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Differential responses of soil phosphorus fractions to nitrogen and phosphorus enrichments: A global meta-analysis

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Abstract

Anthropogenic inputs of nitrogen (N) and phosphorus (P) to terrestrial ecosystems altered soil nutrient cycling. However, the global-scale responses of soil P fractions to N and P inputs and their underlying mechanisms remain elusive.

Here, we conducted a global meta-analysis based on 818 observations of soil P fractions from 99 field N and P addition experiments in forest, grassland, and cropland ecosystems ranging from temperate to tropical zones. In the dataset, two commonly used P fraction extraction methods were employed: the Chang and Jackson inorganic P (Pi) and the Hedley P extraction methods. Our global meta-analysis revealed distinct responses of soil P fractions to N and P enrichments. From studies using the Chang and Jackson method, we found that high N addition promoted the transformation of immobile Pi fractions into Fe/Al-bound Pi and available Pi in surface soils through soil acidification. However, this acid-induced transformation of Pi fractions by N addition was observed only in Ca-rich soils, while in acidic soils, further acidification led to increase P binding by repressing Pi desorption. In contrast, additions of P alone or combined with N significantly increased all soil Pi fractions. Regarding the Hedley P fractions, N addition generally decreased labile organic P by enhancing soil acid phosphatase activity. The response of other P fractions is influenced soil pH, fertilization rates, ecosystem type, and several other factors. P addition increased most soil P fractions. In summary, N inputs can accelerate P transformation in Ca-rich soils but promote P binding in acidic soils, while P inputs directly increase soil available P. These findings are crucial for predicting the effects of future atmospheric N and P deposition on P cycling processes.

Keywords: nitrogen fertilization; phosphorus input; phosphorus fractions; soil acidification; meta-analysis

Key points:

- Nitrogen inputs can accelerate phosphorus transformation in Ca-rich soils but promote P binding in acidic soils
- Soil acidification reduces Pi bioavailability by reducing Pi desorption in acidic soils
- Phosphorus input increases soil labile, moderately labile, and occluded inorganic phosphorus, enhancing soil available P

Plain language summary

Human activities have increased the amount of nitrogen (N) and phosphorus (P) in the environment, which has changed how nutrients cycle in the soil. This study examined the global-scale responses of soil P fractions to N and P inputs using dataset from 99 field experiments worldwide.

The findings revealed distinct responses of soil P fractions to N and P enrichments. High N input resulted in the transformation of immobile inorganic P (Pi) fractions into available Pi in surface soils. This transformation was observed in calcium-rich soils due to soil acidification. In contrast, in acidic soils, the acidification led to increased Pi binding. Moreover, N input generally decreased labile organic P, potentially by enhancing soil enzyme activity. Addition of P alone or combined with N significantly increased soil P fractions. These findings have important implications for predicting the effects of future N and P deposition on P cycling processes and understanding the impacts of nutrient enrichment on soil carbon storage and eutrophication.

1 Introduction

Soil phosphorus (P) is an essential nutrient for plant growth and ecosystem function (Li et al., 2016) and plays a crucial role in various biochemical processes (Turner et al., 2013). However, widespread P limitation exists in global terrestrial ecosystems due to the susceptibility of P to adsorption and immobilization by soil minerals (Vitousek et al., 2010), particularly in tropical and subtropical ecosystems (Augusto et al., 2017; Du et al., 2020). The increasing deposition of atmospheric nitrogen (N) and fertilization have resulted in substantial inputs of exogenous N and P to terrestrial ecosystems (Galloway et al., 2008; Peñuelas et al., 2013; R. Wang et al., 2015), deteriorating soil nutrient cycling with consequences for the global land carbon (C) sink (Wieder et al., 2015) and eutrophication (nutrient excess) of waters and soils (Conley et al., 2009). The faster increase of anthropogenic N inputs to terrestrial ecosystems than P inputs, related to direct and indirect N input into ecosystems, has induced an imbalance between N and P (Penuelas et al., 2020; Peñuelas & Sardans, 2022). Therefore, a comprehensive evaluation of how N and P additions affect different soil P fractions is essential to enhance our understanding and predictions of terrestrial P cycling processes under global environmental changes.

The separation of P fractions with a distinct availability and binding of P represent a powerful approach to elucidate P cycling and environmental sustainability (Helfenstein et al., 2018; Ringeval et al., 2017; X. Yang et al., 2013). Various fractionation techniques are used to separate soil P into different pools based on their chemical properties and availability (Kruse et al., 2015). The Chang and Jackson inorganic P (Pi) and the Hedley P fractionation method are the two most commonly employed approaches in P cycling studies. The Chang and Jackson Pi fractionation method (hereafter Chang and Jackson method), initially developed by Chang and Jackson (1958) and later modified by J. Wang et al. (2010), is a widely applied sequential fractionation technique for separating Pi fractions and used to explore soil Pi mobilization processes in calcareous soil (Kumawat et al., 2022; R. Z. Wang et al., 2022; N. Y. Zhang et al., 2022). It sequentially extracts six Pi fractions from soil samples: soluble (Ca_2-P), exchangeable (Al-P, Fe-P), and precipitated (Ca_8-P, Ca_{10}-P, and Occluded-P) forms. Soluble P is readily available for plant uptake, while exchangeable P is loosely bound to soil particles and can be easily released. Precipitated P forms insoluble compounds, such as Ca-P, which are less available to plants. To better understand the distribution and availability of both Pi and organic P (Po), the Hedley sequential extraction method was proposed (Hedley et al., 1982). This method has undergone refinements and modifications to improve its accuracy and applicability (Tiessen and Moir 1993). The Hedley P fractions can be categorized into labile, moderately labile, and occluded P fractions based on their stability. Now, the Hedley P extraction method is widely used in different soil types and in different ecosystems (Fan et al., 2019; Q. Zhang et al., 2006). In summary, the Chang and Jackson Pi is more commonly used in calcareous soils and can be used to explore the transformation process of mineral-bound Pi (R. Z. Wang et al., 2022), whereas the Hedley P fractions is more widely applicable to a wider range of environments and places more emphasis on the stabilization of both Pi and organic P (Po) in the soil (Guan et al., 2024; Weand et al.,2010; Zheng et al., 2023). Given the characteristics of the two P fraction methods, the effects of anthropogenic N and P additions on soil P fractions can be comprehensively investigated.

Anthropogenic inputs of atmospheric N and P by atmospheric deposition and fertilization to terrestrial ecosystems have altered the available P in soils, resulting in changes in the rate of cycling of multiple nutrients or nutrient imbalances in ecosystems (Peñuelas et al., 2013; Peñuelas et al., 2012; Vu et al., 2008). Several studies have shown that excess N inputs will exacerbate P limitation (Deng et al., 2017; Marklein & Houlton, 2012) with potential consequences for ecosystem functioning (Peñuelas & Sardans, 2022). However, these studies are mostly focused on total soil P (TP), available P (AP), or microbial P (MBP), while there are only relatively few studies based on soil P fractions (Xu et al., 2022; Yu et al., 2022). Moreover, conclusions on the effects of N addition on soil P fractions are ambiguous. Most studies have shown that N additions alter abiotic factors driving soil P fractions such as lowering soil pH, salinity ions, and Fe/ Al oxides (Bowman et al., 2008; Fink et al., 2016; Hou et al., 2018). Other studies have highlighted the role of biological factors controlling soil P fraction transformation, including changes in soil microbial composition, soil enzyme activity, and plant mycorrhizal types (Hu et al., 2022; Q. Wang et al., 2018; Z. L. Zhang et al., 2023). Using the Chang and Jackson Pi fractions, a case study in grassland has revealed that N addition promoted the dissolution of immobile Pi (mainly Ca-bound recalcitrant P) to more available forms of Pi (including Al- and Fe-bound P fractions) by decreasing soil pH in Ca-rich soils (R. Z. Wang et al., 2022). Conversely, Fe and Al ions may be released from soil minerals with soil acidification, and the increased Fe and Al ions may precipitate Pi in the soil solution, thereby reducing the soil AP (Turner et al., 2013). Regarding the Hedley P fractions, simulated N deposition was found to significantly reduce soil labile Pi fractions in temperate forests (K. Yang et al., 2015) and grasslands (Touhami et al., 2022). In contrast, N addition significantly increased the soil available Pi of subtropical broad-leaved evergreen forest soils (Huang et al., 2014). One reason could be that N additions can stimulate phosphatase activity which in turn enhances the release of phosphate from organic P (Fetzer et al., 2022; Hou et al., 2015). However, Weand et al. (2010) found that 10 years of N application did not change soil P fractions in northern hardwood forest.

The inherent level of site N and P natural availability can be also a determinant factor in the response of P cycle in plant soil system to N addition (Fetzer et al., 2022). Increases in P limitation in plants are observed after long-term N deposition (Bragazza et al., 2004) and in experiments simulating N deposition (Braun et al., 2010). In contrast, the effects of N deposition on P limitation in areas with very N-poor soils can remain undetected, as in forests of the northeastern United States (Finzi, 2009) and some areas of Europe (Binkley & Hogberg, 1997).

Although some areas are subjected to simultaneous effects of N and P deposition, the response of soil P fractions to simultaneous N and P additions have rarely been investigated. A recent study has shown that N fertilization combined with P applications exceeding plant requirements cannot mobilize moderately labile inorganic P, which accumulates in high P sorbing soils (Touhami et al., 2022). Overall, these studies suggest that the effects of N addition on soil P fractions can vary depending on many factors, such as soil properties, ecosystem types, N input levels, and the specific P fractionation method used to analyze soil (Fetzer et al., 2022; Hinsinger, 2001; Richardson & Simpson, 2011; Turner, 2008). Therefore, the study of soil P fractions under N and/or P additions is essential for understanding nutrient cycling with the increasing use of fertilizer. In particular, a global perspective is crucial for understanding the general trends in soil P dynamics and identifying factors that modulate the responses of soil P fractions to nutrient enrichment.

This study aims to address this knowledge gap by conducting a comprehensive global meta-analysis on the responses of soil P fractions to N and P fertilization. We compiled and analyzed 99 N and/or P addition experiments and 818 observations of soil P fractions based on the analytical procedures of the Chang and Jackson or Hedley P fractionation methods. By integrating findings from a wide range of studies, we aimed to gain a more robust understanding of the effects of nutrient enrichment on soil P dynamics and underlying mechanisms involved.

2 Materials and methods

2.1 Data source and collection

We employed meta-analysis to investigate the global effects of N and P additions on soil P fractions. A comprehensive literature survey was conducted according to specific search criteria in the Web of Science and China National Knowledge Infrastructure (https://www.cnki.net/) from January 2000 to May 2023. These search keywords are as follows: nitrogen deposition or N deposition or N input or nitrogen addition or N addition or nitrogen fertilization or N fertilization or phosphorus deposition or P deposition or P input or phosphorus addition or P addition or phosphorus fertilization or P fertilization and P fraction* OR phosphorus fraction*. Publications were rigorously screened based on the following criteria: (1) Field studies in terrestrial ecosystems with addition of N only, of P only, and combined N and P additions; (2) each study includes soil P fractionation. By adhering to these criteria and following a PRISMA flow diagram for meta-analysis (**Fig. S1**), a total of 818 observations from 99 publications using either of two P extraction method were identified and compiled to create the dataset (see cited literatures in supplementary materials). In our dataset, soil P fractions had been extracted using the Chang and Jackson method, as well as the Hedley method. Additionally, other variables related to soil P cycling were considered, encompassing soil physicochemical properties, microbial P and N:P ratio, acid phosphatase (ACP), arbuscular mycorrhizal fungi

(AMF), ectomycorrhizal fungi (EMF), and plant P concentrations. The study sites included in this meta-analysis were geographically distributed across a wide range of climatic zones (**Fig. 1**). Furthermore, data on location (latitude and longitude), mean annual temperature (MAT) (1970-2000), mean annual precipitation (MAP), treatment type, intensity, duration of treatments, and soil depth were also extracted. An overview of the basic information included in the analysis was shown in **Table S1**. To extract data from figures, we utilized GetData Graph Digitizer 2.25 (https://getdata-graph-digitizer.com/). For missing standard deviation (SD) data, we employed a linear regression approach to estimate the values based on the log SD and the log of the mean value (Marinho et al., 2015). Whenever MAP and MAT were not reported in the publication, we retrieved this information from the WorldClim database (www.worldclim.com) (Hijmans et al. 2005).

2.2 Data analysis

For observations that only included the standard error (SE), the standard deviation (SD) was estimated with the following formula:

$$SD = SE\sqrt{n} \quad (1)$$

where *n* is the sample size of treatment. The response ratio (RR) of N and P additions on soil P fractions and associated variables were calculated as the natural logarithm-transformed (ln) RR:

$$RR = \ln(\frac{\bar{Y}_T}{\bar{Y}_C}) = \ln(\bar{Y}_T) - \ln(\bar{Y}_C) \quad (2)$$

where the $\bar{Y}_T$ and $\bar{Y}_C$ are the mean of response variables in the treatment and control plots, respectively.

The variance of each RR was calculated as:

$$v = \frac{{SD_T}^2}{n_T{\bar{Y}_T}^2} + \frac{{SD_C}^2}{n_C{\bar{Y}_C}^2} \quad (3)$$

where the n_T and n_C are the sample sizes of the response variables in the treatment and control plots; SD_T and SD_C are the standard deviation of the variables in the treatment and control plots, respectively.

To assess the mean response ratio (RR_{++}) across all studies or within a specific group, we applied a linear mixed-effects model:

$$\mathrm{RR} = RR_{++} + \mu_{site} + e \quad (4)$$

μ_{site} is the random effect of 'site' to explicitly account for between-site heterogeneity, and e is the sampling error. If the 95% confidence interval (CI) of RR_{++} did not overlap zero, the effect of N and P addition on a variable was considered significant at $P < 0.05$. Potential publication bias within each response variable with the data from the entire database was examined using the Egger's test, with sample size as the predictor (Egger et al., 1997). Although we observed publication bias in some variables (**Table S2-5**), the corrected effect sizes were close to original values, indicating that our results were robust to such slight publication biases. To assess the interaction between N and P additions, we used Hedge's d to calculate interaction effect sizes for the response variables (Hedges et al., 1999). Interactions between N and P additions were categorized into three types: additive, synergistic, and antagonistic (Crain et al., 2008). If the 95% confidence interval overlap is zero, the interaction effect is additive. If the individual effects of the N and P additions are negative or in opposite directions, interaction effect sizes >0 were considered antagonistic and <0 were considered synergistic. Linear regression models were used to examine the relationships between RR of soil pH, ACP, and RR of soil P fractions. Furthermore, random-forest analysis was conducted to determine the relatively important factors in affecting the response of soil P fractions to N and P additions. We used percent increase in mean square error (%IncMSE) to rank the predictors in order of importance, and negative values of %IncMSE, which indicate lack of importance. Response ratio and random-forest analysis were performed using the: "metafor" (Viechtbauer, 2010) and "randomforest" (Liaw and Wiener 2002) packages of R, respectively. All statistical analyses were conducted using the software R v.4.2.0 (R core team 2022).

3 Results

3.1 Effects of N and P additions on soil properties, microbial and plant P concentration

Across all studies, N addition, either alone or combined with P, resulted in a decrease in soil pH, while P addition had no significant effect on soil pH (**Fig. 2**). Moreover, N addition increased soil NH_4^--N and NO_3^--N concentrations as well as soil free Fe and Al ions. Notably, N addition did not affect soil available P (AP) and total P (TP) concentrations, whereas additions of P alone or combined with N increased soil AP and TP concentrations. Plant P concentrations were enhanced by both N and P additions, microbial P was increased by P addition, as well as by the combined N and P addition. Nitrogen addition increased microbial N:P ratios and ACP activity, but the combined additions of N and P inhibited ACP activities.

3.2 Effects of N and P additions on soil P fractions

Change and Jackson Pi method sequentially extracts six Pi fractions from soil samples: soluble (Ca_2-P), exchangeable (Al-P, Fe-P), and precipitated (Ca_8-P, Ca_{10}-P, and Occluded-P) forms. Across all studies, N addition did not notably affect the Pi fractions extracted by the Change and Jackson method (**Fig. 3a**). In contrast, additions of P alone or combined with N significantly increased soil Pi fractions whether all study were combined (**Fig. 3b, c**) or grouped (**Fig. S2**). The effects of N addition on soil P fractions were regulated by soil depth, addition rates and durations, and ecosystem types. In surface soil (0-10 cm), N addition increased Ca_2-P, Fe-P, and Al-P, while decreased Ca_8-P and occluded P (**Fig. 4a**). In contrast, in deeper soil (>10 cm), only Al-

P was increased by N addition (**Fig. 4b**). Nitrogen addition at various rates and durations resulted in different changes in P fractions, and these effects also varied among different ecosystems. Low N addition (0-100 kg N ha^{-1} yr^{-1}) decreased only occluded P (**Fig. 4c**), whereas medium N addition (100-200 kg N ha^{-1} yr-1) decreased Al-P as well as occluded P (**Fig. 4d**). High N addition (>200 kg N ha^{-1} yr^{-1}) significantly increased Ca_2-P, Fe-P, and Al-P, while decreasing Ca_8-P and occluded P (**Fig. 4e**). Nitrogen addition for less than five years reduced only occluded P (**Fig. 4f**), whereas both Fe-P and Al-P were increased by N addition between 5 and 10 years (**Fig. 4g**). Among regions, Ca_2-P was reduced by N addition in tropical regions (**Fig. 4i**), Ca_2-P, Fe-P, and Ca_8-P were reduced in subtropical regions (**Fig. 4j**). In contrast, N addition increased Ca_2-P, Fe-P and Al-P, while it decreased occluded P in temperate regions (**Fig. 4k**). In grasslands (**Fig. 4l**), immobile Pi fractions (occluded P and Ca_8-P) was decreased under N addition, while available Pi fractions (Al-P and Ca_2-P) increased.

The Hedley P fractions can be categorized into labile, moderately labile, and occluded P fractions based on their stability. There were overall negative effects of N addition on labile Po ($NaHCO_3$-Po) (**Fig. 3d**), while P addition generally increased soil labile Pi, moderate Pi, and occluded Pi fractions when all data were either combined (**Fig. 3e**) or grouped (**Fig. S3**) **(Table S11-S12)**. Moreover, most soil P fractions showed no remarkable effects of combined N and P addition (**Fig. 3f**), except for a significant increase of H_2O-Pi and resin P, and a reduction for $NaHCO_3$-Po and labile Po. Using Hedge's d to calculate interaction effect sizes for soil P fractions, and we found that the interactions of N and P addition were additive for most soil Hedley P fractions, while synergistic interactions were displayed for labile Pi **(Table S6)**. Nitrogen addition also led to significant declines in soil labile P and occluded P across most subgroups (**Fig. 5**) **(Table S7-S10)**. Specifically, when considering the soil pH range, there was a N-induced decrease of labile Po and occluded Pi when soil pH was less than 4 **(Fig. 5i)**; when soil pH was between 4 and 5 **(Fig. 5j)**, N addition decreased soil labile Po and moderately P. Nitrogen addition reduced labile Pi and occluded Pi when the pH ranged from 5 to 7 **(Fig. 5k)**, and for soil pH greater than 7, it only decreased occluded Pi **(Fig. 5l)**. When N was only added in the form of calcium ammonium nitrate, it reduced most soil P fractions **(Table S7)**. Among ecosystem types in different climatic zones **(Table S8)**, N addition resulted in the reduction of soil labile P (labile Pi and Po) and occluded P (occluded Pi) in tropical forests, labile Po in subtropical forests, and occluded Pi in temperate forests. In temperate grasslands, N addition led to a decrease in labile P (labile Pi and Po) and moderately labile Po, while in subtropical grasslands, it resulted in a decrease in occluded Pi and an increase in occluded Po. Both temperate and subtropical croplands showed a decrease in occluded Pi under N addition, while subtropical croplands also exhibited a decrease in labile Pi. Across different soil types **(Table S9)**, we also found that N addition had negative effects on soil Hedley P fractions in most soil types. However, in fluvo-aquic soils, N addition increased labile Pi and occluded Po while decreasing moderately labile Pi and Po. Moreover, Additionally, in P-poor soils (TP $\leq$ 200 mg kg^{-1}), N addition reduces the soil occluded Pi, while in P-rich soils (TP > 200 mg kg^{-1}), soil labile Po was reduced **(Table S10)**.

3.3 Regulating factors of the effect of N and P additions on soil P fractions

Chang and Jackson Pi fractions showed significant negative correlations between the N responses of soil available Pi fractions (Ca_2-P, Fe-P, and Al-P) and soil pH (**Fig. 5a-c**), while positive correlations existed between soil immobile Pi fractions (Ca_8-P, Ca_{10}-P, and occluded P) and soil pH (**Fig. 5d-f**). This suggests that in Ca-rich soils, soil acidification due to N addition increased soil available Pi fractions while decreasing the soil immobile Pi fractions. Under N addition, all Hedley P fractions (except labile P and occluded Po) were negatively related to soil ACP activities (**Fig. 6**). Among the multiple factors, for the Chang and Jackson Pi fractions (**Fig. 7**), the responses of Ca_2-P, Fe-P, Al-P, and occluded P (Ca_{10}-P) to N and P fertilization were best predicted by fertilizer addition rates; while the response of Ca_8-P was best explained by soil pH. For Hedley P fractions (**Fig. S5**), the predictions for soil labile P, labile Pi, and labile Po were most accurately determined by latitude, soil pH, and soil pH, respectively. For soil moderately labile P, moderately labile Pi, and moderately labile Po, the responses were best predicted by mean annual precipitation, longitude, and soil pH, respectively. Additionally, the responses of soil occluded P, occluded Pi, and occluded Po were primarily influenced by soil pH, mean annual temperature MAT, and soil pH, respectively. Overall, soil pH is a key factor influencing the response of soil P fractions to N and P additions regardless of P extraction methods.

4 Discussion

Given the importance of soil P cycling for terrestrial ecosystems and the inconsistency of methods to extract P fractions, a systematic investigation by a meta-analysis on how N and P enrichments impact soil P fractions is urgently needed. Our global meta-analysis reveals that soil P fractions respond differently to N and P enrichments, but these shifts depend on multiple variables, particularly soil pH. In Ca-rich soils, high N inputs promote the shift from stable P fractions to available fractions. By contrast, in acidic soils, further acidification leads to the binding of soluble P and thus decreases P availability. In support, relating response ratios of P pools to changes of environmental variables **(Fig. 9)** strongly suggest that the changing P pool distribution can be attributed to soil acidification lowering soil pH and an enhanced release of labile Po by increasing phosphatase (ACP) activity. Overall, in the Chang and Jackson Pi fractions, acidification due to N addition promoted the conversion of immobile Pi to available Pi, and P addition, either alone or combined with N, increased soil Pi fractions. The Hedley P fractions revealed generally negative effects on labile P and occluded P, while P addition increased various P fractions. Both P fractionation methods indicated that N input would deplete soil P and thus accelerate the P cycling process. Conversely, P inputs increase most soil P fractions, relieving P limitation.

4.1 Different response of soil P fractions to N and P enrichments

Nitrogen addition had no significant effects on Chang and Jackson Pi fractions across all studies. In specific subgroups (such as surface soil, high N addition, temperate region), we found a consistent pattern that N addition significantly decreased precipitated the Pi fractions (Ca_8-P, Ca_{10}-P, and occluded-P), while increasing the soluble (Ca_2-P) and exchangeable (Al-P, Fe-P) Pi fractions. However, the transformation of soil Pi fraction only occurred in surface soils (0-10 cm) under high N inputs (>200 Kg N $yr^{-1}ha^{-1}$). This finding indicates that N additions alter the distribution among P fractions by an acidification of surface soil induced by high N inputs (Guo et al., 2010; Lu et al. 2014), which could dissolve recalcitrant Pi fractions and dissolute exchangeable Pi fractions to soluble Pi fractions. R. Z. Wang et al. (2022) revealed a similar mechanism of soil P transformation through 10 years of experimentally enhanced N inputs. In addition to soil acidification by the transformation of added NH_4^+, increasing N availability, higher plant growth and P demand could stimulate the release of organic acids from roots to soils to further lower soil pH (Gerke, 2015). However, in temperate grassland with high pH soils, N enrichment mobilized mineral-bound soil Pi, thereby promoting available Pi. By contrast, N addition decreased soil available Pi in both tropical and subtropical areas. In agreement, several new studies also reported that acid addition-induced pH reduction increased the occluded P fractions and decreased the labile P fraction in tropical soil (Hu et al., 2022; Yao et al., 2023). The likely explanation for this pattern is that soil acidification accelerates the solubility of minerals and also results in an enrichment of highly charged exchangeable cations in strongly weathered tropical soils (X. M. Wang et al., 2013), thus enhancing the binding of dissolved Pi to their surfaces. Therefore, future N deposition may lead to a further decrease in soil available P in tropical or subtropical regions characterized by P-poor soils.

In terms of Hedley P fractions, N additions led to significant decline in soil labile P and occluded P across most subgroups, suggesting that N addition does not only dissolves occluded Pi, but also promotes the mineralization of labile Po, especially $NaHCO_3$-Po (H. Z. Zhang et al., 2020), consistent with the generally observed higher ACP activity observed under N addition. However, multiple case studies reported that N addition usually decrease moderately labile Po (NaOH-Po) (Fan et al., 2018; K. Yang et al., 2015), probably because N addition first increases soil labile P (e.g., resin P and $NaHCO_3$-P), at least in part by the mineralization of NaOH-Po related to higher ACP activity. Moreover, the enhanced mineralization of soil moderately labile Po under N addition occurs primarily when soil available Pi is insufficient and the mineralization of $NaHCO_3$-Po does not fully meet the biological requirements (Fetzer et al., 2021). It is important to note that the response of soil P fractions to N addition varied depending on the soil pH range. When the soil pH was below 7, N addition resulted in a decrease in soil labile Pi, labile Po, and occluded Pi. However, when the pH exceeded 7, N addition only decreased occluded Pi, while showing a slight increase in labile Pi, although not reaching a significant level. This aligns with previous studies utilizing the Chang and Jackson Pi fractionation approach, indicating that soil acidification hampers P availability in acidic soils (Hu et al., 2024). The effects of N addition on soil P fractions also exhibited variations across different ecosystem types in different climatic zones. In tropical forests, N addition led to a reduction in both labile P (labile Pi and Po) and occluded P (occluded Pi). Subtropical forests experienced a decrease in labile Po and occluded Pi, while temperate forests showed a decrease in occluded Pi. These results imply that N addition can diminish both immediate and long-term P availability in forest ecosystems, regardless of climatic conditions (Yang et al., 2015; Zeng et al., 2022). In temperate grasslands, N addition resulted in a decrease in labile P (labile Pi and Po) and moderately labile Po, indicating a decline in the pool of easily accessible P for plant uptake. Conversely, subtropical grasslands exhibited a decrease in occluded Pi and an increase in occluded Po, suggesting a potential shift in P sequestration mechanisms in response to N addition (Zhang et al., 2014; Wang et al., 2021). These contrasting responses underscore the significance of accounting for ecosystem type and climatic conditions when evaluating the impacts of N addition on soil P dynamics. The influence of N addition on soil P fractions also varied among different soil types. Overall, N addition had negative effects on soil Hedley P fractions in most soil types, indicating a general reduction in P availability. Furthermore, the effects of N addition on soil P fractions were dependent on the initial soil P content. In P-poor soils (total P ≤ 200 mg kg-1), N addition resulted in a decrease in soil occluded Pi, indicating a potential limitation in the long-term storage of P. In P-rich soils (total P > 200 mg kg-1), N addition led to a reduction in soil labile Po, indicating a disturbance in the pool of readily available P.

Overall, the results of both P fraction methods indicate that N addition depletes soil P, thereby accelerating the soil P cycling. Furthermore, these findings highlight the necessity of considering multiple factors, such as ecosystem type, climatic conditions, soil types, soil pH, and initial soil P content when evaluating the effects of N input on nutrient cycling in ecosystems (Zeng et al., 2022).

In comparison to the complex responses of P fractions to N-additions, both P fraction extraction methods revealed that P addition significantly increased P fractions, especially the Pi fraction, possibly by dissolution of P fertilizers. The lacking P response of organic P fractions agrees with the results of a 65-year P addition experiment (Vu et al., 2008). One explanation could be that the mineralization of Po increases with increasing P inputs at the same rate as the inputs rates of organic P into the soil (through higher plant residue P and microbial P), leading to stable levels of Po (Raguet et al., 2023). Moreover, most Hedley P fractions showed a non-significant response to combined N and P additions. This suggests that P inputs can offset and compensate the soil P depletion promoted by anthropogenic inputs of N. However, the increasing scarcity of P fertilizer may constrain the possibility to perform this compensation effect at great scale.

It is worth considering that the specific P fractions targeted, and the observed effects may vary depending on factors such as soil depth, addition rates and durations, ecosystem types, and climate conditions. Therefore, researchers should carefully select the appropriate extraction method based on their research objectives and account for potential differences in the interpretation of results obtained from different P fractionation methods.

In summary, N addition generally led to a decrease in the labile organic P fraction, likely due to increased microbial activity and uptake. Conversely, P addition increased labile inorganic P fractions, as direct P input enhanced P availability. When examining the combined effects of N and P addition on soil P fractions, most fractions showed no remarkable effects, except for significant increases in H_2O-Pi and resin P, and reductions in $NaHCO_3$-Po and labile Po. The additive effects observed for most soil Hedley P fractions indicate that the impacts of N and P addition on these fractions are independent and do not interact significantly. However, a synergistic interaction was observed for labile Pi, indicating that the combined N and P addition had a more pronounced effect on this specific P fraction (Touhami et al., 2022). These findings suggest that the responses of soil P fractions to N and P addition can vary depending on the specific P fraction analyzed and the interactions between the two nutrient additions.

4.2 Regulation mechanism of soil P fractions to N and P enrichments

The regression analysis based on the Chang and Jackson Pi fractions showed that soil pH was negatively related to soil available Pi fractions, but positively related to recalcitrant Pi fractions. Moreover, our Random Forest Prediction Model (RFPM) has shown that soil pH was a key factor influencing the response of soil P fractions to N and P additions regardless of P extraction method. This suggests that soil pH modified by N addition plays a key role in controlling soil Pi transformation in calcareous soil (Shen et al., 2011), particular in surface soil. Thus, soil acidification induced by N input mobilizes the precipitated Pi fractions and increases soil available Pi in Ca-rich soils. In contrast, N -induced soil acidification may reduce P availability in acidic soils by further increasing the concentrations of reactive Al and Fe phases at lower pH, which promotes the binding of soluble P to their surfaces (Carreira et al., 2000; Wan et al., 2021). The observed dependency of N effects on soil P fractions from the soil type and soil pH has implication for the postulated imbalance between N and P due to chronically high anthropogenic N inputs (Peñuelas et al., 2013). Our meta-analysis strongly suggest that the N-induced P limitation is stronger in acidic soils than in Ca-rich soils, where dissolution of Ca-carbonates binding P may partly compensate for the increasing P shortage. Our study also found that soil phosphatase (ACP) was negatively correlated with most of the Hedley labile and moderate Po, suggesting that N addition led to an increase in soil ACP, which promoted mineralization of labile and moderate Po. This result is consistent with many previous studies of effects of N addition on soil ACP activity (Jian et al., 2016; Marklein & Houlton, 2012; Vitousek et al., 2010). The stimulating effect of N deposition on soil ACP activity has also been identified as one of the main mechanisms for observed changes in soil P fractions in forest soils (Hou et al., 2015) and for the alleviating effect of long-term N loading on P limitation (Chen et al., 2020). Additionally, there are studies showing that mycorrhizal fungi can utilize Po in soil solution and can mobilize soil Fe/Al bound P and mineral P (Becquer et al., 2014; Rosling et al., 2016). However, no significant effect of N addition on arbuscular mycorrhizal or ectomycorrhiza fungi was found in this study, which can partly be related to the few numbers of studies. In addition to soil pH, we also found that the magnitude of N addition was an important factor affecting the transformation of soil P fractions. Low N additions may not lead to significant changes in the soil and may not dissolve and impact the stable mineral-bound P fractions, possibly by their limited acidification effect. Compared to the effect of N addition on soil P fractions, the effect of P addition on soil P fractions is relatively clear. Since the added P forms in the field simulated P deposition experiments were mainly Pi, most of the experimental results showed that the Pi inputs significantly increased the labile Pi, moderate Pi, and occluded Pi in the soil (Kumawat et al., 2022; Vu et al., 2008), while effects on organic P remain small.

5 Conclusion

This meta-analysis reveals that N and P enrichments alter the distribution of P among soil fractions, but these effects depend on soil pH. According to our conceptual framework (**Fig. 8**), high N additions decrease the occluded Pi fractions and enhance soil available Pi fractions in Ca-rich surface soils by reducing soil pH and inducing soil acidification. Additionally, N addition increases ACP activity, promoting the mineralization of labile Po, which contributes to alleviate P limitation. In contrast, in acidic soils, further acidification leads to the formation of reactive surfaces, promoting the binding of soluble P, thereby decreasing P availability. Phosphorus addition directly increases soil labile, moderate, and occluded Pi, enhancing the availability of P in the soil, thereby relieving plant P requirements. These findings should significantly enhance our understanding and predictions of soil P dynamics under future intensified N and P inputs.

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Author contributions

J.F. designed the research; Q.Y. and X.N. collected the data; Q.Y. performed the analyses; Q.Y. wrote the manuscript; F.H., J.P., J.S., C.H., Y.F., X.T., Z.Y., J.Z., C.J., Z.T., M.L and J.F. discussed the design, analyses and results, and edited the manuscript.

Competing interests

The authors declare no competing interests.

Figure captions

Fig.1 Geographical distribution of the studied sites included in this meta-analysis. The circles with different colors represent different fertilization treatment, and the size of the circles indicates the sample size of observations in each site.

Fig.2 Meta-analysis of average effects (%) of N only (a), P only (b), and combined N and P (c) additions on soil properties, microbial P, N:P ratio, mycorrhizal types, ACP, and plant P. ACP, acid phosphatase; AMF, arbuscular mycorrhizal fungi; EMF, ectomycorrhizal fungi. The error bars represent 95% confidence intervals, and the numbers indicate sample sizes of observations. If the 95% CIs do not overlap zero, the effects of N and P additions are considered significant at P <0.05; otherwise, the effects are considered insignificant.

Fig.3 Meta-analysis of overall effects (%) of N only (a, d), P only (b, e), and combined N and P (c, f) additions on soil P fractions according to Chang and Jackson method (a, b, c) and Hedley method (d, e, f).

Fig.4 Meta-analysis of average effects (%) of N only addition on soil P fractions based on Chang and Jackson method across different groups. These groups include different soil depth: 0-10 cm (a), and >10 cm (b); amounts of N addition: 0-100 Kg N yr^{-1} ha^{-1} (c), 100-200 Kg N yr^{-1} ha^{-1} (d), >200 Kg N yr^{-1} ha^{-1} (e); duration of N addition: 0-5 yr (f), 5-10 yr (g), and >10 yr (h); climate zone: tropical (i), subtropical (g), temperate (k); vegetation types: grassland (l), cropland (m).

Fig.5 Meta-analysis of average effects (%) of N only addition on soil P fractions based on Hedley method across different groups. These groups include different soil depth: 0-10 cm (a), and >10 cm (b); amounts of N addition: 0-100 Kg N yr^{-1} ha^{-1} (c), 100-200 Kg N yr^{-1} ha^{-1} (d), >200 Kg N yr^{-1} ha^{-1} (e); duration of N addition: 0-5 yr (f), 5-10 yr (g), and >10 yr (h); soil pH range: pH<4 (i), 4<pH<5 (j), 5<pH<7 (k), pH>7 (l); climate zone: tropical (m), subtropical (n), temperate (o); vegetation types: forest (p), grassland (q), cropland (r).

Fig.6 Relationship of the responses of soil P fractions based on Chang and Jackson method with that of soil pH under N only addition. When the relationships are not significant (i.e. P > 0.05), the regression lines and their 95%confidence intervals are not drawn. The sizes of points are proportional to their corresponding weights. RR, response ratio.

Fig.7 Relationship of the responses of soil P fractions based on Hedley method with that of soil ACP under N only addition.

Fig.8 Random Forest analysis to identify the main predictors of the response ratios of soil P fractions based on Chang and Jackson method (a-f). The percent increase in mean squared errors (%IncMSE) represents the relative importance (%) of main predictors, and negative values of %IncMSE, which indicate lack of importance. Asterisks denote statistics of significance: * $P<0.05$; **$p<0.01$; ***$P<0.0001$; ns, not significant.

Fig.9 Conceptual illustration of different responses processes of soil P fractions to N and/or P additions. High N addition rates would indirectly promote P mobilization through soil acidification. Meanwhile high N addition rates stimulate acid phosphatase (ACP) activity and increase the mineralization of Liable Po thus meet the plant P demands. P addition would directly increase soil labile, moderate, and occluded Pi and increase plant P. Combined N and P additions decreased labile Po and increase H_2O Pi and resin P.

Figure 1

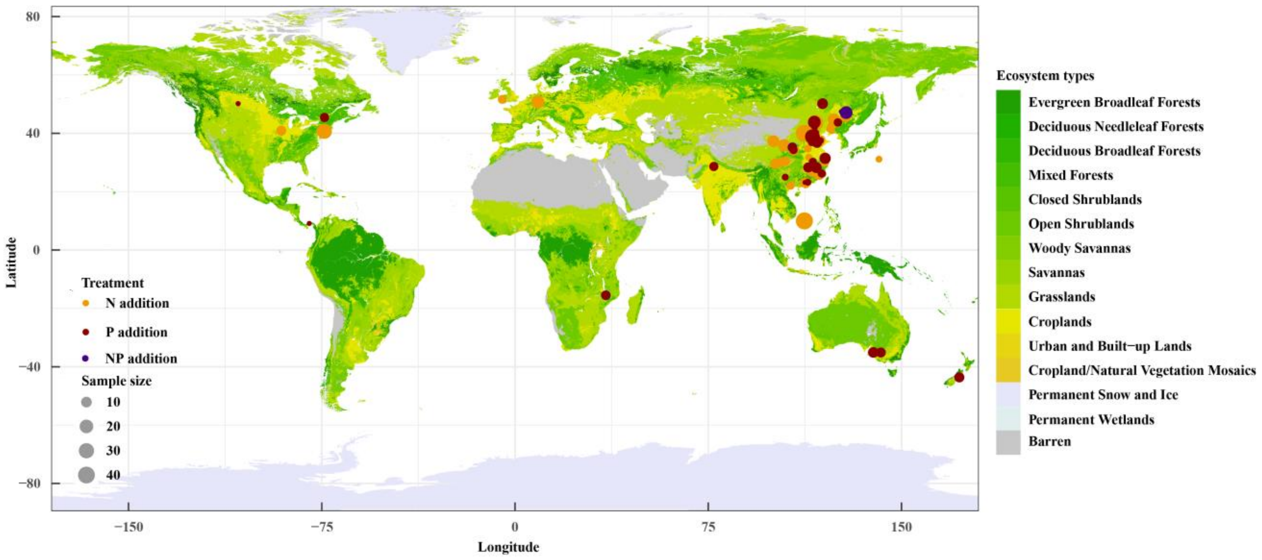

80
40
0
−40
−80
Latitude
−150
−75
0
75
150
Longitude
Treatment
N addition
P addition
NP addition
Sample size
10
20
30
40
Ecosystem types
Evergreen Broadleaf Forests
Deciduous Needleleaf Forests
Deciduous Broadleaf Forests
Mixed Forests
Closed Shrublands
Open Shrublands
Woody Savannas
Savannas
Grasslands
Croplands
Urban and Built−up Lands
Cropland/Natural Vegetation Mosaics
Permanent Snow and Ice
Permanent Wetlands
Barren

Figure 2

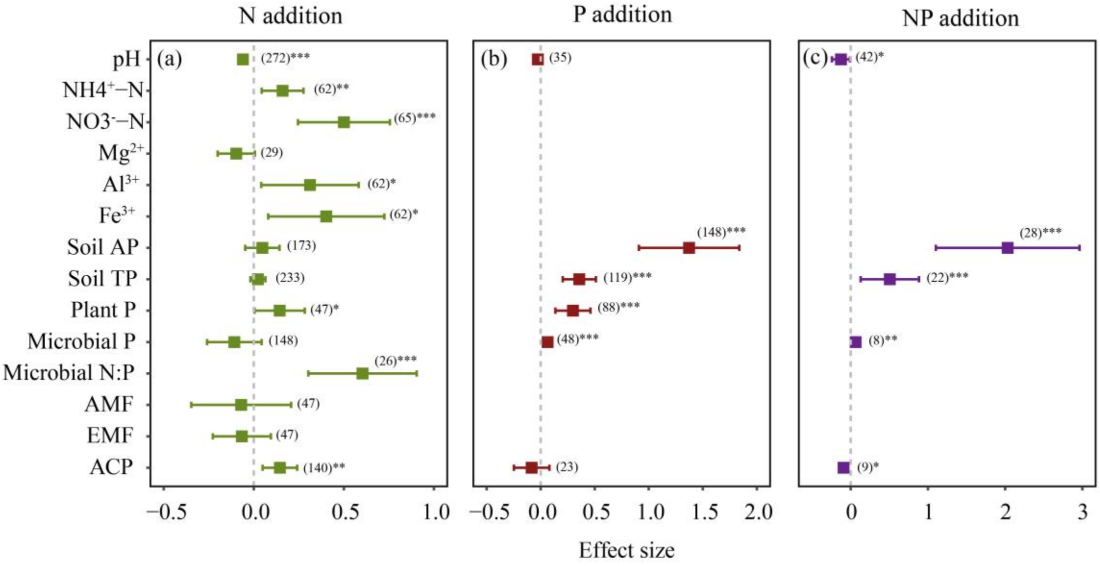
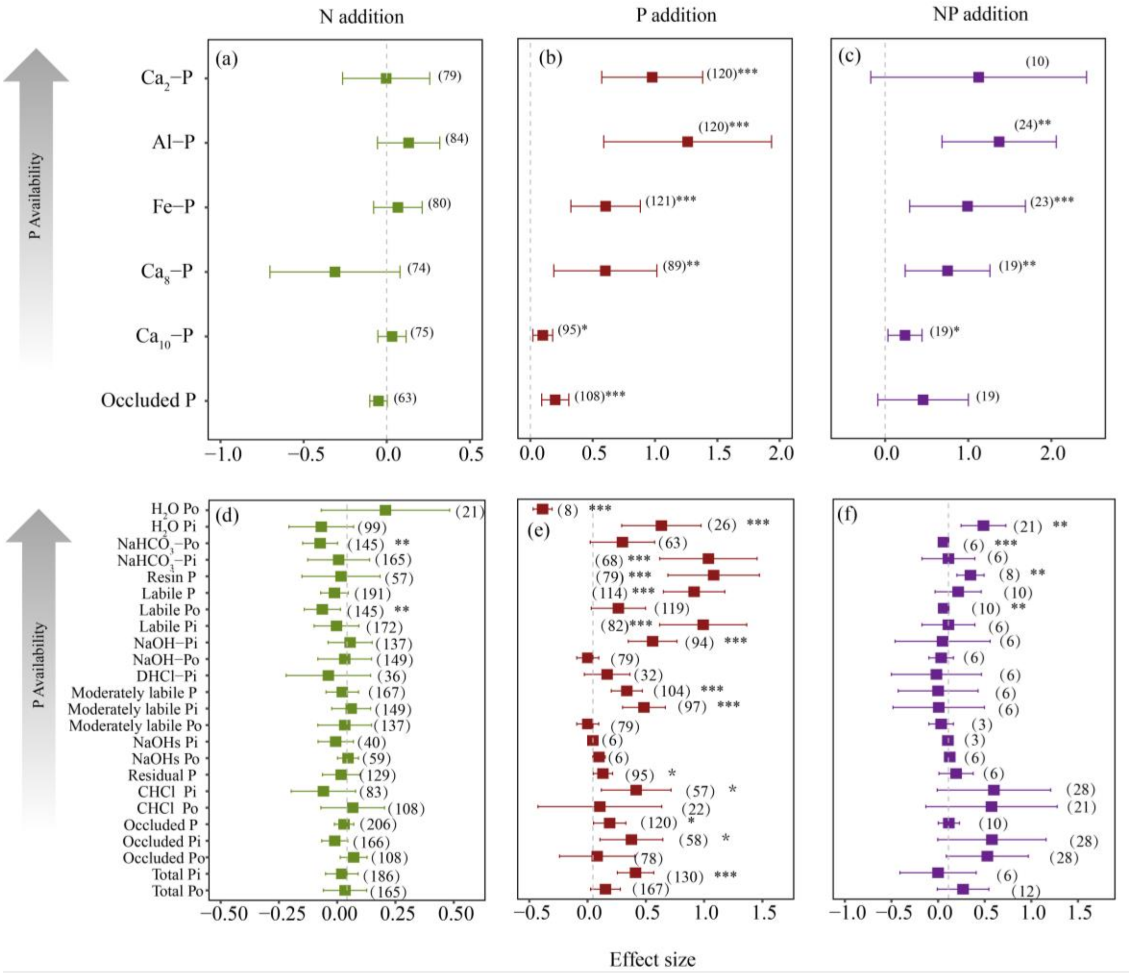

N addition
P addition
NP addition
pH
NH4⁺−N
NO3⁻−N
Mg²⁺
Al³⁺
Fe³⁺
Soil AP
Soil TP
Plant P
Microbial P
Microbial N:P
AMF
EMF
ACP
(a)
(272)***
(62)**
(65)***
(29)
(62)*
(62)*
(173)
(233)
(47)*
(148)
(26)***
(47)
(47)
(140)**
(b)
(35)
(148)***
(119)***
(88)***
(48)***
(23)
(c)
(42)*
(28)***
(22)***
(8)**
(9)*
−0.5
0.0
0.5
1.0
−0.5
0.0
0.5
1.0
1.5
2.0
0
1
2
3
Effect size

Figure 3



N addition
P addition
NP addition
P Availability
(a)
(b)
(c)
Ca$_2$−P
Al−P
Fe−P
Ca$_8$−P
Ca$_{10}$−P
Occluded P
(79)
(84)
(80)
(74)
(75)
(63)
(120)***
(120)***
(121)***
(89)**
(95)*
(108)***
(10)
(24)**
(23)***
(19)**
(19)*
(19)
−1.0 −0.5 0.0 0.5
0.0 0.5 1.0 1.5 2.0
0.0 1.0 2.0
(d)
(e)
(f)
H$_2$O Po
H$_2$O Pi
NaHCO$_3$−Po
NaHCO$_3$−Pi
Resin P
Labile P
Labile Po
Labile Pi
NaOH−Pi
NaOH−Po
DHCl−Pi
Moderately labile P
Moderately labile Pi
Moderately labile Po
NaOHs Pi
NaOHs Po
Residual P
CHCl Pi
CHCl Po
Occluded P
Occluded Pi
Occluded Po
Total Pi
Total Po
(21)
(99)
(145) **
(165)
(57)
(191)
(145) **
(172)
(137)
(149)
(36)
(167)
(149)
(137)
(40)
(59)
(129)
(83)
(108)
(206)
(166)
(108)
(186)
(165)
(8) ***
(26) ***
(63)
(68) ***
(79) ***
(114) ***
(119)
(82)***
(94) ***
(79)
(32)
(104) ***
(97) ***
(79)
(6)
(6)
(95) *
(57) *
(22)
(120) *
(58) *
(78)
(130) ***
(167)
(21) **
(6) ***
(6)
(8) **
(10)
(10) **
(6)
(6)
(6)
(6)
(6)
(6)
(3)
(3)
(6)
(6)
(28)
(21)
(10)
(28)
(28)
(6)
(12)
−0.50 −0.25 0.00 0.25 0.50
−0.5 0.0 0.5 1.0 1.5
−1.0 −0.5 0.0 0.5 1.0 1.5
Effect size

Figure 4

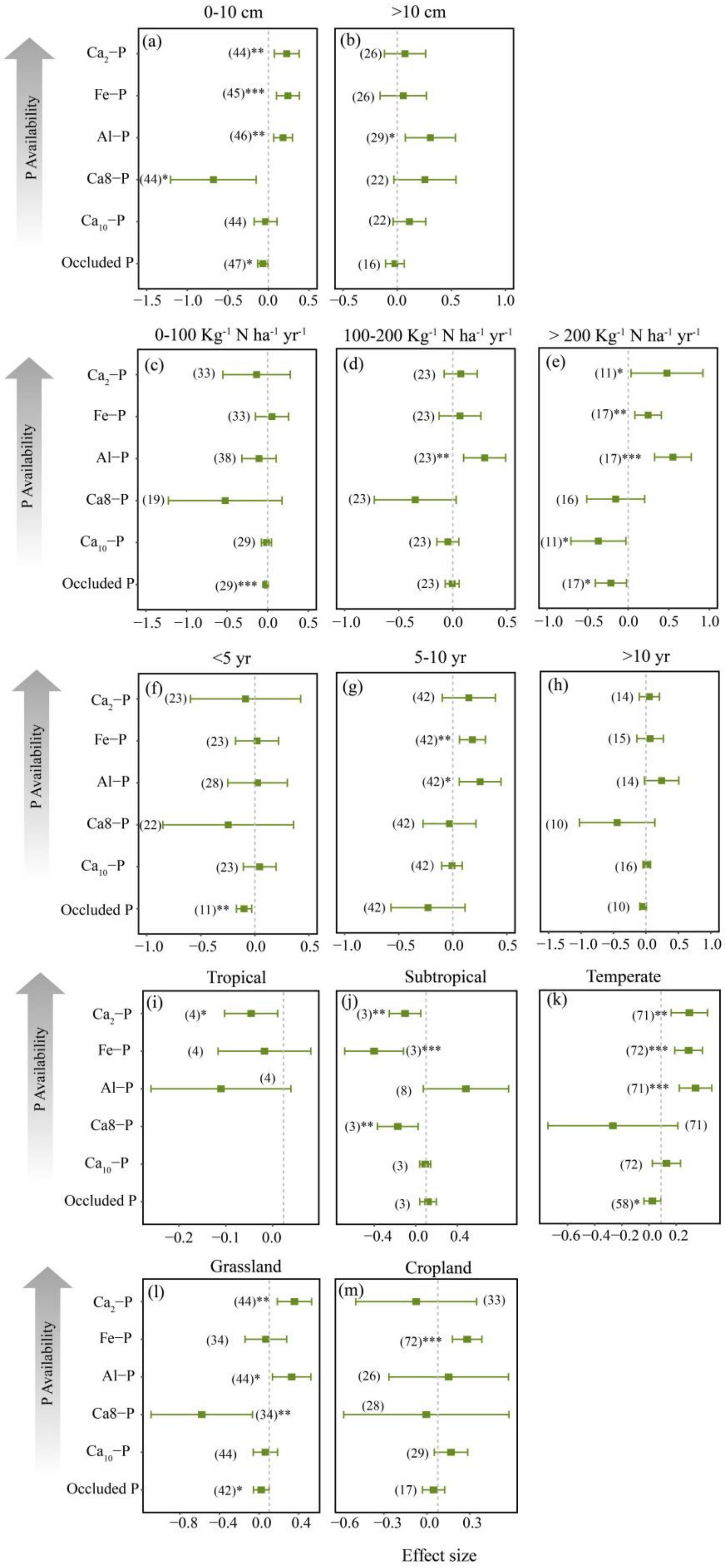
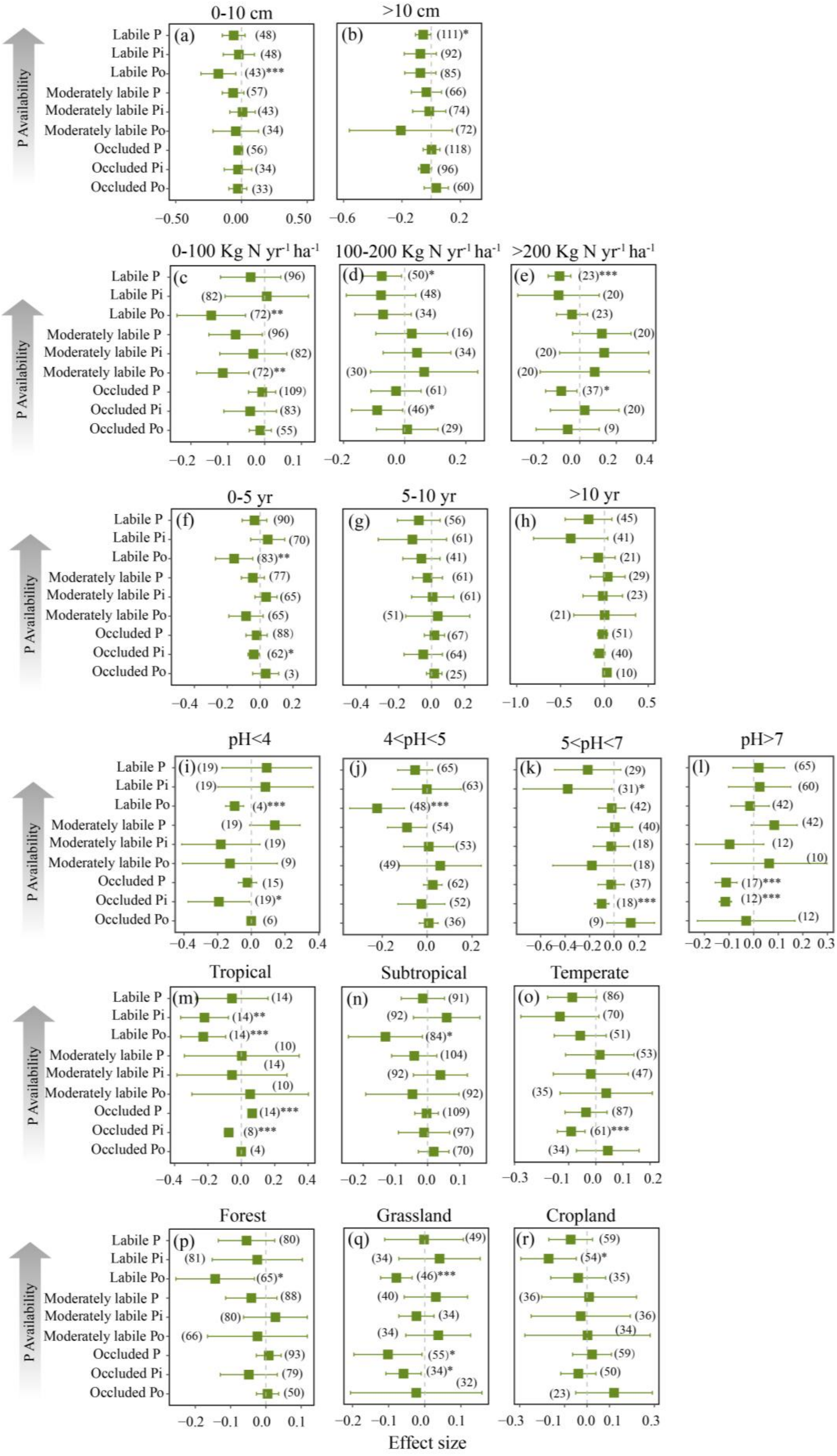

0-10 cm
>10 cm
0-100 Kg-1 N ha-1 yr-1
100-200 Kg-1 N ha-1 yr-1
> 200 Kg-1 N ha-1 yr-1
<5 yr
5-10 yr
>10 yr
Tropical
Subtropical
Temperate
Grassland
Cropland
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
P Availability
Ca2−P
Fe−P
Al−P
Ca8−P
Ca10−P
Occluded P
(44)**
(45)***
(46)**
(44)*
(44)
(47)*
(26)
(26)
(29)*
(22)
(22)
(16)
(33)
(33)
(38)
(19)
(29)
(29)***
(23)
(23)
(23)**
(23)
(23)
(23)
(11)*
(17)**
(17)***
(16)
(11)*
(17)*
(23)
(23)
(28)
(22)
(23)
(11)**
(42)
(42)**
(42)*
(42)
(42)
(42)
(14)
(15)
(14)
(10)
(16)
(10)
(4)*
(4)
(4)
(3)**
(3)***
(8)
(3)**
(3)
(3)
(71)**
(72)***
(71)***
(71)
(72)
(58)*
(44)**
(34)
(44)*
(34)**
(44)
(42)*
(33)
(72)***
(26)
(28)
(29)
(17)
−1.5 −1.0 −0.5 0.0 0.5
−0.5 0.0 0.5 1.0
−1.5 −1.0 −0.5 0.0 0.5
−1.0 −0.5 0.0 0.5
−1.0 −0.5 0.0 0.5 1.0
−1.0 −0.5 0.0 0.5
−1.0 −0.5 0.0 0.5
−1.5 −1.0 −0.5 0.0 0.5 1.0
−0.2 −0.1 0.0
−0.4 0.0 0.4
−0.6 −0.4 −0.2 0.0 0.2
−0.8 −0.4 0.0 0.4
−0.6 −0.3 0.0 0.3
Effect size

Figure 5


0-10 cm
>10 cm
0-100 Kg N yr^{-1} ha^{-1}
100-200 Kg N yr^{-1} ha^{-1}
>200 Kg N yr^{-1} ha^{-1}
0-5 yr
5-10 yr
>10 yr
pH<4
4<pH<5
5<pH<7
pH>7
Tropical
Subtropical
Temperate
Forest
Grassland
Cropland
(a)
(b)
(c
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
(q)
(r)
P Availability
Labile P
Labile Pi
Labile Po
Moderately labile P
Moderately labile Pi
Moderately labile Po
Occluded P
Occluded Pi
Occluded Po
(48) (48) (43)*** (57) (43) (34) (56) (34) (33)
(111)* (92) (85) (66) (74) (72) (118) (96) (60)
(96) (82) (72)** (96) (82) (72)** (109) (83) (55)
(50)* (48) (34) (16) (34) (30) (61) (46)* (29)
(23)*** (20) (23) (20) (20) (20) (37)* (20) (9)
(90) (70) (83)** (77) (65) (65) (88) (62)* (3)
(56) (61) (41) (61) (61) (51) (67) (64) (25)
(45) (41) (21) (29) (23) (21) (51) (40) (10)
(19) (19) (4)*** (19) (19) (9) (15) (19)* (6)
(65) (63) (48)*** (54) (53) (49) (62) (52) (36)
(29) (31)* (42) (40) (18) (18) (37) (18)*** (9)
(65) (60) (42) (42) (12) (10) (17)*** (12)*** (12)
(14) (14)** (14)*** (10) (14) (10) (14)*** (8)*** (4)
(91) (92) (84)* (104) (92) (92) (109) (97) (70)
(86) (70) (51) (53) (47) (35) (87) (61)*** (34)
(80) (81) (65)* (88) (80) (66) (93) (79) (50)
(49) (34) (46)*** (40) (34) (34) (55)* (34)* (32)
(59) (54)* (35) (36) (36) (34) (59) (50) (23)
−0.50 0.00 0.50
−0.6 −0.2 0.2
−0.2 −0.1 0.0 0.1
−0.2 0.0 0.2
−0.2 0.0 0.2 0.4
−0.4 −0.2 0.0 0.2
−0.4 −0.2 0.0 0.2
−1.0 −0.5 0.0 0.5
−0.4 −0.2 0.0 0.2 0.4
−0.2 0.0 0.2
−0.6 −0.4 −0.2 0.0 0.2
−0.2 −0.1 0.0 0.1 0.2 0.3
−0.4 −0.2 0.0 0.2 0.4
−0.2 −0.1 0.0 0.1
−0.3 −0.1 0.0 0.1 0.2
−0.2 −0.1 0.0 0.1
−0.2 −0.1 0.0 0.1
−0.3 −0.1 0.0 0.1 0.3
Effect size

892 Figure 6

893

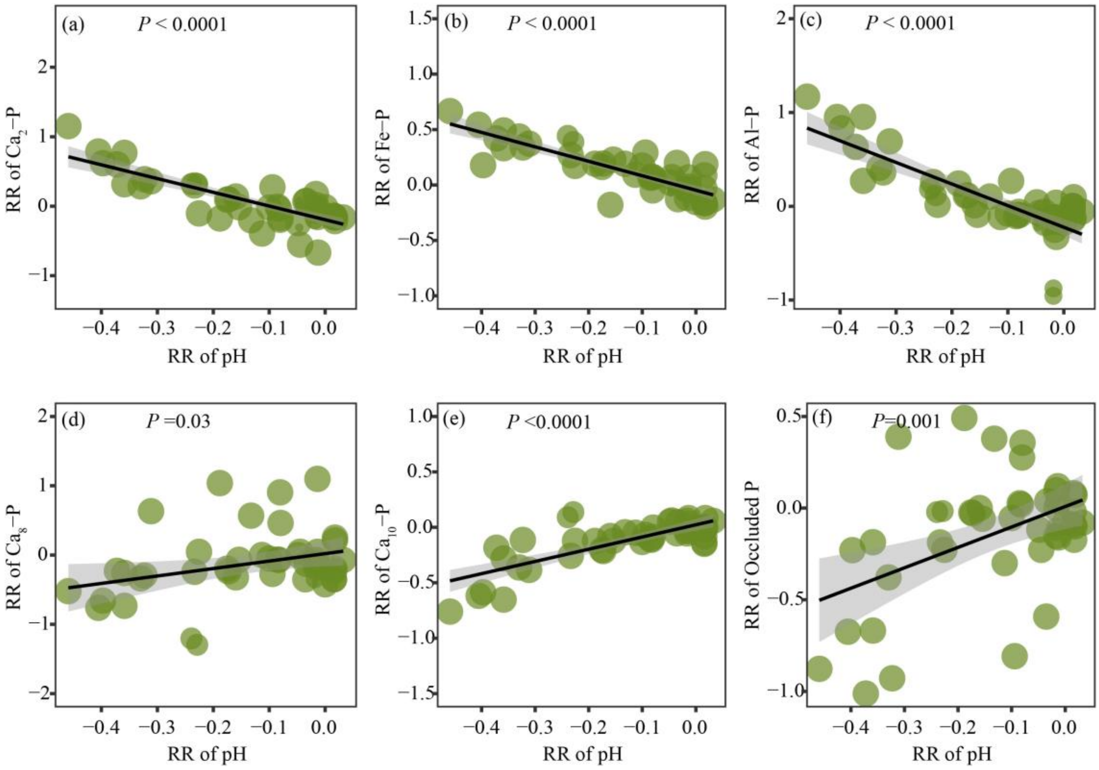


Figure 7

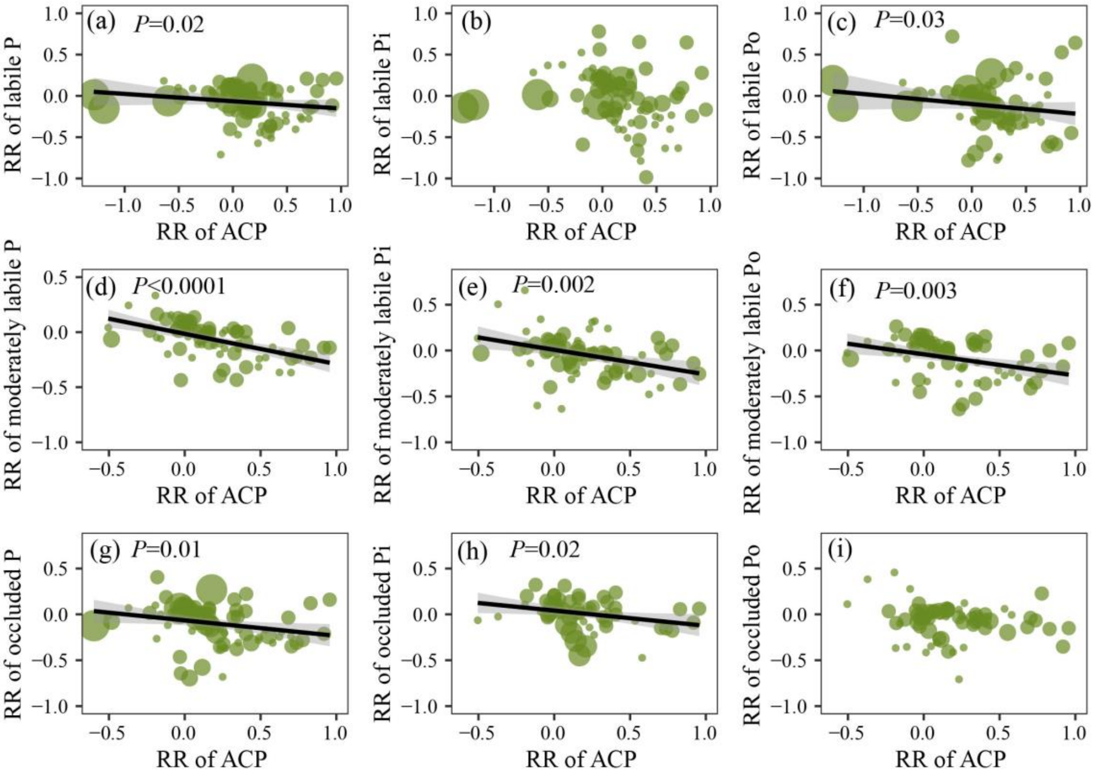

(a) P=0.02
RR of labile P
(b)
RR of labile Pi
(c) P=0.03
RR of labile Po
(d) P<0.0001
RR of moderately labile P
(e) P=0.002
RR of moderately labile Pi
(f) P=0.003
RR of moderately labile Po
(g) P=0.01
RR of occluded P
(h) P=0.02
RR of occluded Pi
(i)
RR of occluded Po
RR of ACP
−1.0 −0.5 0.0 0.5 1.0

Figure 8

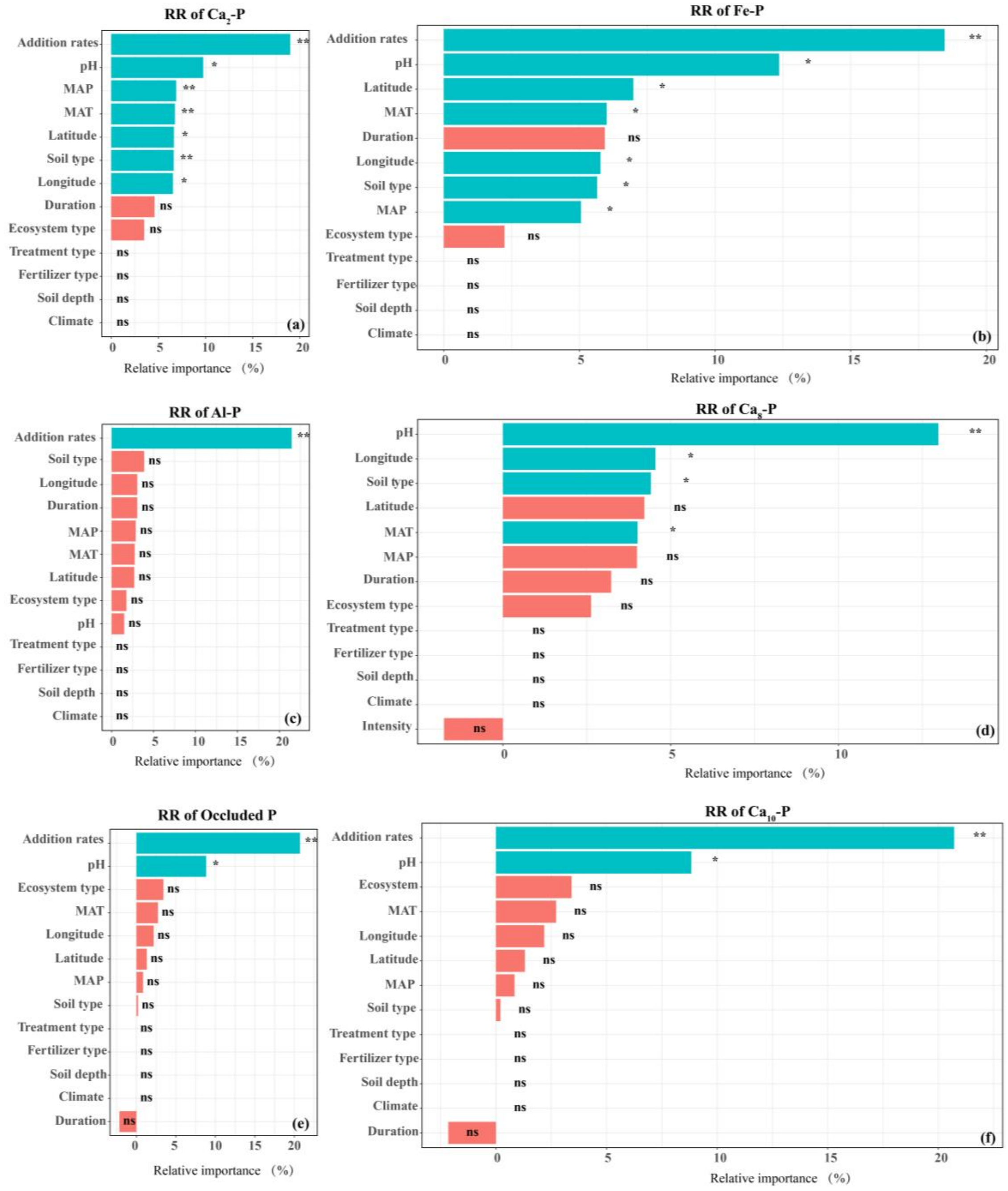
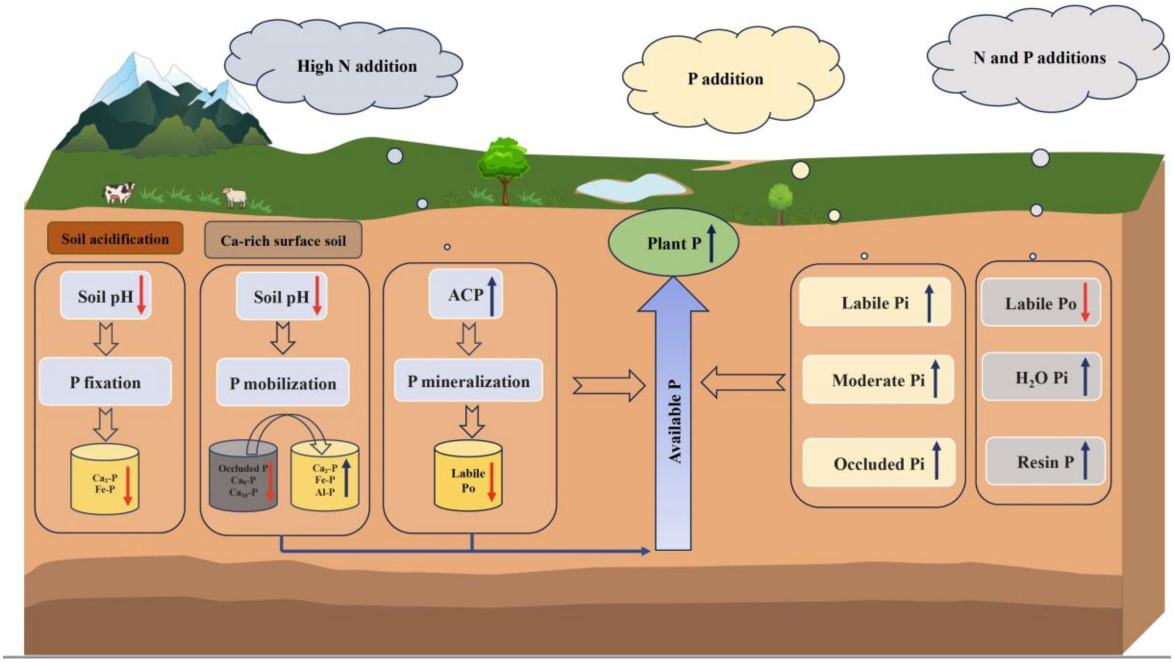

RR of Ca_2-P
Addition rates **
pH *
MAP **
MAT **
Latitude *
Soil type **
Longitude *
Duration ns
Ecosystem type ns
Treatment type ns
Fertilizer type ns
Soil depth ns
Climate ns
(a)
0
5
10
15
20
Relative importance （%）
RR of Fe-P
Addition rates **
pH *
Latitude *
MAT *
Duration ns
Longitude *
Soil type *
MAP *
Ecosystem type ns
Treatment type ns
Fertilizer type ns
Soil depth ns
Climate ns
(b)
0
5
10
15
20
Relative importance （%）
RR of Al-P
Addition rates **
Soil type ns
Longitude ns
Duration ns
MAP ns
MAT ns
Latitude ns
Ecosystem type ns
pH ns
Treatment type ns
Fertilizer type ns
Soil depth ns
Climate ns
(c)
0
5
10
15
20
Relative importance （%）
RR of Ca_8-P
pH **
Longitude *
Soil type *
Latitude ns
MAT *
MAP ns
Duration ns
Ecosystem type ns
Treatment type ns
Fertilizer type ns
Soil depth ns
Climate ns
Intensity ns
(d)
0
5
10
Relative importance （%）
RR of Occluded P
Addition rates **
pH *
Ecosystem type ns
MAT ns
Longitude ns
Latitude ns
MAP ns
Soil type ns
Treatment type ns
Fertilizer type ns
Soil depth ns
Climate ns
Duration ns
(e)
0
5
10
15
20
Relative importance （%）
RR of Ca_{10}-P
Addition rates **
pH *
Ecosystem ns
MAT ns
Longitude ns
Latitude ns
MAP ns
Soil type ns
Treatment type ns
Fertilizer type ns
Soil depth ns
Climate ns
Duration ns
(f)
0
5
10
15
20
Relative importance （%）

Figure 9



High N addition
P addition
N and P additions
Soil acidification
Ca-rich surface soil
Soil pH
P fixation
Ca_2-P
Fe-P
Soil pH
P mobilization
Occluded P
Ca_8-P
Ca_{10}-P
Ca_2-P
Fe-P
Al-P
ACP
P mineralization
Labile Po
Plant P
Available P
Labile Pi
Moderate Pi
Occluded Pi
Labile Po
H_2O Pi
Resin P