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REGULAR ARTICLE

Microbial community shifts trigger loss of orthophosphate in wetland soils subjected to experimental warming

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Abstract

Aims Microbial-driven biogeochemical cycles of phosphorus (P) in wetlands subjected to global climate warming result in a downstream eutrophication risk. However, how warming influences P associated with microbial shifts in wetland soils is largely unknown.

Methods A custom-built, novel microcosm that simulated climate warming was established under ambient temperature and elevated warming conditions (+ 3 °C). ^{31}P nuclear magnetic resonance (^{31}P–NMR) technology was used to characterize different P forms and high-throughput sequencing of 16S rRNA gene was used to identify microbial community and functional potentials in wetland soils varied with nutrition status.

Results Soil P forms were dominated by orthophosphate. The dynamic changes of different P forms in response to warming were mainly observed in high nutrition wetlands. The relative abundance of orthophosphate and polyphosphate (inorganic) significantly ($p < 0.05$) decreased, which was accompanied with increased phosphonate (organic) under warming. Consistently, soil microbial community shifts were also found in high nutrition wetlands, especially in fall with significantly ($p < 0.05$) increased relative abundance of *Alphaproteobacteria* and *Betaproteobacteria* and decreased *Clostridia* under warming. The microbial functions related to catabolism, the transport, degradation and release of P were enriched under warming. Changed microbial community may have altered the overall functional potentials which were responsible for P dynamics.

Conclusions Soil microbial community shifts in response to experimental warming were season-based. Microbial changes and P shifts from high nutrition wetlands were more sensitive to warming. The changed microbial community under warming conditions may trigger the loss of orthophosphate through the altered functional potentials. These findings aid to better understand microbial-driven biogeochemical cycles of P in wetland soils under future climate changes.

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Introduction

Global mean air temperature had increased by approximately 0.85 °C in a period of 1988–2012, and surface temperatures across the earth are predicted to raise an additional 0.3–4.8 °C by the end of this century (Solomon et al. 2007). Many regional ecosystems are vulnerable to rising temperatures (Scheffran and Battaglini 2011). Wetlands are well regarded as transitional zones between aquatic and terrestrial ecosystems, where the chemical, and particularly the nutrient dynamics of shallow groundwater and surface water could be altered by a range of biogeochemical processes. As a result, global warming may impact the inherent biogeochemical balance in wetland ecosystems (Zhang et al. 2012; Wang et al. 2014).

It has been well-known that phosphorus (P) is considered to be a major limiting nutrient for the growth of aquatic organisms, and a major contributor to the eutrophication in freshwater bodies (Yuan et al. 2015). To a large extent, global climate warming would aggravate some symptoms of eutrophication in shallow and enclosed areas of wetland ecosystems, especially when anthropogenic P inputs accumulate on the surface of bottom soils (Feuchtmayr et al. 2009). Some studies have demonstrated that elevated soil temperature promotes the release of soil P into overlying water by enhanced activities of neutral and alkaline phosphatases, and by accelerated anaerobic metabolic pathways in freshwater wetlands, indicating the importance of microorganisms in driving P cycles (Zhang et al. 2012; Zhang et al. 2015). Previously studies largely focused on soluble inorganic and organic P forms using a sequential chemical extraction method. However, this method is destructive and some chemically extracted P fractions may not truly existed in in-situ soils. ^{31}P nuclear magnetic resonance (^{31}P–NMR) spectroscopy is a nondestructive technique which may provide more real and comprehensive information about soil P forms. According to this technology, inorganic P can be divided into orthophosphate, pyrophosphate and polyphosphate, while organic P can be divided into phosphonate, phosphomonoester and phosphodiester (Zhang et al. 2016). The different P forms based on ^{31}P–NMR in response to experimental soil warming have been determined in this study.

Microorganisms are key drivers of the biogeochemical cycle of soil P (Tapia-Torres et al. 2016). For instance, phosphorus-solubilizing microorganisms (PSMs) in soils can promote solubilization of insoluble inorganic P and organic P, and thus increase P availability for plants uptake (García-López et al. 2016). A wide range of PSMs-mediated P solubilization processes are mainly attributed to soil bacteria and fungi, and bacteria are more effective in P solubilization than fungi (Mohammadi 2012). Over the past decades, soil warming studies that have examined microbial community dynamics can be divided into long-term field or mesocosm experiments (1–15 years) with a modest increase in soils temperature (1–3 °C), and short-term lab incubations (6–16 weeks) with soils incubated over a wide range of temperatures (5–40 °C) (Frey et al. 2008). Contrasting effects of soil warming on microbial community composition have been observed among different incubation experiments (Andrews et al. 2000; Schindlbacher et al. 2011). For example, Andrews et al. (2000) showed that the microbial community composition differed across the simulated temperature ranges with varied microbial morphology types, while Schindlbacher et al. (2011) suggested that an increase in soil temperature had no influence on microbial community composition. Warming effects may also vary under different soil types and/or among seasons, indicating the warming-induced microbial responses may depend on studied soils and sampling seasons (Kuffner et al. 2012). Further, soil warming could give competitive advantages to some species adapted to higher temperatures and cause significant increases in their abundance and functional potentials (Kuffner et al. 2012). Until now, we still lack a distinct understanding in how warming will impact microbial community composition and function potentials in wetland soils, and in turn, how these microbial changes will give a feedback to soil P dynamics.

In this study, a novel outdoor microcosm device with high resolution temperature control was used to simulate global warming. ^{31}P–NMR was used for determining different P forms in wetland soils. High-throughput sequencing of 16S rRNA gene was used to identify microbial community composition and associated function potentials. The objectives of our study were (1) to show shifts in soil P forms, microbial community composition and functions via experimental warming,

respectively; (2) to correlate P forms with microbial community composition and functions in order to uncover how microorganisms drive P cycles in wetland soils.

Materials and methods

Study sites, microcosm configuration and samples collection

The information about our established outdoor microcosm device has been described previously (Wang et al. 2014;Wang et al. 2016a, b). In brief, six sites have been selected in the region of Yangtze River Delta in the southeast of China. These sites covered a wide range of nutrition status in soils across subtropical wetlands ecosystems. Among them, YaTang riverine wetland (YT) was in a high nutrition status among six sites. XiaZhuHu (XZ) wetland, XiXi National Wetland Park (XX), BaoYang riverine wetland (BY) were in a moderate nutrition status, while JinHu wetland (JH) and ShiJiu multi-pond wetland (SJ) were in an oligotrophic status. The native vegetation found in these wetlands in-situ included some floating-leaved (e.g., *Lemna minor* and *Trapa spp.*) and emergent (e.g., *Phragmites communis* and *Acorus calamus*) aquatic plants (Online Resource 1).

A custom-built, novel device that simulated climate warming was set up under ambient temperature (control, CK) and elevated warming conditions (+3 °C, warmed, WA), respectively. The details about the configuration of this microcosm system and its corresponding operation were described previously (Zhang et al. 2012). Briefly, transparent polyvinyl chloride plastic columns filled with soils and overlying water collected from these sites were placed in the microcosm device in May 2008, and this device has been operated since then. When incubated in columns, all these soils were under an annual average rainfall of 1380 mm and an annual average air temperature of 27.8 °C in the summer and 6.37 °C in the winter under control scenarios.

After 7-year warming, during 2015–2016, surface soils (0–20 cm deep) were collected in both control and warmed treatments. Each treatment has three replicates, and we collected them from four seasons, i.e., mid-April (spring), mid-July (summer), mid-October (fall) of 2015 and mid-January (winter) of 2016, which corresponded to the ambient temperature of 20.3 °C, 27.8 °C, 20.0 °C and 6.37 °C, respectively. Therefore, there were 144 soil samples in total (6 sites × 2 treatment × 4 seasons × 3 replicates). After collection, these soil samples were immediately transported to the lab on dry ice within one hour. A part of them was stored at −20 °C for sequencing of 16S rRNA gene, and the rest were dried by lyophilization for ^{31}P–NMR analysis.

DNA extraction, 16S rRNA amplicon sequencing and analysis

Total DNA was extracted from each soil sample by using PowerSoil DNA Isolation kit (MoBio Laboratories, USA) according to the manufacturer's instruction. 16S rRNA amplicon preparation and sequencing was according to the previous report (Jiao et al. 2016). Briefly, the V4-V5 hyper-variable regions of 16S rRNA gene was amplified using primers 515F/907R, with reverse primer containing a unique 6 bp barcode at the 5'end. PCR products within 400–450 bp were mixed in equal density ratios and then purified. The purified PCR amplicons were sequenced using the Illumina Hiseq 2500 platform at Novogene Bioinformatics Technology Co., Ltd. (Beijing, China). The QIIME pipelines v1.9.1 (Caporaso et al. 2010) were used for pre-processing of the raw reads. Firstly, the forward and reverse reads were joined using the default setting. Then, the multi-lane Fastq data were de-multiplexed and quality-filtered (Q_{30} >= 75% and Q_{20} = 100%). USEARCHv6.1 was used to identify and remove chimeras. By using a closed-reference operational taxonomic unit (OTU) picking strategy, OTUs were identified at a 97% similarity threshold using UCLUST v1.2.22q to cluster against Greengenes reference database (McDonald et al. 2012). Taxonomy was achieved using RDP Classifier to assign against the same reference (Cole et al. 2009). After OTUs picking and chimera checking, a total of 144,553,052 reads were assigned to 125,532 non-singleton OTUs for a total of 144 samples, which resulted in the classification of 77 taxa at the phylum level and 1490 taxa at the genus level.

For soil samples collected in fall, the functional profiles of microbial communities were further predicted by using PICRUSt according to 16S rRNA marker gene sequences, and NSTI index was kept less than 0.10 to ensure the accuracy of metagenome inference (Langille et al. 2013). The identified KOs related to the transport and metabolism of P, sulfate reduction, and denitrification were examined to show whether they were

significantly changed under warmed treatment. The proportion of microbial taxa contributing to these functions and their relative abundances were further calculated. The raw sequences have been submitted in NCBI database (SUB2131165).

^{31}P–NMR analysis with NaOH-EDTA extracts

After lyophilization, the concentration of soil total P and extractable P was determined. For extractable P, NaOH-EDTA solution was used, and the NaOH-EDTA extracts were further subjected to ^{31}P–NMR analysis according to the previous report (Jin et al. 2016) with slight modifications. Briefly, 3 g lyophilized soil sample and 30 mL solution (0.2 M NaOH and 0.05 M Na_2EDTA) were placed in a 50 mL centrifuge tube, together. The centrifuge tube was shaken gently at 20 °C for 16 h and then centrifuged at 10000 g for 20 min. The supernatant was frozen and lyophilized for 36 h. Approximate 300 mg freeze-dried extract for each soil sample was homogenized, and then re-dissolved in 0.5 mL D_2O, and again mixed with 0.3 mL 10 M NaOH and 0.3 mL NaOH-EDTA extracting solution. Re-dissolved samples were then ultrasonicated for 20 min, centrifuged at 10000 g for 10 min, and then carefully transferred into 5-mm NMR tubes. All samples were prepared within one hour and stored at 4 °C before analysis. ^{31}P–NMR spectra were recorded at 242.9 MHz on a Bruker Ascend 600 spectrometer. The NMR operation parameters were as follows: 90° pulse angle, 0.68 s acquisition time, 4.0 s pulse delay, 17.9 us pulse width, 10 Hz spinning at room temperature of 20 °C. Scans between 2400 and 2800 were performed depending on the total P concentrations in soils. All chemical shifts of signals on spectra were given in parts per million (ppm) relative to 85% H_3PO_4. Solution ^{31}P–NMR spectra were processed with 5 Hz line-broadening on MestReNova8.0 software. To obtain peak areas, different P compounds were identified by their chemical shifts by standardizing orthophosphate peak to 6.0 ppm. Peaks in the raw spectrum with a signal-to-noise ratio exceeding 7 were fitted using the deconvolution method in MestReNova8.0 software. From these peak areas, percentage of individual P compound was calculated by peak areas relative to the sum of all P peak areas based on previous reports (Doolette et al. 2009; Young et al. 2013; Giles et al. 2015).

Statistical analysis

Soil samples based at seasonal and round-year scale under control (CK) and warmed (WA) were assigned into six groups (L-WA, L-CK, M-WA, M-CK, H-WA, H-CK) according to different nutrition status in wetland soils (L: low nutrition status; M: moderate nutrition status; H: high nutrition status). Namely, samples from YT wetland columns were in a high nutrition status (H), samples from XX, XZ, BY wetland columns were in a moderate nutrition status (M), and samples from SJ and JH wetland columns were in an oligotrophic status (L). Then, principal component analysis (PCA) and principal coordinate analysis (PCoA) were conducted to reveal spatial distributions of overall P forms and microbial communities using PAST3.0 software (Hammer et al. 2001). One-way analysis of similarity (ANOSIM) was further conducted to determine the significant differences in P forms and microbial community composition between treatments. Linear discriminant analysis coupled with effect size (LEfSe) was performed to detect significantly different taxa and functions, and to estimate their effect sizes (Segata et al. 2011). Canonical correspondence analysis (CCA) was used to identify the correlations between P forms and major microbial taxa at the class level (i.e., relative abundance >1%). One-way ANOVA with least significant difference (LSD) method at both seasonal scale and round-year scale for P forms, microbial community composition and functions was performed by SPSS17.0 software program (SPSS Inc., USA). All tests were considered statistically significant at the level of 0.05.

Results

Soil P forms in response to warming

The detected peaks have been assigned into six spectrum regions (Fig. 1). Inorganic P compounds were consisted of orthophosphate (Ortho-P, 6.00 ppm), pyrophosphate (Pyro-P, −4.0 to −5.0 ppm) and polyphosphate (Poly-P, −5.5 to −25.0 ppm). Organic P compounds were consisted of phosphonate (Phon-P, 16.0 to 25.0 ppm), phosphomonoester (Mono-P, 2.6 to 5.9 ppm) and phosphodiester (Di-P, 2.5 to −3.8 ppm).

At seasonal scale (Online Resource 2-4), P forms in soils with high nutrition status showed the greatest responses to experimental warming. In low nutrition

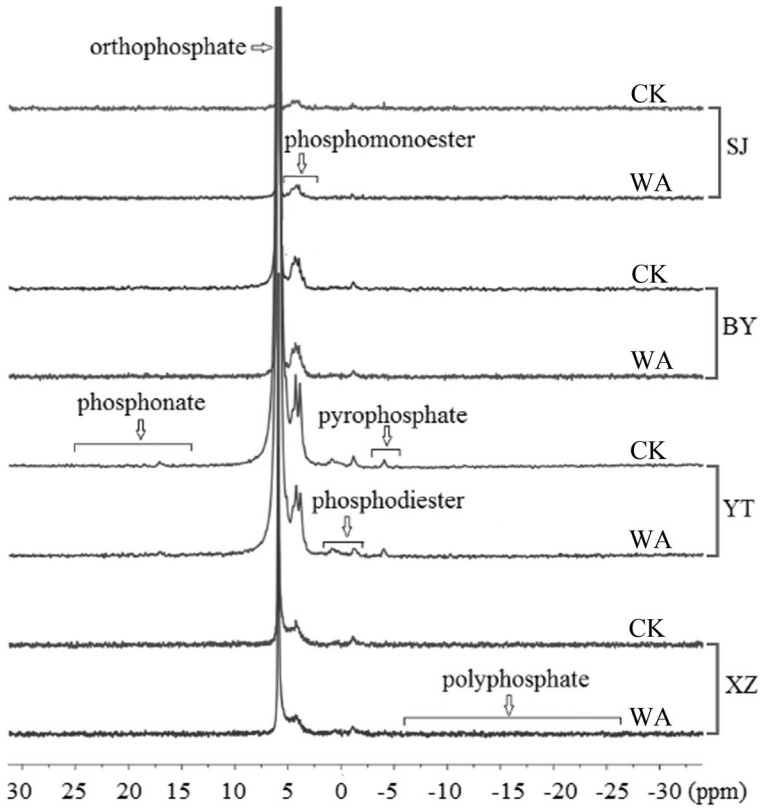

Fig. 1 ^{31}P–NMR spectra of six identified phosphorus forms. The illustrated samples were from ShiJiu multi-pond wetland (SJ, collected in fall), BaoYang riverine wetland (BY, in fall), YaTang riverine wetland (YT, in fall), and XiaZhuhu wetland (XZ, in summer). CK and WA represents control and warmed treatment, respectively. All spectra are plotted with 5 Hz line-broadening and scaled to the orthophosphate peaks (6.0 ppm)

soils, only the relative abundance of Pyro-P was significantly ($p < 0.05$) changed under warming compared to controls in fall (Online Resource 2), while insignificant ($p > 0.05$) changes were found for all individual P forms in soils with moderate nutrition status in each season (Online Resource 3). Further, the relative abundance of P forms in soils with high nutrition status have showed great seasonality to experimental warming (Online Resources 4). The relative abundance of Phon-P (organic) has increased under warming for all seasons (except for spring), while the decreased Ortho-P (inorganic), as well as the increased Mono-P (organic) and Di-P (organic) were found in spring. Overall, different P forms have shown to have distinctly different seasonal patterns under different soil nutrition status when subjected to experimental warming.

At round-year scale, the significant responses to experimental warming were also found in soils with high nutrition status (Fig. 2). Ortho-P and Poly-P (two inorganic P forms) was found to be lower ($p < 0.05$) in warmed treatment than that in control treatment under high soil nutrition status. Warming also resulted in a significant ($p < 0.05$) increase in Phon-P for high nutrition soils. Obviously, P forms from wetlands with high nutrition status were more sensitive to warming. When subjected to warming, the decrease ($p < 0.05$) in the relative abundance of Ortho-P and Poly-P was accompanied with the increase in Phon-P. We further found that the absolute concentration of total P and extractable P (mg per kg dry soil basis) was not significantly ($p > 0.05$) changed for the most treatment/season combination (Online Resource 5), implying P shifts under warming were mainly based on their relative abundance shifts through different P transformations. However, it should be noted that soil P pools were very large compared to those released into water bodies, and poor in repeatability between replicates. Therefore, no significant changes in absolute P amounts do not mean there was no any sorption or leaching of P.

PCA showed a clear and significant (ANOSIM, $p < 0.05$) separation between treatments for all P forms in high nutrition soils along the direction of Axis-1 and Axis-2 in each season (highlighted in circles, Online Resource 6), providing another evidence for P dynamics. Moreover, it was notable that P forms have showed no significant (ANOSIM, $p > 0.05$) separation among

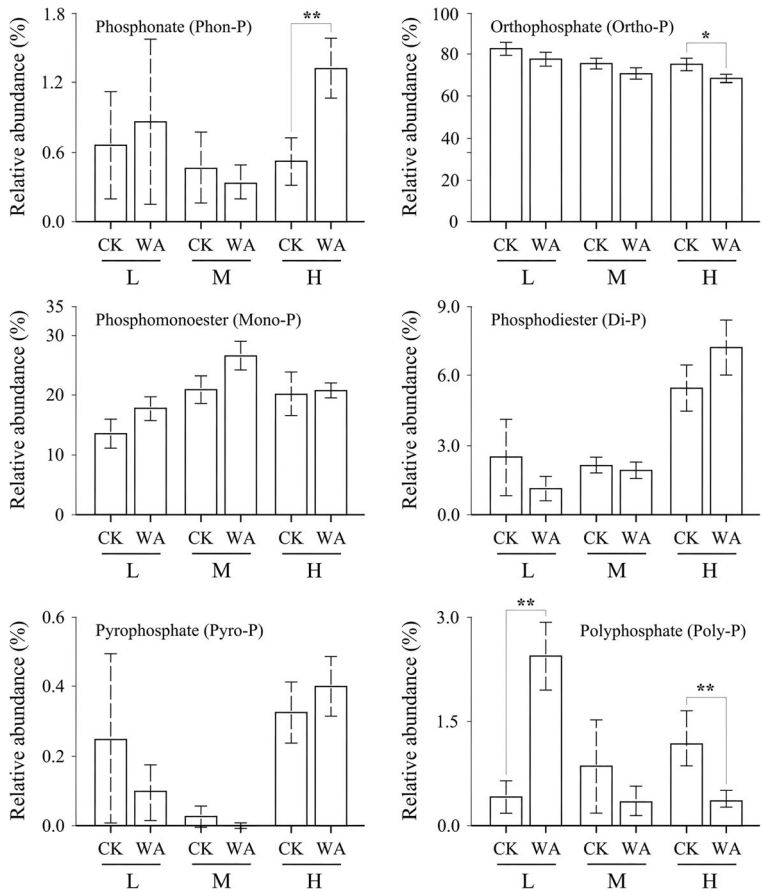

Fig. 2 The relative abundance (%) of six phosphorus forms between control (CK) and warmed (WA) treatment at round-year scale under three soil nutrition status (Low: L; Moderate: M; High: H). The error bar indicates the standard error. Soil phosphorus forms with significant differences between treatments are labeled by asterisk (*, $p < 0.05$; **, $p < 0.01$)

different seasons for each soil nutrition status, indicating seasonal variation may have a minor effect on the overall soil P forms, compared to individual P form changes (Online Resource 2–4).

Features of microbial composition in response to warming

The relative abundance of microbial class as a representative rank was mainly shown, given there were many unknown taxa with their relative abundances even more than 50% for lower ranks. In spring, warming led to the decreased ($p < 0.05$) abundance of *Acidobacteria-6*, *Bacteroidia* and *Deltaproteobacteria* for moderate nutrition soils, while *Betaproteobacteria* and *Nitrospira* increased ($p < 0.05$, Online Resource 8). In addition, warming also triggered decreased ($p < 0.05$) abundance of *Acidobacteria-6* for low nutrition soils (Online Resource 7) and increased ($p < 0.05$) abundance of *Bacteroidia* for high nutrition soils (Online Resource 9). In summer, the increased ($p < 0.05$) taxa included *Anaerolineae* (Online Resource 7) and *Betaproteobacteria* (Online Resource 8) for low and moderate nutrition soils, respectively, while *Dehalococcoidetes* decreased ($p < 0.05$) for moderate nutrition soils (Online Resource 8). In fall under warming, *Clostridia* decreased ($p < 0.05$) by 80%, 75%, and 75% for low, moderate, and high nutrition soils, respectively (Online Resource 7–9). Meanwhile, the increased ($p < 0.05$) taxa included *Anaerolineae* for low nutrition soils (Online Resource 7), and *Nitrospira*, *Alphaproteobacteria*, *Deltaproteobacteria* for moderate nutrition soils (Online Resource 8), and *Deltaproteobacteria*, *Gammaproteobacteria* for high nutrition soils (Online Resource 9). In winter, *Bacteroidia* in high nutrition soils (Online Resource 9) and *Dehalococcoidetes* in moderate nutrition soils (Online Resource 8) decreased ($p < 0.05$) under warming, while *Betaproteobacteria* and *Nitrospira* for moderate nutrition soils (Online Resource 8) and *Nitrospira* for low nutrition soils increased ($p < 0.05$) (Online Resource 7). Besides microbial class, the relative

abundance of major microbial phylum and genus at seasonal scale was further shown in Online Resource 10-11.

At round-year scale (Fig. 3), the increased ($p < 0.05$) taxa at the class level included *Nitrospira* and *Anaerolineae* for low nutrition soils, and *Alphaproteobacteria*, *Betaproteobacteria* and *Nitrospira* for moderate nutrition soils, as well as *Acidobacteria-6*, *Alphaproteobacteria*, *Betaproteobacteria* and *Gammaproteobacteria* for high nutrition soils under warming. In the contrary, *Clostridia* from low nutrition soils, *Gammaproteobacteria*, *Dehalococcoidetes*, *Bacteroidia*, and *Clostridia* from moderate nutrition soils, as well as *Anaerolineae* and *Clostridia* from high nutrition soils were found decreased ($p < 0.05$). Overall, warming has triggered increased ($p < 0.05$) abundance of *Alphaproteobacteria*, *Betaproteobacteria*, and *Acidobacteria-6* as well as decreased ($p < 0.05$) abundance of *Clostridia* mainly in moderate and high nutrition wetland soils.

Comparison of overall microbial composition when subjected to warming

PCoA based on the relative abundances of microbial taxa at class level was further used to show the different patterns of microbial community composition between treatments (Fig. 4). The results showed that in spring, the microbial community composition clearly (ANOSIM, $p < 0.05$) separated along the direction of Axis-1 and Axis-2 among three soil nutrition status in spring, but not between treatments (Fig. 4; spring; comparing H, M and L). However, in fall, microbial community composition was mainly separated between treatments, but not among three soil nutrition status (Fig. 4; fall), suggesting that warming greatly reshaped microbial community in fall. Meanwhile, we also found that microbial community composition in high nutrition soils had a clear separation between treatments for all seasons just like P forms, indicating that the microbial community in high nutrition soils was the most sensitive to experimental warming. Further evidences also showed a significant separation between fall and other seasons for different soil nutrition status using PCA (Online Resource 12), which suggested that warming-induced microbial community shifts were strengthened in fall.

LEfSe analysis of microbial shifts and functional predication using PICRUSt

Since fall was a notable season where most taxa shifts occurred when subjected to warming, we further identified specialized taxa and their associated functions using LEfSe. A total of 13 taxa with LDA scores larger than 2.0 between treatments were identified for low nutrition soils (Online Resource 13; L-WA vs. L-CK). Among them, 6 taxa were significantly enriched under warming for microbial lineages from *Proteobacteria* to *Betaproteobacteria*, and from *Bacteroidia* to *Bacteroidales*. Another 7 taxa were significantly attenuated for microbial lineages from *Firmicutes* to *Clostridium*, and from *Bacilli* to *Bacillales*. In moderate nutrition soils, lineages from *Proteobacteria* to *Rhizobiales*, and from *Nitrospirae* to *Nitrospirales* were enriched under warming (Online Resource 13; M-WA vs. M-CK). In high nutrition soils, a total of 19 taxa with LDA scores larger than 2.0 between treatments were identified (Online Resource 13; H-WA vs. H-CK), showing the most noticeable changes. Overall, the microbial lineage from *Firmicutes* (phylum) to *Clostridium* (genus) generally decreased, while those associated with *Proteobacteria* increased when subjected to experimental warming.

LEfSe also revealed significantly different functions under subsystem hierarchy level III with LDA scores larger than 2.0 between treatments (Online Resource 14). Functions associated with microbial metabolism were found to be enriched mostly in warmed treatment, such as nitrogen metabolism and carbohydrate metabolism (Online Resource 14). Oxidative phosphorylation was found to be enriched under warming mainly in high nutrition soils (Online Resource 14; H-WA vs. H-CK). Since level 3 and higher KEGG categories may obscure the trends in opposing functions within the same category, we further examined individual KOs (KEGG Orthologs) which were associated with P transport and metabolism, as well as sulfate reduction and denitrification of interests (Online Resource 15). We found, just like microbial community shifts, many significantly changed KOs after warming were observed in soils with high nutrition status (Fig. 5). Genes responsible for phosphonate transport were enriched in high nutrition soils under experimental warming (Fig. 5a). In oxidative phosphorylation pathway, genes encoding inorganic pyrophosphatase were attenuated under warming (Fig. 5b & Online Resource 16), while genes encoding

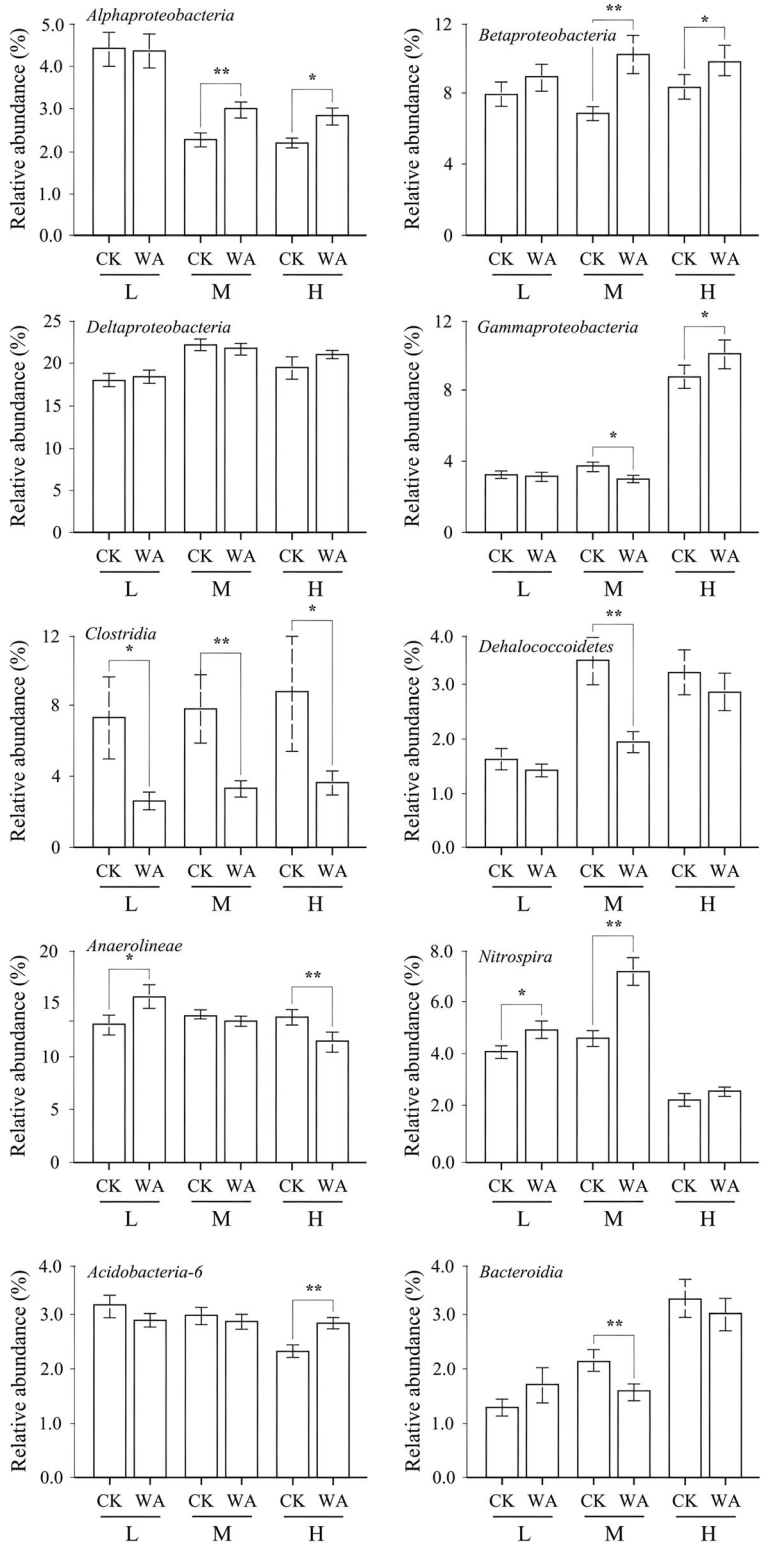

Fig. 3 The relative abundance (%) of the major taxa at the class level between control (CK) and warmed (WA) treatment at round-year scale under three soil nutrition status (Low: L; Moderate: M; High: H). The error bar indicates the standard error. Taxa with significant differences between treatments are labeled by asterisk (*, $p < 0.05$; **, $p < 0.01$)

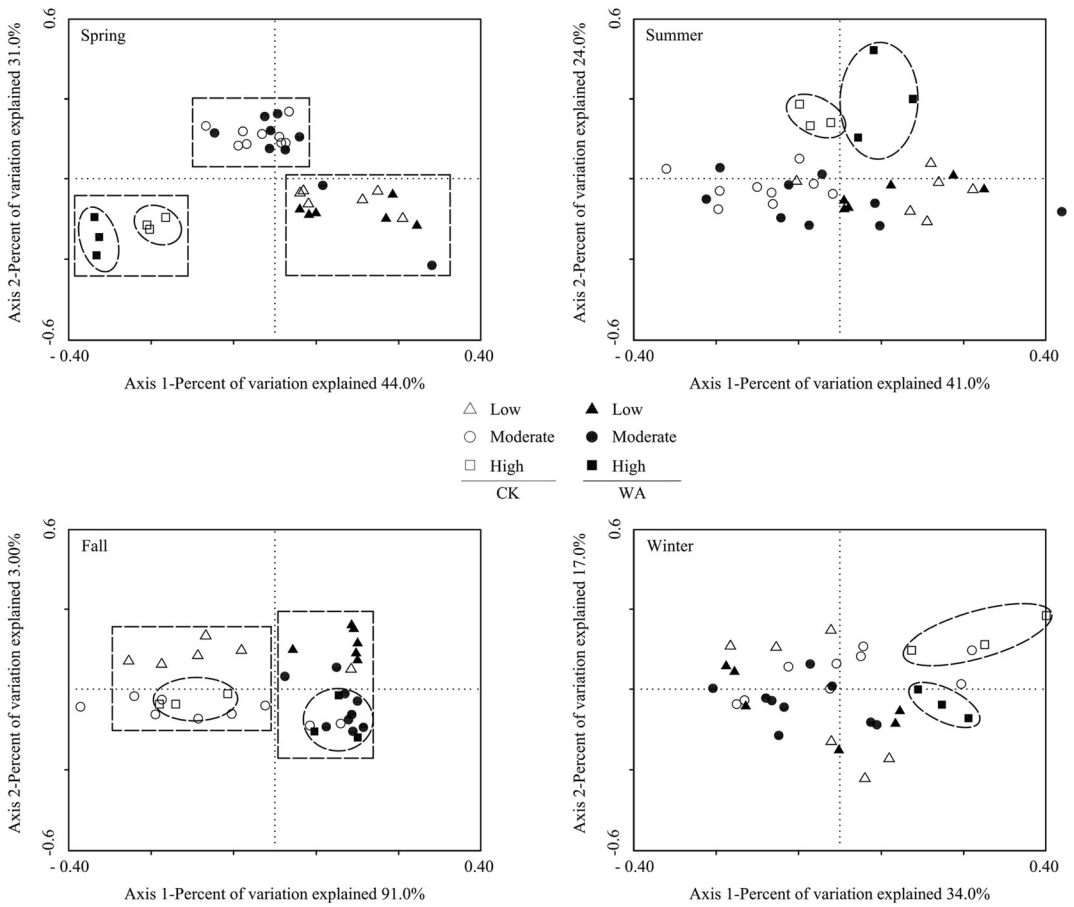

Fig. 4 Principal coordinate analysis (PCoA) shows the clusters of microbial community composition at the class level based on their relative abundances between control (CK, open symbol) and warmed (WA, closed symbol) treatment in spring, summer, fall, and winter. Samples are clustered according to their nutrition status, and/or treatment

polyphosphate kinase were not significantly changed (Online Resource 16). For polyphosphate degradation, genes encoding exopolyphospohatase were enriched in moderate and high nutrition soils under warming (Fig. 5c). For genes related to sulfate reduction and denitrification (Fig. 5d-g), we also found that the certain genes were enriched under experimental warming but not for the overall pathway. Taken sulfate reduction as an example, genes responsible for sulfate adenylyltransferase and dissimilatory sulfite reductase were enriched after warming, while genes encoding adenylylsulfate reductase did not (Online Resource 16).

Effects of microbial community on P forms and its linkage with functional potentials

CCA was mainly performed to identify the potential correlations between P forms and dominated taxa at the class level from high nutrition soils at round-year scale (Fig. 6). Axis-1 and Axis-2 explained 93.5% and 2.67% of variations in all P forms, respectively. Phon-P was positively correlated ($p < 0.05$) with *Bacteroidia*, *Betaproteobacteria*, *Deltaproteobacteria*, *Acidobacteria-6* and negatively correlated ($p < 0.05$) with *Anaerolineae*. Meanwhile, Ortho-P was positively correlated ($p < 0.05$) with *Anaerolineae* and *Clostridia*, and negatively correlated ($p < 0.05$) with *Acidobacteria-6* and *Betaproteobacteria*. Taxa, such as *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, and *Clostridia* were the major taxa affecting the overall P forms as judged by the length of vectors shown in CCA biplots (Fig. 6). Moreover, CCA also revealed a clear separation in overall P forms between control and warmed treatment for high nutrition soils, consistent with those revealed by PCA (Online Resource 6). In order to understand whether there were linkages between changed microbial community and enriched/

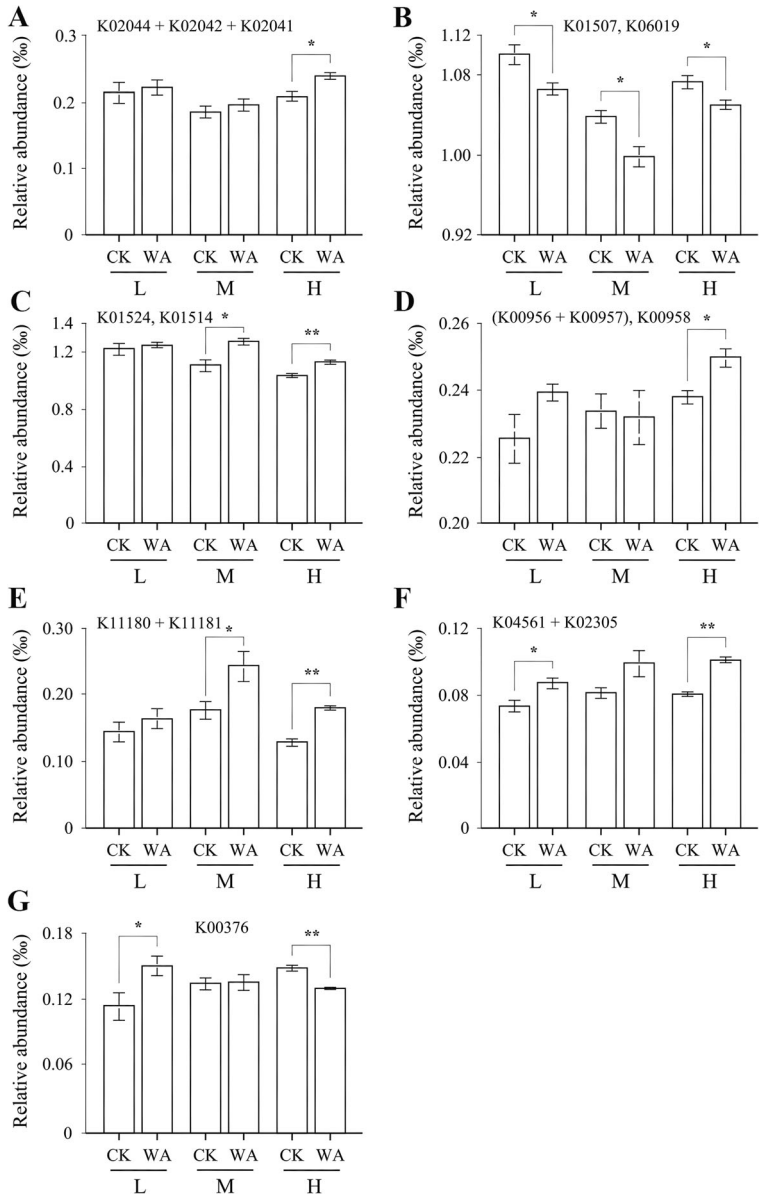

Fig. 5 The relative abundance (1‰) of the predicted genes by PICRUSt between control (CK) and warmed (WA) treatment under three soil nutrition status (Low: L; Moderate: M; High: H). Soil samples were collected in fall. Only significantly changed genes related to phosphorus and other elements cycling of particular interests are shown. Some genes are grouped into pathway module and compared here. Significant differences between treatments are labeled by asterisk (*, $p < 0.05$; **, $p < 0.01$). The error bar indicates the standard error. These genes belong to phosphonate transport (**a**, *phnD*, *phnE*, and *phnC* involved), pyrophosphate metabolism (**b**, *ppa* and *ppaX* involved), polyphosphate metabolism (**c**, *ppx-gppA* and *PPX1* involved), sulfate reduction (**d**, *cysN*, *cysD*, and *sat* involved), sulfate reduction (**e**, *dsrA* and *dsrB* involved), denitrification (**f**, *norB* and *norC* involved), and denitrification (**g**, *nosZ* involved). In each plot, a plus sign (+) between KEGG Orthologs (KOs) indicates different KOs generally combine together to perform functions. See Online Resource 15 for details

attenuated functions, we evaluated which microbial taxa appeared to contribute these aforementioned functions and how their relative abundances were altered by warming. We found that *Deltaproteobacteria*, *Anaerolineae*, *Betaproteobacteria*, and *Gammaproteobacteria* were major contributors to phosphonate transport system, and *Deltaproteobacteria*, *Nitrospira*, and *Betaproteobacteria* were major contributors to dissimilatory sulfite reductase (Fig. 7). The cumulative relative abundances of these major contributors significantly increased under warming (Fig. 7, b & d), which were just consistent with enriched genes (Fig. 5, a & e). This implies that the changed microbial community composition may have altered the associated functional potentials which could in part explain P dynamics in wetland soils.

Discussion

Soil P exists naturally in a wide range of chemical forms. These P forms may have different behaviors and destinies in soils. Although inorganic P has been regarded as the direct source of plant-available P pools, especially for Ortho-P (Shen et al. 2011), the importance of organic P

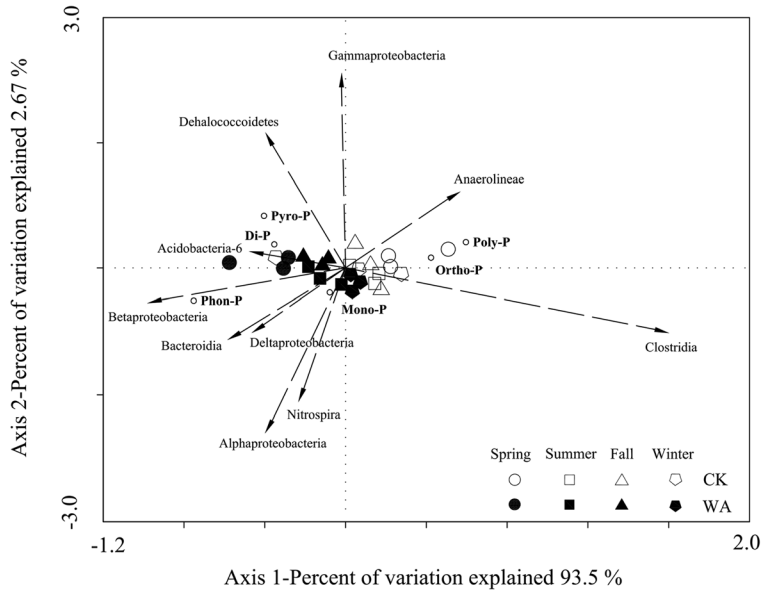

Fig. 6 Ordination diagrams by canonical correspondence analysis (CCA) between six phosphorus forms and the dominated taxa at the class level for high nutrition soils at round-year scale. Open and closed symbols indicate control (control, CK) and warmed (warmed, WA) samples, respectively. Arrows indicate the direction and magnitude of microbial taxa associated with the overall soil phosphorus forms. The small circles indicate six phosphorus forms. The position between symbols (dots) and vectors (arrows) indicate the correlations between microbial taxa and soil phosphorus forms. The length of each vector (arrows) reflects its relative importance in discriminating overall soil phosphorus forms

as potentially bioavailable P has been well recognized (Turner et al. 2005). In this study, Ortho-P and Mono-P were the main inorganic P and organic P forms found in wetland soils, respectively (Online Resource 2–4), which was in accordance with the previous report (Zhang et al. 2016). After 7-year warming, decreased ($p < 0.05$) relative abundance of Ortho-P and Poly-P (two inorganic forms) was found under warming in high nutrition wetland soils, while other P forms, such as Phon-P (organic) have shown increased abundances (Fig. 2 & Online Resource 4). Overall P forms from high nutrition soils seemed to be more sensitive to experimental warming (Fig. 2). Chen et al. (2014) showed that soil warming exerted important effects on the cycling of P in eutrophic soils, which has changed the pathways of P flow and led to increased amounts of P release. Feuchtmayr et al. (2009) also found that on-going warming could lead to the release of soluble Ortho-P from soils to water bodies under elevated soil temperature in eutrophic lakes. Consistently, our previous results also demonstrated that on-going warming can promote the release of total P and dissolved reactive Ortho-P from soils to pore-water, and then into overlying water after 14-months of incubation (Wang et al. 2013). The release of Ortho-P in wetland soils is controlled by combined abiotic and biological process (Lindstrom and White 2011). The major effects of elevated temperature on the release of Ortho-P are usually associated with chemically and microbial regulated redox reactions (Hui et al. 2013). Ortho-P is regarded as the mineralized, mobile and reactive P forms, but it usually binds to Fe (III) oxides and thus deposits in the oxidized surface soil layers (Ahlgren et al. 2005). The classic P cycling model is sensitive to redox reactions based on the coupled features of Fe and P. Warming may accelerate redox reactions, and promote the decomposition and redistribution of mobile P forms in soils or even a decrease in Fe (III)-binding P (Wang et al. 2013).

Studies on the long-term effects of warming on microbial community had been frequently reported in recent years (DeAngelis et al. 2015; Frey et al. 2008), showing that microbial community was more likely to be changed after long-term warming incubation. Particularly, warming-induced taxa changes were preferentially strengthened in fall. We assumed that this result could be closely related with plant growing phases and its nutrient cycling process. Especially, in fall many aquatic annual plant species will wither and die, and a large amount of plant litter will input into soils, which is accompanied by rapid nutrient re-cycling and exchanges. Experimental warming may greatly extend plant growing phases for certain plants (Yu et al. 2010,

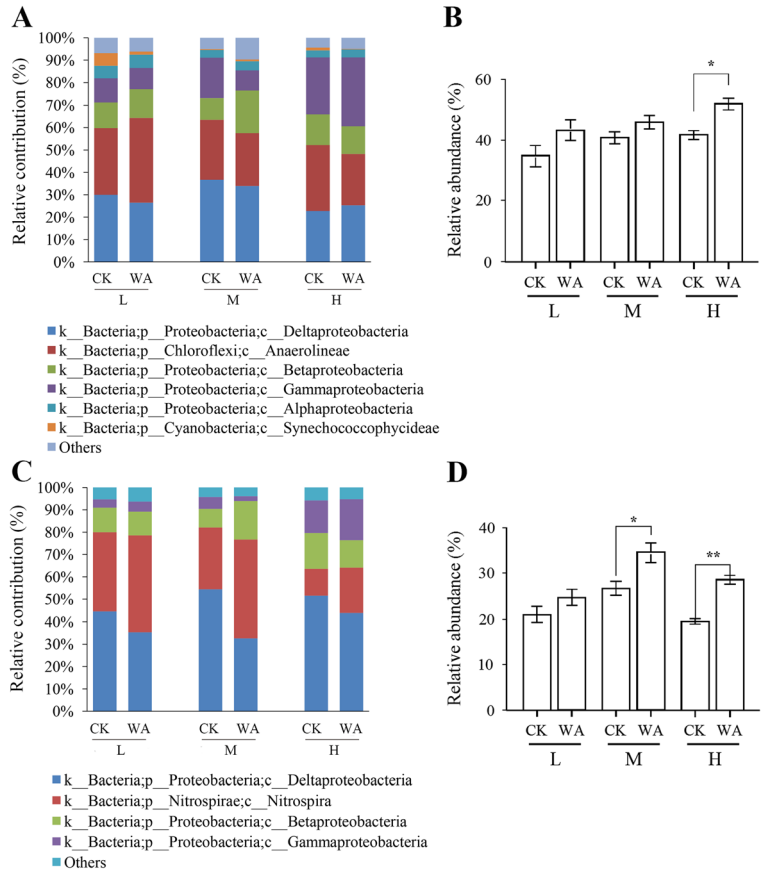

Fig. 7 The relative contribution (%) of the taxa at the class level to phosphonate transport system (K02044 + K02042 + K02041, **a**) and to dissimilatory sulfite reductase (K11180 + K11181, **c**) between control (CK) and warmed (WA) treatment under three different soil nutrition status (Low: L; Moderate: M; H: high). Soil samples were collected in fall. "Others" are the sum of the taxa with the relative contribution less than 1.5%. The cumulative relative abundances of the major contributors (*Deltaproteobacteria*, *Anaerolineae*, *Betaproteobacteria*, and *Gammaproteobacteria*) to phosphonate transport system (**b**), and the major contributors (*Deltaproteobacteria*, *Nitrospira*, and *Betaproteobacteria*) to dissimilatory sulfite reductase (**d**) are compared between treatments. Significant differences are labeled by asterisk (*, $p < 0.05$; **, $p < 0.01$). The error bar indicates the standard error

causing a possible delay in soil nutrient re-cycling. Litter input (mainly *Lemna minor* for high nutrition wetlands) in fall may cause changed microbial communities in response to experimental warming (Jin et al. 2010). However, it is also possible that warming increased the plant biomass accumulation (reaching its peaks in fall), which may alter soil microhabitats and associated microbial community in various ways. Moreover, microorganisms help increase the phosphate availability for plant growth by solubilization (Gyaneshwar et al. 2002). In turn, this process can promote plant rhizospheres to assimilate more soluble ionic phosphate forms and make vegetation compete with the soil microorganisms for nutrients (Kumar et al. 2016). Further, Wang et al. (2016a, b) found that soil microbial population and distribution is significantly different among vegetation types and growing stages, which provides another evidence showing that microbial community would be related with the seasonal growth of vegetation.

As the dominant drivers involved in the biogeochemical cycling of nutrients in various environments, the activities of soil microorganisms directly affect biogeochemistry of P, and also the availability of P levels (Falkowski et al. 2008; Gyaneshwar et al. 2002). With rising temperature, enhanced microbial activities may also result in oxygen depletion, decreased redox potential and weakened capacity of Ortho-P that is bound to Fe (III) oxides (Sondergaard et al. 2003). In one of our previous studies (Zhang et al. 2015), we also found that experimental warming enhanced the functional potentials of anaerobic metabolism by using a comprehensive functional gene microarray (GeoChip 4.0). Sulfate reduction dominated by sulfate-related bacteria were found to indirectly stimulate the release of Fe (III)-binding P (Hupfer and Lewandowski 2008). When sulfate is reduced to sulfide, these sulfide can bind to Fe (III)-oxides and compete for Ortho-P. As a result, Ortho-P will no longer be captured by Fe (III), leading to the release of Ortho-P. Similarly, in this study, we found that genes responsible for sulfate adenylyltransferase and dissimilatory sulfite reductase were enriched after warming (Fig. 5 & Online Resource 16). Some

Deltaproteobacteria is sulfate reducers (Ristova et al. 2017), which was significantly increased in warmed groups comparing with control group in fall for high nutrition soils (Online Resource 9). We further found that *Deltaproteobacteria* was one of the major contributors to dissimilatory sulfite reductase (Fig. 7). This provides a direct evidence from functional perspectives for the release of Ortho-P under on-going warming. Additionally, denitrification processes caused by denitrifying bacteria could also be beneficial to P release. When accumulated nitrate is reduced, this process is accompanied by the reduction of Fe (III) into soluble Fe (II), which liberates Fe (III)-binding P (Zhang et al. 2015). Accordingly, the enriched genes under warming were those responsible for nitric oxide reductase and nitrous-oxide reductase (Fig. 5 & Online Resource 15). *Alphaproteobacteria* and *Betaproteobacteria* as denitrifying bacteria have been found commonly in different lakes sediments (Saarenheimo et al. 2015). They were all enriched in warmed groups at both seasonal (Online Resource 13) and round-year (Fig. 3) scale in high nutrition soils. Ortho-P was negatively correlated with *Betaproteobacteria* as revealed by CCA analysis (Fig. 6), indicating increased *Betaproteobacteria* may be responsible for the release of Ortho-P from soils to water bodies under warming. *Betaproteobacteria* was also one of the predominant classes of phosphate-solubilizing microorganisms (PSMs), which was capable of transforming inorganic insoluble phosphates to plant-available P dissolved in water by acidification, chelation, and other processes (Wei et al. 2016). In addition, these PSMs from soil and plant rhizospheres can assimilate soluble ionic phosphate forms (Kumar et al. 2016). Moreover, *Betaproteobacteria* was found to be one of major contributors to phosphonate transport in this study (Fig. 7). For decreased taxa, that relative abundance of *Clostridia* within the phylum *Firmicutes* decreased ($p < 0.05$) consistently for all soil types in fall (Online Resource 7–9). This taxon was a great contributor causing microbial community composition shifts with obvious differences between fall and other seasons (Online Resource 12). *Clostridia*, as representatives of *Firmicutes* is sensitive to soil warming and seasonal fluctuation (Chernov et al. 2015), implying the interactive effect of soil warming and seasonal variation may give favorable advantages for specific microbial taxa adapted to changed temperatures (Rinnan et al. 2009).

Climate warming exerts significant impacts on soil microbial community and its biodiversity in many ecosystems (Falkowski et al. 2008), and the changed microbial community would also lead to alterations in functional potentials (Fig. 5 & Fig. 7), which in turn affect biogeochemical cycling and ecosystem feedback (Falkowski et al. 2008; Kuffner et al. 2012). The enriched oxidative phosphorylation function under warming (Online Resource 14) is involved with P metabolic process. For some anaerobic bacteria, ATP can be continuously synthesized from ADP and Ortho-P by oxidative phosphorylation (Issartel et al. 1992), suggesting the higher utilization of Ortho-P by certain microbes for catabolism in warmed groups. Enriched genes responsible for oxidative phosphorylation, exopolyphospohatase, and sulfate reduction/denitrification suggest the pathways involved in catabolism, the degradation and the release of P may be preferentially activated under warming. Consistently, P transformations witnessed a significantly decreased orthophosphate and polyphosphate (two inorganic P forms). Wakai et al. (2013) further found the oxidative phosphorylation of genus *Hydrogenophilus* in the class *Betaproteobacteria* was fundamental and advantageous in the biogeochemical cycles occurred in the high temperature geothermal niches, and moreover *Hydrogenophilus* was prevalently distributed in high temperature geothermal niches. These previous findings provided evidences for our study. However, many different enzymes are involved in oxidative phosphorylation, and when exploring into individual KOs, we found genes encoding inorganic pyrophosphatase were attenuated after warming, implying there are maybe opposing trends of functions within this complex pathway when subjected to warming. Overall, the potential responses of P metabolic and releasing processes may provide a new insight into soil P forms in response to on-going experimental warming.

Conclusions

Soil P forms varied differently among different nutrition status and seasons in wetlands. The relative abundance of Ortho-P decreased and Phon-P increased under warming, which was mainly found in high nutrition wetland soils. In spring and summer, microbial community composition showed a clear separation among different nutrition status, however in fall, the major

separation was found between control and warmed treatment, suggesting warming-induced microbial shifts mainly occur in fall, but not in other seasons. Specifically, warming led to an increased relative abundance of *Alphaproteobacteria*, *Betaproteobacteria* and *Acidobacteria-6* as well as decreased abundance of *Clostridia* in high nutrition wetland soils. Changed microbial community may influence the associated functional potentials which then explained P dynamics. This implies a linkage between altered soil P forms and microbial community in response to experimental warming. These findings are beneficial to better understand biogeochemical cycles of P in wetland soils under future climate warming. In the coming studies, a forward verification of the functional profiles of microorganisms using metagenomic sequencing-based approaches is needed to better understand the interrelationship between soil P forms and microorganisms in response to global climate warming.

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