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REGULAR ARTICLE

Sensitivity of soil fungal and bacterial community compositions to nitrogen and phosphorus additions in a temperate meadow

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Abstract Background and aims Soil microorganisms play key roles in soil nutrient turnover and plant community composition; however, the soil microbial community composition and species diversity are often influenced by nutrient enrichment which may affect how soil microbes influence nutrient cycles and the plant community structure. The resistance of soil fungal and bacterial communities to nitrogen (N) and phosphorus (P) additions and whether the responses of the soil microbes and the plant community are simultaneous in a N-limited temperate meadow ecosystem are still unclear.
Methods We carried out a 7-year experiment with N and P additions in a temperate meadow. The community structures of soil bacteria and fungi were examined based on high-throughput sequencing targeting the 16S rRNA and ITS genes, respectively.
Results Nitrogen addition did not influence the community composition or species richness of bacteria, but it did alter the soil fungal community composition and increased fungal operational taxonomic unit (OTU) richness. Phosphorus addition significantly altered the soil fungal and bacterial community compositions, decreased the richness of bacterial OTUs, and increased the OTU richness of fungi. Proteobacteria (38.5%) and Acidobacteria (22.3%) were the most dominant bacteria. Ascomycota were the dominant fungi (42.6%) across all samples. The enrichment of available P in the soil due to P addition reduced the bacterial β-diversity, while the β-diversity of soil fungi was mainly influenced by the concentrations of soil N and P, as well as soil moisture.
Conclusions The sensitivity of soil fungi and bacteria to P addition was stronger than that of N addition, and the response of the soil microbes to N and P additions was more sensitive than that of the plant community. Our results highlight the unequal sensitivity of the soil fungal and bacterial community composition and structure to N and P additions, thereby causing changes in above and belowground community composition and structures in the studied temperate meadow ecosystem.

Keywords Grassland · Nitrogen enrichment · Phosphorus fertilization · Sensitivity · Soil microbial community

Yan Yan and Xiuting Sun contributed equally to this work.

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Introduction

Soil microbes play an important role in determining ecosystem stability and multifunctionality (van der Heijden et al. 2008; Delgado-Baquerizo et al. 2016; Bennett et al. 2017). For instance, soil fungi can reduce greenhouse gas emissions, such as N_2O and CH_4 (Bender et al. 2014, 2015; Thompson et al. 2016; Storer et al. 2018), and alleviate warming potential (Cui et al. 2021). Soil microbial diversity plays an important role in regulating the soil carbon (C), nitrogen (N) and phosphorus (P) cycles because it accelerates the decomposition of litter (Kang et al. 2020) and mineralizes organic P (Jiang et al. 2021), thus affecting plant N and P uptake (Freedman et al. 2013; Mei et al. 2019). However, the community composition and structures of soil microbes are influenced by environmental changes, which should reduce the positive effect of soil microbes on nutrient cycles and alter the plant community structure. To date, how environmental changes influence soil microbial communities is still uncertain.

A series of global change factors such as climate warming, N deposition, and rising atmospheric carbon dioxide concentrations, significantly reduce biodiversity and decrease ecosystem functions (Vellend et al. 2017; Harrison 2020; Yang et al. 2021a, 2021b). For instance, N and P additions have been shown to alter the community composition and reduce the species diversity of soil microorganisms (Wang et al. 2018). The addition of N reduced the bacterial richness in soil by decreasing soil pH but it had no impact on fungal biomass in a tropical forest ecosystem in South China (Wang et al. 2018). Nitrogen addition was also found to alter the bacterial community composition because of changes in the soil pH and in the plant community composition in a temperate steppe (Zeng et al. 2016). Nitrogen deposition reduced the species richness of the active fungal community but had no influence on the bacterial community in a hardwood forest ecosystem, suggesting that the influence of N deposition on the soil bacterial community may be determined in a seasonally or temporally variable fashion (Freedman et al. 2015). However, N addition exerted little influence on soil bacterial diversity in a cedar creek ecosystem (Fierer et al. 2012), and a meta-analysis study also suggested that the effects of N application on soil microbial community compositions were inconsistent (Ramirez et al. 2012). These varying responses of the soil microbial community to N addition suggest that the influence of N enrichment on soil microbial diversity might be ecosystem-specific or be caused by local environmental differences in the soil nutrient status, community composition, and climate.

Increasing evidence has demonstrated that P deposition is becoming a significant P source across the globe (Ahn and James 2001; Vicars et al. 2010; Peñuelas et al. 2013; Zhu et al. 2016), and is a major determinant for the soil microbial community (Wan et al. 2015; Li et al. 2021). The change in soil available P concentration caused by P addition was a key parameter that shift the diversity and composition of the soil microbial community in previous studies (He et al. 2016; Ling et al. 2017). Previous results found that the addition of P increased the abundance of arbuscular mycorrhizal fungi and bacteria due to an increase in carbon availability and pH in subalpine meadows (Huang et al. 2016). Phosphorus addition alters the structure of soil fungal and bacterial communities by affecting phosphate and plant species in acidic grasslands (Rooney and Clipson 2009). Phosphorus addition changed the soil fungal community structure due to fertilization-mediated changes in soil pH in a P-deficient woodland (Nielsen et al. 2015). An increase in soil fungal and bacterial abundance might ameliorate the negative impact of N enrichment on the belowground community (Su et al. 2015) and then positively affect aboveground community composition. However, several studies also found that P addition had little influence on the community composition of soil microbes under N enrichment (He et al. 2016; Wang et al. 2018). These results suggest that the influence of P additions on the soil microbial community is inconsistent and might be determined by local environmental factors and the ecosystem type.

Although some studies have investigated the influence of N and P additions in tropical forests (He et al. 2016; Wang et al. 2018), species-rich meadows (Pan et al. 2014), semiarid steppes (Ling et al. 2017), the influences of N and P additions, and their interactive effects on soil bacterial and fungal community compositions in temperate meadow ecosystems are still not well understood. A previous study showed that N and P additions could alter the plant community structure (Zhao et al. 2019), but whether the response of soil microbes and plants to N and P additions

are coordinated is still unclear. To understand the mechanisms by which N and P additions affect the soil microbial community composition and structure, we conducted a 7-year field experiment with N and P additions in the Songnen meadow, northeastern China. This study aims to clarify the influence of long-term N and P additions, and their interaction on the soil bacterial and fungal communities, to better understand the pathways by which N and P additions affect soil microbes, and to reveal new insights into possible changes in soil ecological functions under N and P additions in a temperate meadow. We hypothesized that: (1) the addition of N would decrease soil bacterial and fungal species diversity and alter the community structure because of a decline in soil pH caused by N addition, whereas P addition would have few impacts (Wang et al. 2018); (2) the soil fungi would be more sensitive than soil bacteria because the closer associations between plants and fungi (Li et al. 2020); and (3) the changes in the soil community structure induced by the addition of N and P would be determined by the changes in plant community composition caused by N and P addition (Cline and Zak 2015).

Material and methods

Experiment site

This experiment was performed in Songnen grassland (123°45′ E, 44° 45′ N), in western Jilin Province, northeastern China. The Songnen grassland is the largest temperate meadow in China, and has been seriously influenced by N deposition (Zhang et al. 2015, 2016; Wen et al. 2020). The altitude of the experimental area is 135–165 m. The annual rainfall at the experimental site is approximately 300–500 mm with a mean of 400 mm (Kang et al. 2020). The annual air temperature on average is 2. 4–2.7 °C. In this region, the soil type is Chernozem soil and it is characterized by a higher pH (7.5–9.0) and a low organic matter content (3–4%) (Zhang et al. 2016). Soil N is limited with a total soil N of 1.8 g kg^{-1} and a soil available P concentration of 2.5 mg kg^{-1} (Mei et al. 2019). The terrain in this area is flat, and the vegetation is relatively uniform. The vegetation is dominated by *Leymus chinensis* and some subordinate species, such as *Carex duriuscula, Polygonum sibiricum, Thalictrum aquilegifolium*, and *Chloris virgata*.

Experimental design

A completely randomized block factorial experimental design was used with two nutrient factors, and N and P additions were included in this experiment. There were four treatments: N addition (N), P addition (P), N + P addition (NP), and one control (C), with three replicates per treatment (Fig. 1). The experimental plot size was 2 × 2 m, with buffer zones (2 m in width) between the plots. Previous studies reported that the saturation rates of soil N and P additions for plant communities were 10.5 g N m^{-2} $year^{-1}$ and 10 g P m^{-2} $year^{-1}$ in grasslands in northern China (Bai et al. 2010; Zhao et al. 2019), respectively. For the additions of N and P, a NH_4NO_3 solution (10 g N m^{-2} $year^{-1}$ in 10 L water) and $Ca(H_2PO_4)_2$ solution (10 g P m^{-2} $year^{-1}$ in 10 L water) was added to the plots before plant germination. In the NP addition treatment, NH_4NO_3 and $Ca(H_2PO_4)_2$ solutions (10 g N and 10 g P m^{-2} $year^{-1}$ in 10 L water) were simultaneously added to the experimental plot. To reduce the effect of water caused by the addition of N and P on the experimental results, the same amount of water (10 L water m^{-2} without N and P) as in N and P treatments was added to the control plots. The experiment began in May 2013.

Sampling and measurements

The soil was sampled in August 2019 and the following parameters were measured soil pH, the concentrations of soil total N, available P, soil moisture, and the community and composition structure of soil bacteria and fungi. In each plot, five soil cores (an inner diameter of 5 cm, 20 cm in-depth) were drilled randomly from three replicate blocks, and then homogenized thoroughly and sieved (2 mm) before chemical analysis. Soil total N and available P were determined according to Mei et al. (2019). Soil pH was measured using a glass electrode.

Plant community composition and productivity

To explore the relationship between the soil and plant community composition under N and P additions, the

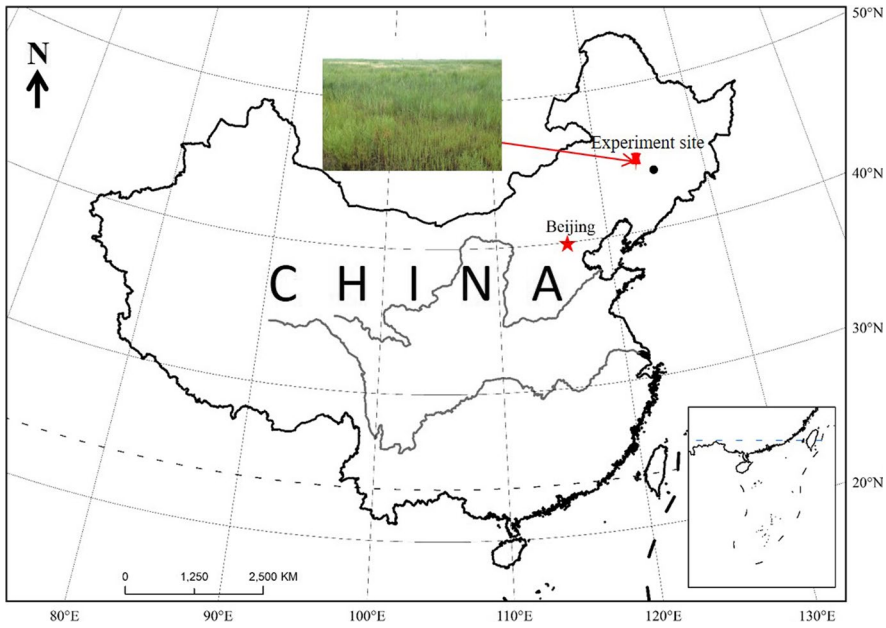

Fig. 1 The experimental site location

plant community composition was studied after seven years of nutrient addition. The plant species in each block were recorded on July 15, 2019 (peak growing season) according to the method of Zhao et al. (2019). Plant species were recorded using a modified point-frame method (1×1 m^2), and the plant species number (species number m^2) and density were recorded to calculate the Shannon–Wiener index *H*. Plants in two quadrants (50×50 cm^2) in each plot were randomly cut in September 2019 to measure the aboveground biomass, which included the dead biomass from the previous year. After cutting the plants in the quadrants, the aboveground plants were weighed after drying for 48 h at 65 °C.

Soil DNA extraction and high-throughput sequencing

A Power Soil DNA Isolation Kit (MO BIO Laboratories) was used to extract soil DNA. The quantity and quality of DNA were evaluated, and the DNA was then stored at −80 °C before use. The 16S rRNA gene of bacteria (in the V3-V4 region) was amplified by the primers 338-F (5′- ACTCCTACGGGAGGCAGCA-3′) and 806-R (5′- GGACTACHVGGGTWTCTAAT-3′) (Mori et al. 2014). We amplified the rRNA gene of fungi (ITS1 region) using ITS1-F (5'-CTTGGTCATTTAGAGGAA GTAA-3′) and ITS2-R (5'-GCTGCGTTCTTCATC GATGC-3′) primers (White et al. 1990; Gardes and Bruns 1993).

We performed PCR amplification in a total volume of 50 µl including the buffer and DNA polymerase (Table S1). A description of the thermal cycling conditions of the first step of PCR can be found in Table S2. We purified the PCR products in the first step using DNA clean beads (VAHTSTM). The amplification PCR of the second round and conditions of thermal cycling can be found in Tables S3 and S4. The sequencing of bacteria and fungi was performed using the Illumina HiSeq2500 platform (2×250 paired ends).

Sequence analyses

The paired-end reads of the fungal ITS gene and bacterial 16S rRNA gene were processed, and the ITS region and 16S sequences were screened for quality control according to the methods of Guo et al. 2019. We clustered all the tags of >97% identity into operational taxonomic units (OTUs). The tags were classified into different taxonomies according to the Silva and UNITE databases for soil bacterial and fungal communities, respectively. There were 17,822 OTUs for soil bacteria and 4986 OTUs for soil fungi after removing those OTUs that did not belong to the soil bacterial or fungal community.

Data analyses

All analyses were performed using R version 3.6.0. (R Core Team 2019). To determine the influence of N and P additions, and their interactive effects on soil total N concentrations, available P concentrations, soil moisture, soil pH, plant species diversity (Shannon–Wiener index, H), aboveground biomass, soil bacterial and fungal α-diversity (the indices of ACE index, Chao1, Shannon and Simpson), and the dominant (> 1%) bacterial and fungal group abundances, two-way ANOVA was performed using R software. The N and P addition effects and their interaction on the community compositions of soil bacteria and fungi were tested by PERMANOVA using the vegan package with 104 permutations. We also visualized how taxonomic frequency and abundances responded to N and P additions using ternary plots. To explore the variations in soil fungal and bacterial species compositions in the fractions illustrated by plant diversity, productivity, soil N and P concentrations, moisture, and pH, we performed distance-based redundancy analysis (db-RDA) based on Bray–Curtis distance. Structural equation modeling (SEM) was performed to explore the pathways by which N and P additions affected soil bacterial and fungal richness according to the methods described by Yang et al. (2021a, 2021b).

Results

Plant and soil parameters

Nitrogen addition highly enhanced the soil total N concentration ($F=4.217$, $P=0.025$) but had no influence on the soil-available P concentration ($F=2.021$, $P=0.27$, Fig. 2a and b). In contrast, phosphorus addition improved the concentrations of both total N ($F=5.01$, $P=0.022$) and available P ($F=10.02$, $P<0.01$) in the soil (Fig. 2a and b). The soil total N ($F=4.327$, $P=0.023$) and available P ($P<0.05$) concentrations in the NP addition treatment were higher than those in the control. For the soil total N concentration, there was no significant difference ($F=1.727$, $P=0.17$) between the P and NP addition treatments (Fig. 2a), and no obvious difference in the soil-available P concentration ($F=0.372$, $P=0.65$) between the P addition and NP addition treatments was detected (Fig. 2b). Significant interactive effects of N and P addition on soil total N concentration were observed ($F=7.371$, $P=0.004$). N and P additions significantly altered the plant community structure (Fig. S4). The addition of N decreased plant species diversity ($F=5.47$, $P=0.018$, Fig. 2c) but significantly increased aboveground biomass ($F=2.478$, $P=0.033$, Fig. 2d). Phosphorus addition did not affect plant species diversity ($F=1.051$, $P=0.271$, Fig. 2c) or aboveground biomass ($F=0.957$, $P=0.375$, Fig. 2d). The addition of NP had no impact on plant species diversity ($F=1.\ 570$, $P=0.145$, Fig. 2c) but led to an increase in aboveground biomass ($F=4.57$, $P=0.012$, Fig. 2d). No interactive effects of N and P additions on plant species richness ($F=0.78$, $P=0.55$, Fig. 2c) or aboveground biomass were detected ($F=1.077$, $P=0.25$, Fig. 2d).

OTU richness and α-diversity

Rarefaction analysis was performed to compare the levels of bacterial and fungal diversities in terms of the total number of OTUs and the Chao 1 index, and the rarefaction results are presented in Supplementary Data Fig. S1. Nitrogen addition had no impact on the soil bacterial OTU richness ($F=1.097$, $P=0.15$), but it was significantly reduced in the P ($F=4.057$, $P=0.021$) and NP ($F=7.907$, $P=0.002$) addition treatments (Fig. 3a). The addition of N and P had no interactive effect on bacterial OTU richness ($F=2.017$, $P=0.045$). Both N ($F=10.101$, $P=0.005$) and P ($F=13.475$, P - 0.003) additions increased the soil fungal OTU richness (Fig. 3b). The interactions between N and P additions significantly affected fungal OTU richness ($F=21.017$, $P=0.001$).

The addition of N ($F=5.201$, $P=0.014$) and P ($F=11.701$, $P=0.002$) remarkably decreased the Chao1 index of soil bacteria (Fig. 3c). The Chao1 index in the NP addition treatment was much lower than that in the N addition ($F=10.011$, $P=0.002$) and control ($F=34.08$, $P<0.001$, Fig. 3c) treatments. A significant primary effect of P addition on the Chao1 index of bacteria was noticed ($F=24.57$, $P<0.001$). The addition of N ($F=4.27$, $P=0.024$) and P ($F=5.18$, $P=0.015$) remarkably enhanced the Chao1 index of soil fungi, and no obvious difference was detected between NP addition and the addition of N and P ($F=1.08$, $P=0.27$, Fig. 3d).

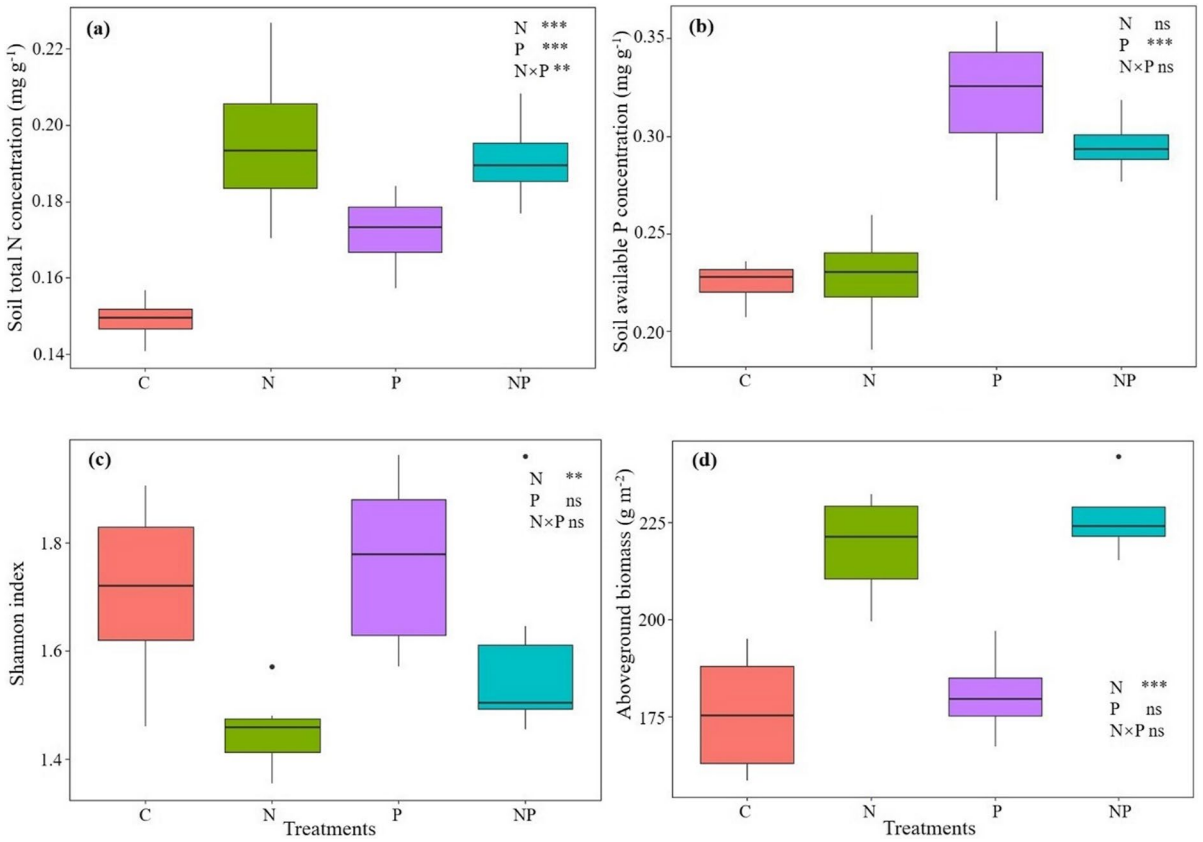

Fig. 2 Effects of the additions of nitrogen (N) and phosphorus (P) on the soil N (**a**) and P concentrations (**b**), plant species diversity (Shannon index, **c**) and aboveground biomass (**d**). C represents the control, N represents N addition, P represents P addition, and NP represents nitrogen plus phosphorus addition. * indicates $P<0.05$; ** indicates $P<0.01$; *** indicates $P<0.001$; ns indicates no significance

Structural equation modeling analysis accounted for 17%, 73%, 29%, 31%, 30%, 80% and 76% of the variations in soil total N, available P, pH, aboveground net primary productivity (ANPP), plant species diversity (Shannon index), and the species richness of bacteria and fungi, respectively (Fig. 4). The addition of N and P caused an increase in soil fungal richness, most likely through their positive effect on soil total N and available P concentrations (Fig. 4). The positive changes in plant species diversity due to the decline in soil pH led to the shift in soil bacterial richness (Fig. 4).

Soil bacterial and fungal community compositions

Proteobacteria (38.5%), Acidobacteria (22.4%), Actinobacteria (14.8%), and Gemmatimonadetes (8.3%) dominated the soil bacterial community across all the treatments (Fig. 5a). Phosphorus addition reduced the abundances of Proteobacteria ($F=3.18$, $P=0.027$) and Gemmatimonadetes ($F=4.31$, $P=0.017$) and increased the abundances of Acidobacteria ($F=7.11$, $P=0.005$) and Actinobacteria ($F=3.07$, $P=0.031$), while neither the addition of N ($F=1.07$, $P=0.095$) nor the addition of NP ($F=2.04$, $P=0.068$) influenced the dominant bacterial taxon abundances. For soil bacteria, Proteobacteria and Gemmatimonadetes were closely tied to P addition (Fig. S2a), while no phyla were closely tied to N addition or the control (Fig. S2a). Several families were affected by N and P additions.

Ascomycota (42.7%), Basidiomycota (11.8%), Gemmatimonadetes (8.3%), and Chloroflexi (7.3%) dominated the soil fungal community across all samples (Fig. 5b). Nitrogen addition increased Ascomycota ($F=6.01$, $P=0.012$) and decreased Basidiomycota ($F=6.01$, $P=0.012$) abundances. The addition of P reduced the abundances of Basidiomycota ($F=3.47$,

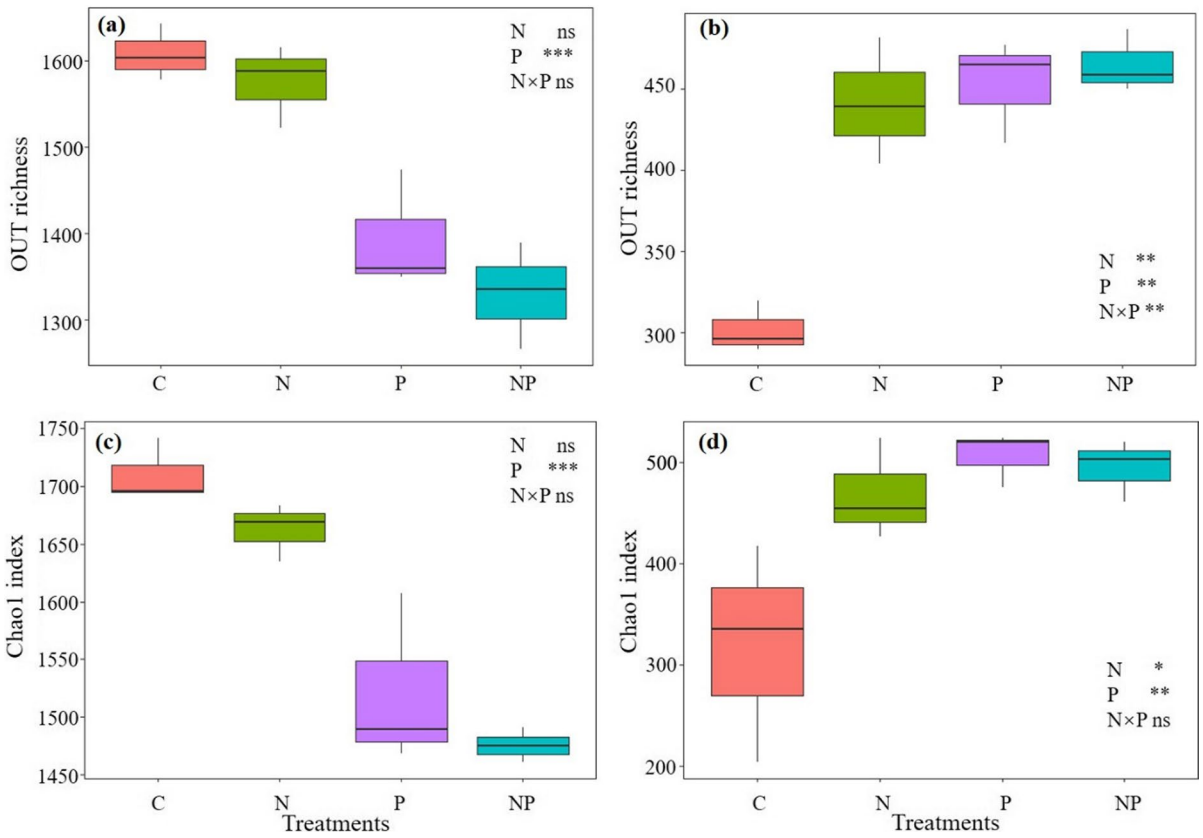

Fig. 3 Effects of the additions of N and P on soil bacterial (**a**) and fungal (**b**) OTU numbers and the Chao1 index of soil bacterial (**c**) and fungal (**d**) communities. C represents the control, N represents nitrogen addition, P represents P addition, and NP represents nitrogen plus phosphorus addition. * indicates $P<0.05$; ** indicates $P<0.01$; *** indicates $P<0.001$; ns indicates no significance

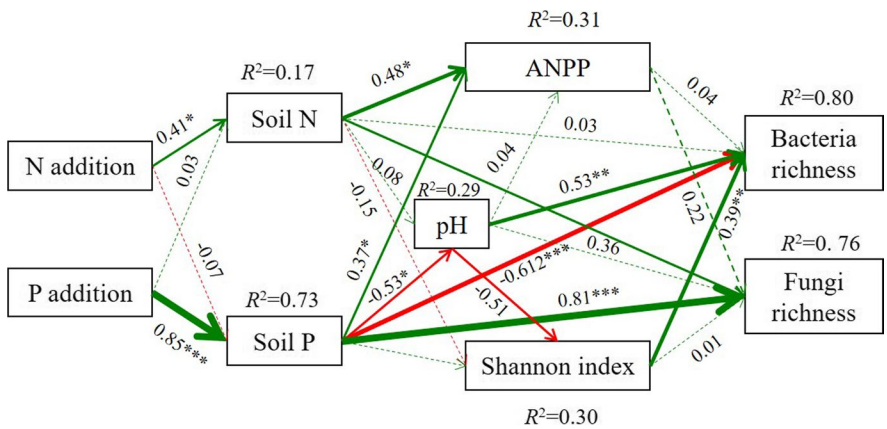

Fig. 4 Structural equation models of N addition and AM fungi as predictors of ecosystem functioning. Solid red arrows represent negative paths, solid green arrows represent positive paths, and dotted red and green arrows represent nonsignificant paths. * indicates $P<0.05$, ** indicates $P<0.01$, *** indicates $P<0.001$, $\chi^2=2.9$, $P=0.40$; root mean square error of approximation (RMSEA) = 0.40, $P=0.27$; Akaike information criteria = 38.93

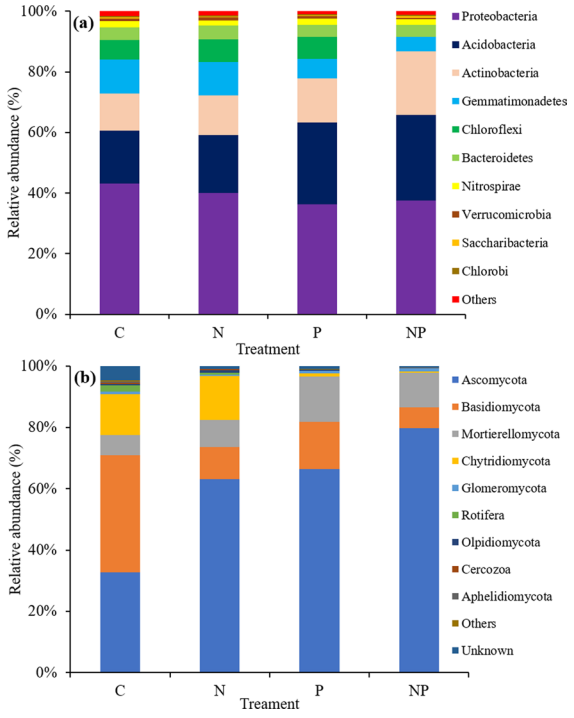

Fig. 5 Effect of N and P additions on the relative abundances of the soil bacterial (**a**) and fungal (**b**) groups. C represents the control, N represents N addition, P represents P addition, and NP represents nitrogen plus phosphorus addition. The dominant groups are shown (relative abundances >1%), while the rare groups (relative abundances <1%) are integrated into "other"

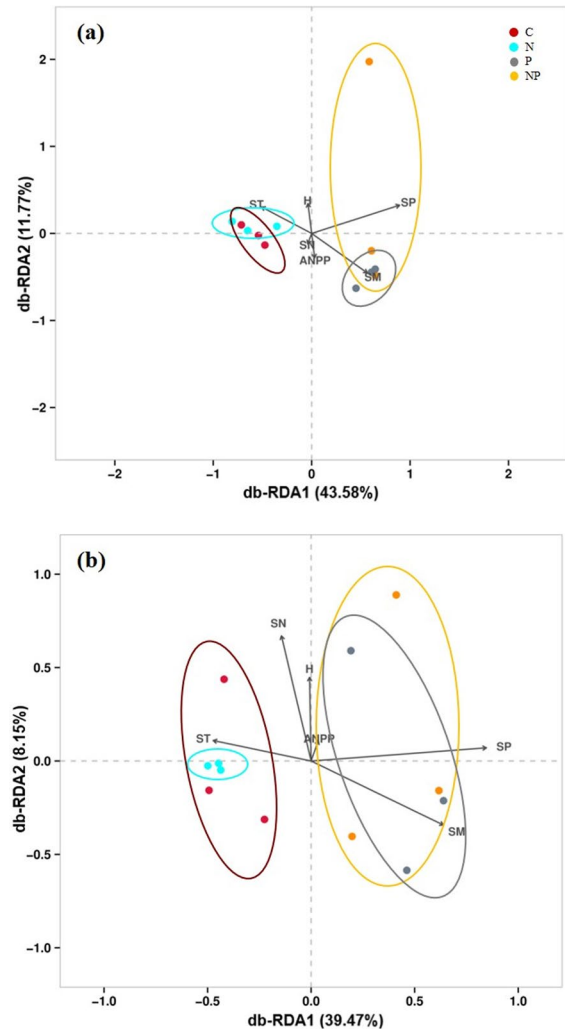

Fig. 6 Soil bacterial (**a**) and fungal (**b**) community compositions and their variation partition ordination plots of db-RDA under additions of N and P in a temperate meadow in northeastern China

$P=0.022$) and Chytridiomycota ($F=26.03$, $P=0.002$). For the soil fungal composition, Ascomycota was closely tied to P addition (Fig. S2b), while no phyla were closely tied to N addition (Fig. S2b).

The db-RDA results showed significant shifts in the community compositions of bacteria (Fig. 6a) and fungi (Fig. 6b). The variation in the bacterial community were mainly influenced by the soil available P content ($F=10.14$, $P=0.004$) and soil moisture ($F=3.13$, $P=0.021$). Soil available P content ($F=8.75$, $P=0.006$), soil total N content ($F=4.22$, $P=0.014$), and soil moisture ($F=3.27$, $P=0.031$) were found to be the most important parameters influencing the community composition of soil fungi. The addition of P ($F=16.07$, $P=0.003$) and NP ($F=4.24$, $P=0.022$)) strongly altered the community composition of bacteria, while the addition of N had no effect ($F=1.03$, $P=0.472$), Fig. 7a). Significant main effects of N ($F=14.37$, $P=0.003$) and P additions ($F=11.13$, $P=0.004$) and interactive effect of P addition × N addition ($F=20.24$, $P=0.001$) on soil fungal community composition were observed (Fig. 7b).

Discussion

The influence of N and P additions on soil bacterial diversity

This study provides new insight into the impacts of N and P additions on bacterial and fungal communities

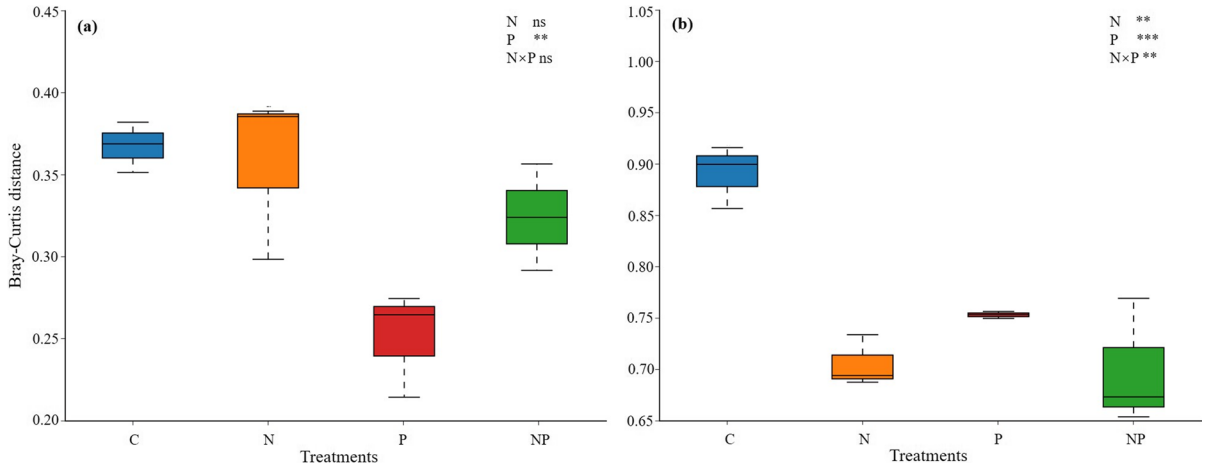

Fig. 7 Results of PERMANOVA testing the effects of the additions of N and P on the bacterial (**a**) and fungal (**b**) communities in soil. * indicates $P < 0.05$; ** indicates $P < 0.01$; *** indicates $P < 0.001$; ns indicates no significance

in a temperate meadow. The addition of N was found to have no influence on soil bacterial OTU richness or α-diversity (Fig. 3), which is inconsistent with previous studies showing that N enrichment reduced soil bacterial richness in tropical forests, temperate steppes, and arctic tundra ecosystems (Campbell et al. 2010; Zeng et al. 2016; Wang et al. 2018; Yan et al. 2018). This might be partly explained by background nutrient availability or soil pH because many previous studies demonstrated that the diversity of soil bacteria is frequently affected by the decline in soil pH caused by N addition (Fierer and Jackson 2006; Wang et al. 2018). The soil pH at our experimental site was much higher than that in the above-studied ecosystem, and N addition did not influence soil pH (Fig. S3). This suggests that N addition has few effects on soil bacterial α-diversity because no significant changes in soil pH resulted from N addition in the highly alkalized N-limited temperate meadow (Fig. S4a). Moreover, soil microbial diversity is likely to increase with the enhancement of plant diversity (van der Heijden et al. 2008). Nitrogen addition highly decreased plant species diversity, but had no impact on soil bacterial richness, suggesting that the sensitivity of soil bacteria to N addition might lag compared to that of plant species. The results also suggest that the effects of N addition on the species diversities of plants and soil bacteria may not be the same (Fierer et al. 2012).

Phosphorus addition significantly reduced soil bacterial OTU richness and α-diversity which is not in agreement with earlier studies showing that P addition did not affect soil bacterial richness (Eo and Park 2016) and that soil bacterial diversity is enhanced with P addition in an agricultural ecosystem (Tan et al. 2013). First, one possible reason for this discrepancy is the competition between soil bacteria and fungi because P addition significantly increased soil fungal diversity, which might have reduced the competition and species diversity of soil bacteria. Second, a significant negative correlation between soil bacterial richness and soil P concentration was detected (Fig. S4b), suggesting that P addition might increase the competition for nutrients between soil bacteria and plants, and thereby reducing soil bacterial richness (Zhang et al. 2014). Moreover, P addition increased the soil available P concentration which might reduce phosphate solubilizing bacteria and indirectly decrease soil bacterial richness. However, the reduction in soil bacterial diversity may not have a negative influence on soil functionality because of the functional redundancies in the soil bacterial community (Pan et al. 2014).

Influences of N and P additions on soil fungal diversity

The addition of N increased soil fungal richness which is in agreement with previous studies that N fertilization highly enhances soil fungal

richness in N-limited ecosystems (Weber et al. 2013; Mueller et al. 2014), this might be related to the increase in soil N availability caused by N addition (Fig. 4). Moreover, the increase in soil fungal richness might be due to the increase in plant aboveground biomass which should favor the growth of soil fungi by increasing the growth of plant belowground biomass and reducing N competition in the soil fungi. The results suggest that some fungal species are more adaptable and tolerant to N addition, and soil N and P concentrations had significant positive influences on soil fungal richness (Fig. S4c, d). The results also indicate that the influence of N addition on soil fungal diversity might depend on the type of grassland ecosystems and the dose of nutrient addition (Zhou et al. 2016).

Phosphorus addition significantly enhanced the soil fungal richness in our present study, which is inconsistent with a previous study that reported that P fertilization reduced the soil fungal species richness (He et al. 2016). One possible reason for this is that soil fungi can increase plant P uptake which might facilitate the associations between soil fungi and plants (Zhang et al. 2014), thereby improving the biomass of soil fungi (Liu et al. 2012). This suggests that P deficiency might be used directly to predict the positive impacts of P addition on soil fungal richness.

Influences of N and P additions on the soil bacterial community composition

Our results showed that N addition had no impact on the community composition of soil bacteria, which agrees with N enrichment impacts on the bacterial community in soil across the globe (Leff et al. 2015). This may be because N addition did not decrease soil pH in the present study, in contrast to many previous studies that reported declines in pH, which is a crucial factor that changes the bacterial community (Wang et al. 2018; Guo et al. 2019). Moreover, the db-RDA results indicated that the changes in the bacterial community were mediated mainly by the soil available P concentration, suggesting that the small changes in soil N addition caused by N input did not directly affect the soil bacterial community composition by decreasing the pH and affecting the soil C/N ratio. Although the addition of N significantly affected the structure of the plant community and productivity in this studied ecosystem (Zhao et al. 2019), the changes in plant community structure and ANPP had no significant impact on the soil bacterial community, suggesting that the responses of soil bacteria to N addition might be lower than those of the plant community (Fig. S5).

In the current study, the addition of P significantly increased Actinobacteria and Acidobacteria abundances and decreased the abundances of Proteobacteria and Gemmatimonadetes. This result is consistent with previous results from a tropical forest (Wang et al. 2018). Several studies have shown that changes in pH caused by P addition play a vital role in influencing the community composition of soil bacteria (Ling et al. 2017; Wang et al. 2018). In the current study, P addition had little effect on soil pH (Fig. S3); however, the soil bacterial community was strongly determined by the soil P concentration with the addition of P and NP, suggesting that an increase in soil P availability and nutrient balance might play a critical role in shaping the soil bacterial community composition. In addition, the increase in Acidobacteria and Actinobacteria might improve plant growth because Acidobacteria have high metabolic activities in rhizosphere soil (Lee et al. 2008), and Actinobacteria may improve plant growth by alleviating soil disease suppression (Palaniyandi et al. 2013); this would increase C input from plants to the soil with the enhancement of soil bacterial activities (Li et al. 2015). However, the influence of varying C/N/P ratios caused by the addition of N and P on the soil bacteria community requires further study.

Influences of N and P additions on the community composition of soil fungi

In the present study, we found that N addition highly increased Ascomycota abundance, but decreased Basidiomycota abundances, which is consistent with previous studies showing that the addition of N can alter the community structure of soil fungi (Leff et al. 2015; Yan et al. 2018; Wu et al. 2021). One reason for this might be related to the increase in soil total N concentration caused by N addition as the soil total N concentration had a positive impact on soil fungal richness (Fig. 4). Ascomycota are saprotrophic fungi that can accelerate soil C decomposition (Xiong et al. 2014), and the increase in Ascomycota induced by N addition increases soil C decomposition and speed up the C cycle. This might explain why N addition led

to the increased litter decomposition of *Leymus chinensis* in the temperate meadow (Gong et al. 2015). Nitrogen addition decreased Basidiomycota abundances, which may have reduced the competition pressures on Ascomycota for resources (Weber et al. 2013). Furthermore, Glomeromycota abundances remarkably declined under N addition suggesting that N addition reduces plant species diversity because most of the species are mycorrhizal plants.

In the present study, P addition significantly affected the community composition of fungi in the soil, which is in agreement with earlier studies (Liu et al. 2012; Nielsen et al. 2015; He et al. 2016). The abundances of Ascomycota and Mortierellomycota significantly increased, but Basidiomycota and Chytridiomycota abundances declined significantly upon P addition. Moreover, the db-RDA results showed that the N and P addition effects on the soil fungal community composition were possibly determined by the soil P concentration (Liu et al. 2018). These results support the previous studies, and changes in the soil fungal community structure alters the ecological function of the soil. For instance, Mortierellomycota can help prevent soil degradation (Li et al. 2019). Additionally, the changes in fungal community structure also supported previous studies that P addition can mitigate the negative impacts of N addition on the plant community structure (Limpens et al. 2004; Pilkingtona et al. 2007; Ceulemans et al. 2014). The current study indicates that changes in the community composition of soil fungi might be a good indicator to explain the impact of P addition on the plant community structure because of the tight association between plant roots and soil fungi. However, how these increased or decreased abundances of soil fungi affect the growth of different functional groups needs further study.

Conclusion

In this study, soil bacterial and fungal diversities responded differently to the addition of N and P in a salinized meadow. The addition of N had little influence on the richness of soil bacteria but had a positive impact on soil fungal richness. Phosphorus addition reduced the soil bacterial richness and increased the soil fungal richness. Nitrogen addition did not influence the bacterial community composition but affected the fungi in the soil. Additionally, both the communities of soil bacteria and fungi shifted due to P addition. The changes in soil P availability induced by N and P additions mainly determined the β-diversity of soil bacteria and fungi. Our findings suggest that the responses of the soil bacterial and fungal communities to 7-year N and P additions were not consistent in the studied ecosystem. Our results highlight that the soil fungal community might be better used to indicate the response of the soil microbial community to N and P enrichment in temperate meadow ecosystems. Moreover, the response of plant community composition to N and P additions was not consistent with the soil bacterial and fungal community composition. These results indicate that P addition might play a key role in affecting the soil microbial community composition in N-limited meadow ecosystems, and that the plant community is more flexible than the soil microbial community in tracking environmental changes.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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