





Metagenomic strategies uncover the soil bioavailable phosphorus improved by organic fertilization in Mollisols

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Highlights

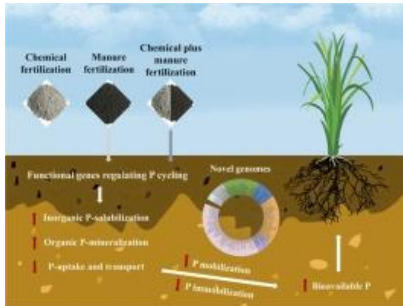
- Manure significantly influenced microbial P cycle-related functional profiles.
- Manure decreased *phnC* gene abundance that inhibited microbial P-uptake and transport.
- Soil microbial inorganic and organic P mobilization was promoted by manure amendments.
- *phnC* gene was found as a biomarker for soil P cycling in black soils.
- Bin44 containing *phnC* gene was a potential indicator regulating microbial P-uptake and transport.

Abstract

Microorganisms play essential roles in soil phosphorus (P) cycling and the regulation of P bioavailability, however, genetic information on microbial P cycling in response to nutrient inputs is largely unclear. Here, metagenomic sequencing and genome binning were used to investigate microbial functional traits under chemical and organic fertilization in three long-term field experiments across black soil region of Northeast China. The results revealed that manure amendments strongly affected microbial P cycle-related functional gene patterns, which were significantly and positively correlated with the contents of soil total P (TP) and available P (AP). Manure addition directly increased soil AP concentrations, and indirectly acted through the alterations of microbial functional genes involved in soil P cycling. Specifically, manure amendments consistently decreased abundances of *phnC* gene and increased gene abundances of *phnP*, *opd*, and *phoN* across three locations, suggesting the potentially inhibition of soil microbial P-uptake and transport and the promotion of soil microbial organic P- mineralization. Manure addition promoted microbial inorganic P-solubilization by enriching the *ppa*, *gcd*, and *pqqC* genes at two out of three locations, while chemical fertilizer (CF) addition slightly stimulated the functional gene abundances involved in microbial P-uptake and transport and P-starvation response regulation. In addition, soil AP content was negatively

correlated with the *phnC* gene abundance but positively correlated with the gene abundances of *opd* and *phoN*. Moreover, 23 metagenome-assembled genomes (MAGs) were reconstructed covering all soil samples, all of which contained the *phnC* gene with the copy numbers varying from 1 to 19. Nevertheless, only bin44 had a negative correlation with soil AP ($r=-0.361$, $P=0.030$) and could be considered as a potential indicator regulating microbial P-uptake and transport. Taken together, manure inputs positively accelerated microbial P-transformations, which was beneficial for the establishment of efficient P management strategies in sustainable-intensive agriculture.

Graphical Abstract



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Keywords

Chemical and organic fertilization; Soil phosphorus cycling; Microbial functional genes; Metagenome-assembled genomes; Mollisols

1. Introduction

Phosphorus (P) is an essential macronutrient for plant growth with important roles in photosynthesis, macromolecular biosynthesis, signal and energy transduction (Ikoyi et al., 2018). Thus, a great deal of P fertilizer is commonly devoted to croplands to maintain high productivity and soil ecological functions (MacDonald et al., 2011). However, only a small proportion of the soil total P is readily bioavailable for plant uptake after fertilization because the rest is rapidly combined into the soil matrix or lost by leaching (Syers et al., 2008). Therefore, it has induced two unprecedented issues in sustaining worldwide food security. One is the scarcity of P as a nonrenewable natural resource and the current lack of substitutes for P (Gilbert, 2009). The other is that the overuse of P fertilizers results in water eutrophication and biodiversity loss (Aubriot et al., 2011). In other words, a better understanding of the mechanisms promoting P bioavailability is essential to ameliorating P limitation in agroecosystems.

Microorganisms with diverse metabolic capacities are involved in soil P transformation and regulating soil P availability (Richardson et al., 2011, McRose and Newman, 2021). Containing a variety of P-cycling genes, soil microorganisms could improve the bio-accessibility of diverse recalcitrant P forms in soils (Richardson and Simpson, 2011). It mainly includes two parts, one is that a set of organic acids (e.g. gluconic acid, citric acid and formic acid) are released by soil microorganisms to solubilize inorganic P forms (Yao et al., 2018), and the other is that a series of microbe-derived enzymes (e.g., phosphatase, phytase and carbon-phosphorus lyase) could mineralize organically fixed P (Barea and Richardson, 2015). Moreover, microorganisms harbor efficient P uptake and transport systems, assimilating inorganic P not only under the P-low but also P-rich environments (Hsieh and Wanner, 2010). Besides, microbial P-starvation response regulation could promote microorganisms to utilize exogenous P (Vershinina and Znamenskaya, 2002). Therefore, the trade-off between microbial P assimilation and mobilization greatly determines

soil P bioavailability for plants. More importantly, the processes of microbial P-transformation are mainly controlled by the relevant microbial gene groups (Bergkemper et al., 2016). To efficiently utilize soil P and maintain agricultural sustainability, it is vital to explore the genetic potential of soil microorganisms in driving soil P cycling.

Fertilization is one of the most common agricultural practices for improving soil P fertility, mainly through the addition of chemical P or organic matter (Lee et al., 2004, Cheng et al., 2020). Amendment of these nutrients leads to changes in soil microbial diversity, community composition and functional potentials involved in C and N cycling (Nemergut et al., 2008, Wang et al., 2021). However, comparatively fewer studies have focused on microbial functional traits relevant to soil P cycling or merely on specific genes, such as *phoD*, which regulates the process of organic P-mineralization (Chen et al., 2019). For example, Liu et al. (2021) reported that total and active *phoD* gene abundances and the associated microbial groups were reduced by long-term mineral fertilizer addition but increased by organic fertilizer amendment, which promoted soil organic P-mineralization. Additionally, using metagenomic method, Dai et al. (2020) revealed that long-term P input promoted P immobilization by reducing the abundances of functional genes involved in P-starvation response regulation, while the addition of N fertilizer reduced the microbial P-solubilizing and mineralizing capacities. Contrarily, organic amendment was reported to promote microbially mediated soil P-solubilization by metagenomics sequencing (Wu et al., 2021). In this regard, different fertilization regimes formed distinct microbial life-strategies shaping soil P cycle processes (Bach et al., 2018). Moreover, microorganisms not only mobilize soil recalcitrant P but also assimilate P into their biomass, which results in their efficiently competing soil available P with crops in agroecosystems (Wanner, 1993). Nevertheless, whether the addition of chemical or organic fertilizers can change the genetic potentials of soil P cycling and whether these processes are linked to the alterations in soil P availability are still poor understood.

Advances in metagenomics have allowed us to investigate multiple microbial genes manipulating soil nutrient cycling processes (Dai et al., 2020). In our previous study, we revealed that long-term chemical and organic fertilization had distinct influences on the microbial functional traits involved in soil C and N cycling in the black soils (also called Mollisols) of Northeast China (Hu et al., 2022). The amendment of chemical fertilizer significantly promoted the genetic potentials of methane oxidation, soil N degradation, nitrification and anammox, while manure fertilizers considerably shifted C fixation and degradation processes, and accelerated assimilatory and dissimilatory nitrate reduction pathways. Moreover, we found that soil P contents were significantly enriched by manure addition, and predominantly affected the C and N cycling patterns, abundances of functional genes and microbial taxa in this region (Hu et al., 2022). In this context, to shed light on the microbial genetic potentials involved in soil P cycling, genome-centric metagenomics was applied to explore how microbial P transformation is affected by long-term chemical and organic fertilizations. Our objectives were to (1) explore microbial functional traits involved in soil P cycling in response to long-term chemical and organic fertilizations, and their links to soil P dynamics; (2) identify the key microbial genes consistently varied across Mollisols and their relevant novel genomes involved in P transformation. We hypothesized that long-term manure input would inhibit microbial P-uptake and transport, and promote P-solubilization and mineralization by shifting the P cycle-related functional genes in Mollisols.

2. Materials and methods

2.1. Field experiments and soil sampling

This study was conducted at three long-term fertilization experimental stations in Gongzhuling (43° 31' N, 124° 48' E), Mingzhuxiang (45° 50' N, 126° 51' E) and Heihe (50° 15' N, 127° 27' E), which corresponded to the southern (SB), middle (MB) and northern (NB) areas of the black soil region in Northeast China, respectively. The three fields have been subjected to continuous fertilization treatments for over 30 years, including non-fertilization (NoF), chemical fertilization (CF), manure fertilization (M) and chemical plus manure fertilization (CFM). The basic conditions of the three fields, fertilizer amendments and crop cultivation were described in our previously published papers (Hu et al., 2017, Hu et al., 2018, Hu et al., 2020, Hu et al., 2022), and were shown in Supplementary Text 1 and Table S1.

A total of 36 soil samples (three locations × four fertilization treatments × three replicates) were collected at a soil depth of 0–20cm in September 2–5 in 2014. The methods for determination of soil properties and the data of soil properties were described in our previous published paper (Hu et al., 2017), which were shown in this study as

supplementary Text 2 and [Table S2](#), respectively.

2.2. DNA extraction, DNA sequencing and metagenomic processing

Soil total DNA was extracted from three replicates per treatment using FastDNA® SPIN Kit for Soil (MP Biomedicals, USA) following the procedures of the manufacturer. The quantity of the extracted DNA was measured by a Qubit 4.0 fluorometer (Invitrogen, USA). The soil DNA purity was analyzed by absorption ratio of A_{260}/A_{280} with a NanoDrop 2000 spectrophotometer (Thermo Scientific, USA). Approximately 1 µg of DNA from each sample was used for preparation of metagenomic libraries. Sequencing was performed on an Illumina HiSeq 4000 platform (Illumina Inc., San Diego, CA, USA) at Majorbio Biopharm Technology Co., Ltd. (Shanghai, China). Raw sequence data with an average of 10Gb (gigabases) were obtained for each sample and deposited into the Genome Sequence Archive (GSA) with accession number [PRJCA006444](#). Data analysis was conducted using previously described methods ([Hu et al., 2022](#)). Briefly, quality control of raw sequences was performed with Fastp (ver. 0.20.0, <https://github.com/OpenGene/fastp>), and the clean reads were de novo assembled into contigs by Megahit (ver. 1.1.2, <http://www.l3-bioinfo.com/products/megahit.html>). Contigs (> 300bp) were used for the prediction of [open reading frames](#) (ORFs) by MetaGene (<http://metagene.cb.k.u-tokyo.ac.jp/>), and redundant genes were removed using CD-HIT (ver. 4.6.1, <http://www.bioinformatics.org/cd-hit/>). The putative protein-coding sequences were searched against Kyoto Encyclopedia of Genes and Genomes (KEGG, ver. 94.2, <http://www.genome.jp/kegg/>) to obtain their functional annotation by Diamond (ver. 0.8.35, <https://github.com/bbuchfink/diamond>). The targeted P cycle-related genes ([Table S3](#)) were retrieved based on published studies ([Dai et al., 2020](#), [Liang et al., 2020](#)). The abundance of P cycle-related genes in each treatment was normalized to 10,000 cells against the total counts of the housekeeping gene ribosomal protein L2 (*rplB*) ([Wang et al., 2015](#)).

2.3. Genome binning, phylogenetic classification and functional annotation

Contigs with length > 1000bp were binned by MetaBAT2 (ver. 2.12.1, <https://bitbucket.org/berkeleylab/metabat>) with default parameters. Genome size, completeness, contamination and GC contents of metagenome-assembled genomes (MAGs) were evaluated by CheckM (ver. 1.0.12, <https://github.com/Ecogenomics/CheckM>). Only MAGs meeting >80% completeness and with <5% contamination were used for further analysis. The taxonomic classification of MAGs was conducted with GTDB-Tk (ver. 1.3.0, <https://github.com/ecogenomics/gtdbtk>). ORFs of high-quality bins were predicted by MetaGene and searched against NCBI-nr and KEGG databases by Diamond for functional annotation. The abundance of each MAG was calculated using its contig depth multiplied by its length ([Uritskiy et al., 2018](#)). Maximum-likelihood [phylogenetic](#) trees were constructed with the reference genomes in GTDB-Tk and visualized by Interactive Tree of Life (i-TOL, ver. 5.0) platform. The genome average nucleotide identity (ANI) of each MAG was calculated by fastANI (ver. 1.0, [Goris et al., 2007](#)). All bins obtained in this study were deposited into the Genome Sequence Archive (GSA) with accession numbers [SAMC797368-797390](#).

2.4. Statistical analysis

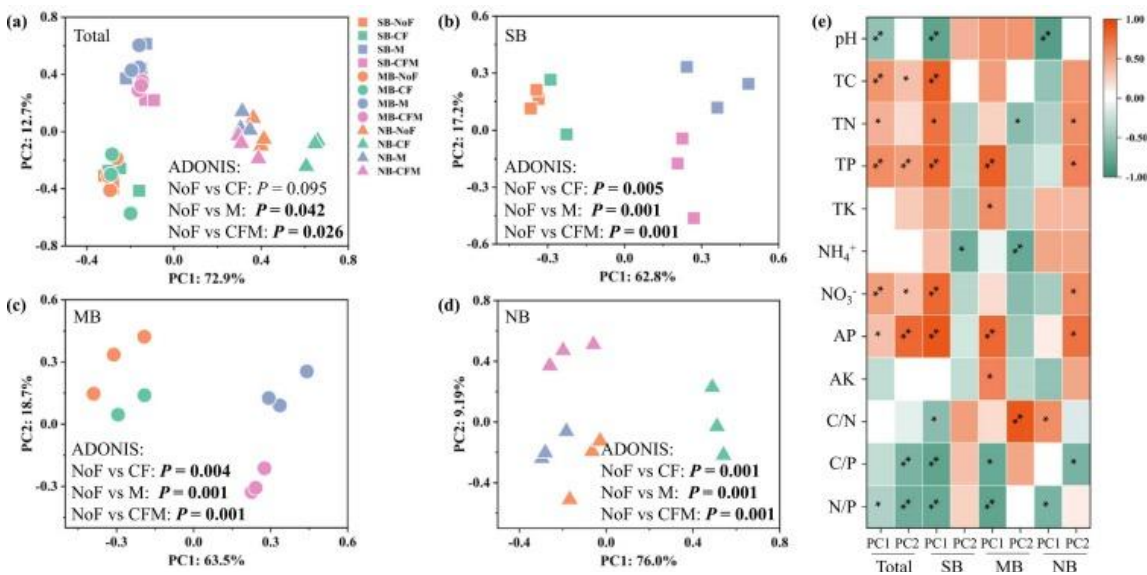
Principal component analysis (PCA) and permutational multivariate analysis of variance using distance matrices (ADONIS) were conducted in R with the vegan package to examine the differences in the gene composition among treatments. Pearson's correlation analysis was used to reveal the correlations between P cycle-related processes, normalized abundances of P cycle-related genes and soil properties, and the correlations were visualized in heatmap plots. Two-way ANOVA was conducted to investigate the interactive effects of fertilization treatments and trial locations on the normalized abundances of P cycle-related genes with *P* values (< 0.05) adjusted by false discovery rate (FDR). The above two analyses were performed in SPSS software (ver. 21.0). The differences in P cycle-related processes and gene abundances between fertilized treatments and NoF treatment were determined by the DESeq2 package in R. The influences of soil properties and P cycle-related processes on soil available P contents were evaluated by linear mixed-effects model analysis (LMM) using the lmerTest package in R. A structural equation model (SEM) was applied to quantify the significant influences (direct or indirect both) of explanatory variables on soil available P using AMOS software (IBM, SPSS AMOS 21.0).

3. Results

3.1. Microbial functional traits involved in P cycling and linkage to soil properties

The soil basic properties across three locations were examined. Briefly, CF significantly decreased soil pH while M increased it in the MB and NB when compared to NoF (Table S2). CF and CFM significantly enhanced soil NH_4^+ -N in the MB and NB, while CFM increased soil NO_3^- -N in the SB and NB. Manure addition (M and CFM treatments) enriched soil TC and TN when compared to NoF, but not all influences were statistically significant across three locations. Notably, compared to NoF, manure addition significantly increased soil TP and AP contents, as consistently detected at three locations (Table S2).

In total, 30 functional genes related to P cycling and their corresponding KEGG orthology (KO) numbers were collected at three locations (Table S3). The PCA at the KO level showed that the functional beta-diversity of NB was separated from those of MB and SB along the PC1 axis, which explained 72.9% of the variation in the whole microbial community (Fig. 1a). With the examination by ADONIS, manure addition (M and CFM treatments, $P < 0.05$) rather than CF ($P = 0.095$) exhibited significantly influenced microbial functional beta-diversity when considering all the samples (Fig. 1a). Individually, all fertilized treatments significantly affected the microbial functional beta-diversity involved in soil P cycling at the three locations (Fig. 1b-d). Furthermore, the contents of soil TP and AP had significant and positive relationships with P cycle-related functional beta-diversity ($P < 0.05$), while the ratios of C/P and N/P exhibited significantly negative correlations ($P < 0.05$) with regarding the three locations together or individually (Fig. 1e).



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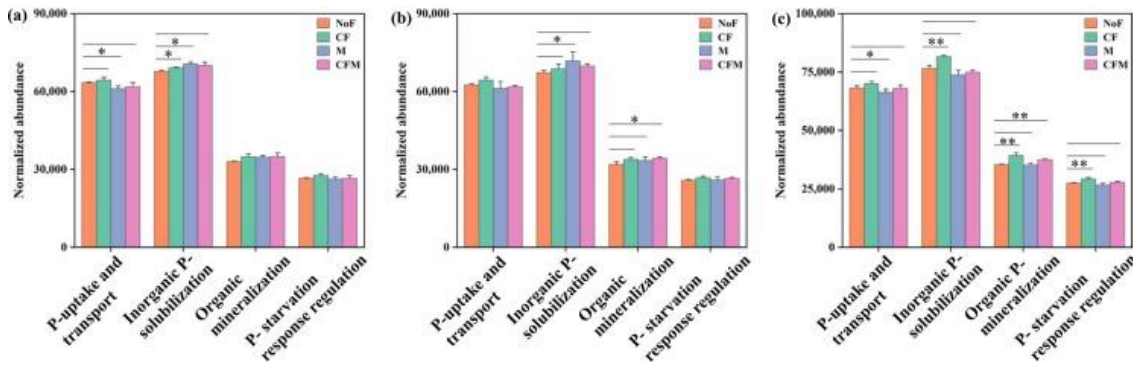
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Fig. 1. Microbial functional beta-diversity involved in soil P cycle identified by principal component analysis (PCA) for all samples (a) and individual location (b-d). Permutational multivariate analysis of variance using distance matrices (ADONIS) was used to examine the differences in microbial functional beta-diversity between fertilized treatments and NoF treatment. Pearson's correlation analysis was used to correlate the microbial P cycle-related functional beta-diversity and soil properties, and the correlations were visualized in the heatmap plot (e). TC, total carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AP, available phosphorus; AK, available potassium. NoF, non-fertilization; CF, chemical fertilization; M, manure fertilization; CFM, chemical plus manure fertilization. SB, MB and NB indicated the three sampling locations in the southern, middle and northern areas, respectively, across the black soil region in Northeast China. *, $P < 0.05$; **, $P < 0.01$.

3.2. Fertilization impact on P cycle-related processes and soil P contents

Microbial functional genes were exclusively retrieved which involved in P cycling, including P-uptake and transport, inorganic P-solubilization, organic P-mineralization and P-starvation response regulation (Table S4). The gene abundances encoding for inorganic P-solubilization and P-uptake and transport were higher than those in the other

two P cycle-related genes across three locations (Fig. 2). Compared to NoF, M treatment significantly decreased the total abundance of genes encoding for P-uptake and transport in the SB and NB (Fig. 2a, c), while an increasing trend of this process was observed under CF treatment (Fig. 2). Besides, M treatment significantly enriched the functional genes encoding for inorganic P-solubilization in the SB and MB (Fig. 2a, b), and CFM treatment significantly increased the total gene abundance of organic P-mineralization in the MB and NB when compared to NoF (Fig. 2b, c). Similarly, CF treatment significantly enhanced the abundance of total genes involved in inorganic P-solubilization in the SB and NB (Fig. 2a, c). CF treatment also significantly increased the total abundance of genes encoding for P-starvation response regulation in the NB and this trend was slightly reflected in the SB and MB (Fig. 2).

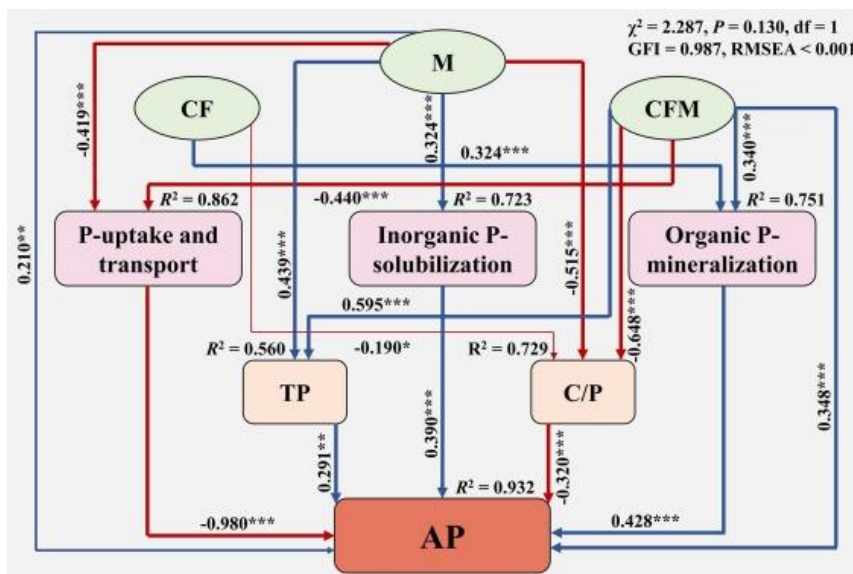


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Fig. 2. The normalized abundance of microbial P cycle-related processes in the SB (a), MB (b) and NB (c). The significant differences between fertilized treatments and NoF treatment were examined by DESeq2 analysis and the cycling processes with significance were marked with asterisks. The p values adjusted by false discovery rate (FDR), *, $P < 0.05$; **, $P < 0.01$. NoF, non-fertilization; CF, chemical fertilization; M, manure fertilization; CFM, chemical plus manure fertilization. SB, MB and NB indicated the three sampling locations in the southern, middle and northern areas, respectively, across the black soil region in Northeast China.

Regarding the whole samples, LMM analysis revealed that soil TP and the ratio of C/P positively and negatively affected the soil AP, respectively (Fig. S1a). Besides, the total abundance of genes encoding for P-solubilization and -mineralization positively influenced the soil AP, while P-uptake and transport exhibited a contrary trend (Fig. S1b). SEM explained 93.2% of the total variance in soil AP (Fig. 3). Manure treatments had direct positive effects on soil AP, while CF treatment had no significant effect (Fig. 3). Besides, the direct effects of soil TP (56.0% explanation) and the ratio of C/P (72.9% explanation) on AP were mainly mediated by manure addition (Fig. 3). Notably, manure treatments indirectly influenced soil AP through their direct positive effect on processes of P-solubilization (72.3% explanation) and -mineralization (75.1% explanation) and negative effect on P-uptake and transport (86.2% explanation).



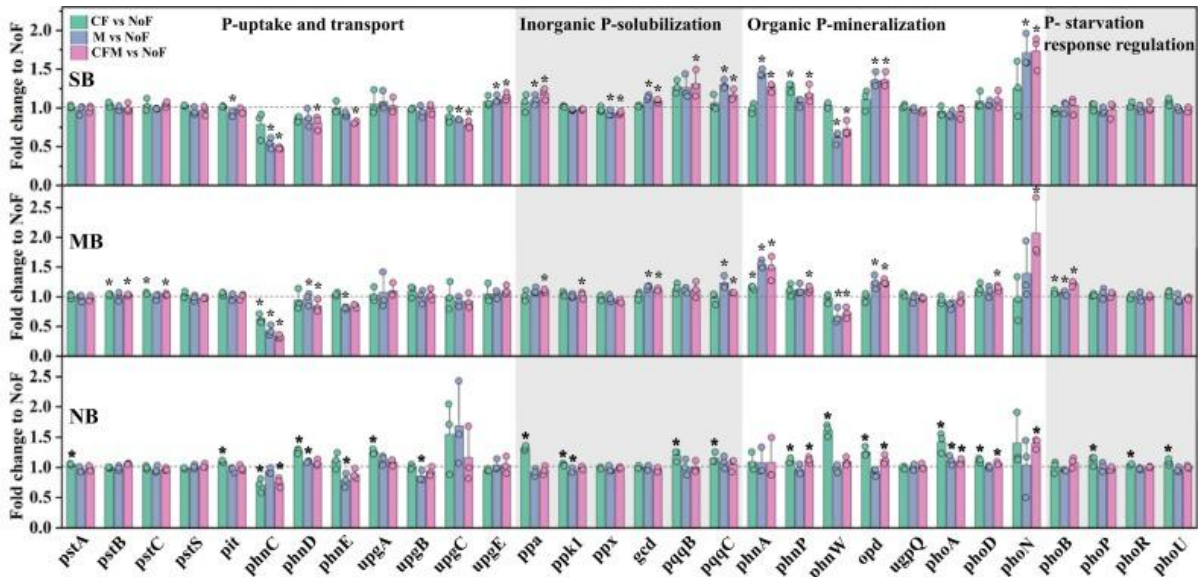
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Fig. 3. Structural equation model (SEM) showing the direct and indirect effects of fertilization regimes on soil available P based on the results of LMM analysis. The width of the solid line was proportional to the significant relationships between variables with blue and red indicating positive and negative relationships, respectively. R^2 values indicated the proportion of the variance explained for the endogenous variable. χ^2 , Chi-square value; df , degree of freedom; GFI , goodness of fit index; $RMSEA$, root mean square error of approximation. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

3.3. Responses of P cycle-related genes to chemical and organic fertilization

Different fertilization treatments induced various influences on the abundance of functional genes involved in P cycling. Compared to NoF, CFM treatment significantly reduced the abundance of *phnC* that involved in P-uptake and transport, but increased the abundances of *phnP*, *opd* and *phoN* for organic P-mineralization across three locations (Fig. 4). Contrarily, no consistent variation in the gene abundance response to CF treatment was observed at the three locations. Besides, regarding two out of three locations, manure addition significantly decreased the *phnE* abundance for microbial P-uptake and transport, while enriched the abundances of *ppa*, *gcd*, *pqqC* for inorganic P-solubilization and the abundances of *phnA* and *phoD* for organic P-mineralization (Fig. 4). CF treatment only significantly increased *phnP* abundance in the SB and NB. Furthermore, the interactive effects of fertilization and location on gene abundances involved in P cycling were examined, which showed that most functional genes largely varied against sampling locations, while fertilized treatments induced stronger effects on the abundances of the *phnC*, *pqqC*, *phnA*, *opd* and *phoN* genes than sampling locations (Table S5).



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Fig. 4. The impacts of different fertilization regimes on microbial functional genes involved in soil P cycling in the SB, MB and NB. The bar indicated the log₂-fold changes (LFCs) in functional genes with three replicates in fertilized treatments relative to NoF treatment. The functional genes with significant LFCs ($P_{adj} < 0.05$) were marked with asterisks. NoF, non-fertilization; CF, chemical fertilization; M, manure fertilization; CFM, chemical plus manure fertilization. SB, MB and NB indicated the three sampling locations in the southern, middle and northern areas, respectively, across the black soil region in Northeast China.

The relationships between the abundance of P cycle-related genes and soil properties were further examined (Fig. S2). When simultaneously considering three locations, *phnC* had a significantly negative correlation with soil AP, while the opposite trend was consistently detected for C/P at the three locations (Fig. S2). The *phoN* gene had significantly positive correlations with soil AP and TP but negative with C/P, and a positive correlation was consistently observed between *opd* and soil AP across three locations.

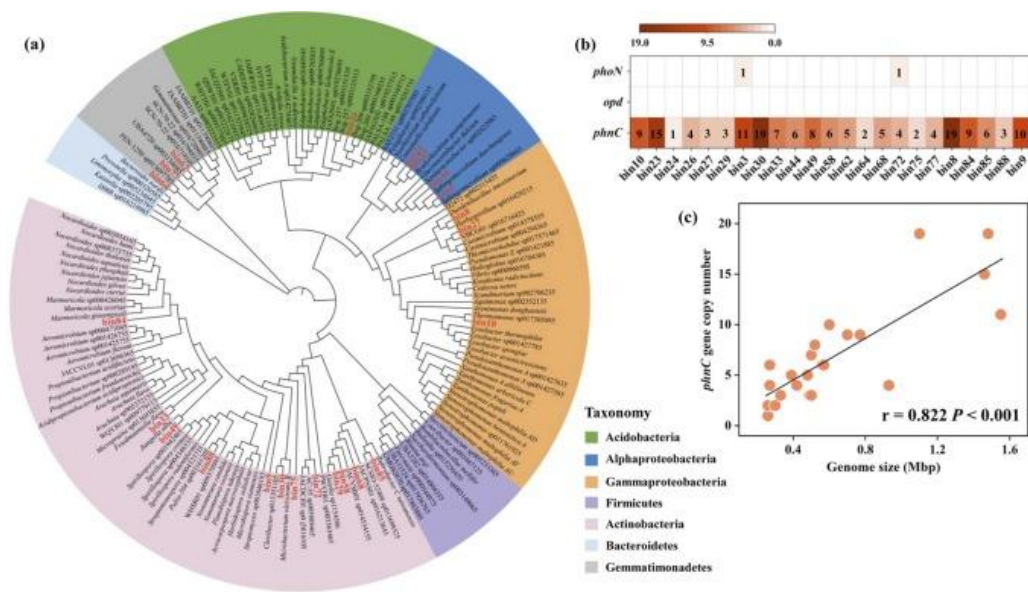
3.4. Metagenome-assembled genomes driving soil P cycling

Twenty-three high-quality MAGs were reconstructed, and taxonomically classified into *Actinobacteria* (12), *Proteobacteria* (7), *Gemmatimonadetes* (3) and *Acidobacteria* (1) (Table 1, Fig. 5a). The average ANI values of all MAGs were less than 95% (77.8–88.5%). The *phnC*, *opd* and *phoN* genes were explored in 23 retrieved MAGs, as they were significantly shifted by fertilizer addition and correlated with soil AP content across three locations. Notably, at least one *phnC* gene (involved in P-uptake and transport) was harbored in all detected MAGs. Among these, bin30 and bin8 contained 19 copy numbers of the *phnC* gene, and were classified into *Clavibacter* and *Herbaspirillum*, respectively (Fig. 5a, b). Subsequently, bin23, bin3 and bin9 contained 15, 11 and 10 *phnC* gene copies and were classified into *Bradyrhizobium*, *Sphingomicrobium* and *Jatrophihabitantaceae*, respectively. Specifically, the copy number of *phnC* gene had a significant and positive correlation with the genome size ($r = 0.822$, $P < 0.001$) (Fig. 5c). Besides, both bin3 and bin72 harbored one *phoN* gene involved in organic P-mineralization, and bin72 was classified into *Actinobacteria* (Fig. 5a, b). Nevertheless, no *opd* gene was detected in any MAGs reconstructed in this study (Fig. 5b). Furthermore, the relative abundance of bin44 containing 6 *phnC* gene copies had a significantly negative correlation with soil AP ($r = -0.361$, $P = 0.030$) (Fig. 5b, Fig. S3). Contrarily, the relative abundance of bin58 containing 6 *phnC* gene copies exhibited a significantly positive correlation with soil AP ($r = 0.754$, $P < 0.001$).

Table 1. Feature summary for high-quality metagenome-assembled genomes reconstructed in this study.

Bins	Genome size (Mb)	Completeness (%)	Contamination (%)	GC (%)	Putative taxonomy
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Bins	Genome size (Mb)	Completeness (%)	Contamination (%)	GC (%)	Putative taxonomy
bin10	0.77	85.9	0.66	0.71	Gammaproteobacteria
bin23	1.46	86.2	1.27	0.61	Alphaproteobacteria
bin24	0.26	94.0	0.00	0.67	Alphaproteobacteria
bin26	0.93	98.9	0.00	0.58	Acidobacteria
bin27	0.33	94.0	0.00	0.68	Gammaproteobacteria
bin29	0.49	98.1	0.00	0.70	Actinobacteria
bin3	1.55	99.1	0.00	0.64	Alphaproteobacteria
bin30	1.10	94.3	0.66	0.67	Actinobacteria
bin33	0.50	83.7	0.00	0.64	Actinobacteria
bin44	0.57	95.1	0.44	0.67	Alphaproteobacteria
bin49	0.52	93.5	0.29	0.68	Actinobacteria
bin58	0.56	94.6	0.00	0.71	Actinobacteria
bin62	0.48	91.9	0.00	0.69	Gemmatimonadetes
bin64	0.30	84.4	0.13	0.66	Gemmatimonadetes
bin68	0.39	99.8	0.00	0.69	Actinobacteria
bin72	0.27	97.6	0.00	0.69	Actinobacteria
bin75	0.26	96.1	1.52	0.74	Actinobacteria
bin77	0.42	96.1	0.19	0.68	Gemmatimonadetes
bin8	1.48	97.7	0.91	0.64	Gammaproteobacteria
bin84	0.70	99.7	0.04	0.71	Actinobacteria
bin85	0.27	94.7	0.07	0.64	Actinobacteria
bin88	0.50	99.7	0.00	0.71	Actinobacteria
bin9	0.60	84.2	0.00	0.67	Actinobacteria



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Fig. 5. **Phylogenetic** tree of reconstructed high-quality metagenome-assembled genomes (MAGs) and reference genomes from GTDB-Tk (a). The MAGs retrieved in our study were marked in red and details on MAGs were provided in [Table 1](#). The heatmap plot display the copy number of genes identified in MAGs that involved in soil P cycling (b). Pearson's correlation between the copy number of *phnC* gene and genome size (c).

4. Discussion

4.1. Manure fertilizations strongly shifted P cycle-related functional traits in Mollisols

The ecosystem services of [soil microorganism](#) are essential pathways in transforming various soil nutrients into plant-available forms ([Whiteside et al., 2009](#), [Scarlett et al., 2021](#)). Especially, fertilization is one of the cornerstones of [agricultural managements](#) for the improvement of sustainable production, and exhibits complex and diverse effects on soil microbiome ([Hartmann et al., 2014](#)). In our previous study ([Hu et al., 2022](#)), we revealed that manure addition rather than chemical fertilizer strongly promoted soil C and N transformations in the black soil region. Accordingly, a similar phenomenon was observed in soil P cycling when considered the whole samples in this study ([Fig. 1a](#)). Besides, the same fertilization treatment significantly changed soil P cycle-related functional patterns across the three locations ([Fig. 1b-d](#)), which suggested that long-term similar nutrient inputs probably assemble soil [microorganisms](#) to share similar nutrient requirements by mediating their survival, growth and productivity, regardless of geographical divergence ([Green et al., 2008](#), [Lauber et al., 2008](#)). Moreover, we found that soil AP and TP were significantly enriched by manure fertilizations ([Table S2](#)), and those two soil factors not only exhibited dominant influences on microbial functional patterns involved in soil C and N cycling ([Hu et al., 2022](#)) but also on soil P cycle-related functional gene assemblages in this study ([Fig. 1e](#)). Our findings demonstrated the view that microbial functional traits involved in soil nutrient cycling strongly could be shaped by soil P [bioavailability](#) ([Yao et al., 2018](#)). Contrarily, the ratios of C/P and N/P showed negative correlations with the P cycle-related functional gene assemblages ([Fig. 1e](#)), which was mainly due to the microbial requirements of balanced intracellular C:N:P [stoichiometry](#) and the need for more rational fertilization regimes based on local nutrient conditions ([Cleveland and Liptzin, 2007](#)).

4.2. Manure addition stimulated the accumulation of soil AP by regulating P cycling traits

Consistent with our hypothesis at the outset, manure fertilizations significantly promoted the genetic potentials for the release of microbial exoenzymes to mineralize soil organic P, and the synthesis of organic acids for microbial inorganic P-solubilization ([Fig. 2](#), [Rodríguez et al., 2006](#); [Chen et al., 2017](#)), which was also reported by other studies ([Grafe et al., 2018](#), [Bi et al., 2020](#)). This finding suggested that microorganisms tend to mobilize soil recalcitrant P rather than compete for bioavailable P with plants under resource-adequate environments. Moreover, we found that manure fertilizations greatly enriched P bioavailability, both directly and indirectly, by influencing soil microbial functional potentials and nutrient conditions ([Fig. 3](#)). Specifically, manure initially contains amounts of labile P and directly increases the content of soil available P, and indirectly reinforces the transformation of stable P to labile P mediated by soil microorganisms ([Yin and Liang, 2013](#), [Yan et al., 2016](#)). Besides, the soils with long-term manure input commonly maintain high microbial biomass, which might store more available P ([Randriamanantsoa et al., 2015](#), [Ma et al., 2020](#)). Consequently, soil P mobilization by functional microorganisms could be of direct importance for plant P acquisition and high crop yields.

Generally, balanced nutrient stoichiometry promotes microbial demand for available P ([Dai et al., 2020](#)). However, our study found that manure addition slightly inhibited the functional potential of P-uptake and transport in the black soils ([Fig. 2](#)). [Brzoska et al., 1994a](#), [Brzoska et al., 1994b](#) revealed that the activity of P-transporter system could be restricted by high concentration of P in microbial cells. This again reflects, under manure fertilizations, the low microbial P-requirement from soils but direct P-assimilation from manure for growth. In this regard, manure addition indirectly promoted the accumulation of soil bioavailable P by weakening the capacity of microbial P-uptake ([Fig. 3](#)). Contrarily, CF addition slightly promoted the functional potential of P-uptake and transport and significantly stimulated P-starvation response regulation ([Fig. 2](#)), which enabled microorganisms to assimilate

external P and might effectively compete for bioavailable P with plants (Richardson and Simpson, 2011). The straightforward reason is that chemical fertilizer does not supply extra energy and carbon sources for microbial balance in utilizing P (Hsieh and Wanner, 2010, Spohn and Kuzyakov, 2013). Besides, CF addition promoted the functional potential of inorganic P-solubilization in the SB and NB (Fig. 2a, c). This is because the significant accumulation of nitrate induced the enhancement of P dissolution and soil P availability (Han et al., 2021). Nevertheless, long-term application of chemical fertilizer causes serious soil degradation (such as soil acidification) and microbial diversity loss (Guo et al., 2010, Hartmann et al., 2014), thus advocating the replacement by manure to improve sustainable agroecosystems (Horrigan et al., 2002).

4.3. Consistent shifts of individual P cycle-related functional genes under fertilizations in Mollisols

Variations in microbial functional genes reflect intrinsic driving forces of soil P cycling processes. In this study, the weakened processes of microbial P-uptake and transport under manure treatments were mainly due to the decrease in *phnC* gene across three locations (Fig. 4). *Phn* is a high-affinity P transport system encoding ATPase for microbial P uptake, and the *phn* genes are generally inhibited when microbes encounter P-adequate environments (Gebhard et al., 2006). Additionally, manure fertilizations significantly increased the gene abundances of *opd* (encoding phosphotriesterase) and *phoN* (encoding acid phosphatase) across three locations (Fig. 4), which could promote the mineralization of phosphonate and phosphate, respectively, suggesting that the organic form is the main component of P in soils with manure addition (Yu et al., 2021). Both addition of chemical and organic fertilizers enriched the *phnP* gene, which encodes C-P lyase to perform C-P cleavage to release free orthophosphate from multiple recalcitrant organic P pools (Bergkemper et al., 2016).

Considering microbial inorganic P-solubilization, the *gcd* gene encoding for glucose dehydrogenase and the *pqq* gene as cofactor encoding for pyrroloquinoline quinone were enriched by manure addition in at least two locations (Fig. 4). Both genes together encode the enzyme PQQGDH, which was repeatedly reported to be the major determinant of hydroxyapatite and rock phosphate solubilization by production of gluconic acid (Khan et al., 2007, Wu et al., 2022b). Moreover, soil available P that was significantly enriched by manure addition had a negative correlation with the *phnC* gene but positive correlations with the *opd* and *phoN* genes (Fig. S2), demonstrating that manure fertilizations strongly favor the accumulation of bioavailable P by regulating the relevant functional genes to inhibit microbial P assimilation and promote microbial P mobilization.

4.4. *phnC* was the biomarker gene regulating soil P cycling under fertilizations in Mollisols

The microbial contributions to soil P cycling need to be investigated in individual microbial species. For this, the functional potential of microbial P-cycling was further evidenced by reconstructed 23 MAGs, and their ANI values were all below 95%, which indicated the potentially novel bacteria obtained in this study (Jain et al., 2018). It should be noted that eukaryotes might be underrepresented in our metagenomic datasets due to gene prediction biases and database limitations, which urgently need to improve the analysis tools for eukaryotic genome assembly and correct identification (Donhauser et al., 2021).

Interestingly, the 23 high quality genomes all contained the *phnC* gene, and 5 MAGs with over 10 *phnC* gene copies were affiliated with Proteobacteria and Actinobacteria (Fig. 5a, b; Table 1). To date, microbial genomes containing genes involved in P cycling are difficult to recover due to highly heterogeneous and diversified soil environments, and have mainly focused on the *gcd* gene that was found to be predominant in soils and considered an indicator of bioavailable soil P (Liang et al., 2020, Wu et al., 2022b). In this regard, our study greatly expanded the known diversity of soil P cycle-related genes and species. Moreover, microorganisms with larger genomes are expected to be linked with greater nutrient demands (Wu et al., 2022a). This strengthened the evidence that certain microbes with higher genome sizes have greater potential for P-uptake and transport (Fig. 5c), and the *phnC* gene as a biomarker for soil P cycling is reasonable in the black soils.

Nevertheless, the existence of the *phnC* gene does not necessarily provide final evidence for microbial function on soil P bioavailability, and only bin44 and bin58 exhibited significant correlations with soil AP (Fig. S3). In accordance with previous statement, soils with high P content decreased the *phnC* gene abundance, and bin44 could be

considered a potential indicator regulating soil microbial P-uptake and transport due to its negative correlation with AP (Fig. S3). In contrast to the result of Wu et al. (2021) that Sphingomonadaceae associated bins had strong positive correlations with soil AP, we found that bin44 affiliated with *Sphingomicrobium* might be a novel species, and its physiological traits need to be further investigated. Additionally, bin58, affiliated with *Gaiella*, had a significantly positive correlation with soil AP (Fig. S3), and this genus has been reported to be a keystone in the production of oxidase and phosphatase to mineralize organic P (Albuquerque et al., 2011), which need further evidences. Although only one *phoN* gene copy was observed in bin3 and bin72, one *cbhA* gene involved in cellulose degradation was further detected in bin72, suggesting the tight coupling of soil P mineralization and C degradation (Chen et al., 2021). In this regard, in response to manure addition and the accumulation of bioavailable P, bin44 and bin72 were representatives of microbial life-strategies, shaping soil P cycling processes for inhibition of microbial P-acquisition and promotion of P-mobilization in the agroecosystem of black soils.

5. Conclusions

Long-term fertilizations, especially manure addition, significantly affected microbial functional patterns involved in soil P cycling. Manure fertilizations contributed to the accumulation of soil available P by direct input of liable P and indirect promotion microbial inorganic P-solubilization and organic P-mineralization, and inhibition of microbial P-uptake and transport. In contrast, addition of chemical fertilizer increased abundances of functional genes involved in microbial P-uptake and transport and P-starvation response regulation. The *phnC* gene, as a biomarker in the process of P-uptake and transport, was significantly decreased under manure fertilizations across three locations and contained in all retrieved MAGs in this study. Among 23 MAGs, only bin44, affiliated with *Sphingomicrobium*, negatively correlated with soil AP and was a potential indicator in regulating soil microbial P-uptake and transport. Additionally, manure amendments obviously enriched the *opd* and *phoN* genes involved in organic P-mineralization across three locations, and the *phoN* gene was detected in two reconstructed MAGs. Among these, bin 72 simultaneously contained *phoN* and *cbhA* gene, demonstrating the coupling of microbial metabolism processes. Taken together, long-term manure fertilizations contributed to microbial P mobilization and reduced microbial P assimilation, ultimately improving soil plant P bioavailability and high crop yields.

Declaration of Competing Interest

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

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Data Availability

No data was used for the research described in the article.

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