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Effects of biochar on phosphorus fraction, phosphatase activity, and phosphorus-solubilizing bacterial abundance: a phosphorus-depleted biochar design

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Purpose: Biochar application is considered a promising strategy for mitigating agricultural phosphorus (P) shortages. However, it remains uncertain whether biochar enhances soil phosphorus availability for crops beyond functioning as an external phosphorus source. Additionally, the role of phosphorus-solubilizing bacteria (PSB) in phosphorus transformation during biochar amendment is poorly understood, including whether PSB exerts a net positive or negative effect.

Methods: Four different soils were incubated with or without phosphorus-depleted biochar (PDB), followed by Hedley phosphorus fractionation and leaching column experiments. Illumina MiSeq high-throughput sequencing targeting the *phoD* gene was used to analyze PSB diversity and community structure. Soil phosphatase activity and related properties were quantified.

Results: Hedley fractionation revealed that PDB application reduced labile phosphorus while increasing HCl-extractable and residual phosphorus across all soils. Leaching experiments confirmed that PDB reduced inorganic and total phosphorus leaching in all soil types. Acid phosphatase activity was inhibited by PDB in upland soils (a peach orchard, a tea plantation, and a vegetable field). *phoD*-based sequencing indicated an increased relative abundance of dominant PSB genera in upland soils but a decreased abundance in paddy soils under PDB treatment. PDB did not significantly alter PSB diversity.

Conclusion: Phosphorus-depleted biochar reduces potentially available phosphorus fractions and mitigates phosphorus leaching, supporting aquatic ecosystem protection. However, it does not enhance short-term soil phosphorus fertility in agricultural systems. Both the mechanisms underlying PSB abundance shifts after biochar application and the ways in which plants respond to the altered P fractions require further investigation.

KEYWORDS

biochar amendment, phosphorus loss, phosphorus fractionation, phosphatase activity, phosphorus-solubilizing microorganisms

1 Introduction

Soil phosphorus (P) depletion poses a growing global threat (Alewell et al., 2020). An estimated 29%–32% of the world's cropland exhibits soil phosphorus deficits, despite intensive fertilizer inputs (Lun et al., 2018; MacDonald et al., 2011). This deficiency primarily stems from the formation of stable soil-bound phosphorus, as explained by the precipitation–particulate and adsorption–penetration theories (Barrow, 2020). Consequently, global phosphorus-use efficiency averages only 46%, with Eastern Asia recording the lowest value (23%) (Lun et al., 2018). Enhancing soil phosphorus utilization efficiency, particularly by converting bound phosphorus to plant-available forms rather than increasing application rates, is therefore a critical strategy for sustainable agriculture.

Biochar soil amendments can modulate plant-available phosphorus pools, especially the inorganic and soluble fractions (Hossain et al., 2020; Zhang et al., 2025). This dynamic carries significant implications for both crop productivity and aquatic ecosystem protection. The prevailing literature suggests that biochar typically increases surface soil available phosphorus by 45%–260% (Gao et al., 2019; Joseph et al., 2021). However, contradictory findings exist (Li et al., 2020), rendering biochar's net impact contentious. Crucially, agricultural constraints more commonly involve scarcity of available phosphorus than insufficiency of total phosphorus. Biochar enriched with inherent phosphorus functionally resembles direct fertilizer application. The core agronomic value of biochar is its ability to mobilize recalcitrant native soil phosphorus to improve utilization efficiency. This function, however, requires that the confounding effects of biochar-borne phosphorus be minimized. Variations in biochar feedstock induce substantial heterogeneity in phosphorus content (Tesfaye et al., 2021), while soil type and biochar–soil interactions further modulate outcomes (Gul and Whalen, 2016).

Phosphate-solubilizing bacteria (PSB) mineralize insoluble phosphorus into plant-accessible forms and may critically mediate phosphorus bioavailability under biochar amendment (Bai et al., 2024; Fan et al., 2025). For instance, rice straw biochar stimulated *Bacillus mucilaginosus* phosphorus solubilization, increasing dissolved phosphorus by 43% versus controls (Lu et al., 2023). PSB exhibits high community diversity across soils (Kour et al., 2021). However, a fundamental question remains unresolved: does biochar amendment enhance or inhibit PSB-mediated phosphorus transformation?

To address this knowledge gap, we conducted an incubation study using four distinct soils amended with phosphorus-depleted biochar (PDB). Through integrated Hedley phosphorus fractionation, leaching experiments, and alkaline phosphatase gene *phoD*-targeted Illumina MiSeq sequencing, we aimed to a) eliminate the confounding effects of biochar-derived phosphorus, b) track transformations among soil phosphorus pools, c) quantify PDB-induced shifts in PSB abundance and diversity, and d) determine cross-soil variability in these responses.

2 Materials and methods

2.1 Preparation of soils and biochar

The sampling sites were located in Danyang City, southern Jiangsu Province, China, under a humid subtropical monsoon

climate (mean annual temperature: 16.5 °C; precipitation: 1,043 mm). Surface soils (0–20 cm depth) were collected in February 2023 from four different field sites: a vegetable field (VF), a tea garden (TG), a rice paddy (RP), and a peach garden (PG). VF, TG, and PG represented upland soils, with VF and TG having a cultivation history of >10 years and PG approximately 5 years. RP represented flooded paddy soil and was sampled post-harvest. For each soil site, three replicate samples were collected randomly. Soils were air-dried, ground, sieved (<2 mm), and stored at 4 °C. Soil pH values were 6.2 (VF), 5.5 (TG), 5.3 (RP), and 5.3 (PG); additional properties (coordinates and phosphorus contents) are provided in [Supplementary Table S1](#). PDB derived from coconut shells (Zhengzhou Niute Agricultural Technology Co., Ltd., Henan, China) was used, exhibiting no detectable phosphorus content ([Table 1](#)).

2.2 Soil incubation and column leaching experiment

PDB was thoroughly mixed into each soil at 5% (w/w), with unamended soils serving as controls. Treatments included four PDB-amended groups (VF + PDB, PG + PDB, TG + PDB, and RP + PDB) and four unamended controls (VF, PG, TG, and RP), each with three replicates. Subsamples from each treatment were allocated to incubation and leaching experiments. The incubation proceeded for 30 days at 20 °C in the dark. For leaching assays, 24 plexiglass columns (internal diameter: 80 mm; height: 500 mm) were prepared with a 5-cm base layer of quartz sand, overlain by 20 cm of soil (1.00 kg). Deionized water (200 mL per event) was applied in five events to simulate rainfall. The next event was initiated only after the leachate from the previous event had completely stopped flowing. The soil was maintained at saturated water content during each leaching event. Inorganic phosphorus (Pi) and total phosphorus (TP) concentrations in leachates were quantified.

2.3 Analysis of Hedley phosphorus fractions and soil properties

After incubation (as described in [Section 2.2](#)), the soil was thoroughly homogenized and quartered to obtain a representative subsample for subsequent extraction. Soil phosphorus fractions were quantified using a modified Hedley sequential extraction procedure (Yang et al., 2024). Soluble P, NaHCO₃-P, NaOH-P, hydrochloric acid-extractable P (HCl-P), and residual P were extracted with deionized water, 0.5 mol·L^{−1} NaHCO₃, 0.1 mol·L^{−1} NaOH, 1.0 mol·L^{−1} HCl, and mixed acid (H₂SO₄ and HClO₄), respectively. The phosphorus concentrations in all extracts were determined by molybdenum antimony colorimetry using a UV-1800 spectrophotometer (Shanghai Mapada Instruments Co. Ltd., China). Soil electrical conductivity (EC) was measured in 1:5 (w/v) soil–water suspensions, while pH was determined electrometrically in 1:2.5 (w/v) suspensions (DDS-11A/PHS-3C, INASE Scientific Instruments Co. Ltd., Shanghai, China). TP was quantified after strong acid digestion using the same colorimetric method.

TABLE 1 Key physicochemical properties of phosphorus-depleted biochar.

Fineness (mesh)	Median diameter (μm)	Specific surface area ($\text{m}^2\cdot\text{kg}^{-1}$)	pH	Electrical conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	Total phosphorus ($\text{g}\cdot\text{kg}^{-1}$)	Soluble phosphorus ($\text{g}\cdot\text{kg}^{-1}$)
200	19.01	243.7	7.50	129.13	N.D.	N.D.

N.D., not detected.

2.4 High-throughput sequencing of phosphate-solubilizing bacteria

Soil DNA was extracted from the incubated samples using a FastDNA™ SPIN Kit for Soil (MP Biomedicals LLC, Santa Ana, CA, United States). The *phoD* gene was amplified with primers phoD-733F/phoD-1083R on a GeneAmp® 9700 Thermal Cycler (Life Technologies, Foster City, CA, United States). Amplicons were sequenced on an Illumina MiSeq PE300 platform (Majorbio, Shanghai, China). The sequencing process is described by Qin et al. (2018). These sequences were deposited in GenBank under the accession numbers SRX3032776–SRX3032779. Using UPARSE (ver. 7.1, <http://drive5.com/uparse/>) at 97% similarity, the sequences were clustered into operational taxonomic units (OTUs) with chimera removal. Taxonomic annotation was performed using the RDP classifier. Alpha diversity was assessed using the Chao1 (richness), Shannon/Simpson (diversity), and coverage indices. The community composition analysis focused on the top eight phyla and genera by relative abundance. Sequence data will be deposited upon manuscript acceptance.

2.5 Analysis of soil acid phosphatase activity

Soil acid phosphatase (ACP) activity was determined using disodium *p*-nitrobenzene phosphate as the substrate. For each assay, 1 g of air-dried soil was incubated with 0.2 mL toluene (to inhibit microbial activity), followed by sequential addition of 4 mL hydrochloric acid buffer (pH 6.5) and 1 mL disodium *p*-nitrobenzene phosphate solution. After 1 h of incubation at 37 °C, ACP activity was quantified by measuring *p*-nitrophenol release at 420 nm using a UV-1800 spectrophotometer (Shanghai Mapada Instruments Co. Ltd., China).

2.6 Statistical analysis

One- and two-way ANOVA (Duncan method) and stepwise regression analysis were performed using IBM SPSS Statistics 18 (IBM, Chicago, IL, United States). Pearson correlation and stepwise regression analyses were also conducted to evaluate the relationships between PSB diversity indices and environmental factors. Redundancy analysis (RDA) was conducted using Canoco 5 software (Microcomputer Power, Ithaca, NY, United States) to examine the associations between environmental factors and PSB community composition. Figures were generated using Origin 8.0 (OriginLab Corporation, Northampton, MA, United States), and the final graphical composition (layout, color editing, and figure assembly) was completed in Adobe Illustrator CS6 (Adobe Systems, San Diego, CA, United States).

3 Results

3.1 Effects of PDB on soil properties and phosphatase activity

A two-way ANOVA demonstrated significant main effects of soil types and PDB amendment on all soil properties (Table 2), with Figure 1 revealing distinct variations across the four different soils. In non-amended soils, TP was highest in VF (2.32 $\text{g}\cdot\text{kg}^{-1}$), significantly exceeding the other treatments, whereas PG showed the lowest TP (0.48 $\text{g}\cdot\text{kg}^{-1}$); the addition of PDB did not significantly alter the TP content. Soil pH in unamended VF (6.21) was significantly higher than in the other untreated soils (5.25–5.46), but PDB amendment increased pH significantly ($p < 0.05$) across all soils tested (VF: 7.12, +0.91 increase; TG: 6.56, +1.10; PG: 7.31, +1.99; RP: 7.21, +1.93). EC exhibited the following pattern: VF (0.214 $\text{mS}\cdot\text{cm}^{-1}$) > RP (0.0615 $\text{mS}\cdot\text{cm}^{-1}$) > PG (0.0325 $\text{mS}\cdot\text{cm}^{-1}$) $\approx$ TG (0.0319 $\text{mS}\cdot\text{cm}^{-1}$), and the addition of PDB significantly elevated EC values by 0.121–0.1868 $\text{mS}\cdot\text{cm}^{-1}$. Crucially, the PDB application significantly reduced acid phosphatase activity ($F = 9.734$; $p < 0.01$), with VF displaying the highest baseline activity (significantly greater than that of RP/PG); after amendment, VF + PDB and TG + PDB showed significant decreases relative to their non-PDB controls. PDB did not affect acid phosphatase activity in RP soil.

3.2 Effects of PDB on soil phosphorus fractions

P fraction changes induced by PDB amendment are shown in Figure 2. A consistent decrease in soluble P ($\text{H}_2\text{O-P}$) occurred across all four soils (a 6.6%–35.6% reduction), whereas the HCl-P and residual P fractions increased by 5.7%–107.3% and 20.5%–62.5%, respectively. Residual P dominated in PG soils, regardless of PDB treatment, while NaOH-P and residual P prevailed in TG and RP soils. The effects of PDB on the NaOH-P and $\text{NaHCO}_3\text{-P}$ fractions were soil-specific: NaOH-P decreased in VF (by 76.0 $\text{mg}\cdot\text{kg}^{-1}$), TG (by 25.3 $\text{mg}\cdot\text{kg}^{-1}$), and RP (by 9.6 $\text{mg}\cdot\text{kg}^{-1}$) soils but increased in PG (by 24.3 $\text{mg}\cdot\text{kg}^{-1}$) soils following PDB addition. Conversely, the $\text{NaHCO}_3\text{-P}$ increased in TG (by 21.5 $\text{mg}\cdot\text{kg}^{-1}$), PG (by 5.9 $\text{mg}\cdot\text{kg}^{-1}$), and RP (by 7.1 $\text{mg}\cdot\text{kg}^{-1}$) soils, yet decreased in VF (by 58.5 $\text{mg}\cdot\text{kg}^{-1}$) soils with PDB amendment.

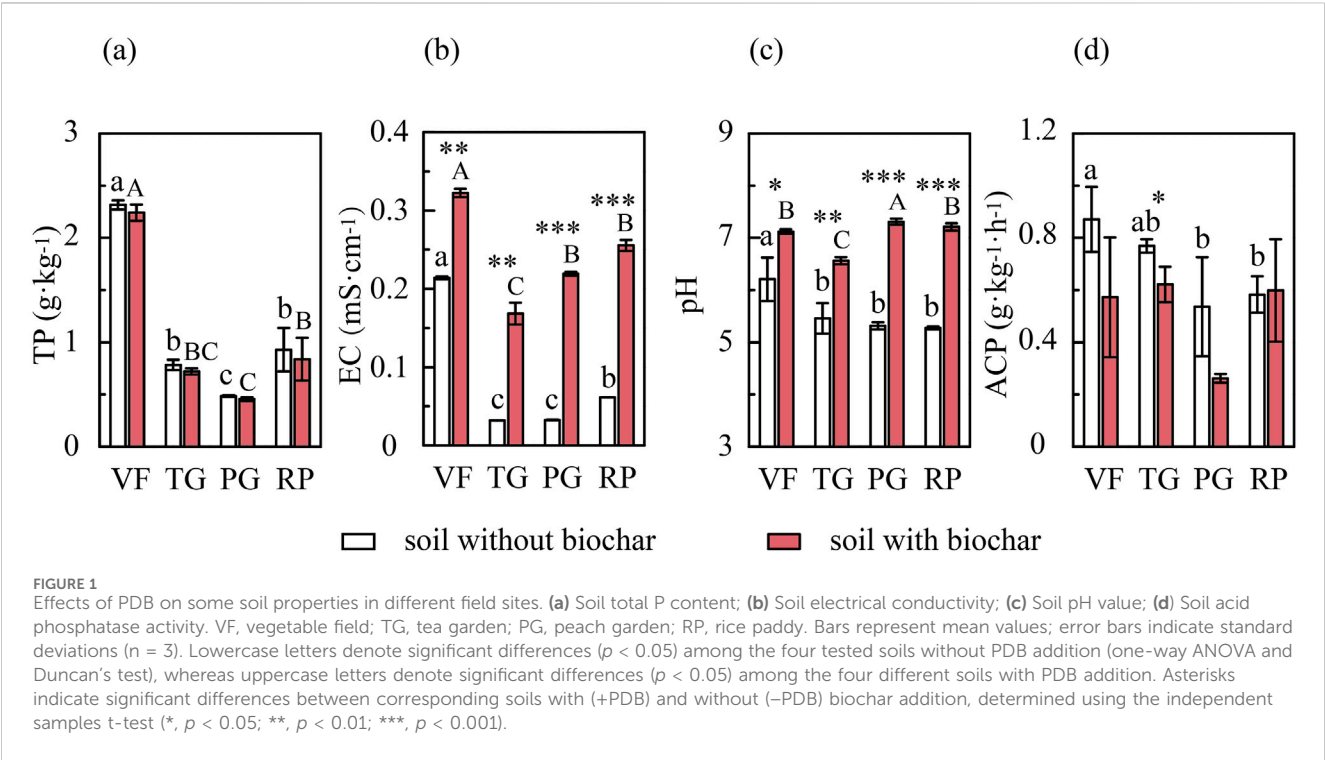
3.3 Effects of PDB on soil phosphorus leaching

Phosphorus leaching responses to PDB amendment across the four tested soils are shown in Figure 3. PDB addition

TABLE 2 Two-way ANOVA of selected soil properties.

Factor	DF	F			
		Acid phosphatase activity	Total P	Electrical conductivity	pH
Soil site(S)	3	6.721*	321.9***	314.5***	12.79***
Biochar (B)	1	9.734**	2.021	1,350***	386.7***
S × B	3	1.631	0.086	17.46***	13.55***

The asterisks represent significant differences based on a two-way ANOVA. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. DF indicates degrees of freedom.



substantially reduced the cumulative losses of TP and Pi in VF soils by 83.7% and 82.7%, respectively. Similarly, TP and Pi losses in TG, PG, and RP soils decreased by 32.95%–61.38% and 1.04%–22.39%, respectively. Notably, without PDB amendment, VF soils exhibited the highest cumulative TP and Pi losses after five rainfall leaching events, significantly exceeding all other soils.

3.4 Effects of PDB on the diversity of soil PSB

The PSB diversity indices (Chao1, Shannon, Simpson, and coverage) presented in Table 3 exhibited significant variation across the soils tested ($p < 0.001$), but PDB amendment did not significantly alter these metrics. Stepwise regression identified NaOH-P content as the primary predictor of α -diversity (Table 4), explaining its critical role in structuring PSB communities.

3.5 Effects of PDB on the relative abundance of soil PSB

The PDB amendment increased the relative abundance of dominant genera in upland soils (VF, TG, and PG; Figure 4). According to the relative abundance data, *Pseudomonas* and *Stenotrophomonas* were the dominant genera in VF soils; *Bradyrhizobium* prevailed in TG; and PG was characterized by *Bradyrhizobium*, *Dactylosporangium*, *Phytohabitans*, and *Actinoplanes*. In contrast, RP soils—dominated by *Bradyrhizobium* and *Nocardioides*—exhibited decreased relative abundances of these genera post-PDB. Redundancy analysis (RDA) at the genus level (Figure 5) indicated that RDA1 (axis 1) and RDA2 (axis 2) collectively explained 50.79% of PSB community variation. NaOH-P, TP, $\text{NaHCO}_3\text{-P}$, and ACP explained 27.6%, 14.9%, 9.5%, and 6.5% of the constrained variance in bacterial community composition, respectively. NaOH-P and TP contents were positively correlated with the abundance of *Pseudomonas* and

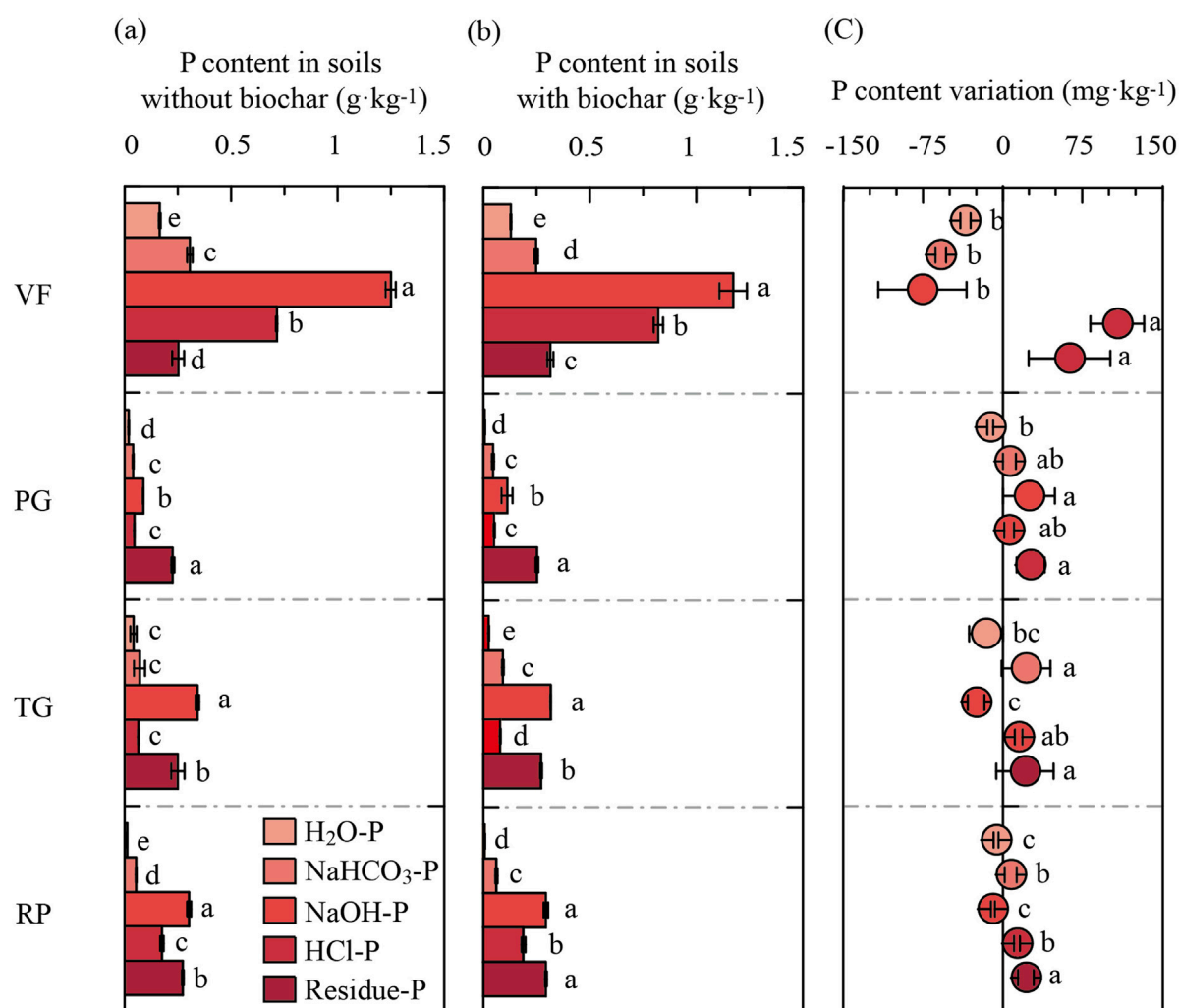


FIGURE 2
Effects of PDB application on soil phosphorus (P) fractions in different soil sites. VF, vegetable field; TG, tea garden; PG, peach garden; RP, rice paddy.
(a) P content in soil P fractions without PDB addition. (b) P content in soil P fractions after PDB addition. (c) Change in P content of each fraction following PDB application relative to non-amended soils. Lowercase letters denote significant differences ($p < 0.05$) among P fractions within the same treatment. Error bars represent standard deviations ($n = 3$).

Stenotrophomonas but negatively correlated with the abundance of *Bradyrhizobium*, *Dactylosporangium*, *Phytohabitans*, *Actinoplanes*, and *Rhodoplanes*.

4 Discussion

4.1 PDB reduces phosphorus bioavailability across different soils

Although conventional biochar typically enhances soil bioavailable phosphorus (Gao et al., 2019; Joseph et al., 2021), this study is the first to demonstrate that PDB—excluding interference from inherent phosphorus—consistently diminished potentially available P fractions in all tested soils. This finding is corroborated by our leaching experiments showing reduced soluble phosphorus loss. Our results suggest that available phosphorus reduction primarily occurs through

the conversion of $\text{H}_2\text{O-P}$ into stable forms, specifically HCl-P and residual phosphorus (Figure 2). The underlying mechanisms might involve PDB-mediated transformation through the following processes: (1) precipitation with surface cations (Mg/Ca in alkaline soils; Fe/Al in acidic soils), which forms insoluble crystals (Chen et al., 2018; Dai et al., 2020) and (2) physical adsorption via porous structures and a high surface area, which limits phosphorus dissolution (Zhu et al., 2005). Crucially, phosphorus-rich biochar increases potentially available P fractions because (i) its exogenous phosphorus directly supplements plant-available pools (Liu et al., 2018) and (ii) pyrolysis-derived phosphorus compounds occupy adsorption sites, increasing the surface's negative charge and inhibiting soil phosphorus adsorption (Zhao et al., 2017). This dual mechanism resolves the apparent contradiction in the literature regarding biochar's phosphorus effects. It is important to note that this was a short-term incubation study, and the findings do not incorporate the potential influences of soil–plant interactions.

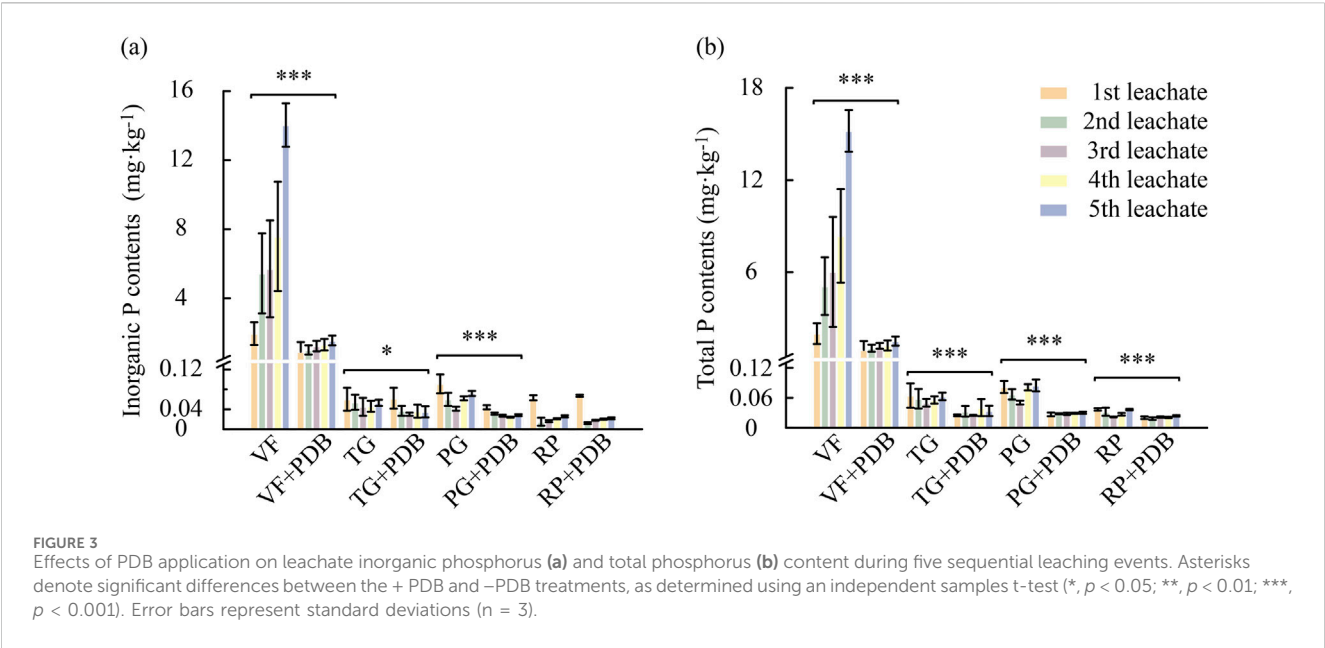


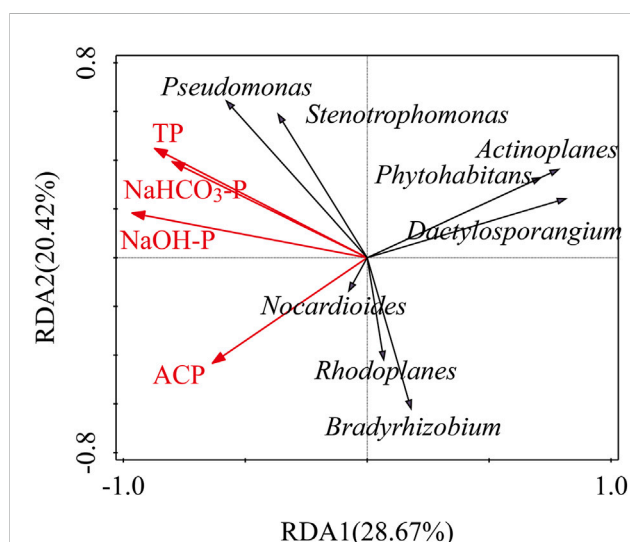
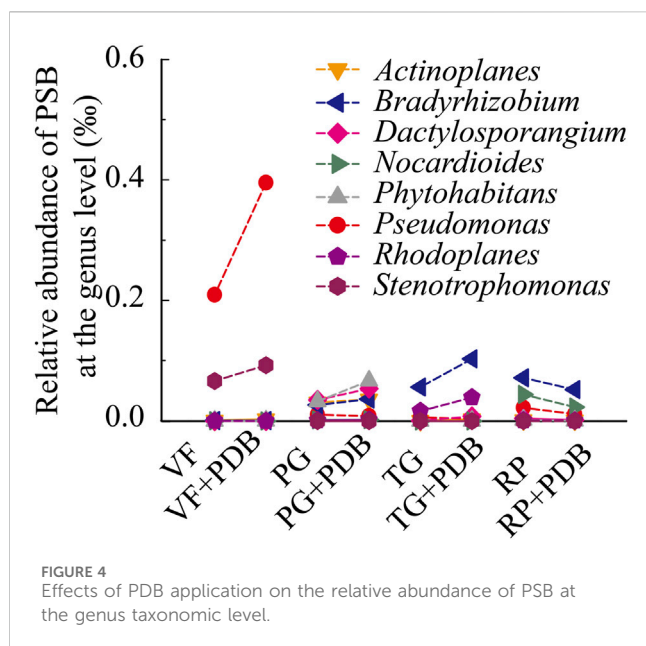
TABLE 3 Response of PSB diversity indices to PDB application in different soil sites.

Soil site	Biochar application	Chao1 index	Simpson index	Shannon index	Coverage index
VF	–PDB	3,333 ± 268 ^a	0.007 ± 0.001 ^c	6.216 ± 0.117 ^a	0.979 ± 0.003 ^c
	+PDB	1705 ± 30 ^b	0.042 ± 0.010 ^c	4.801 ± 0.323 ^b	0.990 ± 0.001 ^b
PG	–PDB	1,614 ± 105 ^b	0.049 ± 0.012 ^c	4.273 ± 0.228 ^c	0.990 ± 0.002 ^b
	+PDB	740 ± 31 ^c	0.140 ± 0.015 ^a	2.957 ± 0.143 ^d	0.995 ± 0.001 ^a
TG	–PDB	3,452 ± 184 ^a	0.006 ± 0.002 ^c	6.279 ± 0.296 ^a	0.978 ± 0.002 ^c
	+PDB	1,580 ± 240 ^b	0.078 ± 0.036 ^b	4.061 ± 0.553 ^c	0.990 ± 0.002 ^b
RP	–PDB	1820 ± 78 ^b	0.046 ± 0.003 ^c	4.465 ± 0.078 ^{bc}	0.988 ± 0.000 ^b
	+PDB	752 ± 46 ^c	0.102 ± 0.002 ^b	3.259 ± 0.082 ^d	0.995 ± 0.001 ^a
	DF	F			
Soil site(S)	3	317.8***	61.16***	134.7***	124.9***
Biochar (B)	1	0.733	0.028	0.171	1.650
S × B	3	1.333	6.253	4.509*	0.160

The data in the table are presented as the mean ± standard deviation, N = 3. Different superscript letters indicate significant differences between treatments. The asterisks represent significant differences based on a two-way ANOVA. *, $p < 0.05$; ***, $p < 0.001$. DF indicates degrees of freedom.

TABLE 4 Stepwise regression analysis between the diversity index and soil environmental factors.

Diversity index	Soil environmental factor
Chao1 index	NaOH-P, soluble P, HCl-P, and pH
Shannon index	NaOH-P, soluble P, and HCl-P
Simpson index	NaOH-P
Coverage index	NaOH-P, soluble P, and NaHCO ₃ -P



4.2 PDB suppresses soil phosphatase activity

ACP mediates organic phosphorus mineralization in acidic soils, a critical process in phosphorus-deficient ecosystems (Eivazi and Tabatabai, 1977; Nannipieri et al., 2011). Although phosphorus-rich biochar inconsistently affects ACP (positive: Masto et al., 2013; Lu et al., 2023; negative: Jin et al., 2016; Song et al., 2020; neutral: Yang et al., 2016; Pokharel et al., 2020), PDB consistently inhibited ACP activity in our study, which could limit the potentially plant-available P-pool in soils. We attribute

this to the following: (1) direct enzyme adsorption: PDB's porous surface adsorbs ACP, inducing conformational changes that reduce activity by >90% (Foster et al., 2018); and (2) microbial mediation: altered electron shuttling and solute transformation impair phosphatase-producing microbes (Yuan et al., 2017). Although we did not observe a significant correlation between pH and ACP, which could be attributed to the constrained sample size, it is necessary to expand the study to confirm these findings in the future.

4.3 PDB alone does not alter PSB α -diversity

Although biochar can enhance bacterial α -diversity by creating distinct microenvironments (e.g., black soil under soybean; Yao et al., 2017), the PDB amendment in our study showed no significant effect on PSB diversity indices (Table 3). This discrepancy may stem from soil-specific factors, particularly moisture and oxygen gradients, which override the influence of biochar on microenvironments. Crucially, stepwise regression identified the NaOH-P content as the primary predictor of α -diversity (Table 4). NaOH-P originates from Al/Fe-bound phosphorus and organic phosphorus in humic/fulvic acids (Qin et al., 2019). Given that NaOH-P acts as a pivotal sink/source of labile-to-stable phosphorus (Zheng et al., 2002) and correlates with dissolved oxygen dynamics (Zhang et al., 2018), we propose that PDB indirectly modulates PSB diversity through oxygen-mediated regulation of NaOH-P fractions, such as Al- or Fe-bound P, along with humic and fulvic acid P, rather than direct microbial habitat alteration.

4.4 Land-use patterns mediate PDB effects on PSB community composition

PDB amendment differentially altered PSB genus-level abundances, with dominant genera increasing in upland soils (VF, TG, and PG) but decreasing in paddy soils (RP) (Figure 4). This divergence underscores a possible effect of land use, such as water management, rather than cropping patterns, as the primary control. For example, *Bradyrhizobium* (a multifunctional genus involved in nitrogen fixation, denitrification, and phosphorus solubilization; Mirriam et al., 2023) exhibited opposing responses to biochar across studies: decreased (He et al., 2021; Yao et al., 2017) versus increased at low application rates (Li et al., 2022). We attribute this to PDB's oxygen-modulating role: in flooded paddy soils, biochar improves porosity and aeration, alleviating hypoxia to favor *Bradyrhizobium* growth. RDA analysis indicated NaOH-P (explaining 27.6% of genus variance; Figure 5) as the key driver, consistent with its oxygen-dependent solubilization dynamics (Zhang et al., 2018). This mechanistically links PDB-induced oxygen shifts to NaOH-P bioavailability and ultimately PSB assemblage. Additionally, a negative correlation between soil total phosphorus and the relative abundance of *Bradyrhizobium* has been documented (Griebsch et al., 2020). However, the specific reasons for this correlation are not yet understood. We acknowledge that other soil properties not measured in this study may also have contributed to these changes.

5 Conclusion

In summary, this study demonstrates that biochar application, irrespective of its phosphorus content, alters soil phosphorus fractions, inhibits soil acid phosphatase activity, and reduces soil phosphorus loss. These findings indicate that biochar holds potential for maintaining soil nutrient status and mitigating non-point source agricultural pollution. Notably, the relative abundance of phosphate-solubilizing bacteria varied significantly across different soils. In addition, the elucidation of specific land-use types is an important field for future research. Further investigation is necessary to elucidate the interactions among biochar, phosphate-solubilizing bacteria, and soil management practices concerning soil phosphorus transformation.

Data availability statement

The authors acknowledge that the data presented in this study must be deposited and made publicly available in an acceptable repository prior to publication. Frontiers cannot accept a manuscript that does not adhere to our open data policies.

Author contributions

HQ: Writing – original draft, Writing – review and editing. XH: Formal analysis, Methodology, Writing – original draft. JC: Data curation, Methodology, Software, Writing – original draft. YZ: Data curation, Investigation, Methodology, Writing – original draft. SW: Data curation, Methodology, Software, Writing – original draft. SL: Methodology, Writing – original draft. YX: Resources, Writing – original draft. XY: Methodology, Writing – review and editing.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2025.1663371/full#supplementary-material>

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