were to (1) examine changes in P fractions; (2) examine changes in fungal community composition, diversity, and function; and (3) show the linkage between P fractions and fungal community structure. It was hypothesized that a strong correlation between soil P fractions and fungal community structure would be found after land use conversions from cropland to grasslands. Studying the impact of different land uses on soil P fractions, fungal community structure, and their relationships would provide a reference for the sustainable development of agriculture and animal husbandry in saline-alkali soil in the Songnen Plain.

## Materials and methods

### Site

This study was carried out at the Songnen Grassland Ecosystem Research Station, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Jilin Province, China. The location has a temperate, semi-arid continental monsoon climate. The average annual temperature is 5.9 °C. The average annual precipitation is 427 mm. The alkali-saline soil is classified as Solonetz in the World Reference Base for Soil Resources [60]. The concentrations of free sodium bicarbonate ( $\text{NaHCO}_3$ ) and sodium carbonate ( $\text{Na}_2\text{CO}_3$ ) in the soil are high, and the pH ranges from 8.0 to 11.0. The vegetation is dominated by *L. chinensis*, *Chloris virgata*, *Puccinellia* spp., and *Polygonum gracilius*. The vegetation coverage is 50–90%. The aboveground biomass is 100–360 g/m<sup>2</sup> of in the peak season [61].

### Experimental design

We conducted the experiment on cropland in May 2011. Due to the plowing before the experiment, soil conditions of the cropland were homogeneous. The initial content of soil organic carbon (SOC) was 7.82 g/kg and 4.86 g/kg in 0–10 cm and 10–20 cm, respectively. The initial soil bulk density was 1.47 g/cm<sup>3</sup> and 1.51 g/cm<sup>3</sup> in 0–10 cm and 10–20 cm, respectively. We designed four land use treatments, maize cropland (MC), alfalfa (*Medicago sativa* L.) grassland (AG), *Leymus chinensis* grassland (LG), and natural restored grassland (RG), in a completed block design with five replicates. The plot area of MC or LG treatment was 600 m<sup>2</sup> (12 × 50 m), and the plot area of AG or RG was 300 m<sup>2</sup> (6 × 50 m). The guard row was 2 m between blocks and the guard row was 1 m between plots. Maize plots were established in May 2011

using traditional cropland practices. The soil was plowed (20 cm) before growth. The treatments of 74 kg N/hm<sup>2</sup>, 22 kg P/hm<sup>2</sup>, and 41 kg K/hm<sup>2</sup> were applied at sowing and mid-July every year. Maize straw was removed from the plots after the annual harvest. Maize residues approximately 137 g/m<sup>2</sup>, including roots, stem bases, and aerial roots, were incorporated into the soil during plowing. In May 2014, the AG plots were established at a sowing density of 1200 seeds/m<sup>2</sup>. The above- and below-ground biomass (to a depth of 20 cm) in the AG plot was 307 g/m<sup>2</sup> and 321 g/m<sup>2</sup>, respectively. In May 2011, the LG plots were sown at a sowing density of 2000 seeds/m<sup>2</sup>. The above- and below-ground biomass (to a depth of 20 cm) in the LG plot was 488 and 638 g/m<sup>2</sup>, respectively. In peak seasons, the aboveground biomass were removed once a year in AG and LG plots. The RG plots had been restored to grass without any disturbance since 2011. *Chloris virgata*, *Sonchus brachyotus*, *Chenopodium glaucum*, and *Phragmites communis* are the dominant species in the RG plot, accounted for more than 85% of above-ground biomass. The above- and below-ground biomass in RG plot was 348 and 397 g/m<sup>2</sup>, respectively. There was no fertilizer applied to the AG, LG, or RG plots. More details on land uses treatments were described in [62].

### Soil sampling

We collected soil samples in September 2020. A soil-drilling sampler (5 cm diameter) was used to collect 5 soil samples from 0–10 cm to 10–20 cm soil layers in each plot. All samples were combined into a composite sample and sieved through a 2 mm screen to remove visible plant materials and other debris. 6 g of each soil sample was placed in a 5 mm polyethylene pipe, immediately transferred to liquid nitrogen for further microbial sequencing, and the remaining sampled soil was used for measurement of soil properties.

The basic soil properties were determined as described by [63]. The determination of soil Pi fractions adopts the procedure of extraction with sodium bicarbonate, ammonium acetate, ammonium fluoride, sodium hydroxide–sodium carbonate, citrate dithionite, and sulfuric acid [64, 65]. These fractions are Ca<sub>2</sub>-P, Ca<sub>8</sub>-P, Al-P, Fe-P, occluded P and Ca<sub>10</sub>-P.

### DNA extraction and Illumina HiSeq sequencing

We extracted soil DNA through FastDNATM SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA, USA). A NanoDrop 2000 (NanoDrop Technologies, Inc., Wilmington, DE, USA) was used to quantify DNA and PCR. The fungal ITS1 region was amplified using primers ITS1-F(5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2-R(5′-GCTGCGTTCATCGATGC-3′), combined with Illumina adapter sequences and barcodes.

We performed PCR in a 30 μL mixture, with 3 μL of each primer (2 μM), 10 μL template DNA (1 ng/μL), 15 μL Phusion® High-Fidelity PCR Master Mix (BioLabs, Inc., New England, USA), and 2 μL water. The following thermal program was used for amplification: 98 °C for 2 min, followed by 25 cycles of 98 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min, and a final extension step at 72 °C for 5 min. We amplified each sample in triplicate, and then pooled and purified PCR products via a Qiagen Gel Extraction Kit (Qiagen, Hilden, Germany). We generated metagenomic sequencing libraries through a TruSeq® DNA PCR-Free Sample Preparation Kit (Illumina, San Diego, CA, USA), and pooled them at an equimolar ratio. PCR amplicons were sequenced with 250 bp paired-end using Beijing Biomarker's HiSeq platform (Illumina, San Diego, CA, USA).

### Sequence data preprocessing

We divided raw sequences into sample libraries via sample-specific barcodes. Then, they were truncated after cutting off the barcode and primer sequences using QIIME v1.9.0 and cutadapt v1.17, respectively. We used FLASH v1.2.7 to merge forward and reverse reads with at least 10-bp overlaps and less than 5% mismatches [66]. Raw tags were quality filtered using Trimmomatic v0.33. We removed sequences shorter than 200 bp with an average quality score below 25 in raw tags. The remaining sequences were subjected to chimera removal using UCHIME v4.2. We classified the operational taxonomic units (OTUs) with 97% similarity level using UCLUST v1.2.22 [67]. We annotated taxonomic identity through a BLAST algorithm on sequences in the Unite Database v7.2 (<https://unite.ut.ee/>) using QIIME software [68]. The classification of sequences that not assigned to kingdom fungi was unknown. All Illumina raw sequence data are in the National Center for Biotechnology Information Sequence Read Archive (NCBI SRA) database with the accession number of SRP132542.

### Statistical analysis

We calculated the index of fungal alpha diversity using Mothur v1.30 [73]. Based on binary Jaccard dissimilarity matrices with the Vegan package, we visualized the structure of fungal community with nonmetric multidimensional scaling (NMDS) [74]. We used one-way ANOVA to assess group means, and performed the Tukey test via IBM SPSS v20.0 statistical software (SPSS, Chicago, IL, USA). Fungal ITS ASVs were designated into functional categories based on their putative life history following ecological guild assignment sensu FUNGuild. To evaluate microbiome complexity in soil treatment groups, network analysis was used. Only fungal OTUs that had a relative abundance >0.005% were analyzed. Correlation

networks were calculated by using the igraph package of R. The co-occurrence network was built by using pair relations with a coefficient  $>0.7$  ( $P < 0.05$ , two-sided). Correlations among OTUs were determined using SparCC analysis. The network structure was explored and visualized with the interactive platform Gephi (v.0.10.1) using the Fruchterman–Reingold layout.

## Results

### Basic soil properties

The AG, LG, and RG treatments significantly increased the contents of SOC, TN, and TP in 0–10 cm and 10–20 cm soils compared to MC treatment ( $P < 0.05$ ). A 36.2% higher of TP content at LG treatment was observed relative to MC treatment in 0–10 cm soil ( $P < 0.05$ ). The contents of Olsen-P and AN in 0–10 cm soil at AG treatment were the highest. The AG treatment increased the content of Olsen-P by 17.7% and 62.6% in 0–10 cm soil compared to LG and RG treatment, respectively ( $P < 0.05$ ) (Table 1).

### Soil inorganic phosphorus (Pi) fractions

The contents of  $\text{Ca}_2\text{-P}$  and  $\text{Fe-P}$  in 0–10 cm soil were significantly increased by the MC treatments. The content of  $\text{Ca}_8\text{-P}$  in 0–10 cm soil at MC treatment was 2.2–5.9 times higher than that at other treatments ( $P < 0.05$ ). The  $\text{Ca}_{10}\text{-P}$  content at MC treatment was 71.4% and 52.2% higher than that at AG treatment in 0–10 cm and 10–20 cm soil layers, respectively ( $P < 0.05$ ). The occluded P content in 0–10 cm soil and  $\text{Al-P}$  content in 10–20 cm soil at RG treatment were the highest ( $P < 0.05$ ). The main Pi fractions in 0–10 cm soil at MC and AG treatments included  $\text{Ca}_{10}\text{-P}$ ,  $\text{Ca}_8\text{-P}$ , and  $\text{Fe-P}$ . The proportions of occluded P and  $\text{Al-P}$  were increased in 10–20 cm soil. The main Pi fractions in 0–10 cm soil at RG treatment included  $\text{Ca}_{10}\text{-P}$ ,  $\text{Al-P}$  and  $\text{Fe-P}$ . However, the proportion of  $\text{Al-P}$  was increased, and the proportion of occluded P was decreased in 10–20 cm soil (Fig. 1).

### Fungal diversity

The Shannon index in 0–10 cm soil by RG and LG treatments was greater than that of MC and AG treatments ( $P < 0.05$ ). The Shannon index at RG treatment was 16.5, 24.1, and 47.4% higher than that at MC, AG, and LG treatment in 10–20 cm soil ( $P < 0.05$ ) (Fig. 2).

In the NMDS plot, land use had significant impacted on the soil fungal communities on average. The samples from AG in 0–10 cm and 10–20 cm soil layers tended to be separated from the MC in 0–10 cm and 10–20 cm soil layers along NMDS1. The samples from AG in 0–10 cm and 10–20 cm soil layers tended to be separated from the LG in 0–10 cm and 10–20 cm soil layers along NMDS2 (Fig. 3).

### Fungal community composition

Illumina HiSeq sequencing of the ITS1 region in all soil samples generated 1,509,112 fungal sequences with 51,246–70,730 rarified reads per sample with average read length of 305 bp.

The dominant fungal phyla for all treatments were Ascomycota and Basidiomycota, and the fungal phyla Chytridiomycota were detected at MC and LG treatments. The highest abundance of Ascomycota in 0–10 cm soil at AG treatment was recorded. The abundances of Mortierellomycota and Glomeromycota were significantly increased at RG and LG treatments ( $P < 0.05$ ) (Fig. 4).

The fungal genera of *Pezizella* was detected at LG treatment, and the abundance of it was greater in 10–20 cm soil rather than 0–10 cm soil. The RG treatment greatly decreased abundances of *Alternaria*, *Cladosporium*, and *Fusarium* in 10–20 cm soil. Higher abundances of *Mortierella* and *Aspergillus* at RG treatment in 10–20 cm soil were observed relative to other treatments ( $P < 0.05$ ) (Fig. 4).

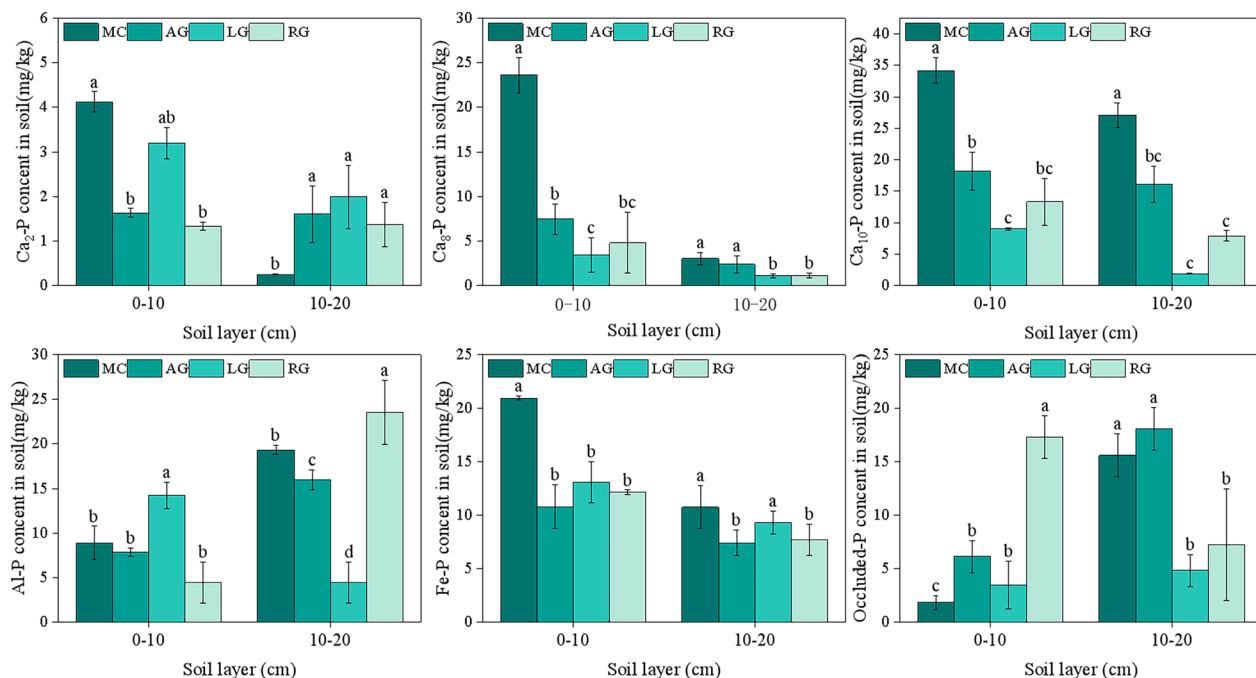
The abundances of animal pathogen at AG and LG treatments in 0–10 cm and 10–20 cm soil were lower than that at other treatments ( $P < 0.05$ ). The LG and

**Table 1** Basic soil properties in different land uses

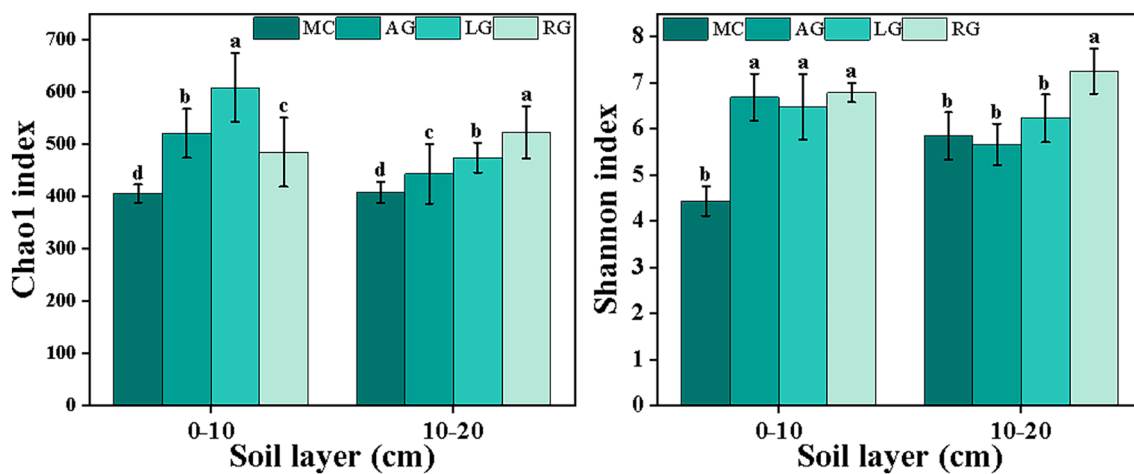
	0–10 cm				10–20 cm			
	MC	LG	AG	RG	MC	LG	AG	RG
SOC (g/kg)	7.46±0.86b	10.69±0.01a	10.50±0.78a	11.29±1.42a	3.96±0.66b	7.21±0.94a	7.72±0.23a	7.52±0.98a
TN (g/kg)	1.30±0.06c	1.36±0.06bc	1.53±0.10ab	1.59±0.08a	0.88±0.12b	1.11±0.10a	1.01±0.06ab	1.22±0.09a
AN (mg/kg)	70.35±3.31b	67.46±6.47b	84.90±5.50a	52.27±2.45c	55.30±6.70a	35.59±5.96b	39.17±5.68b	27.25±3.95b
TP (g/kg)	0.37±0.04b	0.58±0.05a	0.53±0.08a	0.49±0.06ab	0.20±0.05b	0.33±0.05a	0.34±0.04a	0.26±0.05ab
Olsen-P (mg/kg)	51.45±2.80a	44.36±3.33b	52.19±3.84a	32.09±1.09b	26.05±2.78a	24.36±1.72ab	21.69±1.56b	27.18±2.33a

Different lowercase letter indicates that there are significant differences among treatments at 0.05 level

MC maize cropland, LG *Leymus chinensis* grassland, AG alfalfa grassland, RG natural restored grassland. SOC soil organic carbon, TN total nitrogen, AN available nitrogen, TP total phosphorus, Olsen-P available phosphorus



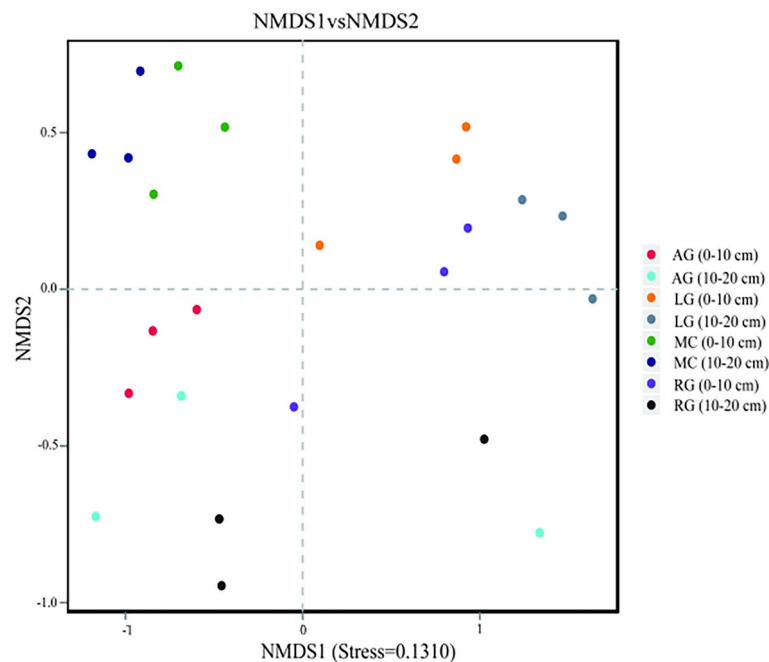
**Fig. 1** Soil Pi fractions in different land uses. MC maize cropland, LG *Leymus chinensis* grassland, AG alfalfa grassland, RG natural restored grassland. Different lowercase letter indicates significant difference at 0.05 level among treatments



**Fig. 2** Estimated Chao 1 index and Shannon index of fungus based on the OTU-generated matrices in different land uses. MC maize cropland, LG *Leymus chinensis* grassland, AG alfalfa grassland, RG natural restored grassland. Different lowercase letter indicates significant difference at 0.05 level among treatments

RG treatments greatly decreased the abundances of Plant Pathogen, while greatly increased the abundances of Saprotroph in 0–10 cm soil ( $P < 0.05$ ). Most abundances of mycorrhizal were detected at RG treatment

in 0–10 cm and 10–20 cm soil. Most abundances of ectomycorrhizal at AG and RG treatments in 0–10 cm and 10–20 cm soil were found (Fig. 4).



**Fig. 3** Nonmetric multidimensional scaling (NMDS) based on binary Jaccard of the fungal community structures in different land uses. *MC* maize cropland, *LG* *Leymus chinensis* grassland, *AG* alfalfa grassland, *RG* natural restored grassland

### Ecological network of fungal community

The topological indices consistently differed under the land uses (Fig. 5 and Fig. 6). In 0–10 cm soil, MC treatment had the highest average degree, and RG treatment had the lowest modularity. The highest of average clustering coefficient and ratio of positive to negative edges were observed at RG treatment. In 10–20 cm soil, LG treatment had the lowest average degree, and RG treatment had the highest modularity.

### Linkages between P fractions and diversity, composition, and function of fungi

The Olsen-P was positively correlated with  $\text{Ca}_8\text{-P}$  ( $r=0.682^{**}$ ),  $\text{Fe-P}$  ( $r=0.622^{**}$ ),  $\text{Ca}_2\text{-P}$  ( $r=0.470^*$ ), and  $\text{Ca}_{10}\text{-P}$  ( $r=0.510^*$ ). The occluded P was negatively correlated with  $\text{Ca}_2\text{-P}$  ( $r=-0.547^{**}$ ) and  $\text{Fe-P}$  ( $r=-0.412^*$ ) (Fig. 7).

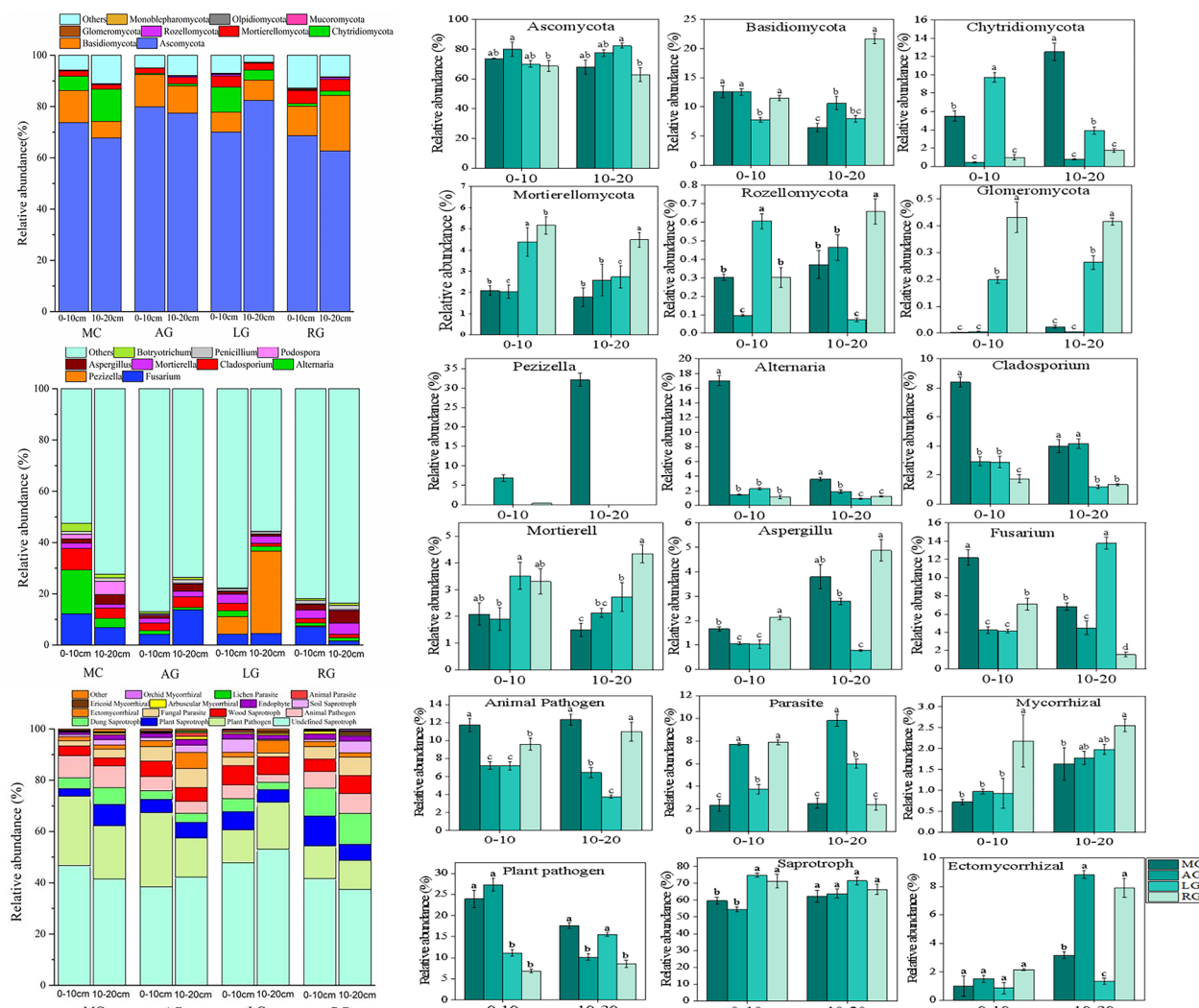
The  $\text{Ca}_8\text{-P}$ ,  $\text{Ca}_{10}\text{-P}$ , and occluded P had negative correlations with Shannon index ( $P<0.05$  or  $P<0.01$ ). The  $\text{Ca}_8\text{-P}$ ,  $\text{Ca}_{10}\text{-P}$ , and Olsen-P had negative correlation with phyla Glomeromycota and had positive correlation with genus *Cladosporium* ( $P<0.01$ ). The  $\text{Fe-P}$  and occluded P was positively and negatively correlated with genus *Alternaria*, respectively ( $P<0.05$ ). The  $\text{Ca}_{10}\text{-P}$  had negative correlation with genus *Mortierella* ( $P<0.05$ ). The Olsen-P,  $\text{Ca}_8\text{-P}$ , and  $\text{Ca}_{10}\text{-P}$  were positively correlated with plant pathogen ( $P<0.01$  or

$P<0.05$ ). The Al-P and occluded P showed positive correlations with Ectomycorrhizal ( $P<0.01$ ), and the  $\text{Ca}_2\text{-P}$  and  $\text{Fe-P}$  showed opposite results. The Olsen-P,  $\text{Ca}_8\text{-P}$ , and  $\text{Fe-P}$  were negatively correlated with Mycorrhizal ( $P<0.01$ ) (Fig. 8).

## Discussion

### Effect of land use conversions on soil P fractions

Existing studies showed that soil properties, plant diversity and/or richness, and microbial activity were significantly changed after land use conversions [34–36, 69–71], which lead to significant changes in phosphorus (P) distribution and availability through increasing P losses or P transfer into recalcitrant pools [26, 31, 81–83]. This study found that the total phosphorus (TP), Olsen-P, and inorganic phosphorus (Pi) fractions varied across different land uses, which suggested that land use conversions from maize cropland to alfalfa, *Leymus chinensis*, and restored grasslands had significant effects on soil P dynamics. One research found that the conversion of native vegetation to cropped land decreased the soil TP content by up to 34% [35]. This study found that land use conversion from maize cropland to grasslands also significantly increased the TP contents in both the 0–10 cm and 10–20 cm soil layers. This might also be attributed to the lack of tillage or low intensity of management in grasslands as well as to increased plant residue inputs [34]. Higher Olsen-P contents in maize cropland and

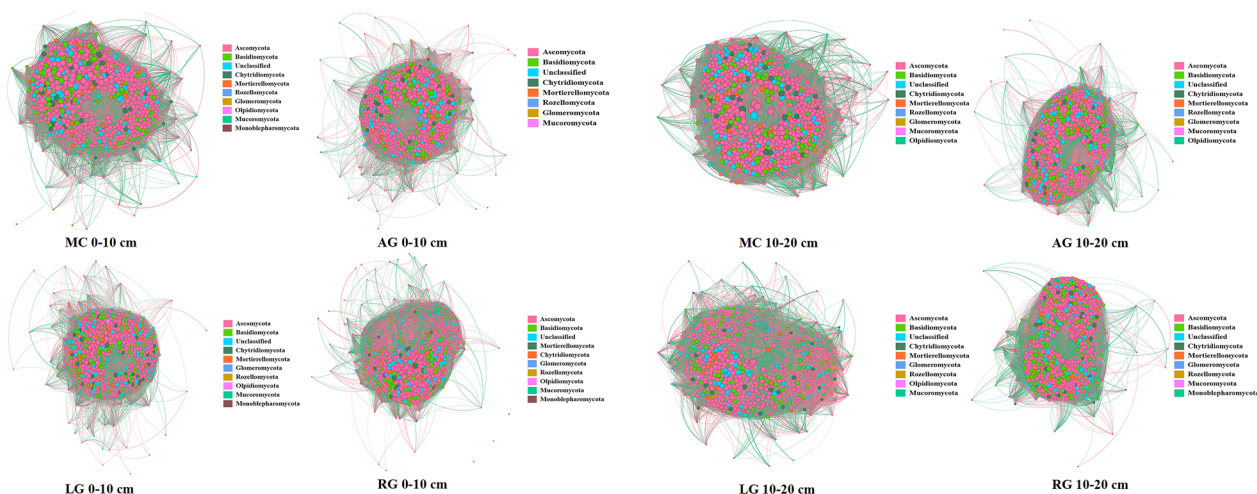


**Fig. 4** Fungal community compositions at phyla level and genus level and fungal functional groups based on FUN guild database in different land uses. MC maize cropland, LG *Leymus chinensis* grassland, AG alfalfa grassland, RG natural restored grassland. Different lowercase letter indicates significant difference at 0.05 level among treatments

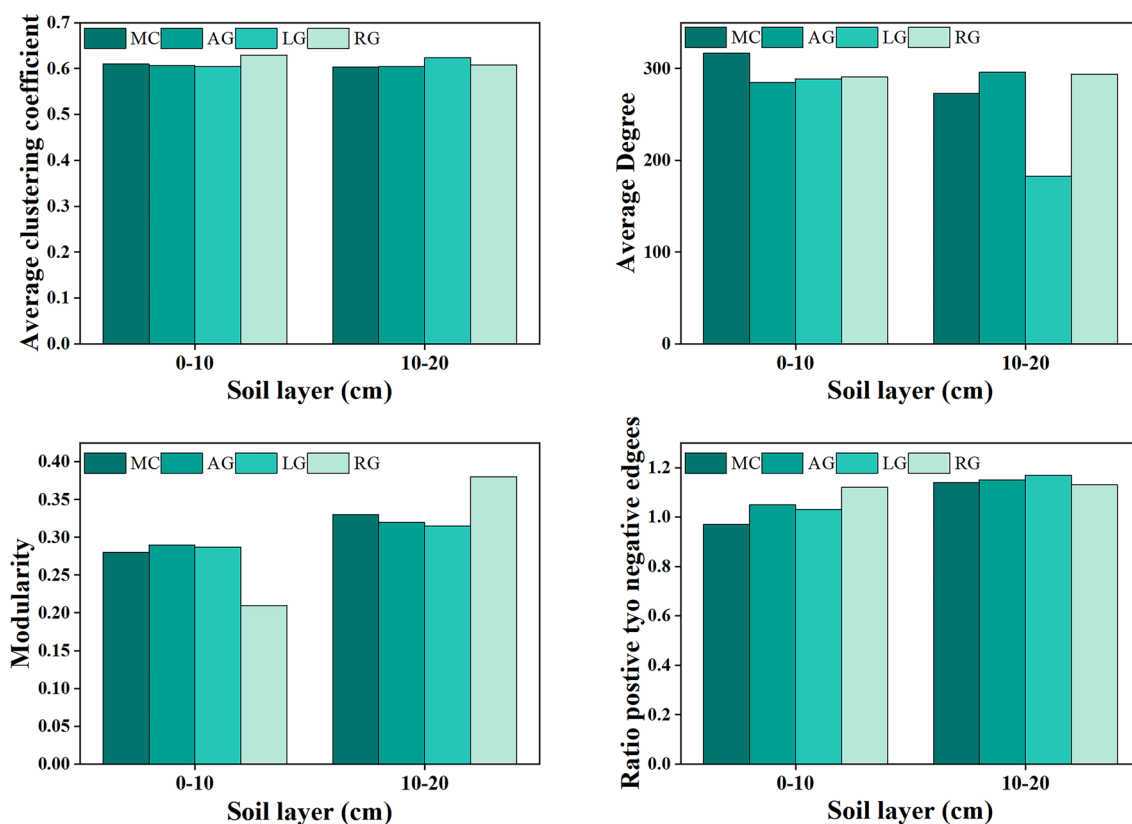
alfalfa grassland were observed in the 0–10 cm soil layer relative to *Leymus chinensis* grassland and restored grassland. This illustrated that maize cropland and alfalfa grassland were capable of supporting high P availability. Maize cropland in this experiment was fertilized annually according to traditional cropland practices. The application of mineral P fertilizer to maize cropland might increase the soluble Pi [72–75]. The Olsen-P increased in the alfalfa grassland was associated with higher AN content. Alfalfa is a good forage because of its high nitrogen and protein content. It can maintain or even improve soil fertility through biological N fixation [76]. In addition, the deep rooting of alfalfa can regulate the P dynamics of grassland ecosystems, transferring P from deeper soil layers to the surface soil [77–79].

The Pi is the main component of total P and can be separated into six fractions. The Olsen-P were positively correlated with Ca<sub>8</sub>-P ( $r=0.682^{**}$ ), Fe-P ( $r=0.622^{**}$ ), Ca<sub>10</sub>-P ( $r=0.510^*$ ), and Ca<sub>2</sub>-P ( $r=0.470^*$ ). Maize cropland accumulated large amounts of Ca<sub>2</sub>-P, Ca<sub>8</sub>-P, Ca<sub>10</sub>-P and Fe-P, which might contribute to the available P pool in the soil. This proved that maize cropland improved P availability, which might not only attribute to the mineral P fertilizer input annually, but also contribute to the lower uptake of P or the higher organic matter decomposition [20, 27, 80]. The highest content of occluded P in the 0–10 cm soil and the highest content of Al-P in the 10–20 cm soil were found in restored grassland. Many studies have found that the restoration of abandoned cropland can decrease the loss of fine particles in





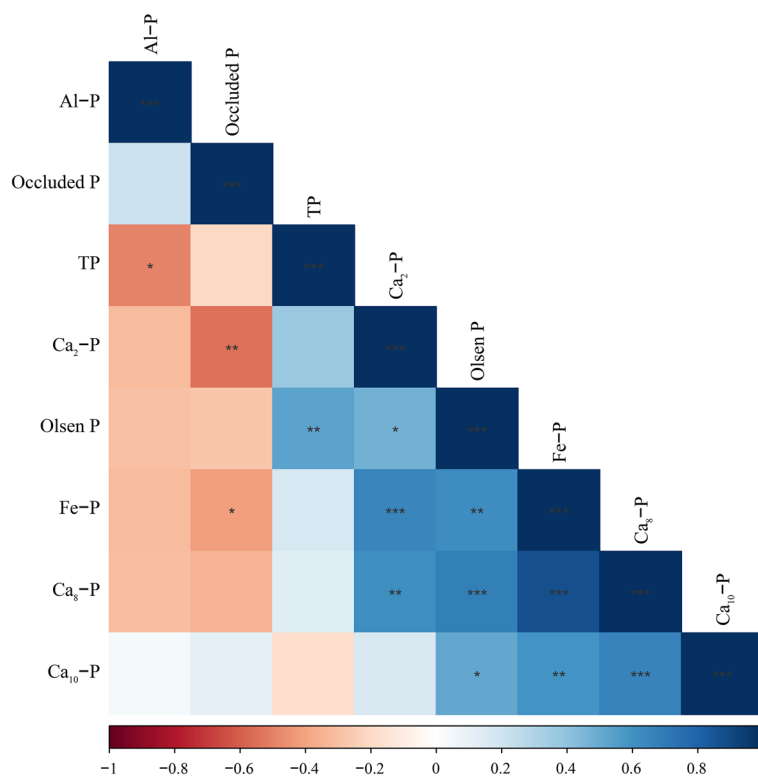
**Fig. 5** Ecological network of fungal communities at the OTU level for soil samples under different land use treatments. MC maize cropland, LG *Leymus chinensis* grassland, AG alfalfa grassland, RG natural restored grassland. Red and green edges indicate significant positive and negative correlations between nodes, respectively ( $P < 0.05$ )



**Fig. 6** Changes of various network topological indices under different land use treatments

soil by increasing plant cover and diversity [30, 82–84]. The fine particles can provide a greater surface area as binding sites, having a higher P adsorption capacity [81, 85–87], which might lead to the lower P availability

in restored grassland. In addition, the soil available P decreased in restored grassland might also be explained by two reasons: (i) larger of plant biomass resulting in an increase in P uptake; (ii) continuous input of plant



**Fig. 7** Correlations among soil P fractions according to Pearson's analysis. Note: \*\*, significant at  $P < 0.01$ ; \*, significant at  $P < 0.05$ . The blue color represents positive correlations, and red color represents negative correlations

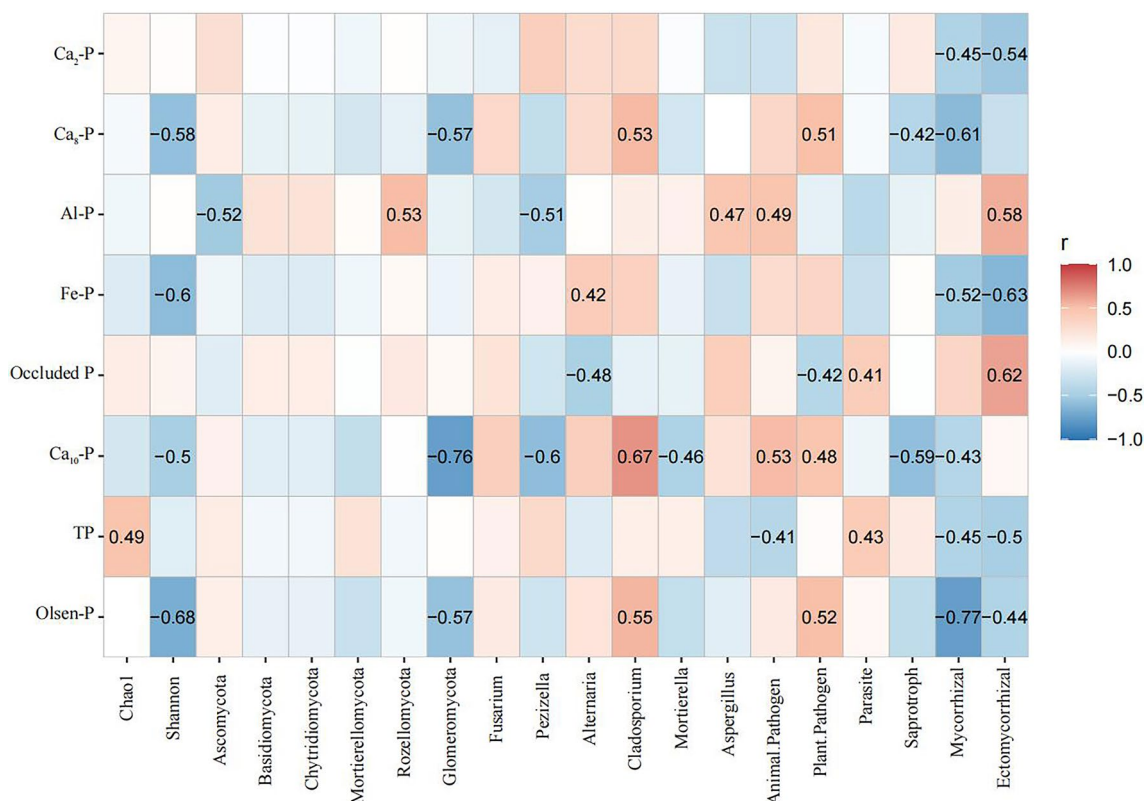
residues resulting in an increase of acidity and release of Al, and then resulting in an Al-P fixation.

### Responses of soil P fractions to fungal diversity and composition

Land use conversions directly affect soil fungal diversity and composition by altering soil environmental conditions via the changes of plant types, biomass, litter quality and amounts [88–96]. The P derives from litter decomposition can remarkably affect the distribution of soil available P [97], which can indirectly influence the assembly of soil microbial communities in land uses. The fungal richness can be greatly affected by the removal of vegetation from natural ecosystems [46, 105], but there are some conflicting results in other studies [98]. Our study found that the Chao 1 index of fungi in 0–10 cm soil had litter changed during land use conversions, while it was significantly decreased in *Leymus chinensis* grassland in 10–20 cm soil. The correlation results in this study showed that there was no significant correlations between Chao 1 index and Pi fractions. Land use conversion from maize cropland to natural restored grassland enhanced the Shannon index of fungi both in 0–10 cm and 10–20 cm soil layers. The significantly negative correlation between Shannon index of fungi and Ca<sub>10</sub>-P

content indicated that the decrease of available P in natural restored grassland might improve the diversity of fungal community. Lots of studies have found that soil fungal diversity was strongly affected by nutritional limitation, especially P limitation [99–101].

The dominant fungi at the phyla level are Ascomycota and Basidiomycota [102–104]. This study found that the relative abundance of Ascomycota in natural restored grassland was lower than other land uses, especially in 10–20 cm soil. This might attribute to the significant increase of Al-P content in natural restored grassland according to the negative correlation between relative abundance of Ascomycota and Al-P content. In addition, land use conversion from maize cropland to alfalfa grassland increased the relative abundance of Ascomycota both in 0–10 cm and 10–20 cm soil layers, which might attribute to the lower Al-P content. Furthermore, the increases in relative abundance of Ascomycota in alfalfa plots might closely relate to the assimilation of root exudates for greater root biomass, as well as biological N fixation of alfalfa and the high TN and N availability in the alfalfa plots [105–115]. The fungal phyla Basidiomycota can degrade cellulose, polyphenolic compounds, and other dissolved organics [116]. This study found that land use conversion from maize cropland to restored



**Fig. 8** Correlations between soil P fractions and fungal diversity, fungal phyla component, fungal genus component, and fungal functional groups (Spearman analysis). \*\*, significant at  $P < 0.01$ ; \*, significant at  $P < 0.05$

grassland greatly increased the relative abundance of Basidiomycota in 10–20 cm soil, which might attribute to plant mediated variation in soil properties [117, 118]. The fungal phyla Glomeromycota can form arbuscular mycorrhizae with plants and promote the host to absorb nutrients [119]. Glomeromycota were detected in natural restored grassland and *Leymus chinensis* grassland in 0–10 cm and 10–20 cm soil layers, which were mainly related to the lower Ca<sub>8</sub>-P, Ca<sub>10</sub>-P, and Olsen-P contents.

The fungal genus *Fusarium* and *Cladosporium* are plant pathogens [120, 121]. Relatively lower abundances of *Fusarium* and *Cladosporium* were found in 0–10 cm soil after land use conversions from maize cropland to grasslands. This suggested that land use conversions from maize cropland to alfalfa, *Leymus chinensis*, and natural restored grasslands could reduce the number of pathogenic fungi. This might attribute to the reduction in P availability due to the positive correlations between fungal genus *Cladosporium* and Ca<sub>8</sub>-P, Ca<sub>10</sub>-P, and Olsen-P ( $P < 0.01$ ). Members of the fungal genus *Mortierella* act primarily as saprotrophs in soil ecosystems. They subsists on rotting leaves, fecal pellets, and other organic materials [122, 123]. The member of fungal genus *Mortierella* also can protect against some plant pathogens [124],

efficiently degrade endosulfan through the hydroxylation pathway, and alleviate the adverse effects of salt on soil enzyme activities and plant growth [125–127]. In this study, the great relative abundance of fungal genus *Mortierella* was recorded in *Leymus chinensis* and natural restored grasslands, which indicated that land use conversions from maize cropland to *Leymus chinensis* and natural restored grasslands could decrease plant pathogens. The lower Ca<sub>10</sub>-P contents in *Leymus chinensis* and natural restored grasslands played important role in the formation of fungal genus *Mortierella* member according to the correlation results.

#### Responses of soil P fractions to fungal functional groups

The variations in fungal functional groups observed in land use conversions from maize cropland to grasslands because of the continued inputs of leaf litter and root material. They provide sufficient energy and substrates for soil microorganisms to stimulate the growth and activity of microbial populations [128]. Most fungal functional groups were positively or negatively correlated with P fractions. The *Leymus chinensis* grassland and natural restored grassland significantly decreased plant pathogens in 0–10 cm soil. This was mainly

mediated by the availability of P such as Ca<sub>8</sub>-P, Ca<sub>10</sub>-P, and Olsen-P saprotrophs are primary degraders of organic matter in soil [129]. A study found that complete removal of vegetation decreased the diversity of saprotrophic fungi in southern China [130]. This study illustrated that land use conversions from maize cropland to *Leymus chinensis* grassland and natural restored grassland greatly increased saprotrophs in 0–10 cm soil, which might contribute to lower Ca<sub>8</sub>-P and Ca<sub>10</sub>-P. Ectomycorrhizae are highly host-specific symbionts of only 4.5% of terrestrial plants, and have evolved several times within Basidiomycota and Ascomycota [131]. Land use conversions from maize cropland to alfalfa grassland and natural restored grassland significantly increased ectomycorrhizal abundance. The correlations analysis showed that Al-P and occluded P were positively correlated with ectomycorrhizal, while Ca<sub>2</sub>-P, Fe-P, and Olsen-P showed opposite results. This illustrated that lower P availability could improve ectomycorrhizal. Mycorrhizal fungi can assist plants in nutrient and water uptake from soil [132], which are affected by land use [133, 134]. Some studies had found that AM fungal diversity in grasslands was higher than that in arable land [135–137]. In the present study, land use conversion from maize cropland to natural restored grassland greatly increased mycorrhizal fungi, which might be associated with low-intensity management and high plant diversity [138]. The previous studies have shown that the variations in mycorrhizal abundance under different land uses could be explained by soil P availability [139]. The Ca<sub>2</sub>-P, Ca<sub>8</sub>-P, Fe-P, Ca<sub>10</sub>-P, and Olsen-P in this study had negative impacts on mycorrhizal fungi [140].

## Conclusions

This paper studied the responses of soil P fractions and fungal community structures to land use conversions from cropland to grasslands in saline-alkali soil in north-eastern China. The Olsen-P was closed with Pi fractions of Ca<sub>8</sub>-P, Fe-P, Ca<sub>2</sub>-P, and Ca<sub>10</sub>-P. Natural restored grassland had higher contents of occluded P and Al-P with low P availability. Natural restored grassland enhanced the fungal diversity and abundance of phyla Mortierellomycota and Glomeromycota, and genus *Mortierella*, while decreased the abundance of genus *Cladosporium*. Moreover, natural restored grassland also reduced plant pathogens and enhanced mycorrhizal and ectomycorrhizal fungi. The lower Olsen-P, Ca<sub>8</sub>-P, and Ca<sub>10</sub>-P resulted in the decrease of plant pathogen, and lower Olsen-P, Ca<sub>2</sub>-P, and Fe-P resulted in higher abundances of ectomycorrhizal and mycorrhizal fungi. This illustrated that land use conversion from maize cropland to natural restored grassland could reduce plant pathogens and

improve useful fungi owing to the low availability of phosphorus.

## Author contributions

Daowei Zhou contributed to the conceptualization of the study. Juan Hu wrote the original draft. Yingxin Huang revised the draft.

## Funding

This research were supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant No. XDA28110202) and the Natural Science Foundation of Jilin Province (20240101258JC).

## Availability of data and materials

The authors confirm that the data supporting the findings of this study are available within the article.

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Received: 14 December 2023 Accepted: 6 April 2024

Published online: 20 April 2024

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