# Invasive and native plants differ in their effects on the soil microbial community and plant-soil phosphorus cycle

**Lingda Zeng**
Huizhou University
**Mengxin Zhao**
Chinese Academy of Agricultural Sciences State Key Laboratory for Biology of Plant Diseases and Insect Pests
**Feng Sun** ( sf0204@163.com )
South China Normal University https://orcid.org/0000-0003-0752-3966

**Research Article**

**Keywords:** Invasion ecology, Soil microbial community, Enzyme activity, Soil phosphorus fractions, Foliar phosphorus fractions

**Posted Date:** September 12th, 2023

**DOI:** https://doi.org/10.21203/rs.3.rs-3151162/v1

# Abstract

Exploring the expansion mechanisms of invasive plants from plant and soil systems is an important ecological research objective; however, plant and soil phosphorus (P) cycling is not well understood. We explored the potential of the soil microbial community to mediate organic P mineralization and allocation to invasive and native plants in South China. Soil samples were collected from three invasive plants of *M. micrantha*, *B. pilosa*, and *I. cairica* and three native plants of *Persicaria chinensis*, *Paederia scandens* and *Pluchea indica*, and soil microbial communities, enzyme activities, and soil P fractions were examined. Plant P concentrations and foliar P fractions were tested to determine P allocation. The results showed that invasive species had higher levels of acid and alkaline phosphomonoesterase and induced a stronger acceleration of soil organic P decomposition. Moreover, the soil glucose dehydrogenase gene of the invasive species was more abundant than that of the native species, allowing it to mineralize more organic P. The invasive species had higher nucleic acid P and metabolic P in the foliar than in the native species because the invasive species allocated more P to photosynthesis. Our study suggests that invasive plants can enhance organic P decomposition by altering the soil microbial communities. In addition, invasive plants may have a higher P utilization efficiency than native plants. These results provide novel mechanistic explanations for the rapid expansion of invasive species in P-poor, lower latitudes.


# Introduction

Exploring the mechanisms underlying the expansion of invasive plants is an important objective of ecological research. Many studies have emphasized the aboveground components of plant invasion and found that invasive plants often increase primary productivity, allelopathic effects, and suppress the growth of native plants (Kaur et al. 2012; Liu et al. 2020). However, most of these studies have focused on the effects of higher photosynthesis and nutrient- and energy-use efficiencies contributing to exotic plant invasion (Liu et al. 2017), while the effects of mineral nutrients on higher photosynthesis and high above ground biomass remain unknown. In addition, most empirical studies have emphasized only the aboveground components and belowground components of plant invasion (Burke et al. 2019; Feng et al. 2009). Exploring the expansion mechanisms of invasive plants based on research on single components is difficult, because the expansion mechanisms of invasive plants are usually superior to those of native plants, not only in terms of aboveground components, but also belowground components (Zhang et al. 2019). Our previous study suggested that exploring the invasion mechanisms of invasive plants should combine the aboveground and belowground components (Liu et al. 2020).

Phosphorus (P) is an essential and limiting macronutrient for plant growth in (sub)tropical ecosystems in highly weathered and old soils (Du et al. 2020). The growth rate hypothesis predicts that plants with faster growth rates require higher amounts of P-rich RNA (Elser et al. 2010). We synthesized data from 49 published field experiments containing 233 invasive plant leaf P concentrations and 207 native plant leaf P concentrations, and found that invasive plant leaf P concentrations were higher than native plant leaf P concentrations in (sub)tropical fields (see Supplementary Figure S1). This could be explained by three

possible reasons: 1) invasive plants have a higher P resorption capacity in resource-poor than in resource-rich environments (Sardans et al. 2017), 2) invasive plants also produce more litter and have faster decomposition rates (Ye et al. 2019), and 3) invasive plants usually accelerate the macronutrient cycling rate by increasing soil microbial activity (Liu et al. 2020; Sun et al. 2019). Additionally, invasive plants have been shown to suppress native plant growth by reducing native plant associations with mycorrhizae (Grove et al. 2017). In (sub)tropical soils, organic P constitutes a large fraction of the total soil phosphorus (Wei et al. 2019). Thus, organic P transformation driven by soil micro-organisms plays an important role in plant P acquisition (Ding et al. 2021). Acid phosphomonoesterase (ACP) and alkaline phosphomonoesterase (ALP) are the dominant enzymes that participate in organic P decomposition. ACP is mainly secreted by fungi and plant roots. ALP is mainly produced by bacteria (Sun et al. 2020). Alternatively, phosphate solubilizing bacteria can liberate phosphate from inorganic compounds by secreting organic acids (Rasul et al. 2019). For example, gluconic acid contributes significantly to the release of P from phosphorus minerals and other inorganic phosphates. The synthesis of gluconic acid from glucose in the direct oxidation pathway is mediated by glucose dehydrogenase, encoded by *gcd* gene, (Sashidhar and Podile 2010). Moreover, invasive plants usually have higher P use efficiency by changing resource investments and allocation in plant tissues, which may explain their invasiveness, especially in P-poor soils (Sun et al. 2022).

The total P in plant tissues is functionally fractionated into structural, metabolic (including inorganic P), nucleic acid, and residual P (Yan et al. 2019). Metabolic P plays a key role in photosynthesis and is useful for studying P limitation and plant growth (Mo et al. 2019). Moreover, plants may adjust the allocation of P among these P fractions to maximize growth and fitness (Hidaka and Kitayama 2011). However, the differences in P fractions between invasive and native plants are unclear. This information may be important for exploring the invasion mechanisms of invasive plants.

In southern China, the rapid increase in economic trade between countries has led to an increasingly frequent exchange of live organisms and seedlings (Gao et al. 2018). Alternatively, the degradation of native vegetation accelerate the expansion of invasive plants. *Mikania micrantha* Kunth, *Bidens pilosa* L., and *Ipomoea cairica* L. are known as the worst invasive species in South China, and have caused serious damage to native ecosystems and economic losses (Sun et al. 2019; Wang et al. 2019; Wang et al. 2011). *M. micrantha* and *B. pilosa* belong to the Asteraceae family and originate from South and Central America, respectively, whereas, *I. cairica* belong to the Convolvulaceae family and originates from North America.

Here, we conducted a comparative study of invasive and coexisting native plants to reveal the effects of invasive plants on soil organic P mineralization and foliar P allocation. We hypothesized that (1) plant invasion would alter soil microbial communities and increase soil organic mineralization, and (2) foliar P allocation of invasive plants would have a higher metabolic P allocation owing to different resource investment strategies.

# Materials and methods

## Study site and sampling

The experiment was conducted in the site of Zhongshan city (22˚29' N, 113˚29' E), Guangdong Province, China. The climate in this region is subtropical monsoon, the mean annual precipitation and annual air temperature is 1759 mm and 21.8 ℃, respectively. We established three experimental blocks in abandoned farmland that had been highly invaded by *M. micrantha*, *B. pilosa* and *I. cairica* for more than 10 years. The distance between each block was more than 50 m. The dominant native species were *Persicaria chinensis* (L.) H. Gross, *Paederia scandens* (Lour.) Merr., and *Pluchea indica* (L.) Less. *Persicaria chinensis* (Polygonaceae) is a perennial herb that grows up to 1 m in subtropical China (Sun et al. 2019). *Paederia scandens* (Rubiaceae) is a herbaceous vine that grows up to 3–4 m in height, and is widely distributed in South China. *Pluchea indica* (Asteraceae) is a perennial herb that grows up to 2–3 m high in the southeastern coastal areas of China.

In each block, five soil cores (5 cm diameter and 10 cm deep) from the rhizosphere of each plant (three invasive and native plants) were taken and mixed together to form a single rhizospheric soil sample. The invasive and native plants were separated from each other by approximately 2 m to avoid rhizospheres influencing each other. Thus, three replicate samples per plant species were taken (18 samples in total). Sampling was performed during the last week of July 2022. One portion of the rhizospheric soil was stored at -20 ℃ for microbial analysis, one portion of the rhizospheric soil was stored at 4 ℃ to measure enzyme activity, and the remaining soil was air dried for chemical analyses. The plant roots, stems and leaves were oven dried at 60 ℃ to determine the plant P concentrations.

## Soil properties analysis

The moist field soil was oven dried at 105 ℃ for 24 h to determine soil moisture content. The soil pH was measured in a 1:2.5 soil: $CaCl_2$ suspension. Soil P fractions were extracted sequentially (Hedley et al. 1982). Briefly, dry soil (0.5 g) was continuously extracted using an anion-exchange membrane, 0.5 M $NaHCO_3$, 0.1 M NaOH, and 1 M HCl; the residual soils were digested with HF-$HClO_4$. The inorganic P (Pi) concentrations in the extracted solution were detected using an inductively coupled plasma optical emission spectrometer (ICP-OES; Optima8300; Perkin Elmer, Waltham, MA, USA). The total P concentrations in the extracted solutions were digested using persulfate, and the concentrations of organic P (Po) were calculated as total P minus Pi. These P fractions are classified as resin-P, $NaHCO_3$-Pi, $NaHCO_3$-Po, NaOH-Pi, NaOH-Po, HCl-Po, and residual P. However, HCl-Pi was not tested in these soils.

## Soil enzyme activity and microbial community analysis

ACP and ALP activities were determined as described by Tabatabai and Bremner (1969) (Tabatabai and Bremner 1969). Briefly, 0.2 mL toluene, 4.0 mL MUB (pH 6.5 and pH 11), and 1.0 mL p-nitrophenyl phosphate solution were added to a 50 mL tube containing 1.0 g fresh soil, and then incubated at 37 ℃ for 1 h. Next, 1.0 mL 0.5 M NaOH and 0.5 M $CaCl_2$ solutions were added. The p-nitrophenol hydrolyzed by

phosphatase activity was determined using a spectrophotometer at 400 nm, and the results were described as μg p-nitrophenol $g^{-1}$ soil $h^{-1}$.

The Power Soil DNA Isolation Kit (MoBio, California, USA) was used to extract DNA from frozen soil (0.5 g) according to the manufacturer's protocol. The phoD gene encodes ALP, the primers ALPS-F730 (5'-CAGTGGGACGACCACGAGGT-3') and ALPS-R1101 (5'-GAGGCCGATCGGCATGTCG-3') were used to analyze ALP-producing bacteria community and phoD gene abundance analysis (Sakurai et al. 2008). The gdh gene encodes glucose dehydrogenase, the primers gcd-FW (5'-CGGCGTCATCCGGGSITIYRAYRT-3') and gcd-RW (5'-GGGCATGTCCATGTCCCAIADRTCRTG-3') were used to analyze the glucose dehydrogenase producing bacteria community and gcd gene abundance analysis. PCR and high-throughput sequencing of the phoD and gcd genes were conducted by the Personalbio Company (Shanghai, China) using the Illumina NovaSeq6000 platform. Sequence reads from each sample were clustered into operational taxonomic units (OTUs) with 97% similarity. The phoD and gcd Chao1 richness and Shannon diversity index were also calculated at the same sequencing depth. The phoD and gcd sequences were deposited in the NCBI Sequence Read Archive under the accession numbers PRJNA (983131) and PRJNA (983235), respectively.

## Plant P fractions analysis

The sequential extraction method was used to determine the plant P fractions (Sun et al. 2022). Then, 0.5 g freeze-dried leves were added to a 50 mL centrifuge tube (1) then extraction mixtures of 7.5 mL chloroform:methanol:formic acid (12:6:1 v/v/v) and 9.5 mL chloroform:methanol:water (1:2:0.8 v/v/v), and 9.5 mL water-washed chloroform were added to extract P fractions. All extractions were transferred to centrifuge tube (2); the upper phase of the extraction was transferred to the centrifuge tube (3), the resultant lower phase was the lipid-rich structural-P. Another 5 mL methanol was added to the tube (1), and the extraction was transferred to tube (3), these extractions were refrigerated at 4 ℃ for 1 h, and then 11 mL trichloroacetic acid (100%) was added and the tubes were centrifuged. The resulting supernatant was used to analyze the metabolic-P. Then, 35 mL of trichloroacetic acid (2.5%, w/v) was uniformly mixed with the residue and was extracted in a thermostatic water bath (95 ℃) for 1 h and then centrifuged. The liquid layer was used to measure nucleic acid-P, and the residue was used to analyze residual-P. All foliar P fractions and plant tissues were digested with $H_2SO_4$, and determined by an ICP-OES (Optima8300; Perkin Elmer, Waltham, MA, USA), the results were described as g $kg^{-1}$.

## Statistical analyses

Statistical analysis was performed using SPSS (version 17.0; SPSS Inc., Chicago, IL, USA). The effects of plant type on soil properties, enzyme activities, microbial communities and plant nutrients were tested using a one-way ANOVA. Differences in microbial community composition (Bray-Curtis dissimilarity matrix) between the invasive and native species were assessed using by permutational multivariate ANOVA (PERMANOVA) and visualized using principal coordinate analysis (PCoA).

# Results

Soil P fractions responses to plant invasion

Invasive *I. cairica* and *B. pilosa* significantly increased the soil pH compared to native *P. indica.* Invasive *M. micrantha* and *B. pilosa* significantly increased soil DOC compared with all native plants, and all invasive plants enhanced soil DON compared with native *P. indica.* Invasive plants did not significantly affect soil water content (Table 1).

Table 1
Responses of soil properties to the invasive and native soils. Different letters indicate significant differences at $P < 0.05$.

| | **Invasive plants** | | | **Native plants** | | |
|---|---|---|---|---|---|---|
| | *M. micrantha* | *I. cairica* | *B. pilosa* | *P. chinensis* | *P. scandens* | *P. indica* |
| SWC | 21.95 ± 1.02 | 20.53 ± 0.79 | 22.72 ± 1.34 | 22.76 ± 1.12 | 21.46 ± 1.1 | 21.78 ± 0.83 |
| pH | 4.72 ± 0.11ab | 4.87 ± 0.14a | 5.02 ± 0.14a | 4.65 ± 0.11ab | 4.62 ± 0.10ab | 4.43 ± 0.11b |
| DOC | 399.66 ± 40.86a | 383.26 ± 37.72ab | 420.3 ± 41.58a | 263.01 ± 45.81b | 268.42 ± 35.37b | 252.37 ± 34.92b |
| DON | 92.17 ± 5.82a | 84.88 ± 6.77a | 93.45 ± 5.73a | 77.81 ± 4.75ab | 75.86 ± 4.55ab | 62.5 ± 6.18b |

DOC: Dissolved organic carbon, DON: dissolved organic nitrogen, SWC: Soil water content.

Table 2
The diversity and richness of ALP-producing bacteria communities and gcd-producing bacteria communities in the invasive and native soils. Different letters indicate significant differences at $P < 0.05$.

| | | Invasive plants | | Native plants | | | |
|---|---|---|---|---|---|---|---|
| | | *M. micrantha* | *I. cairica* | *B. pilosa* | *P. chinensis* | *P. scandens* | *P. indica* |
| phoD | Chao | 2271.8 ± 549.5 | 2854 ± 186.2 | 2221.3 ± 41.1 | 1910.6 ± 177.5 | 2008.5 ± 140.5 | 2035.5 ± 374.9 |
| | Shannon | 8.27 ± 0.37ab | 8.9 ± 0.04a | 8.33 ± 0.17ab | 7.88 ± 0.19bc | 7.19 ± 0.22c | 7.37 ± 0.41c |
| | Simpson | 0.987 ± 0.003a | 0.99 ± 0.001a | 0.984 ± 0.003a | 0.974 ± 0.006ab | 0.955 ± 0.008b | 0.963 ± 0.01b |
| gcd | Chao | 1466.2 ± 144.8ab | 1807.7 ± 136.1b | 1563.3 ± 18.7ab | 1608.3 ± 185.2ab | 1163.9 ± 89b | 1402.6 ± 179.7ab |
| | Shannon | 7 ± 0.1ab | 6.86 ± 0.47ab | 6.96 ± 0.03ab | 7.24 ± 0.09a | 6.51 ± 0.13b | 6.83 ± 0.06ab |
| | Simpson | 0.976 ± 0.005 | 0.957 ± 0.016 | 0.973 ± 0.003 | 0.981 ± 0.003 | 0.972 ± 0.002 | 0.976 ± 0.004 |

NaOH-Pi, NaOH-Po, and residual P were the dominant P fractions in both the invasive and native plants. The concentrations of inorganic P fractions (Resin P, $NaHCO_3$-Pi and NaOH-Pi) in all the invasive plants were higher than those in all the native plants, whereas the organic P fraction of NaOH-Po in all the invasive plants was lower than that in all the native plants (Fig. S2-3). Moreover, the invasive plant *M. micrantha* reduced the concentrations of residual P compared with all native plants. We also calculated the percentages of different P fractions in soil total P. Resin P, $NaHCO_3$-Pi and NaOH-Pi percentages were higher in invasive plants; however, the NaOH-Po percentage in invasive plants was lower than that in the native plants (Fig. 1). Nevertheless, the invasive plants had little influence on the percentages of the other P fractions. Therefore, the data on P fractions and percentages suggest that invasive plants mainly influenced the available P fractions (resin-P, $NaHCO_3$-Pi, and NaOH-Pi) and NaOH-Po.

Microbial responses to plant invasion

All invasive plants showed significantly increased ALP activity compared to native plants, but only the invasive plants *B. pilosa* increased ACP activity (Fig. 2). All invasive plants showed significantly increased phoD gene abundance compared to native plants, and both invasive plants, *M. micrantha* and *B. pilosa* significantly increased gcd gene abundance (Fig. S4).

The PCoA for ALP-producing bacteria showed a significant difference between the invasive and native plants (Fig. S5). The dominant ALP-producing bacteria belonged to the Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria classes (Fig. 3a). We observed a higher relative abundance of Alphaproteobacteria in the invasive plants than in the native plants (Fig. 3a). The dominant

genera were Bradyrhizobium and Cupriavidus, and invasive *M. micrantha* and *B. pilosa* had higher relative abundance of Bradyrhizobium than native plants (Fig. 3b).

The PCoA for gcd-producing bacteria showed a significant difference between the invasive and native plants (Fig. S6). The dominant gcd-producing bacteria belonged to the Alphaproteobacteria and Gammaproteobacteria classes (Fig. 4a). We observed a higher relative abundance of Alphaproteobacteria in the invasive plant *B. pilosa* than in all native plants (Fig. 4a). The dominant genus was Rhizobium; the invasive plants *I. cairica* and *B. pilosa* had a higher relative abundance of Rhizobium than the native plants (Fig. 4b).

In the ALP-producing bacteria and gcd-producing bacterial communities, the relative abundance of Alphaproteobacteria was positively correlated with the concentrations of inorganic P fractions, but negatively correlated with the concentrations of organic P fractions (Fig. S7ab).

Plant responses to plant invasion

The P concentration in the foliar tissue of the invasive plants was higher than that in the native species (Fig. S8); however, there were few differences the stems and roots. For the foliar P fractions, the content and proportion of metabolic P and nucleic acid P were higher in the invasive plants than in native plants (Fig. 5, Fig. S9), and the proportion of structural P was lower in the invasive than in the native species (Fig. 5).

# Discussion

Effects of invasive species on soil organic P mineralization

Organic P mineralization is an important method for plant P uptake in (sub)tropical ecosystems with P limitation (Sun et al. 2022). In this study, soil ACP played an important role in organic P mineralization, suggesting the importance of fungi and ACP in the availability of (sub)tropical soil P (Fan et al. 2019). However, invasive plants not only significantly increased soil ACP activity, but also increased ALP activity, suggesting that bacteria and ALP also contribute to organic P mineralization in (sub)tropical soils (Sun et al. 2020). In this study, the invasive species significantly changed the composition of ALP-producing bacterial communities (Fig. S5), and the relative abundance of Alphaproteobacteria was higher in invasive plant soils (Fig. 3a). The relative abundance of Alphaproteobacteria was positively correlated with alkaline phosphatase ($r = 0.655$, $P = 0.003$). Thus, this shift in soil ALP-producing bacterial communities due to invasive species could facilitate soil organic P mineralization. This was confirmed by the redundancy analysis (Fig. S7a). Alphaproteobacteria are copiotrophic microorganisms, indicating that the growth of microorganisms containing genes coding for alkaline phosphatase is increase in the invasive plant soils, which might be due to the higher soil dissolved organic carbon (Table 1). The redundancy analysis suggested that the relative abundance of Alphaproteobacteria was positively correlated with soil dissolved organic carbon (Fig. S7a). Invasive plants significantly increased the Shannon diversity index of phoD, which indicated a positive relationship with alkaline phosphatase (r =

0.642, $P = 0.004$). Thus, increasing the number of ALP-producing bacteria using invasive species can facilitate soil organic P mineralization.

Alternatively, the glucose dehydrogenase gene encoding glucose dehydrogenase, which plays an important role in the direct oxidation of glucose as a glucose acid, contributes significantly to the mineral phosphate solubilization ability in several gram-negative bacteria (Sashidhar and Podile 2010). In this study, the invasive plants *M. micrantha* and *B. pilosa* showed significantly increased gcd gene abundance (Fig. S4), suggesting that the direct oxidation of glucose by invasive plants is important for mineral phosphate solubilization. This is consistent with a previous study that showed the glucose dehydrogenase gene is responsible for glucose dehydrogenase-mediated phosphate solubilization (Rasul et al. 2019).

Effects of invasive species on soil organic P fractions

Soil P fractions were classified as labile P (resin-P, $NaHCO_3$-Pi, and $NaHCO_3$-Po), moderately labile P (NaOH-Pi and NaOH-Po), or recalcitrant P (HCl-Pi, HCl-Po, and residual-P) (Hedley et al. 1982). In the present study, soil P responded to invasive plants and was associated with the stability of different P fractions. The labile P contents of resin-P and $NaHCO_3$-Pi, the most available P pools in the soil, increased markedly after plant invasion (Fig. 1). This is could likely because moderately labile P fractions play an important role in maintaining the labile P balance. Soil microorganisms can increase Pi availability from moderately labile fractions via the release of hydrolytic enzymes and organic acids (Rasul et al. 2019); subsequently, free Po which can be hydrolyzed by ACP and ALP, leading to a decrease in Po in these P fractions (Fan et al. 2017; Fraser et al. 2017). Indeed, both the content and proportion of moderately labile NaOH-Po were significantly reduced in invasive plant soils, suggesting that moderately labile P can be a resource for available P. Furthermore, a previous study suggested that organic P is abundant in soil and its turnover can supply a considerable fraction of the P taken up by natural vegetation (Turner 2008). These results are consistent with the first hypothesis and imply another important approach for increasing soil available P.

Effects of invasive species on foliar P allocation

The evolution of the increased competitive ability hypothesis suggest that invasive plants with limited resources show trade-offs between growth and defense (Blossey and Nötzold 1995). For example, a study showed that invasive plants of *Ageratina adenophora* increased N allocation to photosynthesis (growth) and reduced N allocation to cell walls, resulting in poorer structural defenses (Feng et al. 2009). In the present study, although the total P content in the stems and roots of invasive plants was not significantly different from that in native plants, the total P content in the leaves of invasive plants was higher than that in native plants. Moreover, the proportions of foliar nucleic acid P and metabolic P in invasive plants were higher than those in native plants. These results suggest that invasive plants have higher P uptake and efficiency in P limited soils (Sun et al. 2022), which may increase the growth and photosynthetic productivity of invasive plants at a lower leaf cost. Consistent with our second hypothesis,

in these tropical plant species, the invasive plants optimize their allocation of P among their foliar P fractions to maintain higher P efficiently in low P soils, and this evolution of adaptive strategies might favor the further success of invasive plants.

Overall, our results suggest that soil organic P mineralization by microorganisms plays a fundamental role in the success of invasive species. In addition, our findings provide new insights into invasive species acclimated to soils with low P availability by remobilizing structural P and residual P to synthesize metabolic P and nucleic acid P to maintain photosynthetic capacity.

# Declarations

This work was funded by the State Key Laboratory for Biology of Plant Diseases and Insect Pests (SKLOF202213) and the National Natural Science Foundation of China (41907023).

### Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

### Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Lingda Zeng, Mengxin Zhao and Feng Sun. All authors read and approved the final manuscript.

# References

1. Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83: 887-889.
2. Burke DJ, Carrino-Kyker SR, Hoke A, Cassidy S, Bialic-Murphy L, Kalisz S (2019) Deer and invasive plant removal alters mycorrhizal fungal communities and soil chemistry: Evidence from a long-term field experiment. Soil Biology and Biochemistry 128: 13-21. doi: 10.1016/j.soilbio.2018.09.031.
3. Ding W, Cong WF, Lambers H (2021) Plant phosphorus-acquisition and -use strategies affect soil carbon cycling. Trends Ecol Evol 36: 899-906. doi: 10.1016/j.tree.2021.06.005.
4. Du E, Terrer C, Pellegrini AFA, Ahlström A, van Lissa CJ, Zhao X, Xia N, Wu X, Jackson RB (2020) Global patterns of terrestrial nitrogen and phosphorus limitation. Nature Geoscience 13: 221-226. doi: 10.1038/s41561-019-0530-4.
5. Elser JJ, Fagan WF, Kerkhoff AJ, Swenson NG, Enquist BJ (2010) Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. The New phytologist 186: 593-608. doi: 10.1111/j.1469-8137.2010.03214.x.
6. Fan Y, Lin F, Yang L, Zhong X, Wang M, Zhou J, Chen Y, Yang Y (2017) Decreased soil organic P fraction associated with ectomycorrhizal fungal activity to meet increased P demand under N

application in a subtropical forest ecosystem. Biology and Fertility of Soils 54: 149-161. doi: 10.1007/s00374-017-1251-8.

7. Fan Y, Zhong X, Lin F, Liu C, Yang L, Wang M, Chen G, Chen Y, Yang Y (2019) Responses of soil phosphorus fractions after nitrogen addition in a subtropical forest ecosystem: Insights from decreased Fe and Al oxides and increased plant roots. Geoderma 337: 246-255. doi: 10.1016/j.geoderma.2018.09.028.
8. Feng YL, Lei YB, Wang RF, Callaway RM, Valiente-Banuet A, Inderjit, Li YP, Zheng YL (2009) Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an invasive plant. Proceedings of the National Academy of Sciences of the United States of America 106: 1853-1856. doi: 10.1073/pnas.0808434106.
9. Fraser TD, Lynch DH, Gaiero J, Khosla K, Dunfield KE (2017) Quantification of bacterial non-specific acid ( phoC) and alkaline ( phoD ) phosphatase genes in bulk and rhizosphere soil from organically managed soybean fields. Applied Soil Ecology 111: 48-56. doi: 10.1016/j.apsoil.2016.11.013.
10. Gao L, Hou B, Cai ML, Zhai JJ, Li WH, Peng CL (2018) General laws of biological invasion based on the sampling of invasive plants in China and the United States. Global Ecology and Conservation 16: e00448. doi: 10.1016/j.gecco.2018.e00448.
11. Grove S, Haubensak KA, Gehring C, Parker IM, D'Antonio C (2017) Mycorrhizae, invasions, and the temporal dynamics of mutualism disruption. Journal of Ecology 105: 1496-1508. doi: 10.1111/1365-2745.12853.
12. Hedley MJ, Stewart JWB, B.S.C. BSC (1982) Changes in Inorganic and Organic Soil Phosphorus Fractions Induced by Cultivation Practices and by Laboratory Incubations. Soil Sci Soc Am J 46: 970-976.
13. Hidaka A, Kitayama K (2011) Allocation of foliar phosphorus fractions and leaf traits of tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu, Borneo. Journal of Ecology 99: 849-857. doi: 10.1111/j.1365-2745.2011.01805.x.
14. Kaur R, Malhotra S, Inderjit (2012) Effects of invasion of Mikania micrantha on germination of rice seedlings, plant richness, chemical properties and respiration of soil. Biology and Fertility of Soils 48: 481-488. doi: 10.1007/s00374-011-0645-2.
15. Liu B, Yan J, Li W, Yin L, Li P, Yu H, Xing L, Cai M, Wang H, Zhao M, Zheng J, Sun F, Wang Z, Jiang Z, Ou Q, Li S, Qu L, Zhang Q, Zheng Y, Qiao X, Xi Y, Zhang Y, Jiang F, Huang C, Liu C, Ren Y, Wang S, Liu H, Guo J, Wang H, Dong H, Peng C, Qian W, Fan W, Wan F (2020) Mikania micrantha genome provides insights into the molecular mechanism of rapid growth. Nature communications 11: 340. doi: 10.1038/s41467-019-13926-4.
16. Liu MC, Kong DL, Lu XR, Huang K, Wang S, Wang WB, Qu B, Feng YL (2017) Higher photosynthesis, nutrient- and energy-use efficiencies contribute to invasiveness of exotic plants in a nutrient poor habitat in northeast China. Physiologia plantarum 160: 373-382. doi: 10.1111/ppl.12566.
17. Mo Q, Li Za, Sayer EJ, Lambers H, Li Y, Zou B, Tang J, Heskel M, Ding Y, Wang F, Ostertag R (2019) Foliar phosphorus fractions reveal how tropical plants maintain photosynthetic rates despite low soil

phosphorus availability. Functional Ecology 33: 503-513. doi: 10.1111/1365-2435.13252.

18. Rasul M, Yasmin S, Suleman M, Zaheer A, Reitz T, Tarkka MT, Islam E, Mirza MS (2019) Glucose dehydrogenase gene containing phosphobacteria for biofortification of Phosphorus with growth promotion of rice. Microbiological research 223-225: 1-12. doi: 10.1016/j.micres.2019.03.004.
19. Sakurai M, Wasaki J, Tomizawa Y, Shinano T, Osaki M (2008) Analysis of bacterial communities on alkaline phosphatase genes in soil supplied with organic matter. Soil Science and Plant Nutrition 54: 62-71. doi: 10.1111/j.1747-0765.2007.00210.x.
20. Sardans J, Bartrons M, Margalef O, Gargallo-Garriga A, Janssens IA, Ciais P, Obersteiner M, Sigurdsson BD, Chen HY, Penuelas J (2017) Plant invasion is associated with higher plant-soil nutrient concentrations in nutrient-poor environments. Global Change Biology 23: 1282-1291. doi: 10.1111/gcb.13384.
21. Sashidhar B, Podile AR (2010) Mineral phosphate solubilization by rhizosphere bacteria and scope for manipulation of the direct oxidation pathway involving glucose dehydrogenase. Journal of applied microbiology 109: 1-12. doi: 10.1111/j.1365-2672.2009.04654.x.
22. Sun F, Ou Q, Yu H, Li N, Peng C (2019) The invasive plant Mikania micrantha affects the soil foodweb and plant-soil nutrient contents in orchards. Soil Biology and Biochemistry 139: 107630. doi: 10.1016/j.soilbio.2019.107630.
23. Sun F, Song C, Wang M, Lai DYF, Tariq A, Zeng F, Zhong Q, Wang F, Li Z, Peng C (2020) Long-term increase in rainfall decreases soil organic phosphorus decomposition in tropical forests. Soil Biology and Biochemistry 151: 108056. doi: 10.1016/j.soilbio.2020.108056.
24. Sun F, Zeng L, Cai M, Chauvat M, Forey E, Tariq A, Graciano C, Zhang Z, Gu Y, Zeng F, Gong Y, Wang F, Wang M (2022) An invasive and native plant differ in their effects on the soil food-web and plant-soil phosphorus cycle. Geoderma 410: 115672. doi: 10.1016/j.geoderma.2021.115672.
25. Tabatabai MA, Bremner JM (1969) Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biology and Biochemistry 1: 301-307.
26. Turner BL (2008) Resource partitioning for soil phosphorus: a hypothesis. Journal of Ecology 96: 698-702. doi: 10.1111/j.1365-2745.2008.01384.x.
27. Wang J, Chen W, Zhu H (2019) Ecological stoichiometry and invasive strategies of two alien species (Bidens pilosa and Mikania micrantha) in subtropical China. Ecological Research 34: 612-623. doi: 10.1111/1440-1703.12027.
28. Wang RL, Zeng RS, Peng SL, Chen BM, Liang XT, Xin XW (2011) Elevated temperature may accelerate invasive expansion of the liana plant Ipomoea cairica. Weed Research 51: 574-580. doi: 10.1111/j.1365-3180.2011.00884.x.
29. Wei X, Hu Y, Razavi BS, Zhou J, Shen J, Nannipieri P, Wu J, Ge T (2019) Rare taxa of alkaline phosphomonoesterase-harboring microorganisms mediate soil phosphorus mineralization. Soil Biology and Biochemistry 131: 62-70. doi: 10.1016/j.soilbio.2018.12.025.
30. Yan L, Zhang X, Han Z, Pang J, Lambers H, Finnegan PM (2019) Responses of foliar phosphorus fractions to soil age are diverse along a 2 Myr dune chronosequence. The New phytologist 223:

1621-1633. doi: 10.1111/nph.15910.

31. Ye XQ, Yan YN, Wu M, Yu FH (2019) High Capacity of Nutrient Accumulation by Invasive Solidago canadensis in a Coastal Grassland. Frontiers in plant science 10: 575. doi: 10.3389/fpls.2019.00575.
32. Zhang P, Li B, Wu J, Hu S (2019) Invasive plants differentially affect soil biota through litter and rhizosphere pathways: a meta-analysis. Ecology letters 22: 200-210. doi: 10.1111/ele.13181.

# Figures

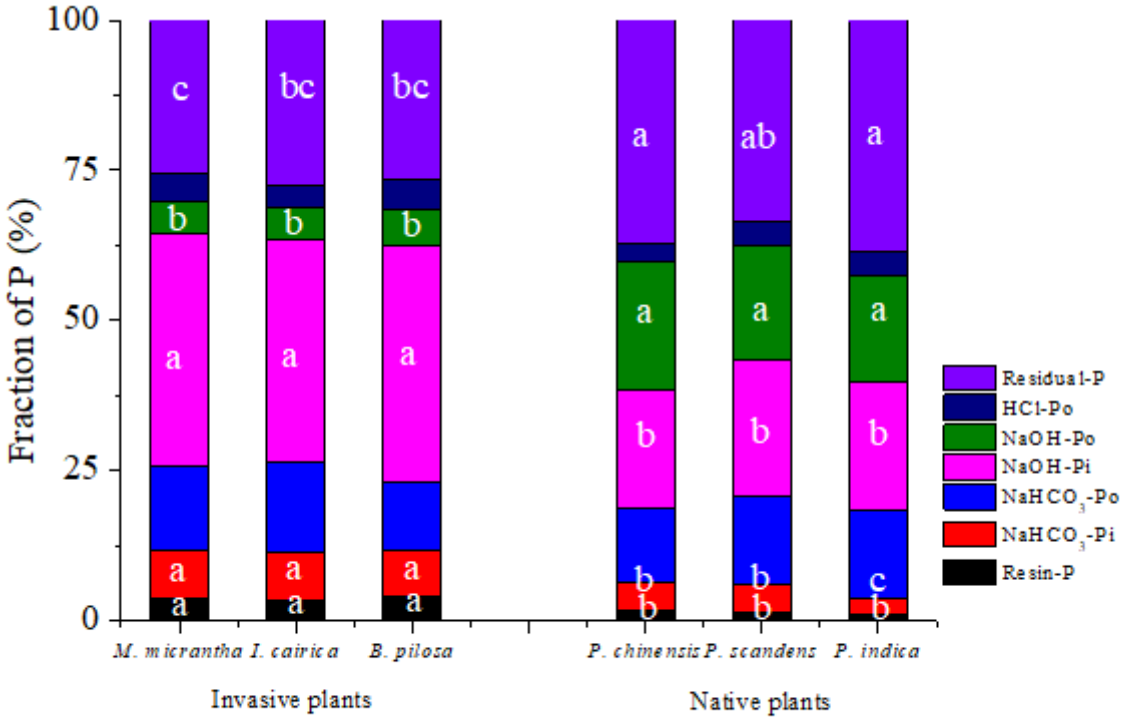
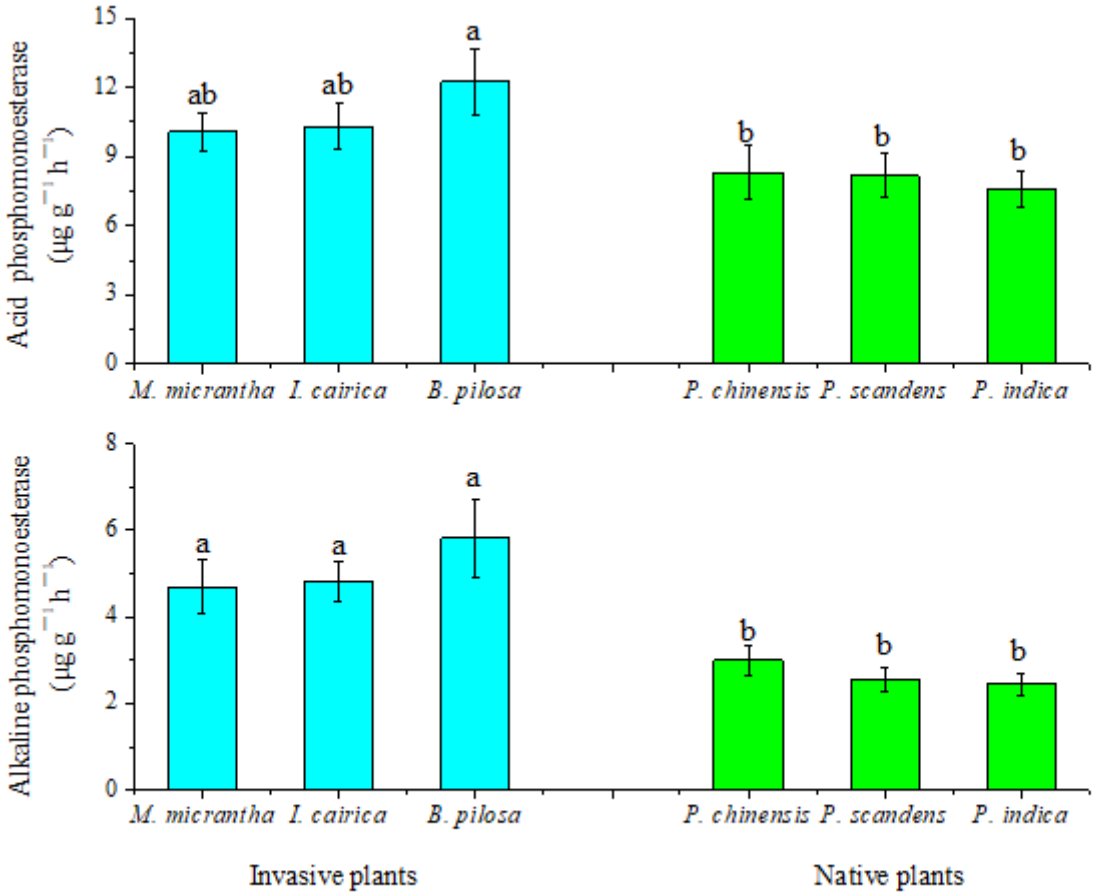


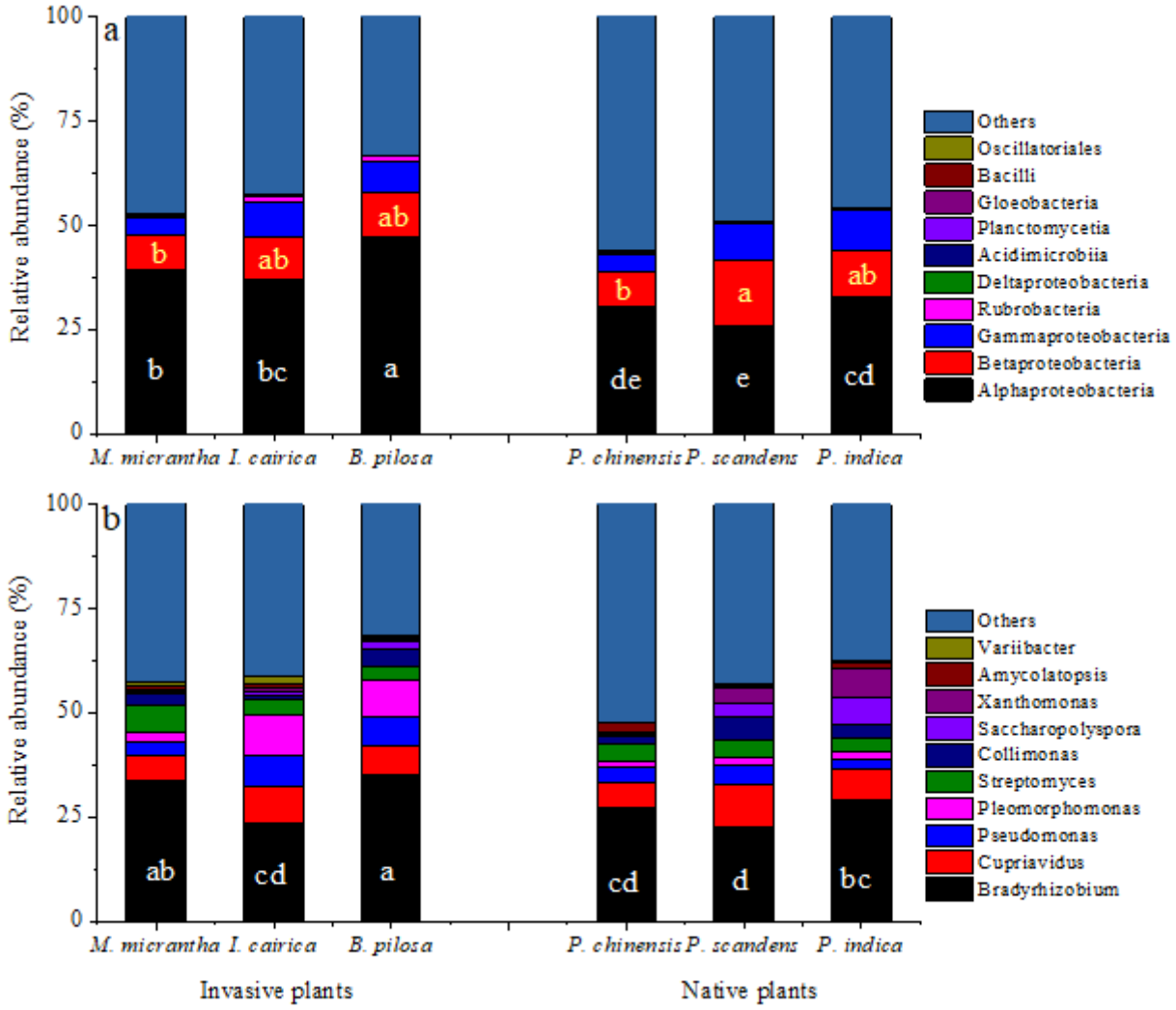

**Figure 1**

Percentages of different P fractions in total P (the sum of all P fractions) in the invasive and native soils. Different letters indicate significant differences at $P < 0.05$.



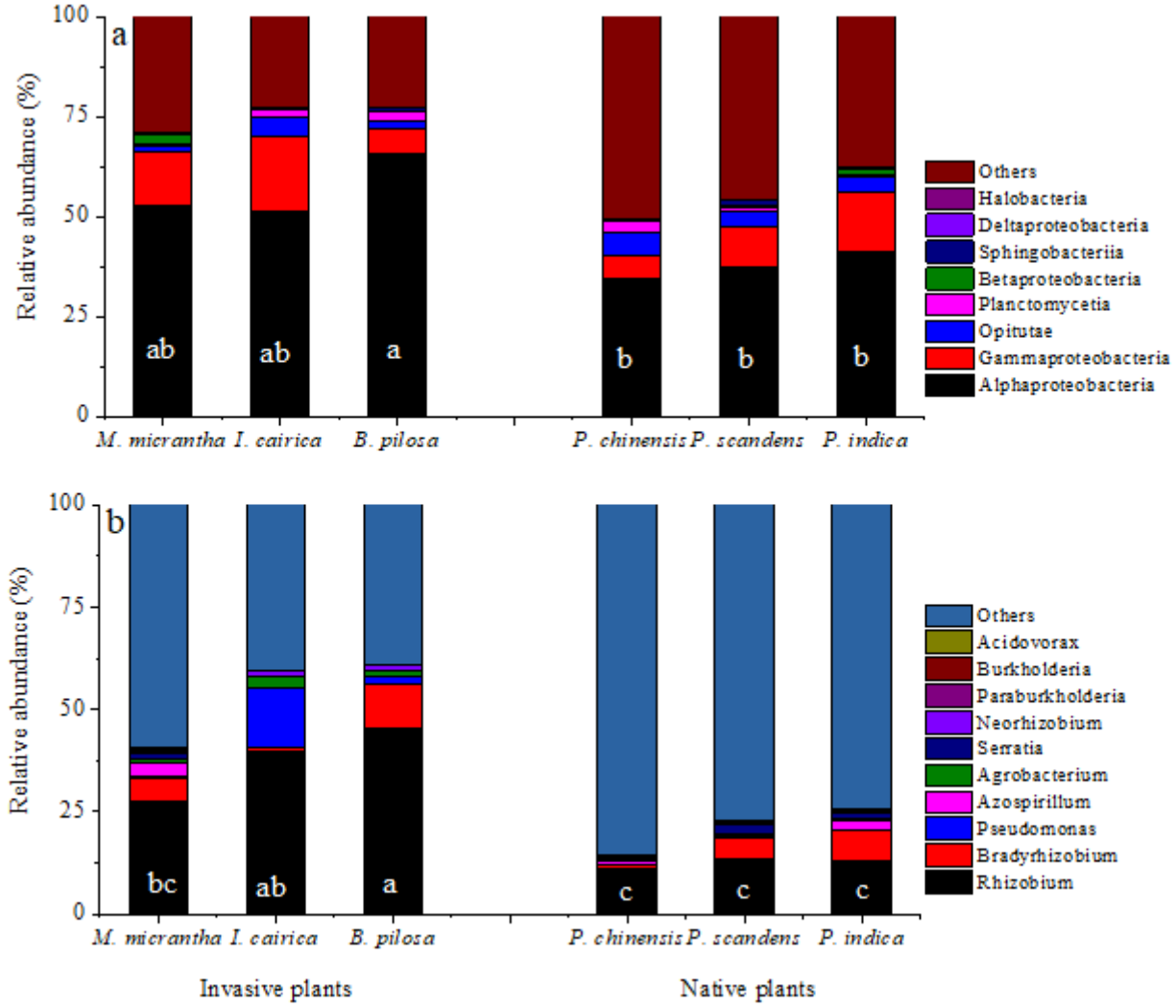

## Figure 2

Changes in soil acid and alkaline phosphomonoesterase activities in the invasive and native soils. Different letters indicate significant differences at $P < 0.05$.




## Figure 3

Changes in taxonomic compositions of the ALP-producing bacteria communities in the invasive and native soils. The relative abundances of ALP-producing bacterial classes (a) and genera (b).




## Figure 4

Changes in taxonomic compositions of the gcd-producing bacteria communities in the invasive and native soils. The relative abundances of gcd-producing bacterial classes (a) and genera (b).

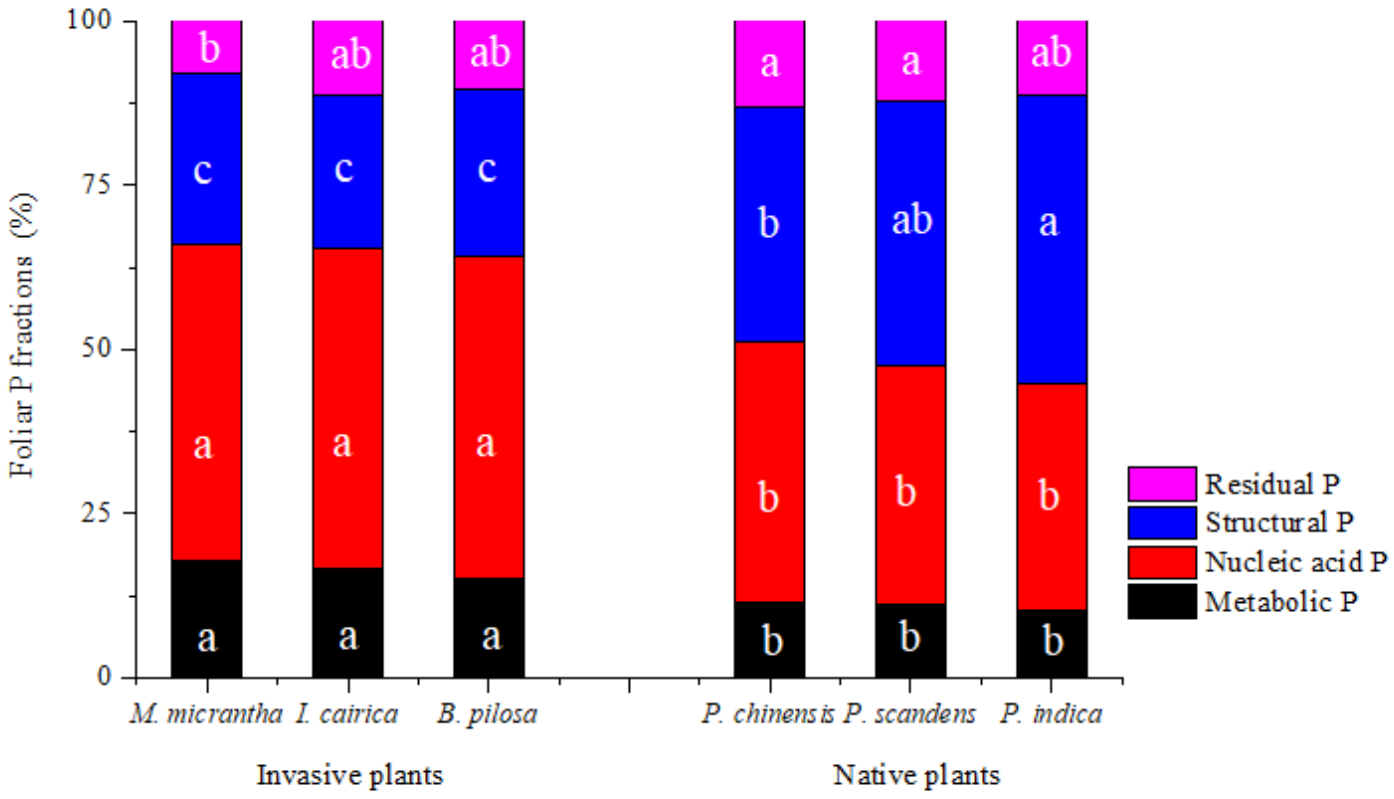



**Figure 5**

Concentrations of foliar P fractions (mg/g dry weight) between the invasive and native plants. Different letters indicate significant differences at $P < 0.05$.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- 1.SupplementaryFigure.doc