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RESEARCH ARTICLE

Global Phosphorus Enrichment Reshapes Terrestrial Phosphorus Cycling

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ABSTRACT

Anthropogenic phosphorus (P) inputs are rapidly altering terrestrial P cycling through plant – soil – microbial interactions; however, global patterns and underlying mechanisms driving these changes remain poorly understood. By performing a global meta-analysis of 1315 observations from 176 studies across diverse natural terrestrial ecosystems, we found that P addition increased P concentrations in foliage, stems, roots, and litter by 62%, 114%, 100% and 63%, respectively. Soil total P, plant-available P, and microbial P concentrations rose by 43%, 221%, and 70%, while leaf P-resorption efficiency and soil phosphatase activity declined by 23% and 15%, respectively. Stem P and soil phosphatase activity exhibited consistent trends across tropical, temperate, and boreal zones, suggesting climate-specific P acquisition strategies. In addition, foliar P responses diverged among ecosystem and plant functional types. These responses were primarily regulated by background soil total P concentration, precipitation, soil pH, and P addition duration and rate. Our findings provide critical insights into the potential consequences of increasing anthropogenic P inputs in natural terrestrial ecosystems, improving our understanding of nutrient cycling and informing future ecosystem management under ongoing global change.

1 | Introduction

Phosphorus (P) is an essential nutrient underpinning terrestrial ecosystem functioning, often limiting plant growth and terrestrial ecosystem productivity (Vitousek et al. 2010; Turner et al. 2018). Over recent decades, anthropogenic P inputs via atmospheric deposition, mineral P fertilizers, and livestock slurry or manure applications have pervasively altered P availability across and within terrestrial ecosystems (Smil 2000). Such changes substantially alter nutrient stoichiometry, disrupt nutrient balance, and shift limitation patterns, ultimately impacting biogeochemical processes that regulate ecosystem productivity and functioning (Linger and Long 2025). Given the tight coupling of carbon (C), nitrogen (N), and P cycles, enhanced anthropogenic P inputs reflect a major driver of environmental change, influencing not only P cycling but also terrestrial C and N dynamics (Treseder and Vitousek 2001; Wang et al. 2010). Indeed, terrestrial C storage is widely recognized as being constrained by both N and P availability (Wieder et al. 2015; Du et al. 2020). However, while many studies have focused on how P addition affects terrestrial C and N cycles (Deng et al. 2017; Feng et al. 2023), uncertainties persist regarding the specific pathways through which external P addition alters the ecosystem P cycling itself, hindering accurate projection of nutrient limitation and C dynamics under ongoing anthropogenic P enrichment.

Ecosystem P cycling comprises a complex network of interlinked pools and processes along the plant – soil – microbial continuum that collectively regulate nutrient uptake and productivity (Helfenstein et al. 2024; Jiang et al. 2024). Numerous field studies have examined the effects of P addition or deposition on individual components of this cycling. For example, external P inputs have been shown to affect plant P concentrations (Firn et al. 2019), P resorption efficiency (PRE) (Zhang et al. 2020), soil P fractions (Li et al. 2016), soil microbial biomass P (Tripathi et al. 2008), and soil phosphatase activity (Mori 2022). However, experimental results are often inconsistent depending on environmental context. Plant P concentrations have been reported to either increase (Aerts et al. 2003) or show no significant change (Alvarez-Clare and Mack 2015) following P inputs. Similarly, responses of plant-available soil P, soil microbial P, and phosphatase activity vary widely among studies, ranging from substantial increases (Xiao et al. 2020) to negligible or even negative changes (Jaerd and Daryl 2020). More importantly, most existing studies have examined only isolated components of P cycling, focusing either on plant or soil processes, without integrating the broader plant – soil – microbial perspective (Marklein and Houlton 2012; Margalef et al. 2021; Mori 2022; Zhang et al. 2022; Wu et al. 2022; Yu et al. 2024). Furthermore, different plant organs, soil P fractions, microbe communities, and enzymes are likely to respond differently to P addition due to their distinct roles in P acquisition, utilization, and storage (Zhang et al. 2018). These complex and interacting responses remain insufficiently understood, such that a generalizable understanding of how the ecosystem P cycle responds to P fertilization and atmospheric deposition, especially across the full plant – soil – microbial system, is still lacking. Addressing this gap requires a comprehensive synthesis of findings from numerous individual studies that together capture the complexity of P cycling processes.

Ecosystem-specific factors such as vegetation structure, physiology, lifespan, management practices, and P acquisition strategies can lead to divergent P cycling responses across different ecosystems or experimental setups (Peng et al. 2023). For example, P addition has been shown to reduce phosphatase activity in tropical forests but had negligible effects in temperate forests and grasslands (Mori 2022), possibly due to the particularly strong P limitation experienced by plants in tropical forests (Camenzind et al. 2018). Plants can acquire P through C resources exchange via mycorrhizal fungi associations (Lambers et al. 2022). However, fungal dominance and P acquisition strategies vary significantly between ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) associations (Plassard and Dell 2010; Carteron et al. 2022), which may result in their contrasting responses to P addition. Likewise, symbiotic N_2-fixing plants generally have a higher P demand due to their high energy (ATP) demand required to produce nitrogenase, making them more sensitive to P availability compared with non-N_2-fixing plants (Toro et al. 2023).

Climate factors, soil properties, and experimental regimes also play key roles in shaping P cycling processes. Plant and soil P cycling processes are sensitive to changes in water availability given its importance for plant P uptake capacity (Reichert et al. 2022; Jiang et al. 2024), soil P leaching dynamics (Liu et al. 2014), soil organic P mineralization (Sun et al. 2020), and the thermodynamic balance of soil P sorption and desorption processes (Barrow 2015), and thus climate can influence the effects of P addition on terrestrial ecosystem P cycling. Variations in soil pH and nutrient availability might also alter P responses in soils and microbial biomass to P addition because soil pH can change redox states (Husson 2013), and regulate soil P availability by affecting the reactivity of soil minerals and microbial activity (Bünemann et al. 2008; Duan et al. 2025). Similarly, soil nutrient availability can shape nutrient balance, microbial community structures, and enzyme activity (Fanin et al. 2015). P addition effects on the ecosystem P cycling may intensify with longer experimental durations and higher P application rates, as plant-soil-microbe systems often require years and sufficient P input to fully adjust to changes in soil P availability (Sun et al. 2022). However, current understanding of these ecological and environmental factors regulating ecosystem P cycling responses to P addition remains fragmented and largely based on limited sites and analyses of isolated factors. Therefore, a comprehensive and quantitative assessment of the relative importance of these drivers at a global scale is urgently needed to improve predictions of ecosystem P dynamics under continued anthropogenic P enrichment.

Here, we compiled a global database comprising 1315 observations from 176 publications that assessed ecosystem P cycling responses to P addition across 159 natural terrestrial ecosystems worldwide (Figure 1). The database includes measurements related to plant, soil, and microbe P cycles, such as concentrations of foliar P, stem P, root P, and litter P, and plant P-resorption efficiency (PRE), as well as soil total P, plant-available P, microbial biomass P, and soil phosphatase activity. Using this database, we tested three hypotheses: (1) P addition would alter ecosystem P strategies and lead to a shift from P recycling to P acquiring strategy, with the effect size and relative sensitivity differing among different ecosystem P cycling variables as added P plays

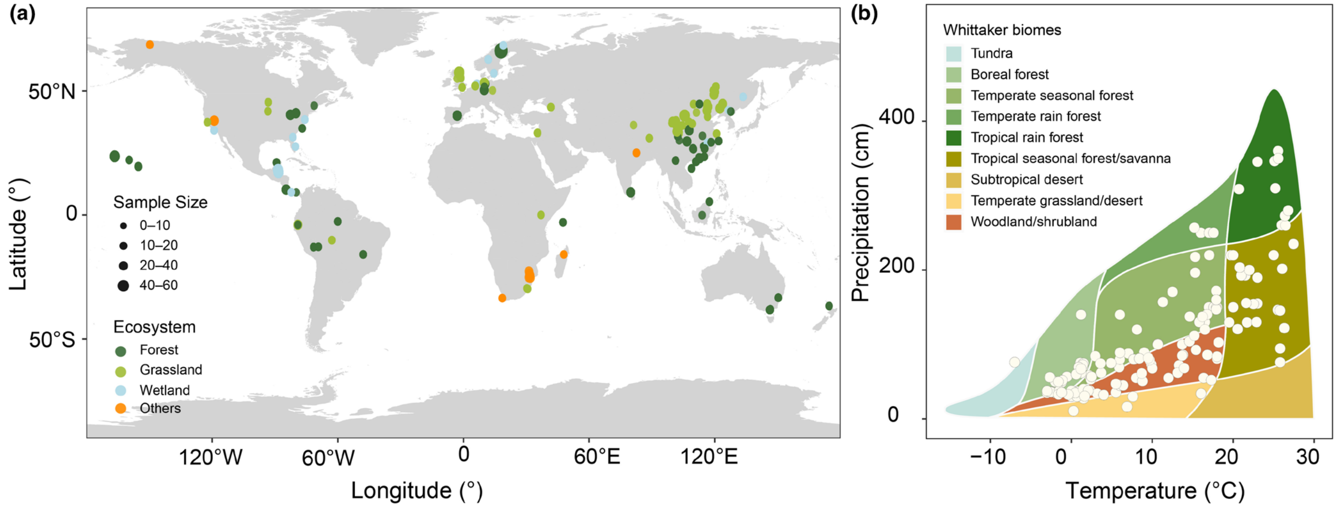


FIGURE 1 | Global site distribution of field phosphorus addition experiments included in this meta-analysis. (a) Location of each sampling site on the background of a world map. Points of different colors and sizes indicate sites with different numbers of samples. This study included a total of 159 sites, with 68 sites for forest, 85 sites for grassland, 19 sites for wetland, and 12 sites for others. (b) Location of each sampling site superimposed upon classic Whittaker biome classification by climate.

different roles in plant, soil, and microbe P cycling processes; (2) ecosystem responses to P addition would also differ across climatic zones, ecosystem types, and plant functional groups because various species growing at different environmental conditions may adopt distinct P acquisition and use strategies; and (3) climatic factors, soil properties, and fertilization regimes would together modulate P responses as they are key regulators of P mineralization, mobilization, adsorption, and desorption in soil, and root uptake and allocation within plant organs. In doing so, our study aims to advance mechanistic understanding of global ecosystem P dynamics and nutrient limitation into terrestrial biosphere models, thereby improving predictions of ecosystem productivity and C dynamics under future global change scenarios.

2 | Materials and Methods

2.1 | Data Collection

We systematically searched for peer-reviewed publications related to the effects of P addition on ecosystem P cycling variables using the Web of Science and China National Knowledge Infrastructure (https://www.cnki.net) databases until March 24, 2023. The searching terms and Boolean combinations used are detailed in Table S1. To expand our dataset, we also screened the reference lists of five prior meta-analysis studies focusing on P addition experiments (Hou et al. 2020; Mori 2022; Zhang et al. 2022; Sun et al. 2022; Feng et al. 2023) and added their relevant data to our newly compiled database.

To minimize selection bias and enhance data comparability, studies were selected based on the following criteria: (i) P addition experiments were conducted under field environments excluding confined environments (e.g., greenhouses, mesocosms or growth chamber), and reported at least one relevant P cycling variables (e.g., foliar, stem, root, or litter P concentration; P resorption efficiency; PRE, calculated using Equation (1); soil total P, plant-available P, microbial P concentrations; or soil phosphatase activity); (ii) Control and P fertilization treatments were conducted under comparable experimental settings, excluding factorial experiments involving additional treatments; (iii) Studies using P fertilizers that also contained N (e.g., diammonium phosphate) were excluded to avoid confounding effects; (iv) Means, standard deviation (SD) or standard error (SE) and sample sizes of ecosystem P cycling variables for both control and P fertilization treatments could be directly extracted or reliably calculated. The study selection process followed the Preferred Reporting Items for Systematic Reviews (PRISMA) guidelines as is illustrated in Figure S1. P resorption efficiency (PRE) was calculated as:

$$PRE = MLCF \times \left(1 - \frac{P_{senesced}}{P_{mature}}\right) \times 100\%, \qquad (1)$$

where P_{mature} and $P_{senesced}$ are the mass-based P concentrations in mature green leaves and senesced leaves, respectively. MLCF (Mass Loss Correction Factor) refers to the mass loss correction factor, defined as the ratio of the dry mass of senesced leaves to that of green leaves (Vergutz et al. 2012).

To comprehensively assess the responses of P cycling under heterogeneous P addition regimes, for each selected publication, we defined one experiment as a multi-level structure of conditions characterized by soil depth, P addition rates, fertilization duration, and experimental sites. In one experiment, we extracted one mean value, sample size and corresponding standard deviation (SD) or standard error (SE) data for different phosphorus (P) variables (e.g., soil total P, foliar P etc.) and named this as one sample When values were presented graphically, data were extracted using WebPlotDigitizer (https://automeris.io). After extraction and compilation, our dataset consisted of 1315 observations from 176 publications (1987–2023), encompassing 159 unique field sites (Figure 1; full data source provided in Appendix S1). Distinct samples were defined as different P variables measured at varying sites, soil depths, P addition rates or experimental duration within a single study. We also recorded environmental variables, geographic coordinates (latitude and longitude) and fertilization regimes from each publication. Environmental data included mean annual temperature (MAT), mean annual precipitation (MAP), background soil pH, background soil organic carbon concentration (SOC), background soil total N concentration (TN), background soil total P concentration (TP) and background plant-available soil P concentration (AP). When not reported, these data were retrieved based on site coordinates from the WorldClim database (http://www.worldclim.org/) and SoilGrids (https://soilgrids.org) databases. Fertilization regime variables included treatment duration (time intervals between the beginning of nutrient addition and sampling date), P fertilization rates, and P fertilizer types. Fertilizer types were categorized as Ca-P (e.g., $Ca(H_2PO_4)_2$), Na-P (e.g., NaH_2PO_4), and K-P (e.g., KH_2PO_4). Fertilizer with unknown composition, listed only as P_2O_5, or mixtures of multiple types were grouped into an “Others” category.

To explore the response variation under different ecological and environmental conditions, we also extracted the information on ecosystem type, climatic zones, plant N_2 fixing status, and mycorrhizal association. Ecosystem types mainly included forests (478 samples), grasslands (651 samples), and wetlands (167 samples); tundra (12 samples) and savanna (14 samples), shrublands (7 samples), and ecotone (2 samples) were grouped as “others” due to limited site numbers. Climatic zones were classified into tropical (23.5°S~23.5°N), temperate (23.5° ~ 46.0°S/N) and boreal (46.0°N~66.0°N) zones following Gwynn et al. (2002) and Yuan et al. (2011). Plant N_2 fixing taxa were classified into N_2-fixing and non-N_2-fixing species using the NodDB database (Kou and Menge 2021; Feng et al. 2023). Mycorrhizal colonizations were categorized into arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), and “Other” based on species-level information from two previous studies (Wang and Qiu 2006; Soudzilovskala et al. 2020). The “Other” category (279 samples) included species with unknown mycorrhizal status, non-mycorrhizal species, and those associated with ericoid mycorrhiza (ErM; 10 samples). Species associated with both AM and EcM associations were classified under EcM, following the approach of Terrer et al. (2021). All species names were verified using The Plant List (http://www.theplantlist.org) prior to classification.

2.2 | Data Analysis

To quantify the effect of P addition on ecosystem P cycling variables, we used the natural logarithmic response ratio (lnRR) as the effect size metric (Hedges et al. 1999). For each sample, the effect size (*lnRR*) was calculated following Equations (2–4):

$$lnRR = \ln\left(\frac{\overline{X_t}}{\overline{X_c}}\right) = \ln\left(\overline{X_t}\right) - \ln\left(\overline{X_c}\right) \tag{2}$$

$$\mathrm{SD} = \mathrm{SE}\sqrt{n} \tag{3}$$

$$v = \frac{\mathrm{SD_t}^2}{\mathrm{n}\overline{\mathrm{X_t}}^2} + \frac{\mathrm{SD_c}^2}{\mathrm{n}\overline{\mathrm{X_c}}^2} \tag{4}$$

where *lnRR*, $\overline{X_t}$ and $\overline{X_c}$ are the logarithm-transformed response ratio, mean value in treatment and control plots of different P cycling variables for each sample, respectively. SD, SE and *n* denote the standard deviation, standard error and sample size of each sample. *v* denotes the variance of each lnRR, which is calculated using both SD (SD_t and SD_c stand for standard deviation of variables in treatment and control plots) and *n*. To evaluate the robustness of our results, we examined publication bias for each P variables using the Egger's test (Egger et al. 1997) and calculated the corrected effect sizes using the trim and fill method (Duval and Tweedie 2000) if publication bias exist. The results showed that correct effect sizes reflected the same trend as their original values (Table S2). We also conducted a Jackknife sensitivity analysis using *leaveout()* function in *metafor* R package to investigate whether individual studies are strong drivers of the results (Basche and Delonge 2019). These analyses confirmed the robustness and stability of our meta-analysis (Figure S2).

To accommodate the dependence arising from the multi-level structure of samples, we employed multi-level random-effects models to consider this hierarchical structure (Harrer et al. 2021; https://bookdown.org/MathiasHarrer/Doing_Meta_Analysis_in_R/). All models were fitted using the rma.mv() function in the metafor R package, with the sampling variance of each effect size supplied as the known level-1 weight.

$$lnRR_{ijk} = \overline{lnRR} + u_{(4)i} + u_{(3)ij} + u_{(2)ijk} + \varepsilon_{ijk} \tag{5}$$

where $lnRR_{ijk}$ refers to the logarithmic response ratio for one single sample; $\overline{lnRR}$ refers to the mean logarithmic response ratio across all samples; ε_{ijk} denotes the level-1 heterogeneity caused by sample errors; $u_{(2)ijk}$ denotes the level-2 heterogeneity deriving from variation in different soil depths, and thus is only adopted in microbial and soil P variables; $u_{(3)ij}$ level-3 denotes the between-experiment heterogeneity from the different designs of the fertilization experiments (i.e., different combinations of P addition rate and duration); $u_{(4)i}$ denotes the level-4 between-site heterogeneity. Residue normality was checked using the “*check_normality*” function in the “performance” package. If residuals violated the normality assumption, 95% confidence intervals (CI) of lnRR were computed using a bootstrapping method with 999 iterations in the “boot” package. An effect was considered significant at $p < 0.05$ if 95% CI did not include zero. To facilitate interpretation, we converted $\overline{lnRR}$ to the percentage change as follows:

$$\text{Percentage change } (\%) = \left(e^{\overline{lnRR}} - 1\right) \times 100\% \tag{6}$$

To explore the variation in response patterns, we examined the scaling relationships among ecosystem P variables using standardized major axis regression (SMA) with *smatr* packages (Rosell et al. 2023).

$$log_{10}Y = \alpha \times \left(log_{10}X\right) + \beta \tag{7}$$

where X and Y represents each of the ecosystem P cycling variables, α and β are the regression slope and intercept, respectively. A slope with 95% CI α overlapping 1 indicates isometry; values significantly above or below 1 indicate faster or slower responses of Y relative to X under P addition (Figure S3).

To investigate the potential roles of biotic and abiotic drivers in conditioning P-addition responses, we implemented mixed-effects models based on Equation (5):

$$lnRR_{ijk} = f(X) + u_{(4)i} + u_{(3)ij} + u_{(2)ijk} + \varepsilon_{ijk} \tag{8}$$

where for classified groups (i.e., climatic zones, ecosystem types, mycorrhizal types and N_2-fixation taxa), X is a fixed factor set as a multi-level factorial variable. For example, if X indicates the climatic zones, then X is a three-level factorial variable containing tropical, temperate and boreal zones; for environmental and experimental factors (i.e., P addition rate, fertilization duration, mean annual precipitation, soil pH, background soil organic C, background soil total N, background soil total P and background plant-available soil P), X is a fixed factor set as a continuous variable.

The random-effects and mixed-effects models described above are listed in Tables S3 and S4. All models are fitted using maximum-likelihood estimation via the rma.mv() function in the metafor R package (Harrer et al. 2021), and the potential influence of each fixed factor was assessed via comparison of likelihood ratio tests (LRTs). In this study, the likelihoods of two candidate models, $L(M_{full})$ and $L(M_{reduced})$, were calculated using Equation R4 and the LRT statistic were calculated through Equation R5 as below:

$$L = P(D \mid \theta, M) \tag{9}$$

$$LRT = 2 \times \ln\left(\frac{L(M_{full})}{L(M_{reduced})}\right) \tag{10}$$

where L denotes the likelihood of the observed data (D) under the model (M) with parameters θ; M_{full} represents the mixed models with more fixed factors while $M_{reduced}$ represents the random models with only random effects. The LRT follows a chi-squared distribution, and a significant value ($p < 0.05$) identifies whether the added fixed factor significantly improves model fit; for example, the effect of climatic zones on stem P concentration.

For the categorical variables (i.e., climatic zones, ecosystem types, mycorrhizal types and N_2-fixation taxa), we compared the mixed-effects models against the random-effects model and list the results in Table S3. For the continuous factors (P addition rate, duration, mean annual precipitation, soil pH, background soil organic C, background soil total N, background soil total P and background plant-available soil P), we list the comparison results in Table S4.

3 | Results

3.1 | Overall Effect of P Addition on Ecosystem P Cycling Variables

Across global terrestrial ecosystems, P addition markedly altered ecosystem P-cycling variables, with positive effects on plant organ P, soil and microbial P and a suppressive effect on PRE and soil phosphatase activity (Figure 2). Among plant organs, P addition increased P concentrations of leaves, stems, and roots, with mean effect sizes of 0.48 (95% confidence interval CI: 0.39–0.57), 0.76 (0.54–0.98), and 0.69 (0.40–0.99), respectively, corresponding to

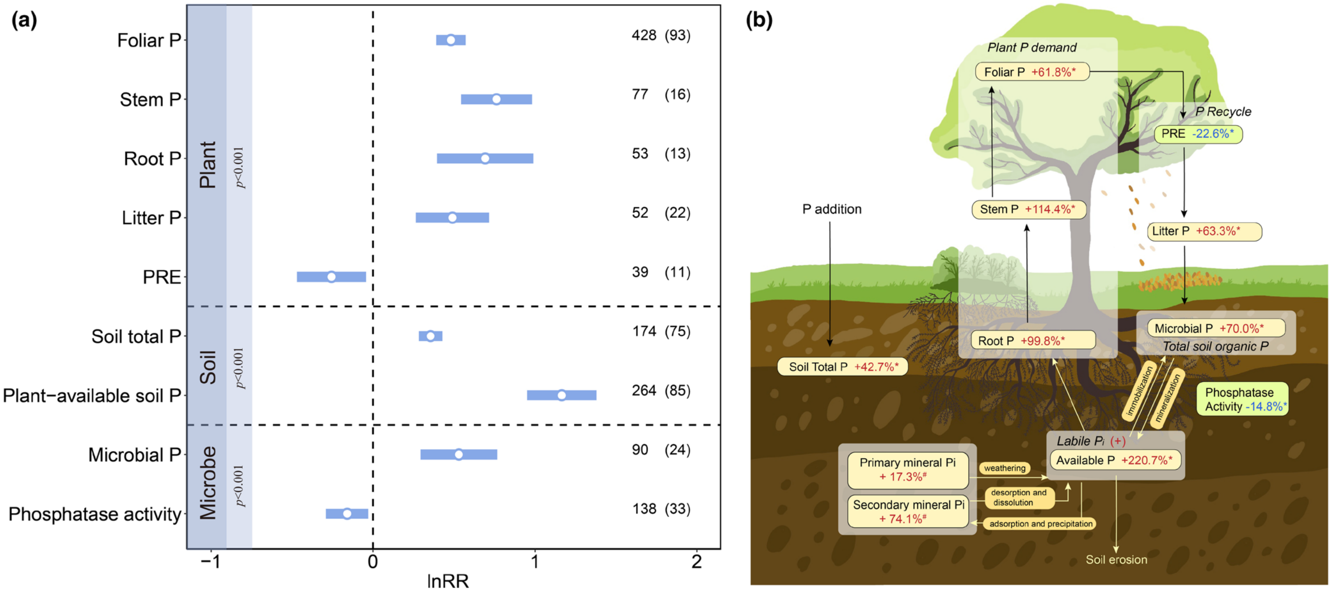


FIGURE 2 | Overall effects of phosphorus (P) addition on ecosystem P cycle. (a) The responses of ecosystem P cycling variables to P addition. Each white point and blue error bar represent the bootstrapped mean and 95% confidence intervals for different variables, respectively. The numbers outside and inside parentheses indicate the numbers of *samples* and *publications*, respectively. (b) A conceptual diagram illustrating how phosphorus (P) addition influences the holistic phosphorus (P) cycling in terrestrial ecosystems. The numbers in boxes represent the average percentage changes of the response variable in the P addition treatment compared with the corresponding values in the control treatment. The asterisk (*) indicates significant effect of P addition on a variable at $p < 0.05$. The symbol "#" indicates the data for primary mineral inorganic phosphorus (Pi) concentration and secondary mineral Pi concentration from Yu et al. (2024). We took the mean effect size of DHCl-Pi as the response for primary mineral P and NaOH-Pi as the response for secondary mineral P (Hou et al. 2018). Symbol "+" and "−" indicate the observed positive and negative effects of P addition, respectively.

relative increases of 61% (48%–77%), 114% (72%–167%), and 100% (48%–169%). For variables associated with internal P recycling processes, litter P concentration also showed a positive response to P addition, with a mean effect size of 0.49 (0.27–0.72), a relative increase of 63% (30%–105%). In contrast, PRE showed a significant decline with a mean effect size of −0.26 (−0.47 to −0.04), dropping by 22% (4%–37%). In soils, P addition significantly elevated soil total P, plant-available soil P, microbial P and suppressed soil phosphatase activity. The mean effect sizes were 0.35 (0.28–0.43) for total soil P, 1.17 (0.95–1.38) for plant-available soil P, 0.53 (0.29–0.77) for microbial P, and −0.16 (−0.29 to −0.03) for phosphatase activity. These correspond to relative changes of 43% (33%–53%), 221% (159%–297%), 70% (34%–115%), and −15% (−25% to −3%), respectively.

To assess relative sensitivities, we examined pairwise relationships among variables using their original values (Figure S3). Among plant organs, stem P concentration was the most sensitive to P addition, followed by litter, foliar, and root P concentrations (Figure S3). Among soil variables, plant-available P was the most responsive, followed by microbial P, total P, and phosphatase activity. The pronounced responsiveness of stem P and plant-available soil P concentrations highlights their potential as sensitive indicators of ecosystem responses to P enrichment.

3.2 | Variations in P Addition Effects Across Climatic Zones, Ecosystem Types and Plant Functional Groups

Ecosystem responses to P addition varied significantly by climatic zones, ecosystem types, and plant functional groups (Figures 3 and 4). Compared with temperate and boreal zones, tropical zones exhibited significantly more sensitivity in stem P ($p < 0.01$) and soil phosphatase activity ($p < 0.001$) (Figure 3a). The mean effect size for stem P was 1.19 in tropical zones, 0.75 in temperate zones, and 0.34 in boreal zones, equivalent to increases of 228%, 112%, and 41%, respectively. For soil phosphatase activity, the mean effect size was −0.60 in tropical zones, −0.02 in temperate zones, and −0.08 in boreal zones, equivalent to decreases of 45%, 2%, and 7%, respectively (Figure 3a). Most ecosystem P cycling variables showed no significant differences among ecosystems and plant functional groups, except foliar P (Figures 3b and 4). Foliar P responses were highest in wetlands (effect size = 0.68, 0.44 to 0.93; 98% increase), followed by grasslands (0.59, 0.46 to 0.71; 80% increase) and forests (0.35, 0.20 to 0.49; 41% increase) (Figure 3b). Similarly, communities dominated by AM plants showed a greater response in foliar P (effect size = 0.56, 0.45 to 0.66; 74% increase) than those dominated by EcM plants (0.31, 0.11 to 0.52; 37% increase) (Figure 4a). Likewise, communities dominated by non N_2-fixers also showed a greater response in foliar P (0.51, 0.42 to 0.61; 68% increase) than those dominated by N_2-fixers (effect size = 0.32, 0.19 to 0.46; 38% increase) (Figure 4b).

3.3 | Environmental and Ecological Drivers of P Addition Effects

We identified key environmental and ecological drivers for the P-addition effect sizes by comparing likelihood ratio tests (LRTs), focusing on variables with sufficient sample size: foliar P, soil total P, plant-available soil P, soil microbial P, and soil phosphatase

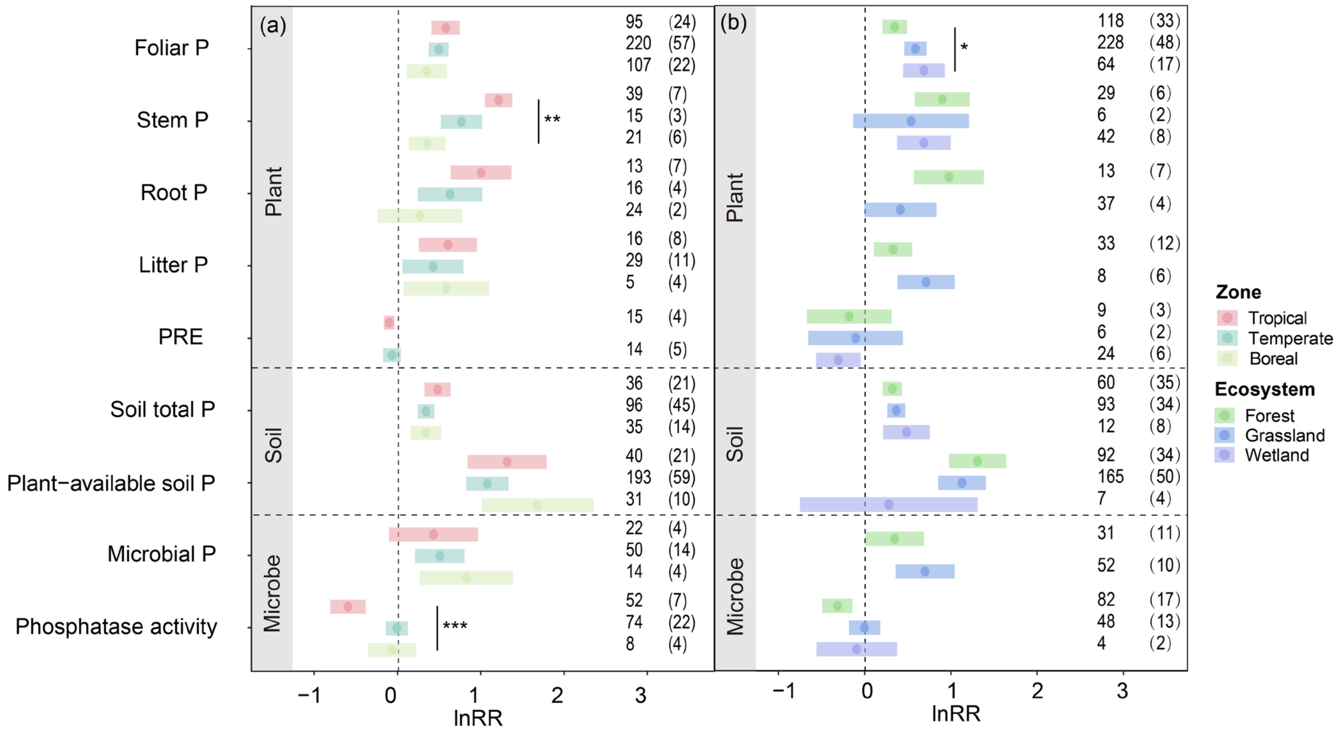


FIGURE 3 | Responses of ecosystem phosphorus (P) cycling variables to P addition among different (a) climatic zones and (b) ecosystem types. The asterisk indicates significant level between different ecosystem types or climatic zones (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). See the caption of Figure R1 for details about the other relevant annotations.

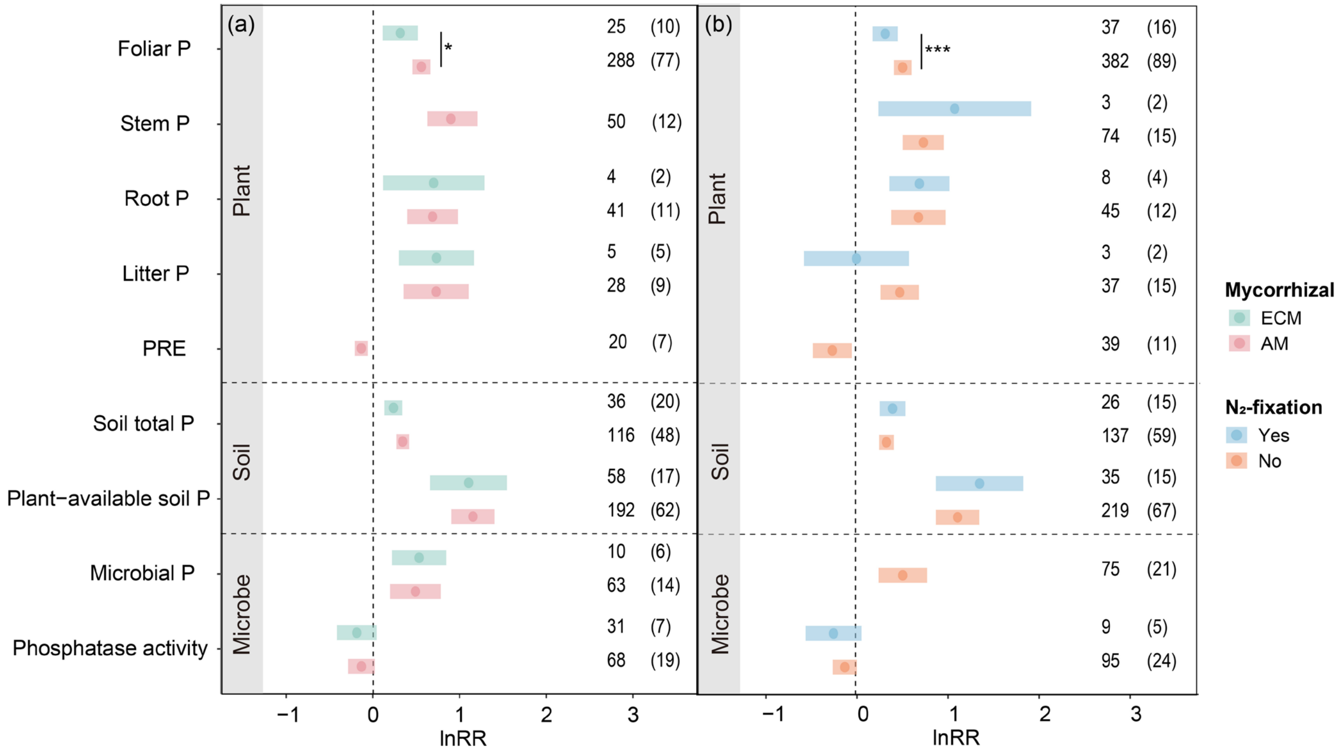


FIGURE 4 | Responses of ecosystem phosphorus (P) cycling variables to P addition among different (a) mycorrhizal types and (b) N_2-fixing taxa. The asterisk indicates significant level among different ecosystem types or climatic zones (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). AM, arbuscular mycorrhiza; ECM, ectomycorrhiza; Yes, symbiotic fixation of atmospheric nitrogen; No, no symbiotic fixation of atmospheric nitrogen. See the caption of Figure R1 for details about the other relevant annotations.

activity. Foliar P concentration was influenced by P fertilizer rate and background soil total N (Figure 5a). Effect sizes increased with P fertilizer rate, but decreased with background soil total N. Plant-available soil P concentration was influenced by P addition rate and duration; the responses increased with P rate and duration (Figure 5b). Soil total P concentration and soil microbial P were both significantly positively associated with P addition rates, increasing as fertilization rates increased (Figure 5c,d). Soil phosphatase activity was shaped by P fertilizer duration, MAP, soil pH, and background soil total P. The negative impacts increased with P fertilization duration and mean annual precipitation but shifted from negative to positive with increasing soil pH and background soil total P (Figure 5e). Collectively, these results reveal that P-addition effects on ecosystem P cycling are modulated by distinct combinations of environmental and ecological drivers for each component, underscoring the complexity of nutrient cycling responses under P enrichment.

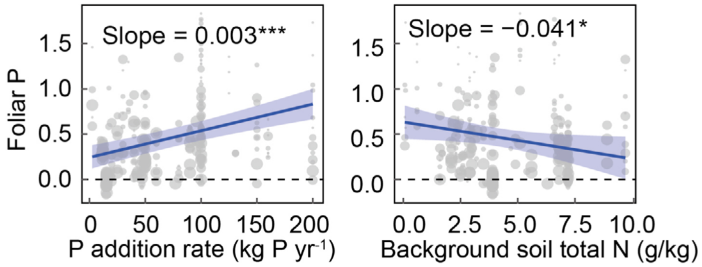
4 | Discussion

4.1 | Shift From P Recycling to P Acquiring

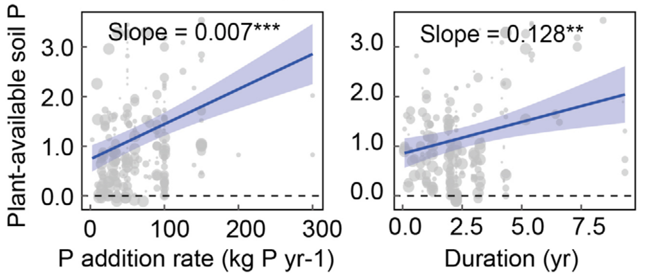
Previous studies have outlined that under P poor conditions ecosystems display more P recycling strategies, while under P rich conditions biological P cycle becomes more open, also called P acquiring strategy (Lang et al. 2016; Helfenstein et al. 2024). Our synthesis reveals that plant–soil-microbial P cycling variables exhibited remarkable divergent responses to P addition across global terrestrial ecosystems (Figure 2). In general, P addition increased plant and soil P concentrations but decreased PRE and soil phosphatase activity. These findings are consistent with previous meta-analyses (Li et al. 2016; Sardans et al. 2017; Margalef et al. 2021; Zhang et al. 2022; Mori 2022), and support the hypothesis that P additions lead to a shift from more P recycling to P acquiring nutrition (Figure 2b). The increases in plant and soil P concentrations are primarily attributed to the direct enhancement of soil P availability by fertilization, which facilitates P uptake by plants (Riskin et al. 2013; Luo et al. 2024). In turn, the alleviation of P limitation reduces the reliance on internal P recycling, leading to lower P resorption efficiency (Feller et al. 2003; Yuan and Chen 2015). Additionally, increased inorganic P availability likely suppresses microbial P limitation, leading to a decline in soil phosphatase activity (Olander and Vitosek 2000; Marklein and Houlton 2012).

Interestingly, non-leaf organs (i.e., stem and root) responded more strongly to P addition than foliar tissue (Figure S3). This may reflect their role as nutrient storage and buffering organs under dynamic environments, and the closer proximity of stem and roots to nutrient resources compared with leaves, which require stable nutrient supplies to support photosynthesis and respiration (Lambers et al. 2008; Schreeg et al. 2014; Sardans et al. 2017). Similarly, plant-available soil P exhibited a higher sensitivity to P addition compared with total soil P, microbial P, and phosphatase activity, consistent with previous findings (Li et al. 2016; Yu et al. 2024). Since P fertilizers typically supply P in inorganic forms, they

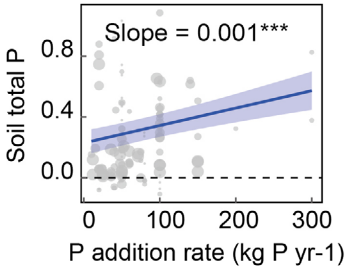
(a) Foliar P (n=304)



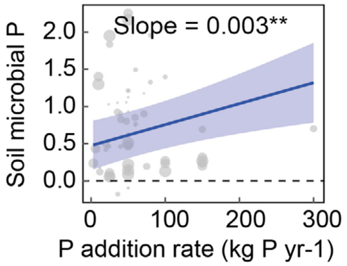
(b) Plant-available soil P (n=220)



(c) Soil total P (n=119)



(d) Soil microbial P (n=58)



(e) Soil phosphatase activity (n=92)

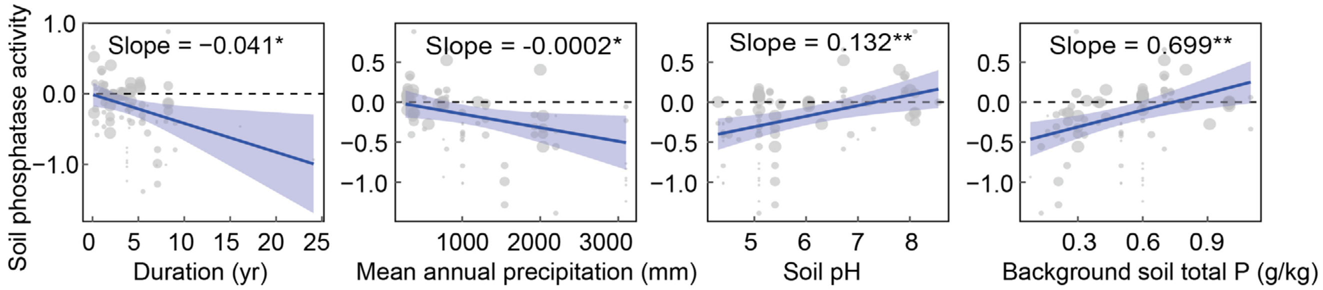


FIGURE 5 | Key predictors in explaining the responses of ecosystem phosphorus (P) cycling variables to P addition. (a) Plant P concentration; (b) Plant-available soil P concentration; (c) Soil total P concentration; (d) Soil microbial P concentration; (e) Soil phosphatase activity. Blue lines and shaded areas represent the mean and 95% confidence intervals of the regression line, respectively. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

directly increase the plant-available P pool (Hou et al. 2020, 2021; Yu et al. 2024), while the majority of total soil P remains bound in forms inaccessible to plants. Collectively, these findings highlight the varying sensitivities of P cycling components, with non-leaf P and plant-available soil P serving as the utmost responsive indicators of nutrient balance under P enrichment.

4.2 | Ecosystem, Climatic, and Plant Functional Group Variation in P Cycling Responses

The magnitude and direction of plant–soil-microbial P cycling responses varied significantly among climatic zones and ecosystem types (Figure 3). In particular, tropical zones showed stronger responses in stem P concentrations and soil phosphatase activity compared to temperate and boreal zones (Figure 3a). These contrasting patterns likely reflect divergent P acquisition strategies prevalent in ecosystems in different climatic zones. Tropical ecosystems with highly weathered and more severe P-limited soils tend to have a very closed P nutrient cycle. With a relatively large fraction of ecosystem P in the biomass relative to the soil, this P is recycled tightly and thus shows more response in plant organ P increase once external P enters (Helfenstein et al. 2024). Similarly, in temperate and boreal zones, P limitation is much less dominant (Vitousek et al. 2010), meaning that these systems often already display less P acquisition strategies and therefore have a smaller decrease in soil phosphatase activity when P is added to the ecosystems. In contrast with climatic zones, ecosystem types and dominant plant functional groups, classified by mycorrhizal associations and N_2-fixing status, exert relatively minor influence on the effect sizes of P addition across most plant – soil – microbial P cycling variables, except for foliar P concentration (Figures 3b and 4). This finding suggests that climate conditions may play a more dominant role than ecosystem types and species traits in governing ecosystem-level responses to P addition. Wetlands exhibited a greater effect size in foliar P than grasslands and forests (Figure 3b). This pattern may stem from the strong P accumulation capacity of wetland plants (Tanner 1996; Vymzal 2007) and reduced P limitation in anaerobic wetland soils (Miller et al. 2001; Vepraskas et al. 2023; Jiang et al. 2024). However, due to limited wetland observations in our datasets, further research is needed to generalize these trends. Grasslands exhibited a greater effect size in foliar P; this may indicate the tendency of trees to show higher resilience and resistance to change under P limitation, owing to the more efficient inorganic P acquisition strategies they have developed to cope with soil inorganic P depletion (thereby expressing smaller responses of foliar P under P enrichment) (Yu et al. 2025).

Communities dominated by AM plants exhibited a greater foliar P response to P addition compared to those dominated by EcM plants (Figure 4a), likely due to higher enzyme investment and C allocation toward P and N acquisition in EcM-dominated ecosystems, thereby experiencing weaker P limitation and consequently showing more attenuated response under P addition (Cheeke et al. 2017). Similarly, communities dominated by non-N_2 fixing species exhibited a greater foliar P response to P addition compared with those dominated by N_2-fixing species (Figure 4b), potentially because N_2-fixing species generally exhibit a larger growth response to P addition, leading to dilution of foliar P concentrations as opposed to reductions in P content per se (Jarrell et al. 1981; Toro et al. 2023).

4.3 | Ecological Factors Regulate the Responses of Ecosystem P Cycling to P Addition

Despite clear global trends, considerable variations existed in the responsiveness of ecosystem P cycling variables to P addition. Our analysis revealed that fertilization regimes, soil background nutrients, MAP, and soil pH were key ecological and environmental drivers of these effect sizes, although their relative contributions differed across specific ecological P cycling components (Figure 5). We suggested that these factors primarily regulated the availability, mobility, and transformation of P in soils, thereby modulating ecosystem responses.

Fertilization regimes, including P application rate and treatment duration, appear to play the most influential roles in regulating ecosystem P addition impacts, as they consistently exhibit significant relationships with P cycling variables responses across plant, soil, and microbial P cycling processes (Figure 5). The positive effects of P addition on foliar P, soil total P, soil plant-available P, and soil microbial P intensified with increasing P application rates. Moreover, longer P fertilization duration further amplified the positive effects on plant-available soil P (Figure 5b) and the negative effects on soil phosphatase activity (Figure 5e). These results align with the previous global syntheses showing that higher-rate and prolonged nutrient additions stimulate plant biomass, soil C accumulation, and shifts in ecosystem C:N:P stoichiometry across global terrestrial ecosystems (Hou et al. 2021; Wu et al. 2022; Sun et al. 2022; Feng et al. 2023). Cumulative P inputs over time may promote plant growth and organic matter inputs (Sun and Chen 2024), which in turn improve soil P retention, water-holding capacity, and cation exchange capacity (Hobbie 2015). These feedbacks can reinforce the increases in plant, soil, and microbial P retention while concurrently suppressing phosphatase activity under sustained P enrichment.

Additionally, P addition effects on foliar P and soil phosphatase activity were also altered by background soil nutrients, MAP and soil pH. P addition impacts on foliar P increased as background soil total N increased (Figure 5a). This trend is consistent with the plant–soil nutrient model described by Perring et al. (2008) that ecosystems experiencing sustained N enrichment tend to shift toward tighter P cycling when (i) the loss rate of available P exceeds that of organic P and (ii) the reactive-P buffering capacity is lower than the minimal critical threshold. Under such conditions, soils conserve P by retaining added P in non-plant-available pools, resulting in reduced translocation of added P to foliage. Thus, in high-N soils where plant and microbial P demand is elevated but soil buffering capacity remains constrained, external P additions would lead to smaller increments in foliar P concentration. The negative effects of P addition on soil phosphatase activity became more pronounced with increasing MAP (Figure 5e). This trend likely reflects intensified P limitation in wetter climates due highly weathered soils, intensified P leaching, and mineral depletion, particularly in humid tropical and subtropical ecosystems (Hou et al. 2018; Helfenstein et al. 2018). Supporting this interpretation, we observed the effects of P addition on soil phosphatase activity shifted from negative to positive along a gradient of rising background soil total P (Figure 5e). Increasing soil pH also shifted the effect of P addition on soil phosphatase activity from negative to positive. This pattern may be due to a shift from organic P mineralization to acid exudation to dissolve calcium-phosphates at higher pH (Eivazi and Tabatabai 1977).

4.4 | Limitations and Future Directions

Although this study provided global-scale analysis for responses of ecosystem P cycling variables to P addition and the associated drivers, some limitations still need to be addressed in future studies. First, our meta-analysis isolates the effects of P addition and does not account for its interactions with other global change drivers (e.g., nitrogen enrichment, warming, altered precipitation, or elevated CO_2), which may jointly regulate P dynamics in natural systems. Second, although our dataset represents the most comprehensive global compilation of plant–soil-microbial P responses to date, the spatial distribution of available field studies remains uneven. This geographic bias may influence the inference of global patterns and the associated drivers. Therefore, expanded field experiments across underrepresented regions are urgently needed to refine predictions of how global P enrichment will alter terrestrial nutrient cycles and ecosystem functioning. Third, our study only investigates the impact of P addition on key P-related variables largely consist of concentrations and phosphatase activity. A more comprehensive mechanistic understanding of the P cycle within the plant–soil-microbial continuum requires integrating detailed indicators that capture P uptake, recycling, and transformation pathways, such as P fluxes and P-related genes abundance. Therefore, further studies focusing on these aspects are needed to fill the current knowledge gaps and provide a more complete picture of ecosystem P dynamics.

5 | Conclusions

This meta-analysis synthesizes the global impacts of P addition on terrestrial ecosystem P cycling and identifies key environmental and ecological drivers shaping plant–soil–microbial responses. P addition consistently increased P concentrations in plant tissues and soils, while reducing P resorption efficiency and soil phosphatase activity, with contrasting sensitivities across P cycling components. Response magnitudes differed among climate zones, ecosystem types, mycorrhizal associations, and N_2-fixing taxa, reflecting context-specific P acquisition strategies. Background nutrient availability, precipitation, and fertilization regimes were dominant modulators of P responses. These findings reveal global patterns and drivers of P cycling under elevated P inputs, providing critical insights into ecosystem P dynamics, limitation, and biogeochemical coupling. The results enhance our ability to predict nutrient cycling, ecosystem productivity, and terrestrial carbon storage under increasing anthropogenic P inputs, particularly for terrestrial biosphere models incorporating P cycling processes.

Author Contributions

Zixin Chen: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing – original draft, writing – review and editing. **Kai Dong:** data curation, formal analysis, visualization, writing – review and editing. **Julian Helfenstein:** investigation, methodology, software, writing – review and editing. **Dafeng Hui:** methodology, validation, formal analysis, writing – review and editing. **Constantin M. Zohner:** formal analysis, methodology, software, writing – review and editing. **Frank Hagedorn:** investigation, methodology, validation, writing – review and editing. **Manuel Delgado-Baquerizo:** software, validation, visualization, writing – review and editing. **Adam R. Martin:** formal analysis, methodology, visualization, writing – review and editing. **Jiguang Feng:** methodology, software, investigation, writing – review and editing. **Nan Yang:** formal analysis, methodology, investigation, writing – review and editing. **Xinli Chen:** investigation, methodology, software, formal analysis, writing – review and editing. **Laurent Augusto:** formal analysis, validation, visualization, writing – review and editing. **Qi Deng:** conceptualization, investigation, methodology, writing – review and editing. **Enqing Hou:** software, investigation, visualization, writing – review and editing. **Mingkai Jiang:** conceptualization, investigation, methodology, writing – review and editing. **Qingshui Yu:** conceptualization, methodology, software, writing – review and editing. **Haihua Shen:** resources, project administration, funding acquisition, methodology, writing – review and editing. **Jordi Sardans:** formal analysis, writing – review and editing, software. **Josep Peñuelas:** formal analysis, writing – review and editing, software. **Hans Lambers:** conceptualization, investigation, visualization, writing – review and editing. **Jingyun Fang:** writing – review and editing, resources, conceptualization, supervision, project administration, funding acquisition, methodology, validation, formal analysis. **Zhengbing Yan:** supervision, resources, project administration, funding acquisition, writing – review and editing, conceptualization, methodology, formal analysis, validation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw data and the R script code demo used in this study have been uploaded in Figshare at https://doi.org/10.6084/m9.figshare.31783327. Mean annual precipitation and mean annual temperature not reported at each site were extracted from the WorldClim database (http://www.worldclim.org/). Soil characteristics not reported were extracted from SoilGrids (https://soilgrids.org) databases.

References

Aerts, R., H. De Caluwe, and B. Beltman. 2003. "Plant Community Mediated vs. Nutritional Controls on Litter Decomposition Rates in Grasslands." *Ecology* 84: 3198–3208. https://doi.org/10.1890/02-0712.

Alvarez-Clare, S., and M. C. Mack. 2015. "Do Foliar, Litter, and Root Nitrogen and Phosphorus Concentrations Reflect Nutrient Limitation in a Lowland Tropical Wet Forest?" *PLoS One* 10: e0123796. https://doi.org/10.1371/journal.pone.0123796.

Barrow, N. J. 2015. "A Mechanistic Model for Describing the Sorption and Desorption of Phosphate by Soil." *European Journal of Soil Science* 66: 9–18. https://doi.org/10.1371/journal.pone.0215702.

Basche, A. D., and M. S. Delonge. 2019. "Comparing Infiltration Rates in Soils Managed With Conventional and Alternative Farming Methods: A Meta-Analysis." *PLoS One* 14: e0215702. https://doi.org/10.1371/journal.pone.0215702.

Bünemann, E. K., R. J. Smernik, A. L. Doolette, et al. 2008. "Forms of Phosphorus in Bacteria and Fungi Isolated From Two Australian Soils." *Soil Biology and Biochemistry* 40: 1908–1915. https://doi.org/10.1016/j.soilbio.2008.03.017.

Camenzind, T., S. Hättenschwiler, K. K. Treseder, A. Lehmann, and M. C. Rillig. 2018. "Nutrient Limitation of Soil Microbial Processes in Tropical Forests." *Ecological Monographs* 88: 4–21. https://doi.org/10.1002/ecm.1279.

Carteron, A., M. Vellend, and E. LalibertÉ. 2022. "Mycorrhizal Dominance Reduces Local Tree Species Diversity Across US Forests." *Nature Ecology & Evolution* 6: 370–374. https://doi.org/10.1038/s41559-021-01634-6.

Cheeke, T. E., R. P. Phillips, and E. R. Brzostek. 2017. "Dominant Mycorrhizal Association of Trees Alters Carbon and Nutrient Cycling by Selecting for Microbial Groups With Distinct Enzyme Function." *New Phytologist* 214: 432–442. https://doi.org/10.1111/nph.14343.

Deng, Q., D. F. Hui, S. Dennis, and K. C. Reddy. 2017. "Responses of Terrestrial Ecosystem Phosphorus Cycling to Nitrogen Addition: A Meta-Analysis." *Global Ecology and Biogeography* 26: 713–728. https://doi.org/10.1111/geb.12576.

Du, E. Z., C. Terrer, A. F. A. Pellegrini, et al. 2020. "Global Patterns of Terrestrial Nitrogen and Phosphorus Limitation." *Nature Geoscience* 13: 221–226. https://doi.org/10.1038/s41561-019-0530-4.

Duan, Y. L., J. B. Zhang, E. Petropoulos, et al. 2025. "Soil Acidification Destabilizes Terrestrial Ecosystems via Decoupling Soil Microbiome." *Global Change Biology* 31: e70174. https://doi.org/10.1111/gcb.70174.

Duval, S., and R. Tweedie. 2000. "Trim and Fill: A Simple Funnel-Plot-Based Method of Testing and Adjusting for Publication Bias in Meta-Analysis." *Biometrics* 56: 455–463. https://doi.org/10.1111/j.0006-341x.2000.00455.x.

Egger, M., G. D. Smith, M. Schneider, and C. Minder. 1997. "Bias in Meta-Analysis Detected by a Simple, Graphical Test." *British Medical Journal* 315: 629–634. https://doi.org/10.1136/bmj.315.7109.629.

Eivazi, F., and M. A. Tabatabai. 1977. "Phosphatases in Soils." *Soil Biology and Biochemistry* 9: 167–172. https://doi.org/10.1016/0038-0717(77)90070-0.

Fanin, N., S. Hättenschwiler, H. Schimann, and N. Fromin. 2015. "Interactive Effects of C, N and P Fertilization on Soil Microbial Community Structure and Function in an Amazonian Rain Forest." *Functional Ecology* 29: 140–150. https://doi.org/10.1111/1365-2435.12329.

Feller, I. C., K. L. Mckee, D. F. Whigham, and J. O'Neill. 2003. "Nitrogen vs. Phosphorus Limitation Across an Ecotonal Gradient in a Mangrove Forest." *Biogeochemistry* 62: 145–175. https://doi.org/10.1023/A:1021166010892.

Feng, J. G., Y. J. Song, and B. Zhu. 2023. "Ecosystem-Dependent Responses of Soil Carbon Storage to Phosphorus Enrichment." *New Phytologist* 238: 2363–2374. https://doi.org/10.1111/nph.18907.

Firn, J., J. M. Mcgree, E. Harvey, et al. 2019. "Leaf Nutrients, Not Specific Leaf Area, Are Consistent Indicators of Elevated Nutrient Inputs." *Nature Ecology & Evolution* 3: 400–406. https://doi.org/10.1038/s41559-018-0790-1.

Gwynn, J. D., B. Saugier, J. Roy, and H. A. Mooney. 2002. "Terrestrial Global Productivity." *Annals of Botany* 89: 797.

Harrer, M., P. Cuijpers, T. A. Furukawa, and D. D. Ebert. 2021. *Doing Meta-Analysis With R: A Hands-On Guide*. Chapman & Hall/CRC Press.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. "The Meta-Analysis of Response Ratios in Experimental Ecology." *Ecology* 80: 1150–1156. https://doi.org/10.1890/0012-9658(1999)080.

Helfenstein, J., B. Ringeval, F. Tamburini, et al. 2024. "Understanding Soil Phosphorus Cycling for Sustainable Development: A Review." *One Earth* 7: 1727–1740. https://doi.org/10.1016/j.oneear.2024.07.020.

Helfenstein, J., F. Tamburini, C. Von Sperber, et al. 2018. "Combining Spectroscopic and Isotopic Techniques Gives a Dynamic View of Phosphorus Cycling in Soil." *Nature Communications* 9: 3226–3234. https://doi.org/10.1038/s41467-018-05731-2.

Hobbie, S. E. 2015. "Plant Species Effects on Nutrient Cycling: Revisiting Litter Feedbacks." *Trends in Ecology & Evolution* 30: 357–363. https://doi.org/10.1016/j.tree.2015.03.015.

Hou, E. Q., C. G. Chen, Y. Q. Luo, et al. 2018. "Effects of Climate on Soil Phosphorus Cycle and Availability in Natural Terrestrial Ecosystems." *Global Change Biology* 24: 3344–3356. https://doi.org/10.1111/gcb.14093.

Hou, E. Q., Y. Q. Luo, Y. W. Kuang, et al. 2020. "Global Meta-Analysis Shows Pervasive Phosphorus Limitation of Aboveground Plant Production in Natural Terrestrial Ecosystems." *Nature Communications* 11: 637. https://doi.org/10.1038/s41467-020-14492-w.

Hou, E. Q., D. Z. Wen, L. F. Jiang, et al. 2021. "Latitudinal Patterns of Terrestrial Phosphorus Limitation Over the Globe." *Ecology Letters* 24: 1420–1431. https://doi.org/10.1111/ele.13761.

Husson, O. 2013. "Redox Potential (Eh) and Ph as Drivers of Soil/Plant/Microorganism Systems: A Transdisciplinary Overview Pointing to Integrative Opportunities for Agronomy." *Plant and Soil* 362: 389–417. https://doi.org/10.1007/s11104-012-1429-7.

Jaerd, L. D., and L. M. Daryl. 2020. "Effects of Elevated pH and Phosphorus Fertilizer on Soil C, N and P Enzyme Stoichiometry in an Acidic Mixed Mesophytic Deciduous Forest." *Soil Biology and Biochemistry* 150: 107996. https://doi.org/10.1016/j.soilbio.2020.107996.

Jarrell, W. M., R. B. Beverly, and N. C. Brady. 1981. "The Dilution Effect in Plant Nutrition Studies." *Advances in Agronomy* 34: 197–224. https://doi.org/10.1016/S0065-2113(08)60887-1.

Jiang, M. K., K. Y. Crous, Y. Carrillo, et al. 2024. "Microbial Competition for Phosphorus Limits the CO_2 Response of a Mature Forest." *Nature* 630: 660–665. https://doi.org/10.1038/s41586-024-07491-0.

Kou, G. S., and D. N. L. Menge. 2021. "Nitrogen-Fixing Trees Increase Soil Nitrous Oxide Emissions: A Meta-Analysis." *Ecology* 102: e03415. https://doi.org/10.1002/ecy.3415.

Lambers, H., F. S. Chapin III, and T. Pons. 2008. "Photosynthesis, Respiration, and Long-Distance Transport." In *Plant Physiological Ecology*, 11–25. Springer.

Lambers, H., P. de Britto Costa, G. R. Cawthray, et al. 2022. "Strategies to Acquire and Use Phosphorus in Phosphorus-Impoverished and Fire-Prone Environments." *Plant and Soil* 476: 133–160. https://doi.org/10.1007/s11104-022-05464-8.

Lang, F., J. Bauhus, E. Frossard, et al. 2016. "Phosphorus in Forest Ecosystems: New Insights From an Ecosystem Nutrition Perspective." *Journal of Plant Nutrition and Soil Science* 179: 129–135. https://doi.org/10.1002/jpln.201500541.

Li, Y., S. L. Niu, and G. R. Yu. 2016. "Aggravated Phosphorus Limitation on Biomass Production Under Increasing Nitrogen Loading: A Meta-Analysis." *Global Change Biology* 22: 934–943. https://doi.org/10.1111/gcb.13125.

Linger, E., and W. Long. 2025. "Phosphorus Limitation Constrains Global Forest Productivity Directly and Indirectly via Forest Community

Structural Attributes: Meta-Analysis." *Global Ecology and Biogeography* 34: e70048. https://doi.org/10.1111/geb.70048.

Liu, R. M., J. W. Wang, J. H. Shi, et al. 2014. "Runoff Characteristics and Nutrient Loss Mechanism From Plain Farmland Under Simulated Rainfall Conditions." *Science of the Total Environment* 468-469: 1069–1077. https://doi.org/10.1016/j.scitotenv.2013.09.035.

Luo, X. Z., A. S. Elrys, L. Zhang, et al. 2024. "The Global Fate of Inorganic Phosphorus Fertilizers Added to Terrestrial Ecosystems." *One Earth* 7: 1402–1413. https://doi.org/10.1016/j.oneear.2024.07.002.

Margalef, O., J. Sardans, J. Maspons, et al. 2021. "The Effects of Global Change on Soil Phosphatase Activity." *Global Change Biology* 27: 5989–6003. https://doi.org/10.1111/gcb.15832.

Marklein, A. R., and B. Z. Houlton. 2012. "Nitrogen Inputs Accelerate Phosphorus Cycling Rates Across a Wide Variety of Terrestrial Ecosystems." *New Phytologist* 193: 696–704. https://doi.org/10.1111/j.1469-8137.2011.03967.x.

Miller, A. J., E. A. G. Schuur, and O. A. Chadwick. 2001. "Redox Control of Phosphorus Pools in Hawaiian Montane Forest Soils." *Geoderma* 102: 219–237. https://doi.org/10.1016/S0016-7061(01)00016-7.

Mori, T. 2022. "Greater Impacts of Phosphorus Fertilization on Soil Phosphatase Activity in Tropical Forests Than in Non-Tropical Natural Terrestrial Ecosystems: A Meta-Analysis." *Pedobiologia* 91-92: 150808. https://doi.org/10.1016/j.pedobi.2022.150808.

Olander, L. P., and P. M. Vitosek. 2000. "Regulation of Soil Phosphatase and Chitinase Activity by N and P Availability." *Biogeochemistry* 49: 175–191.

Peng, Z. Y., Y. T. Wu, L. L. Guo, et al. 2023. "Foliar Nutrient Resorption Stoichiometry and Microbial Phosphatase Catalytic Efficiency Together Alleviate the Relative Phosphorus Limitation in Forest Ecosystems." *New Phytologist* 238: 1033–1044. https://doi.org/10.1111/nph.18797.

Perring, M. P., L. O. Hedin, S. A. Levin, et al. 2008. "Increased Plant Growth From Nitrogen Addition Should Conserve Phosphorus in Terrestrial Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 105: 1971–1976. https://doi.org/10.1073/pnas.0711618105.

Plassard, C., and B. Dell. 2010. "Phosphorus Nutrition of Mycorrhizal Trees." *Tree Physiology* 30: 1129–1139. https://doi.org/10.1093/treephys/tpq063.

Reichert, T., A. Rammig, L. Fuchslueger, L. F. Lugli, C. A. Quesada, and K. Fleischer. 2022. "Plant Phosphorus-Use and -Acquisition Strategies in Amazonia." *New Phytologist* 234: 1126–1143. https://doi.org/10.1111/nph.17985.

Riskin, S. H., S. Porder, C. Neill, A. M. Figueira, C. Tubbesing, and N. Mahowald. 2013. "The Fate of Phosphorus Fertilizer in Amazon Soya Bean Fields." *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 20120154. https://doi.org/10.1098/rstb.2012.0154.

Rosell, J. A., C. R. Marcati, M. E. Olson, et al. 2023. "Inner Bark vs Sapwood Is the Main Driver of Nitrogen and Phosphorus Allocation in Stems and Roots Across Three Tropical Woody Plant Communities." *New Phytologist* 239: 1665–1678. https://doi.org/10.1111/nph.19085.

Sardans, J., O. Grau, H. Y. H. Chen, et al. 2017. "Changes in Nutrient Concentrations of Leaves and Roots in Response to Global Change Factors." *Global Change Biology* 23: 3849–3856. https://doi.org/10.1111/gcb.13721.

Schreeg, L. A., L. S. Santiago, S. J. Wright, and B. L. Turner. 2014. "Stem, Root, and Older Leaf N:P Ratios Are More Responsive Indicators of Soil Nutrient Availability Than New Foliage." *Ecology* 95: 2062–2068. https://doi.org/10.1890/13-1671.1.

Smil, V. 2000. "Phosphorua in the Environment: Natural Flows and Human Interferences." *Annual Review of Environment and Resources* 25: 53–88. https://doi.org/10.1146/annurev.energy.25.1.53.

Soudzilovskala, N. A., S. Vaessen, M. Barcelo, et al. 2020. "Fungalroot: Global Online Database of Plant Mycorrhizal Associations." *New Phytologist* 227: 955–966. https://doi.org/10.1111/nph.16569.

Sun, F., C. J. Song, M. Wang, et al. 2020. "Long-Term Increase in Rainfall Decreases Soil Organic Phosphorus Decomposition in Tropical Forests." *Soil Biology & Biochemistry* 151: 108056. https://doi.org/10.1016/j.soilbio.2020.108056.

Sun, Y., and X. L. Chen. 2024. "Phosphorus Fertilization Enhances Terrestrial Carbon Cycling in Phosphorus-Deficient Ecosystems." *Journal of Environmental Management* 351: 119941.

Sun, Y., C. T. Wang, X. L. Chen, et al. 2022. "Phosphorus Additions Imbalance Terrestrial Ecosystem C:N:P Stoichiometry." *Global Change Biology* 28: 7353–7365. https://doi.org/10.1111/gcb.16417.

Tanner, C. C. 1996. "Plants for Constructed Wetland Treatment Systems–A Comparison of the Growth and Nutrient Uptake of Eight Emergent Species." *Ecological Engineering* 7: 59–83. https://doi.org/10.1016/0925-8574(95)00066-6.

Terrer, C., R. P. Phillips, B. A. Hungate, et al. 2021. "A Trade-Off Between Plant and Soil Carbon Storage Under Elevated CO_2." *Nature* 591: 599–603. https://doi.org/10.1038/s41586-021-03306-8.

Toro, L., A. D. Pereira, A. D. Perez, et al. 2023. "Phosphorus Limitation of Early Growth Differs Between Nitrogen-Fixing and Nonfixing Dry Tropical Forest Tree Species." *New Phytologist* 237: 766–779. https://doi.org/10.1111/nph.18612.

Treseder, K. K., and P. M. Vitousek. 2001. "Effects of Soil Nutrient Availability on Investment in Acquisition of N and P in Hawaiian Rain Forests." *Ecology* 82: 946–954. https://doi.org/10.2307/2679894.

Tripathi, S. K., C. P. Kushwaha, and K. P. Singh. 2008. "Tropical Forest and Savanna Ecosystems Show Differential Impact of N and P Additions on Soil Organic Matter and Aggregate Structure." *Global Change Biology* 14: 2572–2581. https://doi.org/10.1111/j.1365-2486.2008.01702.x.

Turner, B. L., A. T. Brenes, and R. Condit. 2018. "Pervasive Phosphorus Limitation of Tree Species but Not Communities in Tropical Forests." *Nature* 555: 367–370. https://doi.org/10.1038/nature25789.

Vepraskas, M. J., M. Polizzotto, and S. P. Faulkner. 2023. "Redox Chemistry of Hydric Soils." In *Wetland Soils: Encyclopedia of Soils in the Environment*, edited by C. W. van Huyssteen, M. J. Goss, and M. Oliver, 125–128. Academic Press.

Vergutz, L., S. Manzoni, A. Porporato, et al. 2012. "Global Resorption Efficiencies and Concentrations of Carbon and Nutrients in Leaves of Terrestrial Plants." *Ecological Monographs* 82: 205–220. https://doi.org/10.1890/11-0416.1.

Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. "Terrestrial Phosphorus Limitation: Mechanisms, Implications, and Nitrogen–Phosphorus Interactions." *Ecological Applications* 20: 5–15. https://doi.org/10.1890/08-0127.1.

Vymzal, J. 2007. "Removal of Nutrients in Various Types of Constructed Wetlands." *Science of the Total Environment* 380: 48–65. https://doi.org/10.1016/j.scitotenv.2006.09.014.

Wang, B., and Y. L. Qiu. 2006. "Phylogenetic Distribution and Evolution of Mycorrhizas in Land Plants." *Mycorrhiza* 16: 299–363. https://doi.org/10.1007/s00572-005-0033-6.

Wang, Y. P., R. M. Law, and B. Pak. 2010. "A Global Model of Carbon, Nitrogen and Phosphorus Cycles for the Terrestrial Biosphere." *Biogeosciences* 7: 2261–2282. https://doi.org/10.5194/bg-7-2261-2010.

Wieder, W. R., C. C. Cleveland, W. K. Smith, and K. Todd-Brown. 2015. "Future Productivity and Carbon Storage Limited by Terrestrial Nutrient Availability." *Nature Geoscience* 8: 441–444. https://doi.org/10.1038/ngeo2413.

Wu, W. C., F. Wang, A. Q. Xia, et al. 2022. “Meta-Analysis of the Impacts of Phosphorus Addition on Soil Microbes.” *Agriculture, Ecosystems & Environment* 340: 108180. https://doi.org/10.1016/j.agee.2022.108180.

Xiao, H., B. Wang, S. Lu, et al. 2020. “Soil Acidification Reduces the Effects of Short-Term Nutrient Enrichment on Plant and Soil Biota and Their Interactions in Grasslands.” *Global Change Biology* 26: 4626–4637. https://doi.org/10.1111/gcb.15167.

Yu, G. C., M. H. Zheng, Y. P. Wang, et al. 2025. “Trees Show Higher Resilience Than Herbs Under Phosphorus Deficit Induced by 12-Year Simulated Acid Rain.” *Ecology* 106: e70071. https://doi.org/10.1002/ecy.70071.

Yu, Q. S., F. Hagedorn, J. Penuelas, et al. 2024. “Differential Responses of Soil Phosphorus Fractions to Nitrogen and Phosphorus Fertilization: A Global Meta-Analysis.” *Global Biogeochemical Cycles* 38: e2023gb008064. https://doi.org/10.1029/2023GB008064.

Yuan, Z. Y., and H. Y. H. Chen. 2015. “Negative Effects of Fertilization on Plant Nutrient Resorption.” *Ecology* 96: 373–380. https://doi.org/10.1890/14-0140.1.

Yuan, Z. Y., H. Y. H. Chen, and P. B. Reich. 2011. “Global-Scale Latitudinal Patterns of Plant Fine-Root Nitrogen and Phosphorus.” *Nature Communications* 2: 344. https://doi.org/10.1038/ncomms1346.

Zhang, J. H., N. Zhao, C. C. Liu, et al. 2018. “C:N:P Stoichiometry in China's Forests: From Organs to Ecosystems.” *Functional Ecology* 32: 50–60. https://doi.org/10.1111/1365-2435.12979.

Zhang, M. X., L. Y. Zhang, X. Y. Yao, et al. 2022. “Co-Evaluation of Plant Leaf Nutrient Concentrations and Resorption in Response to Fertilization Under Different Nutrient-Limited Conditions.” *Diversity* 14: 385. https://doi.org/10.3390/d14050385.

Zhang, Y., G. S. Yang, F. X. Shi, and R. Mao. 2020. “Biomass Allocation Between Leaf and Stem Regulates Community-Level Plant Nutrient Resorption Efficiency Response to Nitrogen and Phosphorus Additions in a Temperate Wetland of Northeast China.” *Journal of Plant Ecology* 14: 58–66. https://doi.org/10.1093/jpe/rtaa077.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb70827-sup-0001-DataS1.docx. **Table S1:** Search keywords and their combinations used for identifying studies relating to phosphorus (P) addition effects on P-cycling variables in terrestrial ecosystems until March 2023. **Table S2:** Examination of publication bias using Egger's test. **Table S3:** Comparison between random-effects models and mixed-effects models for Figures 3 and 4. **Table S4:** Comparison between random-effects models and mixed-effects models for Figure 5. **Figure S1:** Preferred Reporting Items for Systematic Reviews (PRISMA) Flow Diagram showing the process of study selection in this meta-analysis. **Figure S2:** Jackknife sensitivity of the estimated P addition response effect size (LnRR). **Figure S3:** Heatmap showing the standard major axis correlations between different ecosystem phosphorus (P)-cycling variables under both the control conditions and P-addition treatments. **Figure S4:** Violin Plot showing the differential effects of phosphorus (P) addition on the concentrations of plant P, soil total P and plant-available soil P under various P-fertilizer conditions. **Figure S5:** Heatmap showing the Pearson correlations for environmental predictors. **Data S2:** Appendix references.