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Microbial mechanisms enhancing soil phosphorus bioavailability through vermicompost application for sustainable agriculture

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KEYWORDS

Bioavailable phosphorus, earthworm casting, legacy phosphorus, mineralization of organic phosphorus, phosphorus-solubilizing bacteria, solubilizing inorganic phosphorus.

HIGHLIGHTS

- Vermicompost-derived microorganisms secrete solubilizing agents that mobilize soil P.
- Soil properties changed by vermicompost application stimulate native microbes to enhance P availability.
- Microbial cell lysis releases dissolved P, an overlooked but vital contributor to soil P availability.
- Findings lay the groundwork for developing P-solubilizing microbial inoculants for sustainable agriculture.

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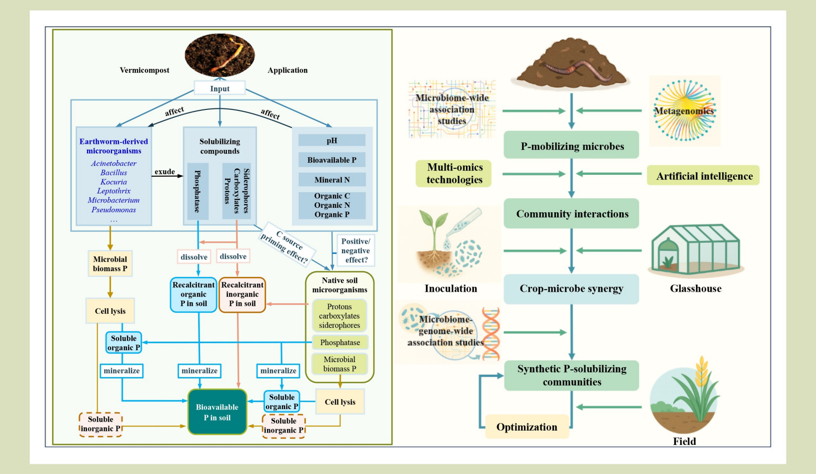
GRAPHICAL ABSTRACT



ABSTRACT

Although the chemical and biochemical pathways of phosphorus (P) mobilization following vermicompost application are relatively well-documented, the microbial processes that drive the release of sparingly-soluble P remain insufficiently explored. Consequently, this study examined key microbial mechanisms that enhance soil-P bioavailability in response to

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vermicompost application. First, vermicompost-derived microorganisms can mobilize inorganic P by releasing solubilizing compounds such as protons, siderophores, and carboxylates. Second, vermicompost-derived microorganisms mobilize organic P by exuding phosphatases. Resident soil microorganisms can also contribute to these processes when they are stimulated by the changed soil properties following vermicompost application, including pH and the concentrations of mineral nitrogen (N) and organic carbon (C). Additionally, microbial cell lysis can increase dissolved P concentrations in the soil solution, particularly as microbial biomass expands with vermicompost-derived organic matter inputs. Moreover, the study further explored how microbial mineralization of organic P is facilitated by carboxylates and the C:N ratio in vermicompost. Interactions between vermicompost-derived microorganisms and resident soil microbial communities are crucial, as competition or cooperation between them can significantly affect inorganic-P solubilization and organic-P mineralization. The rapid advancement of multi-omics technologies and the development of synthetic microbial community approaches provide opportunities to identify and optimize efficient P-solubilizing microorganisms. Future research should focus on elucidating microbial interactions and long-term effects of vermicompost-derived microorganisms on soil-P cycling, particularly in agricultural systems. This will provide a foundation for developing tailored, highly efficient P-solubilizing microbial inoculants, effectively translating theoretical insights into practical applications for sustainable agriculture.

1 Introduction

Phosphorus (P) is an essential macronutrient for plant growth[1] and its adequate supply is critical for crop health and yield[2]. However, about one third of agricultural soils globally lack sufficient bioavailable P[3], posing a significant challenge for long-term agricultural productivity. Large quantities of mineral fertilizers are typically applied to meet crop P needs[4,5]. Under a business-as-usual scenario, it is estimated that the global P requirement exceed P-fertilizer supply by around 2040[6]. Also, due to the strong sorption of P by soil minerals, the P-acquisition efficiency of many crops is low, leading to the accumulation of P in soil known as legacy P[7]. Although legacy P is not readily accessible to crops[8], it can be transformed into dissolved forms and transported to rivers and lakes via runoff. This process contributes to environmental issues such as algal blooms[9–11]. Therefore, improving the effective use of legacy P not only reduces agricultural fertilizer costs but also mitigates non-point source pollution from croplands, thereby supporting the sustainable development of agriculture[12–14].

The introduction of earthworms to soil improves its structure, enhances P bioavailability and promotes soil biological activity[15–17]. However, directly adding earthworms to cropland soils is often impractical due to the widespread use of pesticides in modern agriculture. Vermicompost is a nutrient- and microorganism-rich organic fertilizer and soil conditioner produced through the natural decomposition of organic waste by earthworms. It provides superior efficacy in enhancing soil-P bioavailability compared to conventional organic fertilizers, characterized by: (1) elevated bioavailable-P content[18–20], and (2) enhanced phosphatase activity and carboxylic acid utilization capacity in soil[21]. Critically, vermicompost provides superior sustained P supply capacity compared to mineral fertilizers. In the tomato-wheat rotation system, single superphosphate-amended soils exhibited a significantly greater reduction in bioavailable-P content than vermicompost-treated soils[22]. Consequently, vermicompost is often applied to mobilize legacy P and enhance both P bioavailability and crop P-use efficiency[23].

There are several mechanisms through which vermicompost enhances soil-P bioavailability. First, earthworms have selective feeding behavior[24] and the microorganisms within their gut mobilize P, resulting in greater concentrations of total and bioavailable P in vermicompost than in the surrounding soil[25–31]. For example, a meta-analysis revealed that the concentration of bioavailable P in vermicompost is 84% higher than that in surrounding soil[32], indicating significant implications for promoting plant growth and enhancing crop yield[16,33]. Second, vermicompost can increase the release of dissolved inorganic P by altering soil pH and reducing the active surface area available for P sorption, thus improving P bioavailability[28,34]. Third, vermicompost contains phosphatases[35–38] that mineralize organic P, releasing inorganic P that can be taken up by plants. These mechanisms are widely recognized and have been summarized in several reviews[23,28,32].

With the advancement of molecular biological techniques, recent research has increasingly focused on the role of microorganisms in vermicompost in enhancing soil-P bioavailability. Alterations in the microbial community composition within earthworm intestines[39] and the presence of efficient P-solubilizing microorganisms in vermicompost[21,40] are critical factors contributing to enhanced P bioavailability in soil[41]. Although previous reviews have addressed the effects of earthworm activity on soil microbial communities and the P cycle[42,43], systematic summaries of the mobilization of sparingly-soluble P in soil following vermicompost application and the microbial mechanisms involved remain lacking. In addition, a research framework specifically aimed at enhancing legacy-P utilization through microorganisms in vermicompost is yet to be developed.

This review examines the effects of vermicompost on soil-P bioavailability and explores the underlying microbial mechanisms. The specific objectives are: (1) to review the key microbial mechanisms through which vermicompost application enhances soil-P bioavailability and (2) to identify knowledge gaps and to propose future research directions.

2 Potential microbial mechanisms of soil-P mobilization after vermicompost application

The application of vermicompost to soil enhances P bioavailability via three primary mechanisms: (1) the secretion of P-solubilizing compounds by microorganisms that dissolve inorganic P, (2) the release of phosphatases that mineralize organic P, and (3) microbial cell lysis that releases bioavailable P. These processes are further affected by the altered biotic and abiotic conditions resulting from vermicompost application (Fig. 1).

2.1 Microbial dissolution of inorganic P following vermicompost application

The microbial dissolution of inorganic P in soil occurs through several mechanisms. These includes the direct release of protons (H^+) that dissolve sparingly-soluble P minerals, the secretion of carboxylates and siderophores that exchange with metal-bound inorganic P. These processes are impacted by a series of interconnected mechanisms (Fig. 1).

Following the application of vermicompost, P-solubilizing compounds in the soil originate primarily from two sources (Fig. 1). First, earthworm gut harbors a variety of P-solubilizing microorganisms[44,45]. When these microorganisms are introduced into soil, they can release protons[46] and carboxylates, further enhancing the bioavailability of soil inorganic P. The examples provided[22,47,48] are excellent for illustrating the diversity of P-solubilizing microorganisms. Pathma and Sakthivel[47] isolated 52 strains of P-solubilizing bacteria from vermicompost made from rice straw and sheep manure, and Parastesh et al.[22] isolated 18 bacterial strains capable of dissolving calcium phosphate from vermicompost produced from cow manure and sycamore leaf litter. Mejía-Guerra et al.[48] identified 28 P-solubilizing bacterial strains in vermicompost derived from tea leaves, predominantly in genera such as *Acinetobacter, Bacillus, Kocuria, Leptothrix, Microbacterium, Micrococcus, Pantoea, Pseudomonas, Rahnella, Serratia* and *Streptomyces*. Bhattacharya et al.[49] isolated 30 P-solubilizing fungal strains from *Eisenia fetida* vermicompost, with *Aspergillus nidulans* V1 being the most efficient, capable of dissolving 13% to 36% of four P-containing minerals after just three days of incubation. *Lichteimia corymbifera* is another fungal species with strong P-solubilizing abilities[48].

Second, vermicompost has a substantial concentration of carboxylates, which, upon incorporation into soil, facilitate the dissolution of inorganic P. Fourier-transform infrared spectroscopy and ^{13}C-CP MAS NMR analyses have confirmed

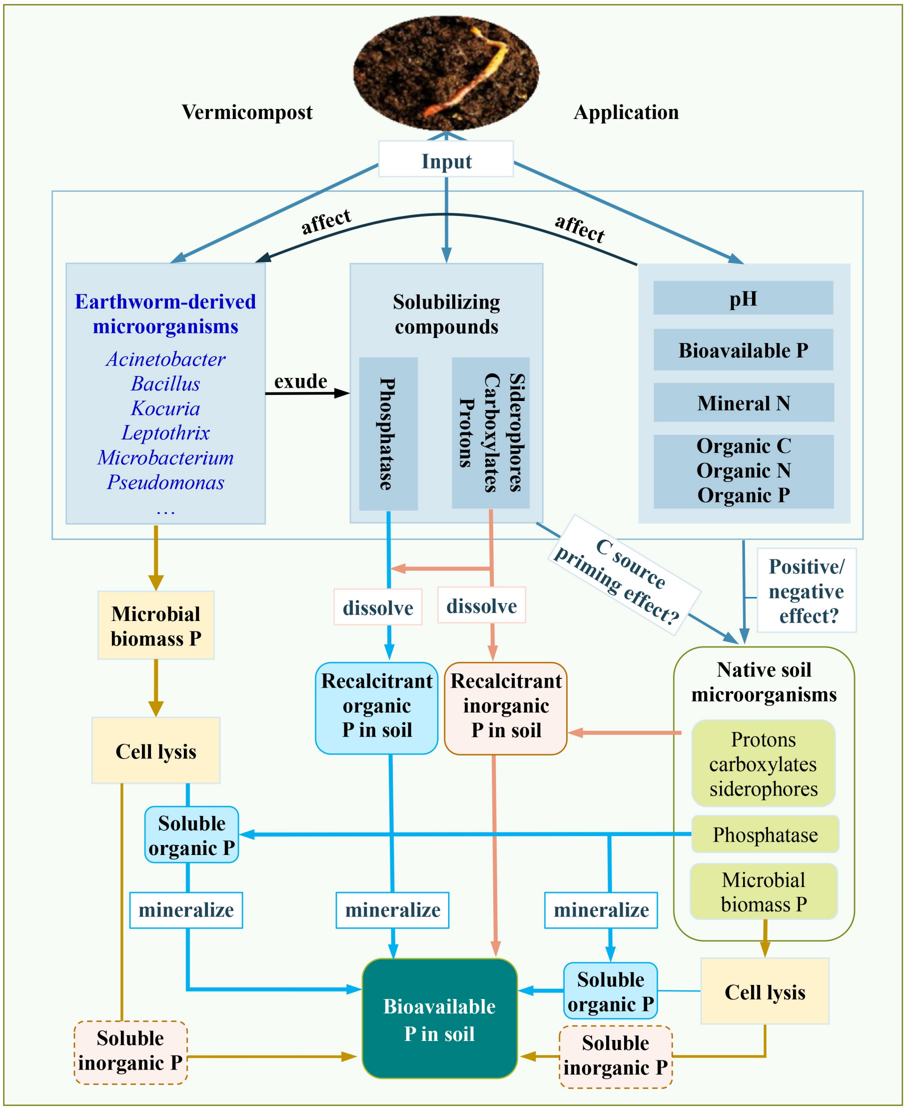

Fig. 1 Possible microbial mechanisms of soil phosphorus (P) mobilization after vermicompost application.

the presence of abundant carboxylates in vermicompost[50,51]. The degradation of macromolecular organic matter by earthworms and their gut microorganisms during the composting process increases the carboxylate concentration in vermicompost[50]. However, few studies have reported the chemical nature of these carboxylates and it remains unclear how earthworm species and composting substrates influence the quantity and composition of these compounds.

Although the precise contributions of vermicompost-derived versus microorganism-derived carboxylates are not fully understood, the rapid increase in bioavailable soil P after vermicompost application can be attributed to the carboxylates in vermicompost. In the long-term, however, microbial-released carboxylates are expected to be more significant in the dissolution of inorganic P. This is because carboxylates are rapidly degraded[52]; vermicompost-derived carboxylates in soil likely exist for a relatively short time, however, microorganisms can continue to release carboxylates.

Microorganisms in vermicompost can release siderophores[22,47,48,53], which can mobilize iron-bound P into bioavailable P through ligand exchange[54]. The release of siderophores by microorganisms in vermicompost thus represents another potential pathway for enhancing soil P-bioavailability.

The microbial dissolution of inorganic P can be influenced by changes in soil properties induced by vermicompost application (Fig. 1). Following the addition of vermicompost, bioavailable soil P, organic carbon (C) and nitrogen (N) concentrations typically increase[32]. The increase in bioavailable P can reduce the need for microbial release of carboxylates to dissolve P, and the increased organic C and N concentrations provide an energy and N source for microorganisms[55,56], potentially enhancing microbial activity yet immobilizing P in microbial biomass. Whether these changes exert a positive or negative impact on microbial P solubilization requires further investigation.

Given that bacterial communities and their functions are highly sensitive to pH[26,57] and vermicompost often differs in pH from the resident soil, its addition can significantly modify soil pH[29], thereby reshaping the microenvironment for both earthworm-associated and indigenous microorganisms. Several studies have shown that soil pH strongly influences P-mobilizing bacterial communities having *pqqC* genes[58–60], which serves as a widely recognized molecular marker for identifying microorganisms capable of solubilizing inorganic P. Deng et al.[61] further reported that elevated soil pH promotes the activity of a small group of *pqqC*-possessing bacteria, particularly *Burkholderia*, *Variovorax*, *Bradyrhizobium* and *Leptothrix*, which are key in reducing mineral-occluded and chelated inorganic-P fractions. Despite these insights, the specific effects of pH alterations induced by vermicompost application on the composition, diversity, and P-solubilizing activity of soil microbial communities remain poorly understood. Further studies are required to elucidate how vermicompost-mediated pH shifts regulate P-mobilizing microorganisms and, consequently, influence soil-P dynamics.

In alkaline soils, inorganic legacy P is typically bound to calcium (Ca^{2+}), whereas in acidic soils legacy P is predominantly bound to iron (Fe^{3+}) and aluminum (Al^{3+}) (hydr)oxides[62,63]. Therefore, in alkaline soils, proton-mediated dissolution of inorganic P can be the dominant process by which microbes increase the solubilization of legacy P whereas carboxylate-mediated ligand exchange and other dissolution processes are likely to be more prevalent in acidic soils. The relative contribution of protons and carboxylates to the dissolution of legacy inorganic P depends on the strength of soil-P sorption[64]. Under conditions of medium to high adsorption strength of minerals, carboxylate dissolution is more significant, whereas proton-mediated acidification becomes more so under low to medium sorption strength.

2.2 Organic-P mineralization following vermicompost application

The secretion of phosphatases by vermicompost-associated microorganisms is a crucial mechanism influencing soil-P bioavailability (Fig. 1). Many studies have demonstrated that the activity of acid and alkaline phosphatases is greater in vermicompost than in bulk soil[35,36,57,65–67]. Both pot and field experiments have shown that vermicompost application significantly increases soil phosphatase activity[68–73]. In addition, vermicompost application was found to sustain elevated alkaline phosphatase activity over extended periods. In tomato-cultivated soils amended with vermicompost, alkaline phosphatase activity increased from 326 ± 2.3 to 609 ± 23.7 $\mu g \cdot h^{-1} \cdot g^{-1}$ PNP after 100 d, and further rose to 804 ± 198 $\mu g \cdot h^{-1} \cdot g^{-1}$ PNP following an additional 90-d wheat rotation[22]. Although the individual contribution of vermicompost, vermicompost-derived microorganisms and resident soil microorganisms to phosphatase activity remains unclear, it is plausible that vermicompost-derived phosphatases introduced into the soil are rapidly deactivated by protease degradation[74,75]. Phosphatases adsorbed onto soil minerals can retain their activity over extended periods. However, their ability to hydrolyze organic P is highly dependent on specific mineral surfaces that effectively concentrate both the enzymes and organic-P substrates[76]. Consequently, over longer periods, the contributions of vermicompost-derived microorganisms and resident soil microorganisms to phosphatase activity can become more pronounced, leading to a greater impact on soil-P bioavailability.

The concentrations of C and N in vermicompost can also influence microbial secretion of phosphatases (Fig. 1). Several studies have reported a significant positive correlation between the C:N ratio in composting substrates or vermicompost and phosphatase activity[65,74,77,78]. For example, adding glucose to aged vermicompost significantly increased both microbial biomass and enzyme activity[75]. In contrast, a field trial revealed that 5 years of continuous vermicompost application (2.4 $t \cdot ha^{-1} \cdot yr^{-1}$) did not significantly increase soil phosphatase activity whereas treatments with 10-fold the amount of organic fertilizer resulted in a significant increase in phosphatase activity[79]. This highlights the role of vermicompost C and N concentrations, as well as their ratio, in influencing microbial mineralization of organic P.

The bioavailable P in vermicompost can influence the secretion of phosphatases by microorganisms (Fig. 1). Controlled experiments have shown that the addition of bioavailable P inhibits the secretion of phosphatases[80,81]. In the early stages after the addition of vermicompost, the high bioavailable-P concentration can inhibit microbial phosphatase synthesis and activity. However, as bioavailable-P concentrations decrease[82], microbial phosphatase secretion and organic-P mineralization can increase. The increase in soil mineral N concentration from vermicompost can also promote microbial mineralization of organic P. According to microbial stoichiometric theory[83], an increase in bioavailable N concentration can lead to a higher microbial demand for bioavailable P, which would induce phosphatase secretion[84], enhancing the mineralization of organic P.

Another important factor influencing microbial mineralization of soil organic P is carboxylates. Although some studies have indicated that phosphatases can directly hydrolyze organic P on soil particle surfaces[76,85], while others proposed a two-step mechanism for soil organic-P mineralization. The first step involves carboxylates forming organic-metal complexes with polyvalent metals such as Ca, Al and Fe, releasing organic P into the soil solution. The second step involves extracellular phosphatases catalyzing the hydrolysis of organic P in the soil solution, releasing soluble inorganic P[86,87]. Therefore, the extent of organic-P mineralization by microorganisms might also depend on the dissolution capabilities of carboxylates and siderophores, as discussed above. Vermicompost-derived microorganisms, which can secrete both carboxylates and phosphatases, are likely key participants in this process.

2.3 Microbial cell lysis following vermicompost application contributes to soil-P bioavailability

After application of vermicompost, microbial death and cell lysis can release dissolved P into the soil solution, thereby enhancing soil-P bioavailability (Fig. 1). The released dissolved P includes both inorganic and organic forms of P[88]. Although inorganic P is immediately available for uptake by plants and microorganisms, dissolved organic P requires prior hydrolysis by phosphatases to release dissolved inorganic P for plant uptake. Numerous studies have demonstrated that the application of vermicompost to soil significantly increases both the number of soil microorganisms[21,22,40,67,89] and microbial biomass[68,71,74,90–92]. This increase is partly due to the direct introduction of microorganisms from vermicompost into the soil[93,94] and partly due to the added mineral N, organic C and P, which promote the growth and activity of resident soil microbial populations[95,96]. In addition, substances such as carboxylates and phosphatases in vermicompost serve as high-quality C and N sources for soil microorganisms, potentially inducing priming effects[97,98] and leading to further increases in microbial abundance and activity.

Although there is some variation, soil bacteria typically have a higher P concentration (18 ± 4 to 23 ± 6 g·kg^{-1} P freeze-dried material) than fungi (7.6 ± 1.9 to 9.5 ± 3.2 g·kg^{-1} P freeze-dried material)[99,100]. The proportion of soluble inorganic P in fungi (31% ± 28% to 39% ± 15%) is higher than that in bacteria (13% ± 12% to 27% ± 18%) whereas the P in bacterial biomass is primarily organic P (72% ± 18% to 84% ± 12%). Microbial biomass P, although constituting a small fraction (< 5%) of total soil P in agricultural systems[83,101], has a high turnover rate[102]. In some natural ecosystems, microbial biomass P is even a major biological P pool[103,104]. Turner et al.[88] demonstrated that P released from lysed bacterial cells accounted for about 88% of the increase in water-extractable P following soil drying and Achat et al.[105] similarly observed that microbial death under desiccation elevated inorganic-P concentrations in organic matter-rich soils. Although no studies have provided a quantification of the contribution of vermicompost-derived microbial cell lysis to soil-P bioavailability, those findings collectively suggest that an increase in soil microbial biomass following vermicompost application could substantively contribute to enhancing P availability. Nevertheless, this potential mechanism remains poorly understood, and further empirical studies are needed to evaluate its quantitative significance in soil-P cycling.

3 Overview, research gaps and perspectives

3.1 Overview

This paper has reviewed the primary microbial mechanisms by which vermicompost application mobilizes legacy P in agricultural soil and thus affects bioavailable soil P. First, vermicompost-derived microorganisms can secrete P-solubilizing substances, including protons, siderophores and carboxylates, that dissolve inorganic soil P. Second, these microorganisms secrete phosphatases that mineralize organic P. Notably, the mineralization of organic P by phosphatases can be influenced by the solubilization of stable organic P through substances like siderophores and carboxylates. Additionally, resident soil microorganisms can also be stimulated to contribute to the above P-mobilizing processes following the input of vermicompost-derived organic matter. Finally, this review has highlighted a previously insufficiently-examined mechanism: microbial cell lysis, which releases dissolved P and significantly contributing to the formation of the bioavailable-P pool. The occurrence of these mechanisms is influenced by changes in soil physical and chemical properties following vermicompost application, including pH, bioavailable-P concentration, and the concentrations of mineral N, organic C, N and P (Fig. 1). Amid the global P fertilizer crisis and the growing accumulation of legacy P in soils resulting from years of repeated fertilizer application[106], elucidating these processes is crucial for improving crop utilization of soil legacy P. Such understanding will contribute to reducing P fertilizer dependency in agricultural production and mitigating P loading in downstream aquatic ecosystems.

3.2 Research gaps and perspectives

3.2.1 Identifying and harnessing highly efficient P-solubilizing microorganisms derived from vermicompost

To enhance soil-P bioavailability in croplands through the use of vermicompost, future research should focus on identifying and harnessing highly efficient P-solubilizing microorganisms derived from vermicompost for sustainable agricultural applications. Although numerous individual P-solubilizing strains have been isolated, microbial communities as functional consortia often outperform single strains due to their greater adaptability, metabolic flexibility and resilience under variable environmental conditions[107]. However, the diversity and abundance of P-solubilizing microorganisms in vermicompost remain insufficiently characterized[49]. Also, most previous studies have concentrated on vermicompost effects on genes encoding N-cycling enzymes, but research on functional genes involved in P cycling is still limited[44]. Notably, even when vermicompost from the same earthworm species is applied to different soils, a core microbial community tends to persist[108], yet it remains unclear whether a distinct core community specializing in P solubilization exists.

Emerging approaches such as metagenomics and microbiome-wide association studies (MWAS)[109,110] offer promising ways to uncover efficient P-solubilizing microorganisms within vermicompost-derived communities and to link them with functional genes encoding P-cycling enzymes (Fig. 2). Shotgun metagenomics allows high-resolution profiling of microbial taxa and their functional genes involved in P solubilization and cycling. Annotation of metagenomic reads against curated databases (e.g., KEGG[111], eggNOG[112] and MetaCyc[113]) enables identification of genes encoding key P-cycling enzymes, such as *phoD*, *phoA*, *ppx*, *gcd* and *pqqC*, as well as genes associated with the biosynthesis of P-solubilizing compounds, including organic acids, siderophores and exopolysaccharides. Quantitative analysis of these genes across microbial populations can reveal taxa that significantly contribute to P mobilization. MWAS further complements this approach by statistically linking microbial taxa, gene abundances, or metabolic pathways with experimentally measured P-solubilization traits, such as soluble phosphate release, phosphatase activity or shifts in soil-P fractions. Integrating metagenomics and MWAS with ecological network analyses can reveal co-occurrence patterns and synergistic interactions among taxa involved in P transformation. Collectively, these approaches enable the identification of keystone microorganisms and genetic determinants of P-solubilizing capacity, facilitating the development of targeted microbial inoculants or synthetic consortia for enhancing soil-P bioavailability in vermicompost-amended systems.

3.2.2 Explore the mechanisms of microbial interactions following vermicompost application

Understanding the mechanisms of microbial interactions following vermicompost application is essential for constructing complementary and efficient P-solubilizing microbial communities (Fig. 2). Vermicompost-derived microorganisms can interact dynamically with resident soil microbiota, jointly influencing community structure and ecosystem functioning[24,114,115]. For example, Liu et al.[116] reported that vermicompost amendments significantly altered bacterial and fungal communities by increasing the relative abundance of *Acidobacteria* while reducing *Proteobacteria* and *Chloroflexi*, and by enriching *Basidiomycota* and *Glomeromycota* while suppressing *Ascomycota*. Similarly, Zuo

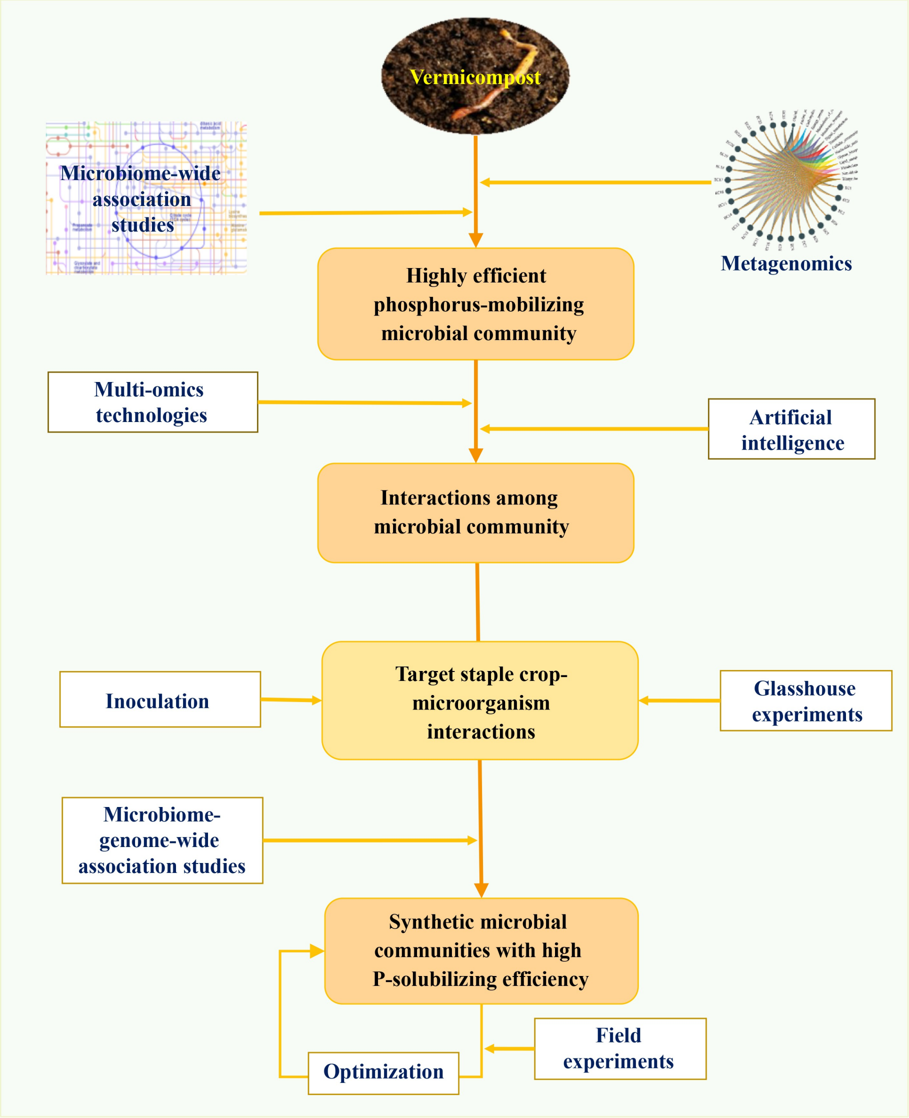

Fig. 2 Priority research directions of vermicompost-derived phosphorus-mobilizing microorganisms toward sustainable agriculture.

et al.[92] found that vermicompost-derived microbes increased the abundance of beneficial soil bacteria, particularly P-solubilizing groups, and de Celis et al.[117] indicated that these effects can persist for months. In addition, vermicompost-derived beneficial microorganisms can competitively exclude pathogenic fungi such as *Fusarium* spp. and *Penicillium* spp[26,89]. Zhao et al.[19] also found that vermicompost addition reduced the abundance of *Fusarium solani* and *Acrocalymma vagum* while maintaining a relatively high abundance of beneficial *Trichoderma* spp. Conversely, Sasse et al.[118] proposed that vermicompost-derived and resident microorganisms can have complementary rather than competitive resource utilization patterns, and Lipiec et al.[119] demonstrated that vermicompost microbial communities show higher metabolic activity toward C sources compared with resident soil microbiota. Despite this evidence, whether the relationship between vermicompost-derived and resident P-solubilizing microorganisms is primarily cooperative or competitive remains unresolved, as does the overall effect of these altered interactions on soil-P transformation.

Recent advances in multi-omics technologies, including metagenomics, transcriptomics, proteomics and metabolomics, combined with mathematical modeling[120] and artificial intelligence techniques[121,122], offer powerful means to elucidate these complex microbial interactions. Metagenomics can reveal community composition and functional potential, whereas transcriptomics identifies actively expressed genes and pathways mediating microbial communication and nutrient cycling. Proteomics links gene expression to enzymatic function, and metabolomics characterizes signaling and metabolic exchanges (e.g., organic acids, phytohormones and secondary metabolites) that shape microbial interactions and soil nutrient dynamics. Integration of these omics layers provides a systems-level perspective of microbial ecology that transcends single-level analyses. Meanwhile, mathematical modeling and artificial intelligence, through network inference, machine learning and predictive modeling, can synthesize multi-omics data to identify key interaction hubs, infer causal relationships and predict community responses to environmental change. Together, these approaches promise to unravel the mechanistic basis of microbial cooperation and competition in vermicompost-amended soils, thereby advancing the design of data-driven management strategies for soil health and sustainable nutrient cycling.

3.2.3 Developing synthetic microbial communities with high P-solubilizing efficiency from vermicompost-derived microorganisms

Developing synthetic microbial communities with high P-solubilizing efficiency from vermicompost-derived microorganisms represents a crucial step toward translating fundamental research into practical agricultural applications (Fig. 2). Given that rhizosphere processes can vary widely between crops and strongly influence soil microbial community structure and function[107,117,118,120], the effectiveness of vermicompost-derived P-solubilizing communities most likely depends on crop species and soil conditions[121]. Synthetic microbial communities, by contrast, offer advantages of simplicity, controllability, reproducibility and functional specificity, enabling targeted enhancement of plant nutrient acquisition[122,123].

Building upon insights given above, the development of such communities should begin with the systematic screening of vermicompost-derived microorganisms across soils differing in legacy P forms. Promising isolates should then be tested for their interactions with target crops using advanced tools such as microbiome-genome-wide association studies[107]. Once key functional strains are identified, synthetic microbial communities can be rationally assembled following established frameworks (e.g., Jing et al.[124]) and optimized for synergistic performance. Field trials under real-world agricultural conditions should then by used to evaluate their effectiveness in improving P bioavailability, crop productivity and soil health, with iterative refinement based on observed outcomes. Ultimately, vermicompost-based synthetic microbial communities could form the foundation for scalable and sustainable biofertilization strategies that promote efficient P utilization and long-term soil fertility.

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Compliance with ethics guidelines

Hong-Qiu Du, Hongyang Sun, Jun Zhou, Hongtao Zhong, Xiao-Long Li, Shuang Wu, Fei Peng, Benjamin L. Turner, and Hans Lambers declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

REFERENCES

1. Hawkesford M, Horst W, Kichey T, Lambers H, Schjoerring J, Møller I S, White P. Functions of macronutrients. In: Marschner P, ed. Marschner’s Mineral Nutrition of Plants (Third Edition). Amsterdam: *Elsevier*, 2012, 135–189
2. Kvakić M, Pellerin S, Ciais P, Achat D L, Augusto L, Denoroy P, Gerber J S, Goll D, Mollier A, Mueller N D, Wang X, Ringeval B. Quantifying the limitation to world cereal production due to soil phosphorus status. *Global Biogeochemical Cycles*, 2018, **32**(1): 143–157
3. Lun F, Liu J, Ciais P, Nesme T, Chang J, Wang R, Goll D, Sardans J, Peñuelas J, Obersteiner M. Global and regional phosphorus budgets in agricultural systems and their implications for phosphorus-use efficiency. *Earth System Science Data*, 2018, **10**(1): 1–18
4. Chen G, Xiao L, Yue K, Wang Y, Wang S, Zhu Y, Kai L. Optimizing phosphate application to improve soil quality and reduce phosphorus loss in rice-wheat rotation. *Agriculture, Ecosystems & Environment*, 2025, **378**: 109310
5. Demay J, Ringeval B, Pellerin S, Nesme T. Half of global agricultural soil phosphorus fertility derived from anthropogenic sources. *Nature Geoscience*, 2023, **16**(1): 69–74
6. Nedelciu C E, Ragnarsdottir K V, Schlyter P, Stjernquist I. Global phosphorus supply chain dynamics: assessing regional impact to 2050. *Global Food Security*, 2020, **26**: 100426
7. Turner B L, Kim P J. Terminology for residual and legacy phosphorus. *Plant and Soil*, 2024, **501**(1): 237–239
8. Zhang L, Chen J, Chu G. Legacy phosphorus in calcareous soil under 33 years of P fertilizer application: implications for efficient P management in agriculture. *Soil Use and Management*, 2022, **38**(3): 1380–1393
9. Alewell C, Ringeval B, Ballabio C, Robinson D A, Panagos P, Borrelli P. Global phosphorus shortage will be aggravated by soil erosion. *Nature Communications*, 2020, **11**(1–2): 4546
10. Sharpley A, Jarvie H P, Buda A, May L, Spears B, Kleinman P. Phosphorus legacy: overcoming the effects of past management practices to mitigate future water quality impairment. *Journal of Environmental Quality*, 2013, **42**(5): 1308–1326
11. Zhao L, Fu D, Li T, Yuan X, Wang S, Liu C, Duan C. Temporal variations of N and P losses via surface runoff from Chinese farmland after fertilisation. *Soil & Tillage Research*, 2025, **246**: 106338
12. Helfenstein J, Ringeval B, Tamburini F, Mulder V L, Goll D S, He X, Alblas E, Wang Y, Mollier A, Frossard E. Understanding soil phosphorus cycling for sustainable development: a review. *One Earth*, 2024, **7**(10): 1727–1740
13. McDowell R W, Haygarth P M. Soil phosphorus stocks could prolong global reserves and improve water quality. *Nature Food*, 2025, **6**(1): 31–35
14. Stackpoole S M, Stets E G, Sprague L A. Variable impacts of contemporary versus legacy agricultural phosphorus on US river water quality. *Proceedings of the National Academy of Sciences of the United States of America*, 2019, **116**(41): 20562–20567
15. Ferron L M E, Van Groenigen J W, Koopmans G F, Vidal A. Can earthworms and root traits improve plant struvite-P uptake A field mesocosm study. *Agriculture, Ecosystems & Environment*, 2025, **377**: 109255
16. Ratsiatosika O, Trap J, Herinasandratra V, Razafimbelo T, Bernard L, Blanchart E. Earthworms enhance the performance of organic amendments in improving rice growth and nutrition in poor ferralsols. *Soil Biology & Biochemistry*, 2024, **195**: 109477
17. Pelosi C, Taschen E, Redecker D, Blouin M. Earthworms as conveyors of mycorrhizal fungi in soils. *Soil Biology & Biochemistry*, 2024, **189**: 109283
18. Chowdhury R, Barman S, Choudhury M, Kim K H, Bhattacharya S S. Earthworm modifies microbial community and functional genes for lignocellulosic waste valorization: isolating plant-growth-promoting bacteria via next generation sequencing. *International Biodeterioration & Biodegradation*, 2024, **193**: 105854
19. Zhao H T, Li T P, Zhang Y, Hu J, Bai Y C, Shan Y H, Ke F. Effects of vermicompost amendment as a basal fertilizer on soil properties and cucumber yield and quality under continuous cropping conditions in a greenhouse. *Journal of Soils and Sediments*, 2017, **17**(12): 2718–2730
20. Nieto-Cantero J, García-López A M, Recena R, Quintero J M, Delgado A. Recycling manure as vermicompost: assessing phosphorus fertilizer efficiency and effects on soil health under different soil management. *Journal of Soil Science and Plant Nutrition*, 2025, **25**(2): 5046–5061
21. Zhao F, Zhang Y, Li Z, Shi J, Zhang G, Zhang H, Yang L. Vermicompost improves microbial functions of soil with continuous tomato cropping in a greenhouse. *Journal of Soils and Sediments*, 2020, **20**(1): 380–391
22. Parastesh F, Ali Alikhani H, Etesami H. Vermicompost enriched with phosphate-solubilizing bacteria provides plant with enough phosphorus in a sequential cropping under calcareous soil conditions. *Journal of Cleaner Production*, 2019, **221**: 27–37
23. Vidal A, Blouin M, Lubbers I, Capowiez Y, Sanchez-Hernandez J C, Calogiuri T, van Groenigen J W. The role of earthworms in agronomy: consensus, novel insights and remaining challenges. In: Sparks D L, ed. Advances in Agronomy. Amsterdam: *Elsevier*, 2023, 1–78

24. Vos H M J, Koopmans G F, Beezemer L, de Goede R G M, Hiemstra T, van Groenigen J W. Large variations in readily-available phosphorus in casts of eight earthworm species are linked to cast properties. *Soil Biology & Biochemistry*, 2019, **138**: 107583
25. Arumugam K, Renganathan S, Babalola O O, Muthunarayanan V. Investigation on paper cup waste degradation by bacterial consortium and *Eudrillus eugeinea* through vermicomposting. *Waste Management*, 2018, **74**: 185–193
26. Iordache M. Chemical composition of earthworm casts as a tool in understanding the earthworm contribution to ecosystem sustainability—A review. *Plant, Soil and Environment*, 2023, **69**(6): 247–268
27. Jouquet P, Bottinelli N, Podwojewski P, Hallaire V, Tran Duc T. Chemical and physical properties of earthworm casts as compared to bulk soil under a range of different land-use systems in Vietnam. *Geoderma*, 2008, **146**(1–2): 231–238
28. Ros M B H, Hiemstra T, van Groenigen J W, Chareesri A, Koopmans G F. Exploring the pathways of earthworm-induced phosphorus availability. *Geoderma*, 2017, **303**: 99–109
29. Trap J, Blanchart E, Ratsiatosika O, Razafindrakoto M, Becquer T, Andriamananjara A, Morel C. Effects of the earthworm *Pontoscolex corethrurus* on rice P nutrition and plant-available soil P in a tropical Ferralsol. *Applied Soil Ecology*, 2021, **160**: 103867
30. Walia S S, Kaur T. Earthworms and vermicomposting. In: Walia S S, Kaur T, eds. Earthworms and Vermicomposting. Singapore: *Springer Nature Singapore*, 2024, 1–5
31. Wu D, Du E, Eisenhauer N, Mathieu J, Chu C. Global engineering effects of soil invertebrates on ecosystem functions. *Nature*, 2025, **640**(8057): 120–129
32. Van Groenigen J W, Van Groenigen K J, Koopmans G F, Stokkermans L, Vos H M J, Lubbers I M. How fertile are earthworm casts? A meta-analysis. *Geoderma*, 2019, **338**: 525–535
33. Vos H M J, Koopmans G F, Ferron L M E, Oenema O, van Groenigen J W. Do earthworms increase grass biomass production and phosphorus uptake under field conditions. *Applied Soil Ecology*, 2022, **180**: 104598
34. Vos H M J, Hiemstra T, Prado Lopez M, van Groenigen J W, Voegelin A, Mangold S, Koopmans G F. Earthworms affect reactive surface area and thereby phosphate solubility in iron-(hydr)oxide dominated soils. *Geoderma*, 2022, **428**: 116212
35. Chiba A, Vitow N, Baum C, Zacher A, Kahle P, Leinweber P, Schloter M, Schulz S. Earthworm activities change phosphorus mobilization and uptake strategies in deep soil layers. *Applied Soil Ecology*, 2024, **193**: 105168
36. Jiang D, Wu C, Wang S, Zhang Y, Chen Z, Jiang N, Zhang Y, Xie H. Vermicompost derived from mushroom residues improves soil C/P cycling, bacterial community, and fungal abundance. *Global Change Biology. Bioenergy*, 2023, **15**(12): 1437–1449
37. Vos H M J, Zweig R, Margenot A J, Koopmans G F, van Groenigen J W. Phosphatase activity in the drilosphere and its link to phosphorus uptake by grass. *Geoderma*, 2023, **439**: 116690
38. Yang Z, Luo Y, Chen H, Zhang Y, Wu S, Yang M, Jia J, Zhou C, Zhou Y. Vermicompost addition improved soil aggregate stability, enzyme activity, and soil available nutrients. *Journal of Soil Science and Plant Nutrition*, 2024, **24**(4): 6760–6774
39. Kliszcz A, Kuźniar A, Wolińska A, Jurczyk S, Kruczyńska A, Puła J. Future frontiers of agroecosystem management: shifts in microbial community after passage through the gut of earthworms reveals enhanced abundance of cereal endophytes. *Applied Soil Ecology*, 2024, **203**: 105666
40. Hodson M E, Brailey-Crane P, Burn W L, Harper A L, Hartley S E, Helgason T, Walker H F. Enhanced plant growth in the presence of earthworms correlates with changes in soil microbiota but not nutrient availability. *Geoderma*, 2023, **433**: 116426
41. Raymond N S, Gómez-Muñoz B, van der Bom F J T, Nybroe O, Jensen L S, Müller-Stöver D S, Oberson A, Richardson A E. Phosphate-solubilising microorganisms for improved crop productivity: a critical assessment. *New Phytologist*, 2021, **229**(3): 1268–1277
42. Medina-Sauza R M, Álvarez-Jiménez M, Delhal A, Reverchon F, Blouin M, Guerrero-Analco J A, Cerdán C R, Guevara R, Villain L, Barois I. Earthworms building up soil microbiota, a review. *Frontiers in Environmental Science*, 2019, **7**: 81
43. Kooch Y, Kuzyakov Y. Earthworms for soil organic matter mineralization and carbon sequestration. In: Kooch Y, Kuzyakov Y, eds. Earthworms and Ecological Processes. Cham: *Springer Nature Switzerland*, 2024, 373–394
44. Bhakta J N, Sarkar B, Brahma P. Isolation and characterization of potential phosphate solubilizing bacteria from earthworm (*Metaphire posthuma*) for applying as biofertilizer. *Organic Agriculture*, 2022, **12**(3): 431–444
45. Biswas J K, Banerjee A, Rai M, Naidu R, Biswas B, Vithanage M, Dash M C, Sarkar S K, Meers E. Potential application of selected metal resistant phosphate solubilizing bacteria isolated from the gut of earthworm (*Metaphire posthuma*) in plant growth promotion. *Geoderma*, 2018, **330**: 117–124
46. Prabhu N, Borkar S, Garg S. Phosphate solubilization by microorganisms: overview, mechanisms, applications and advances. In: Meena S N, Naik M M, eds. Advances in Biological Science Research. Amsterdam: *Elsevier*, 2019, 161–176
47. Pathma J, Sakthivel N. Molecular and functional characterization of bacteria isolated from straw and goat manure based vermicompost. *Applied Soil Ecology*, 2013, **70**:

33–47

48. Mejía-Guerra P A, Salas-Sanjuán M C, Martínez-Gallardo M R, Jurado M M, Estrella-González M J, López-González J A, Suárez-Estrella F, López M J. Microbial biofertilizers and biopesticides from vermicompost tea and rhizosphere of organic soilless melon crop: *in vitro* assessment. *Biocatalysis and Agricultural Biotechnology*, 2025, **63**: 103453
49. Bhattacharya S S, Barman S, Ghosh R, Duary R K, Goswami L, Mandal N C. Phosphate solubilizing ability of *Emericella nidulans* strain V1 isolated from vermicompost. *Indian Journal of Experimental Biology*, 2013, **51**(10): 840–848
50. García A C, Tavares O C H, Balmori D M, dos Santos Almeida V, Canellas L P, García-Mina J M, Louro Berbara R L. Structure-function relationship of vermicompost humic fractions for use in agriculture. *Journal of Soils and Sediments*, 2018, **18**(4): 1365–1375
51. Sengupta S, Bhattacharyya K, Mandal J, Chattopadhyay A P. Complexation, retention and release pattern of arsenic from humic/fulvic acid extracted from zinc and iron enriched vermicompost. *Journal of Environmental Management*, 2022, **318**: 115531
52. Lambers H, Hayes P E, Laliberté E, Oliveira R S, Turner B L. Leaf manganese accumulation and phosphorus-acquisition efficiency. *Trends in Plant Science*, 2015, **20**(2): 83–90
53. Gopalakrishnan S, Vadlamudi S, Bandikinda P, Sathya A, Vijayabharathi R, Rupela O, Kudapa H, Katta K, Varshney R K. Evaluation of *Streptomyces* strains isolated from herbal vermicompost for their plant growth-promotion traits in rice. *Microbiological Research*, 2014, **169**(1): 40–48
54. Vassilev N, Vassileva M, Nikolaeva I. Simultaneous P-solubilizing and biocontrol activity of microorganisms: potentials and future trends. *Applied Microbiology and Biotechnology*, 2006, **71**(2): 137–144
55. Musarrat J, Khan M S. Factors affecting phosphate-solubilizing activity of microbes: current status. In: Khan M S, Zaidi A, Musarrat J, eds. Phosphate Solubilizing Microorganisms. Cham: *Springer International Publishing*, 2014, 63–85
56. Scervino J M, Papinutti V L, Godoy M S, Rodriguez M A, Della Monica I, Recchi M, Pettinari M J, Godeas A M. Medium pH, carbon and nitrogen concentrations modulate the phosphate solubilization efficiency of *Penicillium* purpurogenum through organic acid production. *Journal of Applied Microbiology*, 2011, **110**(5): 1215–1223
57. Hoeffner K, Santonja M, Cluzeau D, Monard C. Epi-anecic rather than strict-anecic earthworms enhance soil enzymatic activities. *Soil Biology & Biochemistry*, 2019, **132**: 93–100
58. Bi Q F, Li K J, Zheng B X, Liu X P, Li H Z, Jin B J, Ding K, Yang X R, Lin X Y, Zhu Y G. Partial replacement of inorganic phosphorus (P) by organic manure reshapes phosphate mobilizing bacterial community and promotes P bioavailability in a paddy soil. *Science of the Total Environment*, 2020, **703**: 134977
59. Shi W, Xing Y, Zhu Y, Gao N, Ying Y. Diverse responses of pqqC- and phoD-harbouring bacterial communities to variation in soil properties of Moso bamboo forests. *Microbial Biotechnology*, 2022, **15**(7): 2097–2111
60. Yang L, Du L, Li W, Wang R, Guo S. Divergent responses of phoD- and pqqC-harbouring bacterial communities across soil aggregates to long fertilization practices. *Soil & Tillage Research*, 2023, **228**: 105634
61. Deng P, Zhou Y, Chen W, Tang F, Wang Y. Microbial mechanisms for improved soil phosphorus mobilization in monoculture conifer plantations by mixing with broadleaved trees. *Journal of Environmental Management*, 2024, **359**: 120955
62. Solangi F, Zhu X, Khan S, Rais N, Majeed A, Sabir M A, Iqbal R, Ali S, Hafeez A, Ali B, Ercisli S, Kayabasi E T. The global dilemma of soil legacy phosphorus and its improvement strategies under recent changes in agro-ecosystem sustainability. *ACS Omega*, 2023, **8**(26): 23271–23282
63. Doydora S, Gatiboni L, Grieger K, Hesterberg D, Jones J L, McLamore E S, Peters R, Sozzani R, Van den Broeck L, Duckworth O W. Accessing legacy phosphorus in soils. *Soil Systems*, 2020, **4**(4): 74
64. Oburger E, Jones D L, Wenzel W W. Phosphorus saturation and pH differentially regulate the efficiency of organic acid anion-mediated P solubilization mechanisms in soil. *Plant and Soil*, 2011, **341**(1–2): 363–382
65. Buck C, Langmaack M, Schrader S. Nutrient content of earthworm casts influenced by different mulch types. *European Journal of Soil Biology*, 1999, **35**(1): 23–30
66. Satchell J E, Martin K. Phosphatase activity in earthworm faeces. *Soil Biology & Biochemistry*, 1984, **16**(2): 191–194
67. Tiwari S C, Tiwari B K, Mishra R R. Microbial populations, enzyme activities and nitrogen-phosphorus-potassium enrichment in earthworm casts and in the surrounding soil of a pineapple plantation. *Biology and Fertility of Soils*, 1989, **8**(2): 178–182
68. Lv M, Li J, Zhang W, Zhou B, Dai J, Zhang C. Microbial activity was greater in soils added with herb residue vermicompost than chemical fertilizer. *Soil Ecology Letters*, 2020, **2**(3): 209–219
69. Rashid M I, Shah G A, Iqbal Z, Shahzad K, Ali N, Rehan M, Alhakamy N A A, Klemeš J J. Nanobiochar reduces ammonia emission, increases nutrient mineralization from vermicompost, and improves maize productivity. *Journal of Cleaner Production*, 2023, **414**: 137694
70. Rezaei-Chiyaneh E, Amirnia R, Fotohi Chiyaneh S, Maggi F, Barin M. , Razavi B S. Improvement of dragonhead (*Dracocephalum moldavica* L.) yield quality through a coupled intercropping system and vermicompost application

along with maintenance of soil microbial activity. *Land Degradation & Development*, 2021, **32**(9): 2833–2848

71. Saha S, Mina B L, Gopinath K A, Kundu S, Gupta H S. Relative changes in phosphatase activities as influenced by source and application rate of organic composts in field crops. *Bioresource Technology*, 2008, **99**(6): 1750–1757
72. Srivastava P K, Gupta M, Upadhyay R K, Sharma S, Shikha, Singh N, Tewari S K, Singh B. Shikha, Singh N, Tewari S K, Singh B. Effects of combined application of vermicompost and mineral fertilizer on the growth of *Allium cepa* L. and soil fertility. *Journal of Plant Nutrition and Soil Science*, 2012, **175**(1): 101–107
73. Yang L, Zhao F, Chang Q, Li T, Li F. Effects of vermicomposts on tomato yield and quality and soil fertility in greenhouse under different soil water regimes. *Agricultural Water Management*, 2015, **160**: 98–105
74. da Silva L F, da Silva E F, Morais F M S, Portela J C, de Oliveira F H T, de Freitas D F, de Almeida Ferreira E, Gurgel M T, Pinheiro A M, Lima R B, Vasconcelos A A, de Sousa Antunes L F. Potential of vermicomposting with mixtures of animal manure and vegetable leaves in the development of *Eisenia foetida*, microbial biomass, and enzymatic activity under semi-arid conditions. *Journal of Environmental Management*, 2023, **330**: 117169
75. Aira M, Monroy F, Domínguez J. Ageing effects on nitrogen dynamics and enzyme activities in casts of *Aporrectodea caliginosa* (Lumbricidae). *Pedobiologia*, 2005, **49**(5): 467–473
76. Olsson R, Giesler R, Loring J S, Persson P. Enzymatic hydrolysis of organic phosphates adsorbed on mineral surfaces. *Environmental Science & Technology*, 2012, **46**(1): 285–291
77. Flegel M, Schrader S. Importance of food quality on selected enzyme activities in earthworm casts (*Dendrobaena Octaedra*, Lumbricidae). *Soil Biology & Biochemistry*, 2000, **32**(8-9): 1191–1196
78. Tejada M, Gómez I, Hernández T, García C. Utilization of vermicomposts in soil restoration: effects on soil biological properties. *Soil Science Society of America Journal*, 2010, **74**(2): 525–532
79. Albiach R, Canet R, Pomares F, Ingelmo F. Microbial biomass content and enzymatic activities after the application of organic amendments to a horticultural soil. *Bioresource Technology*, 2000, **75**(1): 43–48
80. DeForest J L, Smemo K A, Burke D J, Elliott H L, Becker J C. Soil microbial responses to elevated phosphorus and pH in acidic temperate deciduous forests. *Biogeochemistry*, 2012, **109**(1–3): 189–202
81. Xie X, Li H, Chen X, Lang M. Rhizosphere phosphatase hotspots: microbial-mediated P transformation mechanisms influenced by maize varieties and phosphorus addition. *Plant and Soil*, 2025, **512**(1–2): 1577–1593
82. Scheu S. Microbial activity and nutrient dynamics in earthworm casts (Lumbricidae). *Biology and Fertility of Soils*, 1987, **5**(3): 230–234
83. Cleveland C C, Liptzin D C. N: P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass. *Biogeochemistry*, 2007, **85**(3): 235–252
84. Margalef O, Sardans J, Maspons J, Molowny-Horas R, Fernández-Martínez M, Janssens I A, Richter A, Ciais P, Obersteiner M, Peñuelas J. The effect of global change on soil phosphatase activity. *Global Change Biology*, 2021, **27**(22): 5989–6003
85. Annaheim K E, Rufener C B, Frossard E, Bünemann E K. Hydrolysis of organic phosphorus in soil water suspensions after addition of phosphatase enzymes. *Biology and Fertility of Soils*, 2013, **49**(8): 1203–1213
86. Clarholm M, Skyllberg U, Rosling A. Organic acid induced release of nutrients from metal-stabilized soil organic matter—The unbutton model. *Soil Biology & Biochemistry*, 2015, **84**: 168–176
87. Gerke J. The acquisition of phosphate by higher plants: effect of carboxylate release by the roots. A critical review. *Journal of Plant Nutrition and Soil Science*, 2015, **178**(3): 351–364
88. Turner B L, Driessen J P, Haygarth P M, McKelvie I D. Potential contribution of lysed bacterial cells to phosphorus solubilisation in two rewetted Australian pasture soils. *Soil Biology & Biochemistry*, 2003, **35**(1): 187–189
89. Przemieniecki S W, Zapałowska A, Skwiercz A, Damszel M, Telesiński A, Sierota Z, Gorczyca A. An evaluation of selected chemical, biochemical, and biological parameters of soil enriched with vermicompost. *Environmental Science and Pollution Research International*, 2021, **28**(7): 8117–8127
90. Das D, Abbhishek K, Banik P, Swain D K. Comparative evaluation of changes in soil bio-chemical properties after application of traditional and enriched vermicompost. *Environmental Technology & Innovation*, 2022, **28**: 102956
91. Zhang F, Wang R, Yu W, Liang J, Liao X. Influences of a vermicompost application on the phosphorus transformation and microbial activity in a paddy soil. *Soil and Water Research*, 2020, **15**(4): 199–210
92. Zuo Y, Zhang J, Zhao R, Dai H, Zhang Z. Application of vermicompost improves strawberry growth and quality through increased photosynthesis rate, free radical scavenging and soil enzymatic activity. *Scientia Horticulturae*, 2018, **233**: 132–140
93. Hussain N, Das S, Goswami L, Das P, Sahariah B, Bhattacharya S S. Intensification of vermitechnology for kitchen vegetable waste and paddy straw employing earthworm consortium: assessment of maturity time, microbial community structure, and economic benefit. *Journal of Cleaner Production*, 2018, **182**: 414–426
94. Zhou Y, Li H, Guo W, Liu H, Cai M. The synergistic effect

between biofertility properties and biological activities in vermicomposting: a comparable study of pig manure. *Journal of Environmental Management*, 2022, **324**: 116280

95. Shi J, Gong J, Li X, Zhang Z, Zhang W, Li Y, Song L, Zhang S, Dong J, Baoyin T T. Phosphorus application promoted the sequestration of orthophosphate within soil microorganisms and regulated the soil solution P supply in a temperate grassland in northern China: a ^{31}P NMR study. *Soil & Tillage Research*, 2023, **227**: 105612
96. Aira M, Domínguez J. Earthworm effects without earthworms: inoculation of raw organic matter with worm-worked substrates alters microbial community functioning. *PLoS One*, 2011, **6**(1): e16354
97. Kuzyakov Y, Friedel J K, Stahr K. Review of mechanisms and quantification of priming effects. *Soil Biology & Biochemistry*, 2000, **32**(11-12): 1485–1498
98. Wang C, Kuzyakov Y. Soil organic matter priming: the pH effects. *Global Change Biology*, 2024, **30**(6): e17349
99. Bünemann E K, Smernik R J, Doolette A L, Marschner P, Stonor R, Wakelin S A, McNeill A M. Forms of phosphorus in bacteria and fungi isolated from two Australian soils. *Soil Biology & Biochemistry*, 2008, **40**(7): 1908–1915
100. Makarov M I, Haumaier L, Zech W, Marfenina O E, Lysak L V. Can 31P NMR spectroscopy be used to indicate the origins of soil organic phosphates. *Soil Biology & Biochemistry*, 2005, **37**(1): 15–25
101. Xu X, Thornton P E, Post W M. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography*, 2013, **22**(6): 737–749
102. Achat D L, Morel C, Bakker M R, Augusto L, Pellerin S, Gallet-Budynek A, Gonzalez M. Assessing turnover of microbial biomass phosphorus: combination of an isotopic dilution method with a mass balance model. *Soil Biology & Biochemistry*, 2010, **42**(12): 2231–2240
103. Turner B L, Lambers H, Condron L M, Cramer M D, Leake J R, Richardson A E, Smith S E. Soil microbial biomass and the fate of phosphorus during long-term ecosystem development. *Plant and Soil*, 2013, **367**(1–2): 225–234
104. Wang J, Wu Y, Zhou J, Bing H, Sun H, He Q, Li J, Wilcke W. Soil microbes become a major pool of biological phosphorus during the early stage of soil development with little evidence of competition for phosphorus with plants. *Plant and Soil*, 2020, **446**(1–2): 259–274
105. Achat D L, Augusto L, Gallet-Budynek A, Bakker M R. Drying-induced changes in phosphorus status of soils with contrasting soil organic matter contents—Implications for laboratory approaches. *Geoderma*, 2012, **187–188**: 41–48
106. Wasaki J. Low phosphorus tolerance of plants forming root clusters: can the specialized functions be used to resolve the phosphorus crisis. *Soil Science and Plant Nutrition*, 2025, **71**(6): 643–658
107. Xu H, Liu W, He Y, Zou D, Zhou J, Zhang J, Bai Y. Plant-root microbiota interactions in nutrient utilization. *Frontiers of Agricultural Science and Engineering*, 2025, **12**(1): 16–26
108. Aira M, Pérez-Losada M, Crandall K A, Domínguez J. Composition, structure and diversity of soil bacterial communities before, during and after transit through the gut of the earthworm *Aporrectodea caliginosa*. *Microorganisms*, 2022, **10**(5): 1025
109. Yang J, Schrader S, Tebbe C C. Legacy effects of earthworms on soil microbial abundance, diversity, and community dynamics. *Soil Biology & Biochemistry*, 2024, **190**: 109294
110. Matuszyńska A, Ebenhöh O, Zurbriggen M D, Ducat D C, Axmann I M. A new era of synthetic biology-microbial community design. *Synthetic Biology*, 2024, **9**(1): ysae011
111. Kanehisa M, Goto S. KEGG Kyoto encyclopedia of genes and genomes. *Nucleic Acids Research*, 2000, **28**(1): 27–30
112. Huerta-Cepas J, Szklarczyk D, Heller D, Hernández-Plaza A, Forslund S K, Cook H, Mende D R, Letunic I, Rattei T, Jensen L J, von Mering C, Bork P. eggNOG 5.0: a hierarchical, functionally and phylogenetically annotated orthology resource based on 5090 organisms and 2502 viruses. *Nucleic Acids Research*, 2019, **47**(D1): D309–D314
113. Caspi R, Billington R, Fulcher C A, Keseler I M, Kothari A, Krummenacker M, Latendresse M, Midford P E, Ong Q, Ong W K, Paley S, Subhraveti P, Karp P D. The MetaCyc database of metabolic pathways and enzymes. *Nucleic Acids Research*, 2018, **46**(D1): D633–D639
114. Wang X W, Sun Z, Jia H, Michel-Mata S, Angulo M T, Dai L, He X, Weiss S T, Liu Y Y. Identifying keystone species in microbial communities using deep learning. *Nature Ecology & Evolution*, 2024, **8**(1): 22–31
115. Wang X W, Wang T, Liu Y Y. Artificial intelligence for microbiology and microbiome research. arXiv, 2024: 2411.01098
116. Liu M, Wang C, Wang F, Xie Y. Maize (*Zea mays*) growth and nutrient uptake following integrated improvement of vermicompost and humic acid fertilizer on coastal saline soil. *Applied Soil Ecology*, 2019, **142**: 147–154
117. de Celis M, Fernández-Alonso M J, Belda I, García C, Ochoa-Hueso R, Palomino J, Singh B K, Yin Y, Wang J T, Abdala-Roberts L, Alfaro F D, Angulo-Pérez D, Arthikala M K, Corwin J, Duan G L, Hernandez-Lopez A, Nanjareddy K, Pasari B, Quijano-Medina T, Rivera D S, Shaaf S, Trivedi P, Yang Q, Zaady E, Zhu Y G, Delgado-Baquerizo M, Milla R, García-Palacios P. The abundant fraction of soil microbiomes regulates the rhizosphere function in crop wild progenitors. *Ecology Letters*, 2024, **27**(6): e14462
118. Sasse J, Martinoia E, Northen T. Feed your friends: do plant exudates shape the root microbiome. *Trends in Plant Science*, 2018, **23**(1): 25–41

119. Lipiec J, Frąc M, Brzezińska M, Turski M, Oszust K. Linking microbial enzymatic activities and functional diversity of soil around earthworm burrows and casts. *Frontiers in Microbiology*, 2016, **7**: 1361

120. Wei S, Jacquiod S, Philippot L, Blouin M, Sørensen S J. Spatial analysis of the root system coupled to microbial community inoculation shed light on rhizosphere bacterial community assembly. *Biology and Fertility of Soils*, 2021, **57**(7): 973–989

121. Jacquiod S, Nesme J, Ducourtieux C, Pimet E, Blouin M. Artificially selected rhizosphere microbiota modify plant growth in a soil-independent and species-dependent way. *Plant and Soil*, 2025, **510**(1–2): 641–660

122. Castrillo G, Teixeira P J P L, Paredes S H, Law T F, de Lorenzo L, Feltcher M E, Finkel O M, Breakfield N W, Mieczkowski P, Jones C D, Paz-Ares J, Dangl J L. Root microbiota drive direct integration of phosphate stress and immunity. *Nature*, 2017, **543**(7646): 513–518

123. Zhang J, Liu Y X, Zhang N, Hu B, Jin T, Xu H, Qin Y, Yan P, Zhang X, Guo X, Hui J, Cao S, Wang X, Wang C, Wang H, Qu B, Fan G, Yuan L, Garrido-Oter R, Chu C, Bai Y. NRT1.1B is associated with root microbiota composition and nitrogen use in field-grown rice. *Nature Biotechnology*, 2019, **37**(6): 676–684

124. Jing J, Garbeva P, Raaijmakers J M, Medema M H. Strategies for tailoring functional microbial synthetic communities. *ISME Journal*, 2024, **18**(1): wrae049