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ORIGINAL PAPER

Shifts in bacterial and fungal diversity in a paddy soil faced with phosphorus surplus

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Abstract

Abundant phosphorus (P) has been applied to paddy fields in the red soil region of subtropical China. Microbial communities play important roles in soil nutrient cycling; however, the effects of P surplus on soil microbial diversity and community composition are still unclear. Soils collected from paddy fields in subtropical China was incubated and subjected to four P treatments: 33 kg ha^{-1} (CK), 66 kg ha^{-1} (P1), 132 kg ha^{-1} (P2), and 264 kg ha^{-1} (P3). Changes in bacterial and fungal diversity and community composition were evaluated by high-throughput sequencing. The different P rates had no significant effect on bacterial diversity, whereas fungal richness and diversity indexes declined significantly by increasing P rates. Principle coordinate analysis (PCoA) also indicated a shift in fungal community composition when P rates were higher than 132 kg ha^{-1}. Available P (AP) was the dominant factor affecting fungal community composition as evaluated by canonical correspondence analysis (CCA). Multivariate regression trees (MRT) revealed that the key threshold of 53.6 mg kg^{-1} of AP divided treatments into two distinct groups. Linear discriminant analysis effect size (LEfSe) showed that abundances of *Pseudogymnoascus* and *Geomyces* increased, but those of *Penicillium* and an unknown genus of *Trichocomaceae* decreased when AP was ≥ 53.6 mg kg^{-1}.

Keywords Subtropical China · Different P rates · Microbial community composition · High throughput sequencing · Indicator species

Introduction

As one of the elements limiting crop production, P fertilizer is intensively applied to obtain high crop yield in conventional agriculture. It was predicted that by 2050, global P fertilizer input would increase by 64% compared to that in 2000 and reach 23 Tg year^{-1} (Bouwman et al. 2013). However, only 10–20% fertilizer P is recovered by crop in the short term and a large portion of input soluble P is fixed and accumulated in soil (Bouwman et al. 2009). It has been reported that soil P surplus could increase by 54% and reach 18 Tg year^{-1} by 2050 (Bouwman et al. 2013). The red soil region is the main grain-producing area in subtropical China and paddy fields are the major land use sites in this region. To obtain and maintain high rice yield, abundant P is added to paddy fields. Red soil is rich in ferric and aluminum ion; thus, applied soluble P is strongly fixed and its utilization efficiency is low (Zhang and Li 1998). This has led to P accumulation up to 300% in subtropical China (Lu et al. 2000). This P surplus may not only brings potential environmental problems, such as eutrophication, but also affects soil ecological processes. For example, N fixation and soil respiration often increased with P availability (Cleveland et al. 2011). Phosphorus also affected organic carbon, microbial biomass, microbial community composition, and metabolic activity of soil (Liu et al. 2013; Wakelin et al. 2017).

Microorganisms play essential roles in nutrient cycling, and microbial community composition is closely related to soil ecosystem processes and functions (Brussaard et al. 2007). Conversely, nutrient availability, particularly N and P, also has effects on microbial properties. However,

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contradictory effects of P on soil microbial diversity have often been observed. For instance, P addition was shown not only to increase (Tan et al. 2013; Zhong and Cai 2007) but also decrease the microbial Shannon diversity indexes in soil (Chhabra et al. 2013). Moreover, several studies showed that P amendments can affect biomass, activity, and composition of microbial communities (Beauregard et al. 2010; Chen et al. 2016; Huang et al. 2016; Liu et al. 2012; Wakelin et al. 2017), while others revealed no obvious changes in microbial community composition under P addition (Hamel et al. 2006; Huang et al. 2016; Shi et al. 2012).

These contradictory results depend on different P fertilization rates, crop rotation, or land use and also on the method used for microbial community analysis. For example, Beauregard et al. (2010) discovered that there was no significant effect of P input on the microbial community composition based on phospholipid fatty acid analysis, whereas the composition of bacterial and fungal communities was influenced by P addition and crop season as determined by denaturing gradient gel electrophoresis. In addition, different sensitivities of bacteria and fungi to P addition make estimation of the overall microbial response more complicated.

In the present study, incubation experiments using different P fertilizer rates were carried out with a paddy soil sampled from the red soil region of subtropical China. High throughput sequencing of amplified bacterial 16S rDNA and fungal Internal Transcribed Spacer (ITS) region was done to get information on the diversity of the two microbial communities under P surplus. The specific objective of this study was to test the hypothesis that responses in composition of bacterial and fungal communities were different with different P fertilization rates.

Materials and methods

Site and soil collection

Paddy fields accounted for 30% China arable land and more than 90% of which were located in tropical or subtropical of China (Jia et al. 2010). Thus, a typical paddy filed in Yingtan, Jiangxi Province, subtropical China (28° 15′ 30″ N, 116° 55′ 30″ E) was selected as sampling site. Double rice was continuously cultivated before sampling. A red soil derived from Quaternary Red Clay was collected (0–15 cm) at the end of October. After sampling, soil was mixed thoroughly for the subsequent incubation experiment, air-dried at room temperature, and sieved (< 2 mm). The soil organic carbon (SOC), total N (TN), and total P (TP) contents were 40.7, 2.48, and 0.69 g kg^{-1}, respectively, while the available N (AN) and P (AP) contents were 207 and 29.7 mg kg^{-1}, respectively. The water holding capacity of soil was 61.0%.

Incubation experiment and soil measurement

Incubation experiment

The local P fertilization rate of the red soil region was 33 kg ha^{-1} P. We carried out the following four treatments: 33 kg ha^{-1} (CK), 66 kg ha^{-1} (P1), 132 kg ha^{-1} (P2), and 264 kg ha^{-1} (P3) of P; to get these rates, 36, 72, 144, and 288 mg calcium superphosphate (6% P) were mixed thoroughly with 190 g soil at a 40% water holding capacity gravimetrically. Additionally, 22 mg urea (46% N) and 19 mg potassium chloride (43% K), equivalent to 150 kg ha^{-1} N and 124 kg ha^{-1} K, respectively, were incorporated into soil. The mixture was then settled in a 600-ml plastic bottle sealed with a gas-permeable membrane. Each treatment was replicated three times. After incubation at 25 °C for 60 days, portions of the fresh samples were collected to be analyzed for microbial properties. The remaining soil samples were air-dried to determine the chemical characteristics.

Chemical property measurement

Soil pH was measured in 1:2.5 soil-to-water solutions (*w*/*v*) using the potentiometric method. After digesting with 0.8 M $K_2Cr_2O_4$/concentrated H_2SO_4 (*v*/*v*, 1:1) SOC was measured using the Tyrin method (Pansu and Gautheyrou 2006). Kjeldahl and the alkali-hydrolysis diffusion methods were used to determine TN and AN (Pansu and Gautheyrou 2006). Soil was heated at 850 °C with anhydrous sodium carbonate, then TP was dissolved with 5 M sulfuric acid and detected by molybdenum-blue colorimetry (Pansu and Gautheyrou 2006). Soil AP was extracted by 0.5 M sodium bicarbonate and measured by molybdenum-blue colorimetry (Pansu and Gautheyrou 2006).

Microbial biomass P measurement

Microbial biomass P (MBP) was measured using the chloroform fumigation-extraction method (Brookes et al. 1982). Briefly, 5 g of non-fumigated and 5 g of chloroform fumigated soil samples were extracted by 0.5 M $NaHCO_3$, as well as 5 g of spiked soil sample treated with KH_2PO_4 (equivalent to 25 mg P kg^{-1} soil). The extracted inorganic P was determined by molybdenum-blue colorimetry. MBP was calculated as $MBP = E_P / (K_P \times R_P)$, where E_P was the value of fumigated P minus non-fumigated P, K_P was 0.4, representing 40% microbial P fractions extracted after fumigation, and R_P was the P recovery efficiency estimated with the spiked soil.

DNA extraction, PCR amplification, and Miseq Illumina sequencing

Microbial genomic DNA was extracted from 0.5 g fresh soil using a FastDNA™ SPIN Kit (MP Biomedicals, Santa Ana, CA, USA). Bacterial primers 515F (5′-GTGC CAGCMGCCGCGGTAA -3′) and 806R (5′-GGAC TACHVGGGTWTCTAAT-3′) with a barcode marker were used to amplify the genes targeting the V4 region of the 16S rRNA genes (Caporaso et al. 2011). Fungal primers ITS5-1737F (5′-GGAAGTAAAAGTCGTAACAAGG-3′) and ITS2-2043R (5′-GCTGCGTTCTTCATCGATGC-3′) with a barcode marker were used to amplify the genes targeting the ITS1 region (Schmidt et al. 2013; White et al. 1990). Phusion® High-Fidelity PCR Master Mix with GC Buffer (New England Biolabs, Beverly, MA, USA) was used for the amplification reaction. The PCR cycling conditions were 98 °C for 1 min, 30 cycles of 98 °C for 10 s, 50 °C for 30 s, 72 °C for 30 s, and 72 °C for 5 min. Amplicons were purified using the GeneJET kit (Thermo Scientific, Waltham, MA, USA) and a library was constructed using a NEB Next® Ultra™ DNA Library Prep Kit for Illumina (New England Biolabs). High-throughput sequencing was performed on the Illumina MiSeq PE250 platform.

Sequencing raw data were processed using the Quantitative Insights Into Microbial Ecology (QIIME) software package (Caporaso et al. 2010). First, reads were filtered by QIIME quality filters to remove primers, barcodes, low-quality sequences (quality score $Q < 25$), or ambiguous nucleotides as evaluated by the database. Sequences with ≥ 97% similarity were then assigned to the same OTUs. A representative sequence for each OTU was then selected and taxonomic information was annotated by RDP classifier (Wang et al. 2007). Each sample was then rarefied to the same number of sequences for subsequent analyses. Finally, 10,947 high-quality sequences were grouped into 3859 OTUs for bacteria and 27,388 high-quality sequences were grouped into 547 OTUs for fungi for each sample. Sequences (raw data) of bacteria and fungi were submitted to Sequence Read Archive (SRA) of NCBI with the accession numbers SRP112637 and SRP112647.

Statistical analyses

Significant differences among treatments were determined by one way ANOVA with Duncan's post hoc test at $P < 0.05$ (SPSS, Chicago, IL, USA). Microbial α and β diversity were analyzed by R (version 3.2.3; R Development Core Team). The Chao1 richness and Shannon diversity indexes were calculated by using the phyloseq package. Principal coordinate analysis (PCoA) and canonical correspondence analysis (CCA) was performed with the vegan package. The effects of P rates on the composition of microbial communities were determined by permutational multivariate analysis of variance (PERMANOVA) using adonis function within the vegan package. The vif.cca function was used to remove the high autocorrelation variables when CCA was conducted. Significant effects of total and specific edaphic properties on the microbial community were determined by the anova.cca and envfit functions within the vegan package. Multivariate regression trees (MRT) were generated with the mvpart package (De'Ath 2002). To identify indicator species in soils with different P availability, the linear discriminant analysis (LDA) effect size (LEfSe) method was used (http://huttenhower.sph.harvard.edu/lefse/) (Segata et al. 2011).

Results

Changes in edaphic properties and MBP under different P fertilization rates

Except for treatment P3, in which AN content was significantly higher than CK, there was no obvious difference in AN contents among the other P rates (Table 1). The total and available P contents were 0.69–0.81 and 41.4–75.0 mg kg^{-1}, respectively, and these increased obviously with P fertilization rates (Table 1). The MBP was 14.0–21.0 mg kg^{-1}, which was also significantly higher in treatments with higher than lower P rates (Table 1). The C/P and N/P ratios were 123–151 and 6.92–8.09, respectively, under different P fertilization rates (Table 1).

Changes in microbial diversity and community composition under different P fertilization rates

Bacterial Chao1 and Shannon indexes were not significantly affected by different P fertilization rates (Table 2). However, when input rates were > 132 kg ha^{-1}, fungal Chao1 and Shannon indexes decreased markedly.

The first and second axes of PCoA explained 46.8 and 14.5% of the variation in the bacterial community composition, respectively. The bacterial communities were not clearly separated by the different P rates (Fig. 1). Axes 1 and 2 of PCoA interpreted 88.2 and 2.3% of changes in the composition of the fungal community. The fungal community of P2 and P3 treatments was separated from that of CK and P1 treatments along PCoA 1 (Fig. 1).

Different P rates did not affect bacterial community composition as evaluated by PERMANOVA analysis ($P > 0.05$, Table 3). When P input rates were higher than 132 kg ha^{-1}, the soil fungal community composition was significantly different from that of CK as evaluated by PERMANOVA analysis ($P = 0.02$, Table 3).

Table 1 Properties of paddy soil treated with different P rates

	pH	SOC g kg^{-1}	TN g kg^{-1}	TP g kg^{-1}	AN mg kg^{-1}	AP mg kg^{-1}	MBP mg kg^{-1}	C/N	C/P	N/P
CK	4.77 ± 0.12 a	40.2 ± 1.6 a	2.47 ± 0.03 a	0.69 ± 0.01 c	252 ± 11 b	41.4 ± 0.9 d	14.0 ± 0.1 c	19.0 ± 1.0 a	151 ± 7 a	7.94 ± 0.15 ab
P1	4.73 ± 0.08 a	39.0 ± 1.0 a	2.55 ± 0.16 a	0.70 ± 0.02 c	268 ± 19 ab	48.3 ± 0.8 c	17.4 ± 1.3 b	17.9 ± 0.9 a	145 ± 0 ab	8.09 ± 0.42 a
P2	4.75 ± 0.05 a	38.7 ± 0.7 a	2.43 ± 0.04 a	0.72 ± 0.02 b	258 ± 11 ab	58.6 ± 0.8 b	21.0 ± 2.8 ab	18.6 ± 0.6 a	138 ± 6 b	7.45 ± 0.09 b
P3	4.75 ± 0.10 a	38.4 ± 0.7 a	2.52 ± 0.14 a	0.81 ± 0.02 a	282 ± 4 a	75.0 ± 2.2 a	20.3 ± 0.6 a	17.8 ± 0.8 a	123 ± 1 c	6.92 ± 0.29 c

Different lowercase letters in the same column indicate a significant difference at < 0.05

CK P fertilization rate of 33 kg ha^{-1}, *P1* P fertilization rate of 66 kg ha^{-1}, *P2* P fertilization rate of 132 kg ha^{-1}, *P3* P fertilization rate of 264 kg ha^{-1}, *SOC* soil organic C, *TN* total N, *TP* total P, *AN* available N, *AP* available P, *MBP* microbial biomass P

Impact factors for fungal community changes under different P fertilization rates

The first and second axes of CCA explained 77.6 and 4.7%, respectively, of the variation in the composition of fungal community by soil properties and MBP. Except for high autocorrelation variants, pH, TN, TP, AN, AP, C/N, and MBP as a whole contributed to changes in the composition of fungal community based on ANOVA ($P = 0.01$). Among above soil properties, only AP content ($P = 0.001$), TP content ($P = 0.002$), and MBP content ($P = 0.005$) were those most affecting fungal community composition changes (Fig. 2).

Fungal communities of the different treatments were divided into two groups according to a threshold of 53.6 mg kg^{-1} of AP by MRT analysis (Fig. 3). The community of the CK and P1 treatments grouped together for AP content less than 53.6 mg kg^{-1}, and those of P2 and P3 treatments grouped together over this value (Fig. 3). When the AP content was higher than 53.6 mg kg^{-1}, abundances of *Dothideomycetes*, *Leotiomycetes*, and *Sordariomycetes* increased, but those of *Eurotiomycetes*, *Un-s-Ascomycota sp*, *IS-s-Mortierella sp FSU10537*, *Agaricomycetes*, *Lecanoromycetes*, *IS-s-Mortierella sp FMR23_12*, and *Un-s-fungal sp. K6* decreased (Fig. 3).

According to the results of MRT, we defined treatments CK and P1 as group 1 (soil P availability < 53.6 mg kg^{-1}) and treatments P2 and P3 as group 2 (soil P availability ≥ 53.6 mg kg^{-1}). When LDA effect size scores were < −4.5, *Penicillium* and an unknown genus of *Trichocomaceae* were

Table 2 Bacterial and fungal alpha diversity in soil treated with different P rates

	Bacteria		Fungi	
	Chao1	Shannon	Chao1	Shannon
CK	1419 ± 117 a	5.70 ± 0.12 a	369 ± 17 a	2.42 ± 0.06 a
P1	1470 ± 89 a	5.80 ± 0.16 a	326 ± 25 b	2.39 ± 0.23 a
P2	1510 ± 101 a	5.86 ± 0.20 a	85.5 ± 4.5 c	0.61 ± 0.01 c
P3	1477 ± 95 a	5.78 ± 0.07 a	99.2 ± 19.6 c	0.91 ± 0.18 b

Different lowercase letters in the same column indicate a significant difference at < 0.05

CK P fertilization rate of 33 kg ha^{-1}, *P1* P fertilization rate of 66 kg ha^{-1}, *P2* P fertilization rate of 132 kg ha^{-1}, *P3* P fertilization rate of 264 kg ha^{-1}, *Chao1* species richness index, *Shannon* Shannon diversity index

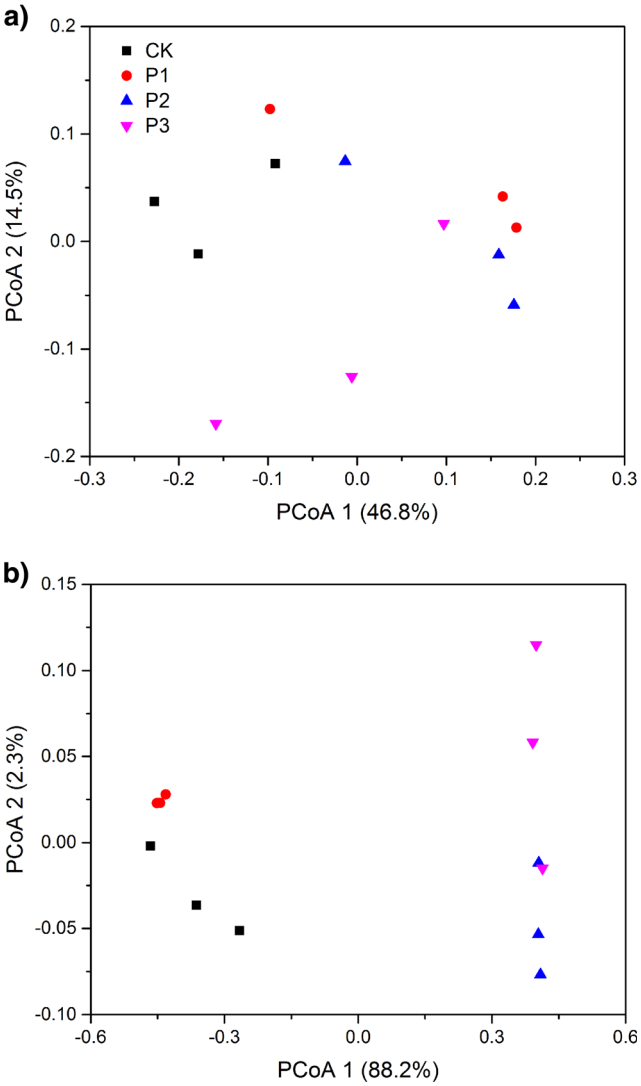

Fig. 1 Principal coordinate analysis of changes in bacterial (**a**) and fungal (**b**) diversity on the basis of the Bray-Curtis distance of communities in a paddy soil treated with different P rates. CK, P fertilization rate of 33 kg ha^{-1}; P1, P fertilization rate of 66 kg ha^{-1}; P2, P fertilization rate of 132 kg ha^{-1}; P3, P fertilization rate of 264 kg ha^{-1}

Table 3 Differences of bacterial and fungal community composition in soil treated with different P rates based on the dissimilarity test of Adonis

	Bacteria		Fungi	
	R^2	P	R^2	P
CK–P1	0.43	0.11	0.42	0.09
CK–P2	0.55	0.10	**0.98**	**0.02**
CK–P3	0.34	0.19	**0.95**	**0.02**
P1–P2	0.17	0.48	0.99	0.10
P1–P3	0.26	0.20	0.97	0.10
P2–P3	0.28	0.32	0.52	0.12

Numbers in bold indicate a significant difference

CK P fertilization rate of 33 kg ha^{-1}, *P1* P fertilization rate of 66 kg ha^{-1}, *P2* P fertilization rate of 132 kg ha^{-1}, *P3* P fertilization rate of 264 kg ha^{-1}, R^2 coefficients of determination

distinguished as an indicator fungi for group 1 by LEfSe analysis. Conversely, when LDA effect size scores were > 4.5, *Pseudogymnoascus* and *Geomyces* were considered indicator fungi for group 2 (Fig. 4).

Discussion

Effect of P fertilization rates on microbial diversity

The response of MBP to high P fertilization rates confirmed what was observed by Huang et al. (2016) in a forest soil. This may occur because microorganisms can accumulate P in their biomass over their physiological demand (Docampo et al. 2010; Khan and Joergensen 2012; Ryazanova et al. 2009). For instance, intracellular polyphosphate accumulated rapidly in arbuscular mycorrhizal fungus with P application (Ezawa et al. 2003). Usually, P is taken up by soil solution and transferred to the vacuoles of arbuscular mycorrhizal fungus and transformed to polyphosphate (Ezawa et al. 2002).

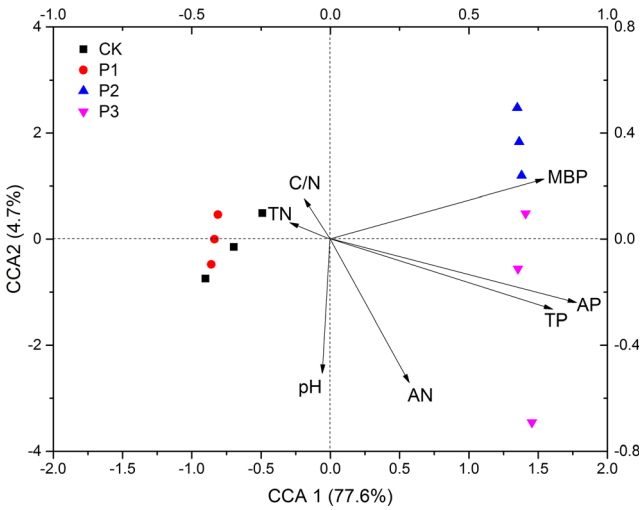

Fig. 2 Canonical correspondence analysis of the effects of soil properties on the composition of fungal communities in a paddy soil treated with different P rates. MBP, microbial biomass P; AP, available P; TP, total P; AN, available N; TN, total N; CK, P fertilization rate of 33 kg ha^{-1}; P1, P fertilization rate of 66 kg ha^{-1}; P2, P fertilization rate of 132 kg ha^{-1}; P3, P fertilization rate of 264 kg ha^{-1}

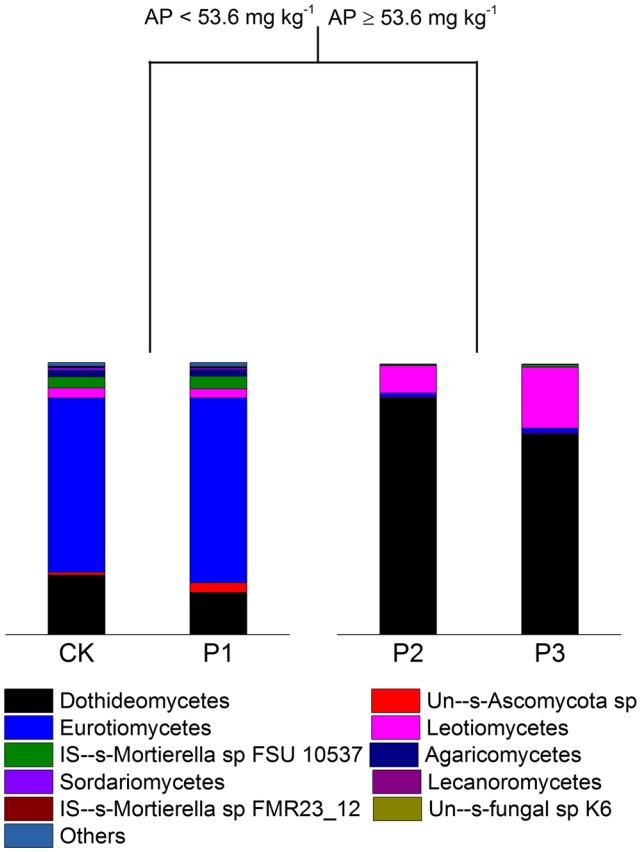

Fig. 3 Multivariate regression trees of fungal community in a paddy soil treated with different P rates, partitioned by available P. Bar plots indicated relative abundance of fungi classes. AP, available P; CK, P fertilization rate of 33 kg ha^{-1}; P1, P fertilization rate of 66 kg ha^{-1}; P2, P fertilization rate of 132 kg ha^{-1}; P3, P fertilization rate of 264 kg ha^{-1}

Long-term application of P increased bacterial diversity in pasture soil (Tan et al. 2013), whereas high P fertilization decreased bacterial Shannon diversity indexes in barley rhizosphere soil (Chhabra et al. 2013). Phosphorus addition also changed total and alkaline phosphomonoesterases-harboring bacterial population in the ryegrass rhizosphere (Lagos et al. 2016). However, effect of P fertilization on fungal diversity has been less studied than on bacterial diversity. For example, He et al. (2016) reported P addition to soil affected fungal diversity more than N addition. Lin et al. (2012) found that long-term P application decreased arbuscular mycorrhizal fungal diversity in an arable soil. On the contrary, phospholipid fatty acid analyses revealed no changes in soil microbial composition after different P fertilization regimes (Huang et al. 2016; Shi et al. 2012). Denaturing gradient gel electrophoresis has shown a significant impact of P addition on

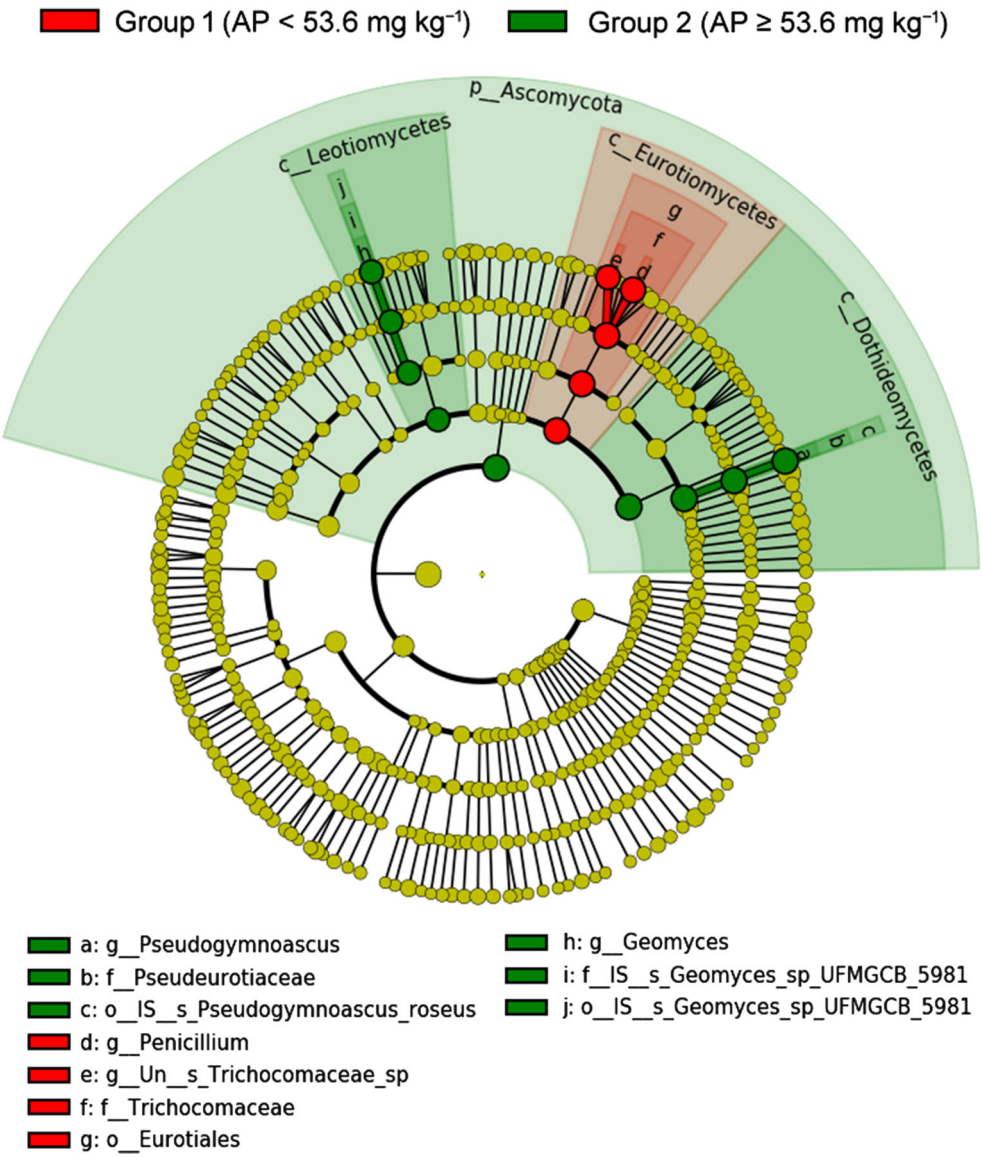

Fig. 4 Cladogram of linear discriminant analysis effect size showing the fungal indicators with different abundances among treatments. Group 1 and group 2 included treatments with soil available P lower and higher than 53.6 mg kg^{-1}, respectively. Circles from inside root to outside indicated six fungal taxonomical levels from kingdom to genus. Red and green represent different fungal indicators in corresponding groups. Prefixes of each fungal taxonomic name such as p, c, o, f, and g were the initial letters of phylum, class, order, family, and genus, respectively

bacterial and fungal community composition (Beauregard et al. 2010). In the present study, bacterial diversity was not affected by P, whereas fungal diversity changed markedly when P application rates were higher than 132 kg ha^{-1}. The reason for the different responses of bacteria and fungi might be due to the fact that fungi are more sensitive than bacteria to soil fertility and P addition (He et al. 2008; Li et al. 2015). Usually, fungal hyphae can extend into soil and increase the surface area for water and nutrient absorption. Therefore, easy accessibility to soil available and even immobile P might contribute the sensitivity of fungi to P addition.

The critical soil properties affecting fungal diversity

Microbial diversity can be affected by soil properties such as moisture, temperature, pH, and organic or inorganic nutrient supply (Hamel et al. 2006). In the present study, fungal diversity was significantly affected by soil P-related factors. For example, regression analysis showed that fungal richness and diversity indexes were correlated to the AP content (Supplementary Table S1). The AP content was also the most important factor influencing fungal community composition as evaluated by CCA analysis. Similarly, soil P content was the second most important driver of bacterial and fungal diversity in soil (Siciliano et al. 2014). Moreover, extractable P concentration affected changes in fungal diversity in soils across different land use types (Lauber et al. 2008; Siciliano et al. 2014). The effect of P availability on fungal diversity may depend on: (i) changes in soil pH or osmotic potential (Liu et al. 2013; Thirukkumaran and Parkinson 2000); however, soil pH did not change in the present study; (ii) increased organic C availability by the increased litter fall or root exudate, due to the increased plant growth promoted by the increased available P (Huang et al. 2016); however, this can be

excluded since no plants were involved in the incubation; (iii) and an increase in the abundance of soil fungivore, which subsequently altered competitive patterns between different fungal group (He et al. 2016). Probably, the AP content and the increase in soil fungivore abundance affected fungal diversity in this study; the effect of the AP content probably occurred by changing the osmotic potential; the impact of fungivore might take place by exerting the selective pressures on fungal communities and by changing the competitive interactions (Crowther et al. 2011).

Recent studies indicated that soil P accumulation can influence biological diversity of terrestrial ecosystems (Ceulemans et al. 2014; Kuramae et al. 2011). For example, microbial communities of grassland soil with neutral pH and soil under different plant succession were separated by the soil AP content (Kuramae et al. 2011). When AP content was higher than 100 mg kg^{-1}, specific bacterial members became dominant (Kuramae et al. 2011). However, this AP value was not reached in our study and the red soil has different properties than the neutral pH soil used by Kuramae et al. (2011). We found the threshold of 53.6 mg kg^{-1} to be the AP value causing a significant shift in the fungal diversity.

Fungal indicators of different P availability

Phosphorus availability might influence microbial diversity by changing the presence of specific microorganisms in soil. For example, when soil AP content was greater than 100 mg kg^{-1}, soil-borne *copiotrophic* bacteria were dominant in arable field soils (Kuramae et al. 2011). Increasing AP also stimulated the growth of *r*-strategy microorganisms in soils under long-term fertilization (Malý et al. 2009). The results of LEfSe indicated that *Penicillium* (belonging to class *Eurotiomycetes*) and unknown *Trichocomaceae* (belonging to class *Eurotiomycetes*) were fungal indicator of soils with AP < 53.6 mg kg^{-1}, whereas *Pseudogymnoascus* (belong to *Dothideomycetes*) and *Geomyces* (belong to *Leotiomycetes*) were indicators for soils with AP ≥ 53.6 mg kg^{-1}. Many strains of *Penicillium* are considered phosphate-solubilizing fungi contributing to the solubilization phosphate rocks (Gómez-Muñoz et al. 2017; Illmer et al. 1995; Rice et al. 1994). Some isolates of *Trichocomaceae*, including *Aspergillus* and *Penicillium*, can also use complex P sources, such as phytic acid and DNA (Daynes et al. 2008). Some members of *Pseudogymnoascus* and *Geomyces* were previously reported to be involved in decomposition of organic matter. For instance, *Pseudogymnoascus roseus* was related to the degradation of wood and its abundance increased in the rhizosphere of tree stumps (Kwasna 2001, 2004; Sigler et al. 2000). Moreover, some strains of *Geomyces* were reported to be involved in the decomposition and nutrient cycling in Antarctica (Arenza et al. 2006).

In soil ecosystem, fungi contribute to the degradation of lignocellulose in leaf litter and wood (Hammel 1997); mycorrhizal fungi help plant growth by P uptake (Schachtman et al. 1998). Hence, fungal diversity changes may play important roles in ecological processes under P surplus. However, this study did not give the evidence that fungi can affect C and P transformation. Lagos et al. (2016) detected the phosphomonoesterase encoding genes in bacteria as corresponding enzymes can mineralized organic P and increase soil available P. Some fungi such as *Trichocomaceae* also have the phosphomonoesterase activities and can grow on organic P (Daynes et al. 2008). Reduction of certain fungi may lead to the decrease of these enzyme activities with the subsequent effect on soil P.

Conclusion

The AP content was the most important soil property influencing fungal α and β diversity. When the AP content was ≥ 53.6 mg kg^{-1}, *Penicillium* and *Trichocomaceae* decreased but *Pseudogymnoascus* and *Geomyces* increased. Fungi might play important roles in organic matter decomposition and P cycling under P surplus.

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