Linkage between tree species richness and soil microbial diversity improves phosphorus bioavailability

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An increase in the availability of soil phosphorus (P) has recently been recognized as an underling mechanism of the positive relationship between plant diversity and ecosystem functioning. The effect of plant diversity on the bioavailable forms of P involved in biologically mediated rhizospheric processes and how the link between plant and soil microbial diversity facilitates soil P bioavailability, however, remain poorly understood. We quantified four forms of soil bioavailable P in subtropical mature forests using a novel biologically based approach and soil microbial diversity based on high-throughput Illumina sequencing. Tree species richness was positively correlated with the four forms, which was more pronounced in organic than mineral soil. A model of the link between plants and soil microbes for each form indicated that soil bacterial and fungal diversities played dominant roles in mediating the effects of tree species richness on the bioavailability of soil P. The increasing biodiversity of trees and soil bacteria and fungi could maintain the bioavailability of soil P in forest ecosystems and alleviate the limitation of soil P.

Many studies have reported that plant biodiversity enhances ecosystem functions, particularly above- and belowground biomass or productivity[1, 2]. Increases in biomass and productivity (e.g. overyielding) in ecosystems with many species of plants can be attributed to sampling (or selection) effects of the dominant species and to complementarity effects among species[3-5]. The sampling effects are species-specific impacts on biomass due to the higher probability of having highly productive species included and dominant in more highly diverse ecosystems[3, 4, 6]. The complementarity effects refer to the various forms of niche partitioning among species for acquiring resources in ways that are spatially or temporally complementary, or plant-plant facilitation for increasing resource availability or other growing conditions, and therefore increasing productivity[3, 4, 6]. Phosphorus (P) is an important nutrient for various

physiological processes and components[7] (e.g. energy metabolism, signal transduction, energy carriers, nucleic acids and membranes) needed for plant growth but is often deficient to meet the demands of plants[8, 9]. An increase in soil P availability has therefore recently been recognized as an underlying mechanism for the positive effects of plant diversity on ecosystem biomass and productivity[10]. P, however, occurs in many inorganic and organic forms in the soil, and the use of multiple forms of P by plants is complex and poorly understood[11]. Understanding how plant diversity affects the availability of multiple forms of bioavailable P, as opposed to single forms of available P or total P[12, 13], may facilitate the development of sustainable strategies to alleviate limitations of soil P.

Plants develop a range of mechanisms accompanied by microbial processes in response to P deficiency to increase the mobility and bioavailability of soil P[8, 11]. Four potential mechanisms can be generalized: (1) modification of root morphology and formation of mycorrhizae[14-16], (2) exudation of organic acids[9, 17-19], (3) exudation of enzymes (e.g. phosphatase and phytase) [19-21] and (4) exudation of $H^+/OH^-/HCO_3^-$[18, 22, 23] in the rhizosphere by plant roots and soil microbes. The forms of bioavailable P involved in mechanisms 1 to 4 are defined as $CaCl_2$-P, citric-P, enzyme-P and HCl-P, respectively[9].

Increases in soil P bioavailability in ecosystems with diverse plant species are hypothesized to involve plant-plant facilitation[24], where P-mobilizing species improve P nutrition for themselves and neighboring non-P-mobilizing species by secreting organic acids, protons and enzymes into the rhizosphere to desorb and solubilize phosphates[10, 12, 24]. Facilitation has recently been identified in two-species intercropping ecosystems[10, 24, 25]. Forests are P self-nourishing ecosystems that depend on P retained in their own biomass and supplied from litter decomposition[26]. The facilitation of soil P bioavailability, however, has not yet been reported for forest ecosystems, which often consist of more than two plant species or even dozens of species.

Soil microbes play important roles in returning nutrients to the soil by the decomposition of litter (leaves and roots) and root exudations, which are key processes that bridge the link between plant and soil P nutrition[12, 16, 24], namely plant-microbe-soil interaction[24] (Extended Data Fig. 1). Diverse plant communities produce litter composed of more diverse traits of leaves and roots (in amount and quality) and release more diverse root exudates[27]. The litter and exudates can also influence soil organic carbon (SOC)[24] and directly affect soil microbial composition and activity[12, 24, 28, 29]. Bioavailable soil P clearly has simultaneous multiple forms[9], and these forms can be mediated in natural ecosystems by the biodiversity of soil microbes. For example, ectomycorrhizal (ECM) fungi are widely considered the main factor for improving P uptake by plants[24, 30, 31], and saprotrophic fungi are responsible for litter decomposition and play a crucial role in the mobilization of organic P[32]. Bacteria can solubilize mineral P or immobilize it in their biomass[33]. Plant and soil microbial communities and their interactions can shape multiple forms of bioavailable P, but identifying and quantifying their relative effects is difficult, perhaps because soil microbes obtain C compounds from plants in exchange for mineral nutrients, including P[30, 33]. Plant-microbe-soil interactions may thus be key mechanisms for understanding the biogeochemical processes involved in P bioavailability in diverse plant ecosystems.

Bioavailable-P plant-plant facilitation and plant-microbe-soil interactions may strengthen as forest stands develop[34]. We selected a total of 94 subplots (with areas of 10 × 10 m) along diversity gradients from 1 to 12 tree species in three mature subtropical forests[35] (Extended Data Fig. 2) to quantify the four forms of soil bioavailable P ($CaCl_2$-P, citric-P, enzyme-P and HCl-P), tree species richness, soil bacterial and fungal diversity (Shannon index) and many of the drivers hypothesized to be important for regulating their variation. We plotted bivariate relationships to determine the influence of biodiversity on bioavailable P. We identified the underlying mechanism of the effect of tree species richness on bioavailable P by formulating

a theoretical framework for the interconnections among all drivers and using structural equation models (SEMs) to empirically evaluate the theoretical framework (Extended Data Fig. 1). More details of the methodology are provided in the Methods section.

Tree species richness was positively associated with soil P bioavailability (Fig. 1), consistent with other studies[4, 13]. Tree species richness may have been positively correlated with bioavailable P because diverse tree species may produce more and diverse litter (leaves and roots) to form SOC (Fig. 2), have various root morphological characteristics for secreting more exudates (i.e. organic acids, phosphatases and $H^+/OH^-/HCO_3^-$) and increase tree growth (i.e. basal area (BA), see Fig. 2), thereby increasing the requirements of the nutrients, including P, that drive root exudation and intensify soil microbial activities. The positive effects of tree species richness on bioavailable P were more pronounced in organic than mineral soil (Fig. 1), reinforcing the premise that forests with many tree species generate diverse quantities and qualities of litter[24] and increase the density of fine roots distributed in the organic horizon, which greatly increases P exudation.

The effects of tree species richness on bioavailable P varied with the form of bioavailable P[8] (Figs. 1 and 2). $CaCl_2$-P is a labile P that is easily available to plants and is then depleted in the rhizospheric soil[14, 16]. A $CaCl_2$-P concentration gradient formed between the rhizosphere and bulk soil, which could drive the mobilization of $CaCl_2$-P from bulk soil to the rhizosphere. Citric-P is an active form of inorganic P, adsorbing to clay particles and weakly binding to Ca, Fe or Al precipitates, which can be easily released by organic acids[9, 18, 19]. Organic acids are commonly secreted by living plants or dead roots, and their secretions are plant species-specific. HCl-P is a recalcitrant inorganic P that can be solubilized by $H^+/OH^-/HCO_3^-$ root exudates. $H^+/OH^-/HCO_3^-$ are secreted when roots take up ions in unbalanced proportions, which is also plant species-specific[8]. More and diverse root morphological characteristics, organic acids and $H^+/OH^-/HCO_3^-$ may increase the bioavailability of $CaCl_2$-P, citric-P and HCl-

P in diverse species communities (Fig. 2a, b and d). Enzyme-P, however, is an organic form of P that will only be taken up by plants if mineralized by phosphatases[9, 36]. Phosphatase exudation by plants consumes energy and depends on the demand for P[21, 37]. If $CaCl_2$-P, citric-P and HCl-P increased by high diverse trees is sufficient for supporting P requirements of plants, they contribute to reduce energy and substrate consumption[36], and there is a weak relationship between enzyme-P and tree species richness.

Our results indicated a strong, positive and linear correlation between the amount of bioavailable P and bacterial and fungal diversity (Fig. 3), but the effect of microbial diversity on bioavailable P differed among microbial taxa. The solubilization and immobilization of inorganic P are the main mechanisms responsible for bacterial P bioavailability[33]. Bacterial diversity also directly increased the amounts of the three forms of inorganic P ($CaCl_2$-P, citric-P and HCl-P; Fig. 2). The ability to solubilize inorganic P depends on the development of extraradical mycelia by ECM fungi and the release of organic acids and $H^+/OH^-/HCO_3^-$[30, 33]. Fungal diversity contributed more than bacterial diversity to the bioavailability of enzyme-P (Fig. 3), suggesting that fungal communities had a dominant role in enzyme-P bioavailability by the exudation of phosphatases. The effects of fungal diversity on citric-P and HCl-P were similar to those of bacterial diversity and tree species richness, indicating that organic acids and $H^+/OH^-/HCO_3^-$ are commonly released by plants and microbes. A specific functional group of ECM fungi has been documented as an important P predator and helped plants take up P[24, 30, 31]. In addition, $CaCl_2$-P is a readily absorbed and used form of inorganic P[9], so the lack of significant impacts of fungal diversity on $CaCl_2$-P was not surprising, because highly efficient $CaCl_2$-P uptake by ECM fungi can offset the positive effects of other functional groups of fungi.

Soil microbial diversity mediated the effects of tree species richness on soil bioavailable P by three biological mechanisms (Figs. 2 and 4). Firstly, the roots of diverse tree species

release diverse exudates in rhizospheric soil as a "booster" for soil microbial activity and diversity[8]. Our analysis found that tree species richness directly increased bacterial diversity. Secondly, the plants in tree-rich communities have long fine roots, which provide more and multiple hosts for soil microbes and thus multi-host-multi-microbe interactions[38]. Our results indicated that tree species richness increased the length of fine roots and bacterial and fungal diversity. Thirdly, tree species richness increased tree basal area (aboveground biomass) and fine-root biomass, which would produce larger amounts and varieties of litter and thus more SOC, which would then decrease bacterial and fungal diversity. The higher amounts of litter produced by highly diverse species communities could affect resource availability or litter leachates and alter microclimatic conditions, including soil-water content and temperature, which might suppress the growth of some common microbial species or decrease their competitive ability, thus lowering microbial diversity[39]. In contrast to diversity, microbial activity and biomass could increase as the amounts of litter[39] and SOC[36] increased, which could also increase mycorrhizal formation and exudation of organic acids, phosphatases and $H^+/OH^-/HCO_3^-$ to increase the amount of bioavailable P.

SOC had positive and direct effects on citric-P, enzyme-P and HCl-P[24] (Fig. 2 and Extended Data Figs. 3-6). Both biological and physical processes can account for this result. Among the biological processes, communities with diverse tree species producing more SOC[36] lead to higher microbial activity and thereby the production of more organic acids, phosphatases and $H^+/OH^-/HCO_3^-$. The physical processes vary depending on the form of bioavailable P. Citric-P and HCl-P bind weakly or create stable Fe and Al precipitates[9] at elevated concentrations of SOC in acidic forest soils, which can easily form soluble C compounds-Fe(Al)-P complexes in which P is readily liberated[40]. The positive correlation between SOC and enzyme-P may be due to the ability of SOC to adsorb phosphatases in an active form[41] and then maintain a high rate of enzyme-P mineralization.

The bivariate plots of tree species richness could only explain less than 7, 22, 7 and 12% of the variation in $CaCl_2$-P, citric-P, enzyme-P and HCl-P (Fig. 1), but the SEMs could explain 18, 41, 25 and 45% of the variation in $CaCl_2$-P, citric-P, enzyme-P and HCl-P, respectively. The SEM results indicated that the effects of tree species richness on bioavailable P were mediated by other biotic and abiotic factors, such as soil microbes and SOC concentrations. Not all of the variability of bioavailable P could be explained by the variables in these SEMs. Other variables (e.g. soil pH; Extended Data Figs. 7 and 8) not included in these SEMs may thus have also contributed to the effects of tree species richness on bioavailable P.

To the best of our knowledge, this study is the first to explore the mechanism of soil P bioavailability in subtropical forests with diverse tree species by identifying the links between trees, microbes and soil. Our findings have three important implications for understanding the interactions between biodiversity and bioavailable P. Firstly, the increase in tree species richness increased soil bioavailable P, including $CaCl_2$-P, citric-P, enzyme-P and HCl-P, which were more pronounced in organic than mineral soil. Secondly, soil bacterial and fungal diversity can mediate the effects of tree species richness on bioavailable P. Tree species richness can directly affect bacterial diversity and indirectly affect bacterial and fungal diversity by increasing tree basal area and fine-root biomass and length, thereby affecting bioavailable P. Thirdly, the SEMs indicated that SOC served as a link between tree species richness and soil microbial diversity to affect bioavailable P, suggesting that soil abiotic factors may be key drivers controlling the relationships between biodiversity and bioavailable P. More observations and experiments that link plant and soil biodiversity to bioavailable P will certainly be needed in the near future to evaluate and predict P bioavailability and mobilization in forest ecosystems, because the loss of biodiversity is continuing and soil properties are changing in forest ecosystems.

Online content Methods, additional Extended Data items and source data are available in the online version; references unique to these sections appear only in the online version.

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Extended Data are available in the online version.

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Author contributions Concept and study design: WX; data collection and analysis: HW, SO, TG, BZ, LC, LP, SZ, LC and YZ; manuscript writing: HW, WX, DIF, JP and CP.

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METHODS

Site description. This study was carried out in the Dashanchong Forest Park (28°23′58″-28°24′58″N, 113°17′46″-113°19′08″E) in Changsha County, Hunan Province, China. The altitude ranges from 55 to 17 m a.s.l. The park has a mean annual precipitation of 1416 mm and a mean annual temperature of 17.3 °C. The soil is a well-drained red clayey loam classified as an Alliti-Udic Ferrosol. Details of the site are provided by Jiang et al.[42] and Zhu et al.[43].

No activities of human disturbance, such as firewood collection, have been allowed in the park since the late 1950s. Secondary forests have developed after decades of forest protection, dominated by *Pinus massoniana*, *Choerospondias axillaris*, *Cyclobalanopsis glauca*, *Lithocarpus glaber* and *Loropetalum chinense*. A 1-ha permanent plot was established in 2013 for each of three secondary forests: *P. massoniana* ï *L. glaber* coniferous and evergreen broadleaved mixed forest (PLF), *C. axillaris* deciduous broadleaved forest (CAF) and *L. glaber* – *C. glauca* evergreen broadleaved forest (LGF) at early, middle and late successional stages. Forest ecosystems are highly complex, with many microsites varying in environmental factors[34, 35]. We established a network of forest plots along gradients of tree species richness within the forests to account for environmental factors[34, 44, 45]. Each plot was subdivided into a grid of 100 subplots of 10 × 10 m. The locations of trees were mapped within each subplot, and the species, diameter at breast height (DBH) and height (H) of all trees were recorded. A similar experimental design was used to examine the effects of plant functional diversity on forest ecosystem function[46]. Detailed information of stand characteristics is available in Ouyang et al.[35] and Zhu et al.[43].

Sample collection. We selected 31 subplots based on their tree species richness along a diversity gradient from 2 to 9 species in PLF, 31 subplots along a diversity gradient from 1 to 12 species in CAF and 32 subplots along a diversity gradient from 1 to 11 species in LGF (Fig.

S2), for a total of 94 subplots containing 40 species (Extended Data Table 1). We avoided adjacent subplots as much as possible to eliminate edge effects but used a five-point mixed sampling method to eliminate edge effects when not possible. The five sampling points included the center of the subplot and four points equidistant from the center toward the corners of the plots (Extended Data Fig. 9). Samples of organic soil were collected within areas 50 × 50 cm at each point after the litter was removed. Samples of mineral soil were then collected from the 0-10 cm soil layer. All mixed soil samples were sieved to pass through a 2-mm mesh and divided into three subsamples. One subsample was air-dried for the determination of soil organic-carbon (SOC) concentration, soil available-P concentration and soil pH; one subsample was stored at 4 °C for measuring the amount of bioavailable P and one subsample was stored at -80 °C for measuring microbial diversity. Fine roots (<2 mm in diameter) were collected from the 0-10 cm soil layer at the five points in each subplot using an auger and were transported to the laboratory for further analysis.

Chemical analysis. Four fractions of bioavailable P ($CaCl_2$-P, citric-P, enzyme-P and HCl-P) were measured using the extraction method reported by Deluca et al.[9]. Each P fraction was measured in parallel by shaking 0.5 g of fresh soil with each extract (10 ml) in separate 15-ml centrifuge tubes for 3 h on a reciprocal shaker at 180 rpm. The extracts were then centrifuged (4000 *g*, 25 °C, 30 min) to obtain supernatants containing the four forms of bioavailable P. $CaCl_2$-P was assessed using a 10 mM $CaCl_2$ solution, citric-P was assessed using a 10 mM citric acid solution, enzyme-P was assessed using a final concentration of 0.02 enzyme units ml^{-1} solution mixed with phosphatase and phytase and HCl-P was assessed using a 1 M HCl solution. Citric-P extracts were diluted 10-fold, and HCl-P extracts were diluted 20-fold. The $CaCl_2$-P and enzyme-P extracts were not diluted. All extracts were analyzed colorimetrically (630 nm) by the malachite-green method[58] using a multiscan spectrum (Tecan Infinite® 200

Pro).

Soil pH was measured at a soil:water (deionized) ratio of 1:2.5 using an FE20 pH meter (Mettler Toledo, Shanghai, China). Air-dried soil was ground and sieved through a 0.25-mm mesh. The SOC concentration was measured using $K_2Cr_2O_7$-H_2SO_4 oxidation. Soil available P concentrations were determined using 0.05 mol L^{-1} HCl and 0.025 mol L^{-1} (1/2 H_2SO_4)[59]. Soil properties are presented in Extended Data Table 2. Fine roots were separated as described by Liu et al.[47], and their biomass and length were then quantified.

Assessment of microbial diversity. DNA was extracted from 0.5 g fresh weight of thawed soil samples using the E.Z.N.A.® soil DNA Isolation Kit (Omega Bio-tek, Norcross, USA) following the manufacturer's protocol. The diversity of the soil microbial communities was analyzed by DNA sequencing using the Illumina MiSeq platform. Bacterial 16S rDNA genes were amplified using the primer pair 515F (5′-GTGCCAGCMGCCGCGG-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′)[48]. Fungal ITS genes were amplified using the primer pair ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (2043R) (5′-GCTGCGTTCTTCATCGATGC-3′)[49]. Raw fastq files were demultiplexed and then quality-filtered using QIIME (version 1.17) with the following criteria. (i) Reads of 300 bp were truncated at sites receiving an average quality score <20 over a 50-bp sliding window, discarding the truncated reads that were <50 bp. (ii) Exact barcode matching, two mismatched primer nucleotides and reads containing ambiguous characters were removed. (iii) Only sequences that overlapped by >10 bp were assembled based on their overlap sequence. Reads that could not be assembled were discarded. Operational taxonomic units (OTUs) were clustered with a cutoff of 97% similarity using UPARSE (version 7.1 http://drive5.com/uparse/), and chimeric sequences were identified and removed using UCHIME. The taxonomy of each 16S rRNA gene sequence was analyzed by RDP Classifier

(http://rdp.cme.msu.edu/) against the SILVA (SSU115) 16S rRNA gene database using a confidence threshold of 70%[50]. The fungal ITS OTUs were assigned to taxa using the BLAST interface against the UNITE database V6.9.7. ($E<10^{-5}$)[51]. The Shannon diversity index, calculated for these rarefied OTU taxonomies using QIIME (version 1.17), was selected for this study because it provides a robust and informative estimate of taxonomic diversity for soil bacterial and fungal communities[52].

Statistical analysis. We first determined the relationships between the four forms of bioavailable P and soil available P using Pearson correlations (Extended Data Table 3). We next assessed the relationships between biodiversity, bioavailable P, tree basal area, fine-root biomass, fine-root length and SOC (Extended Data Figs. 3-6 and Extended Data Table 4) using linear regressions. We then identified the effects of tree species richness, tree basal area, fine-root biomass and length, soil bacterial and fungal diversity and SOC on bioavailable P; individual variables were subjected to multiple regression model selection based on the corrected Akaike information criterion (AIC) (Extended Data Table 5).

Structural equation models (SEMs) were used to analyze the direct and indirect relationships between the four forms of bioavailable P and tree species richness, tree basal area, fine-root biomass and length, soil bacterial and fungal diversity and SOC. The first step in an SEM requires establishing an *a priori* model based on known effects and the relationships among the driving variables (Extended Data Fig. 1 and Extended Data Table 5). In our model, we only considered the bottom-up effect of tree species richness on soil bioavailable P using tree basal area, fine-root biomass and length, soil bacterial and fungal diversity and SOC. Data manipulation was required before modeling. The distributions of endogenous variables were estimated, and their normality was tested. Tree basal area, fine-root biomass and length, citric-P, HCl-P and SOC were log-transformed to satisfy the requirement of normality. The R

software platform[53] and the lavaan[54] and lavaan.survey[55] packages were used to analyze our SEMs. Each pathway in the final model was evaluated for significant contributions to the model. Indices of model fit were the χ^2-test (a lower χ^2 indicates a better model), *P* (traditionally > 0.05), the root mean square error (RMSE) of approximation (RMSEA; the model has a good fit when RMSEA <0.05) and the 90% confidence intervals (CI90). Details of the SEMs are shown in the Extended Data Notes.

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Figure legends

Figure 1 | The correlations of tree species richness with $CaCl_2$-P (a), citric-P (b), enzyme-P (c) and HCl-P (d). The red and blue fitted lines are from linear regression (n=94). Only significant fitted lines are shown on the graphs. Significance indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Figure 2 | Structural equation models of tree species richness, tree basal area (tree BA), fine root length, fine root biomass, soil organic carbon (SOC), bacterial diversity and fungal diversity on soil $CaCl_2$-P (a), citric-P (b), enzyme-P (c) and HCl-P (d) in organic soil (n=94). The fit indices of the four models were the same; χ^2_2=1.112, P=0.573; RMSEA=0.000, CI90 (0.000; 0.172). Numbers in the endogenous variable indicate the explained variance (R^2). Numbers next to the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of path coefficients. Significance indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Figure 3 | The correlations of soil bacterial diversity and fungal diversity with $CaCl_2$-P (a, b), citric-P (c, d), enzyme-P (e, f) and HCl-P (g, h). The red and blue fitted lines are from linear regression (n=94). Only significant fitted lines are shown on the graphs. Significance indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Figure 4 | The correlations of tree species richness with soil bacterial diversity (a) and fungal diversity (b). The red and blue fitted lines are from linear regression (n=94). Only significant fitted lines are shown on the graphs. Significance indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

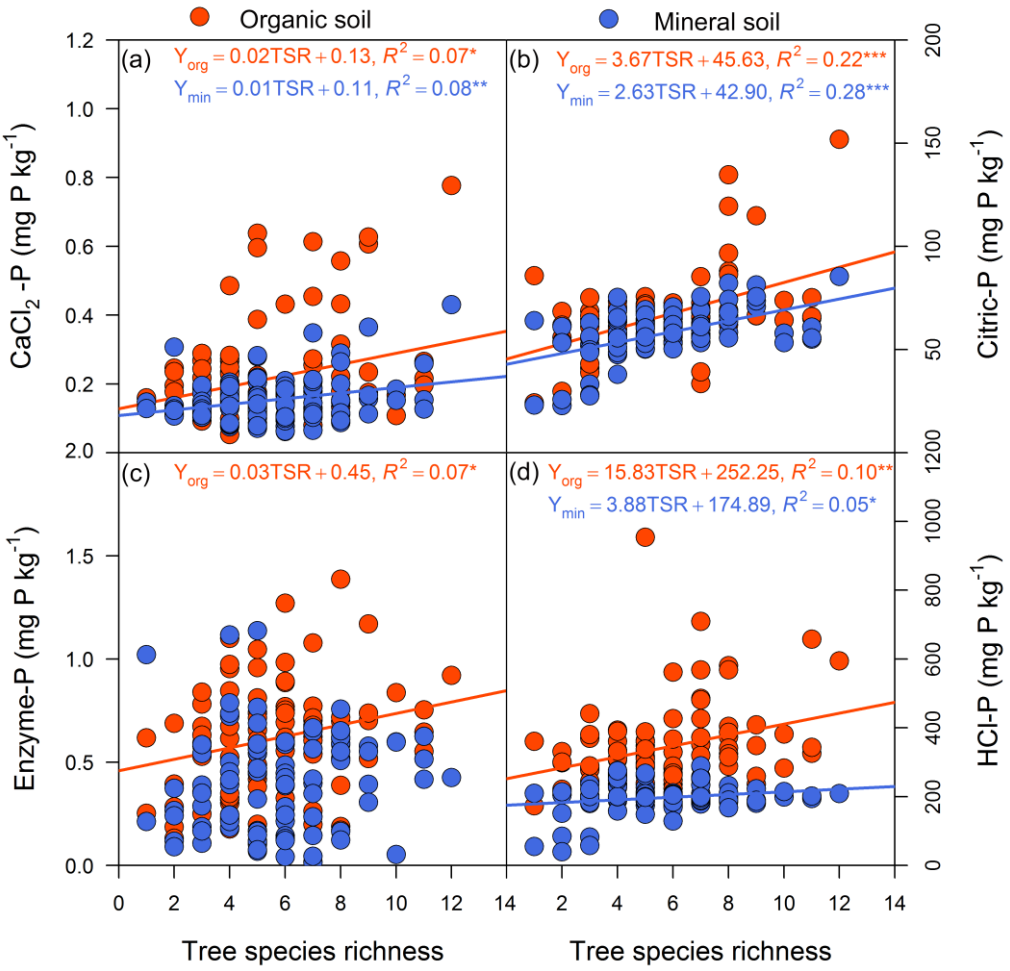


Figure 1 | Correlations of tree species richness with $CaCl_2$-P (a), citric-P (b), enzyme-P (c) and HCl-P (d). The red and blue lines are the fitted regression lines (n=94). Only significant fitted lines are shown. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

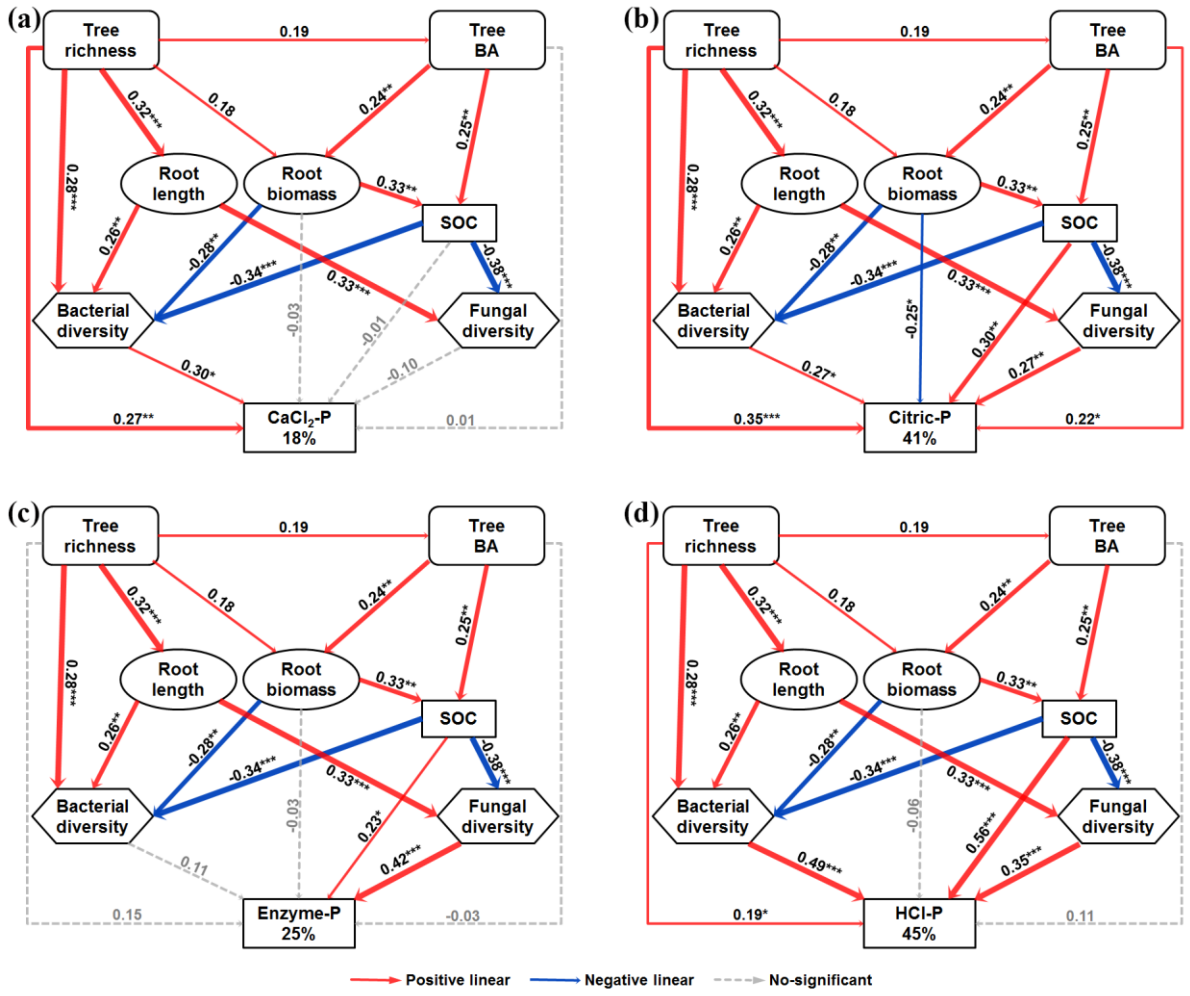
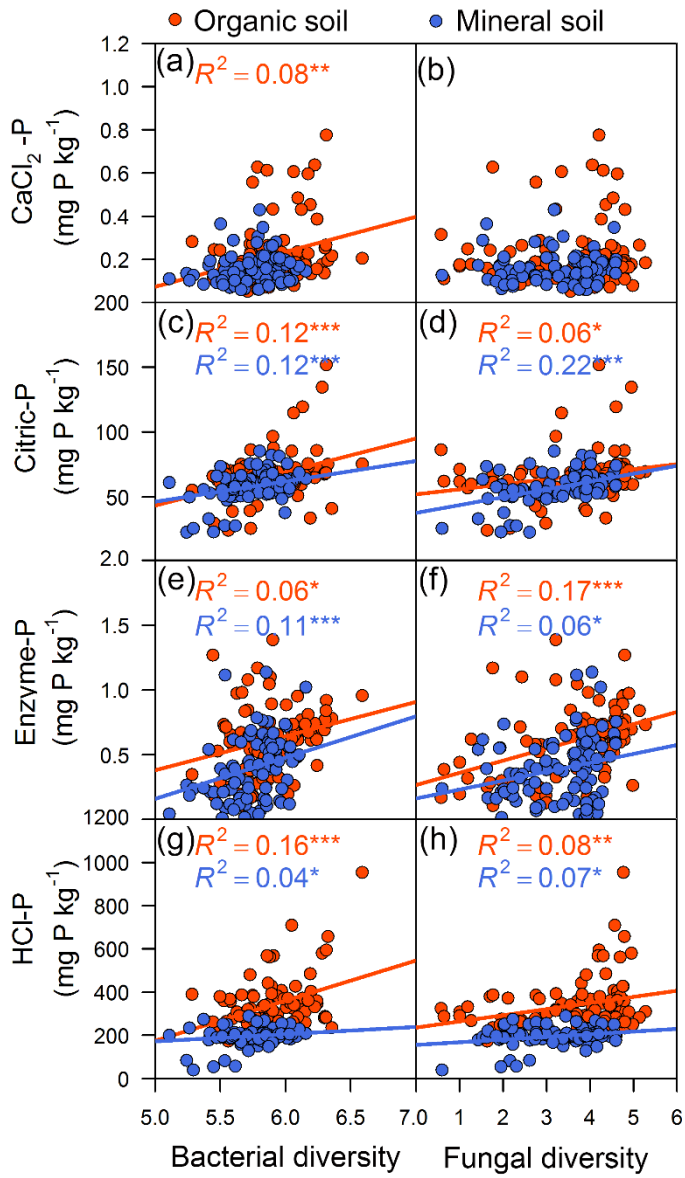


Figure 2 | Structural equation models of the effects of tree species richness, tree basal area (Tree BA), fine-root length, fine-root biomass, soil organic carbon (SOC), bacterial diversity and fungal diversity on soil $CaCl_2$-P (a), citric-P (b), enzyme-P (c) and HCl-P (d) in organic soil (n=94). The fit indices of the four models were the same; χ^2_2=1.112, *P*=0.573; RMSEA=0.000, CI90 (0.000; 0.172). The numbers for the endogenous variables indicate the explained variance (R^2). The numbers on the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of the path coefficients. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.



476

477 **Figure 3 | Correlations of soil bacterial diversity and fungal diversity with $CaCl_2$-P (a, b),**

478 **citric-P (c, d), enzyme-P (e, f) and HCl-P (g, h).** The red and blue lines are the fitted

479 regression lines (n=94). Only significant fitted lines are shown. * $P < 0.05$, ** $P < 0.01$, ***

480 $P < 0.001$.

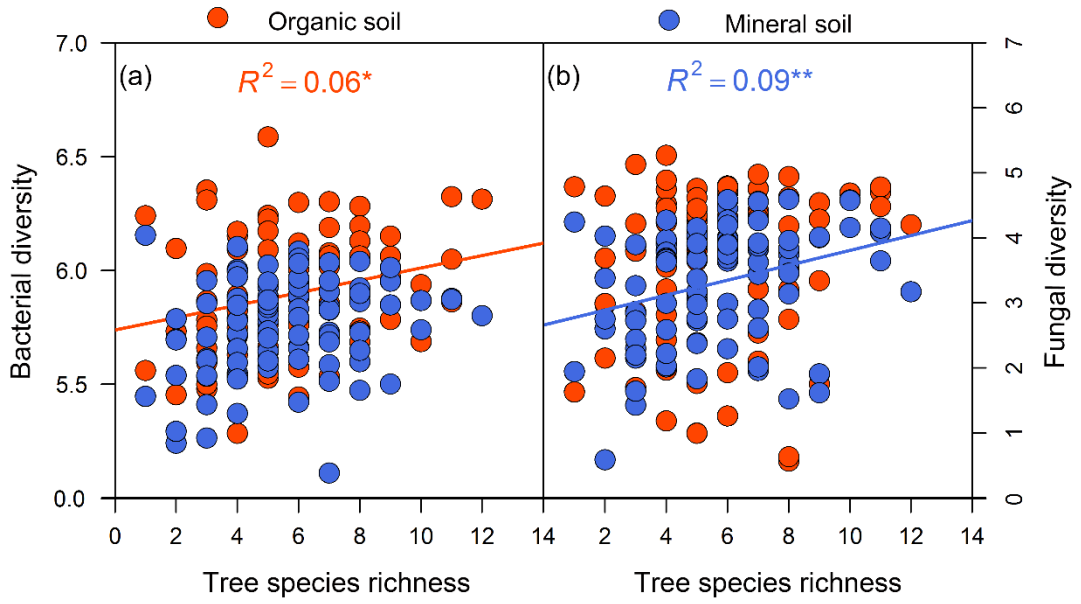


Figure 4 | Correlations of tree species richness with soil bacterial diversity (a) and fungal diversity (b). The red and blue lines are the fitted regression lines (n=94). Only significant fitted lines are shown. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.