



Increase of soil phosphorus bioavailability with ectomycorrhizal tree dominance in subtropical secondary forests

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ABSTRACT

Many forest tree species form symbiotic associations with either arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi to increase access to nutrients. ECM and AM differ in strategies for acquiring nitrogen (N) and phosphorus (P), however, little is known about the degree to which mycorrhiza mediate the effects of tree species on soil P bioavailability outside of the temperate zone. Here, we established a natural gradient with increasing ECM tree dominance in subtropical secondary forests, and investigated the linkages between the ECM tree dominance and soil bioavailable P content. We quantified the contents of four soil bioavailable P pools (CaCl₂-P, citric-P, enzyme-P and HCl-P) using the recently developed biologically-based P extraction method, as well as acid phosphatase activity, litter biomass and quality, microbial biomass carbon (C), and soil abiotic variables. We found that CaCl₂-P, citric-P and HCl-P increased with ECM tree dominance, while enzyme-P did not. Specially, ECM-dominated soils displayed markedly higher (1.2–2.9 times) citric-P and HCl-P than AM soils, indicating that ECM forests can effectively obtain inorganic P by releasing organic acids and through proton excretion. The acid phosphatase involved in the acquisition of organic P had similar activity between AM and ECM forests. Structural equation models indicated that increasing ECM tree dominance increases litter C/N ratio and soil organic matter, but decreases pH and microbial biomass C/P ratio, all of which are critical in mediating P bioavailability. Collectively, our findings confirm that tree mycorrhizal associations affect soil P bioavailability, which have implications for understanding species coexistence and guiding forest managements in subtropics.

1. Introduction

Phosphorus (P) is an indispensable nutrient for various physiological processes and components that are necessary for tree growth (Zavišić et al., 2016). Globally, soil P availability is a primary limiting factor of forest productivity (Kochian, 2012; Hou et al., 2020), especially in highly weathered tropical and subtropical soils due to large amounts of P being occluded by iron and aluminum oxides (Fisk et al., 2015; Turner et al., 2007; Du et al., 2020). Despite these conditions of chronically low soil P availability, tropical and subtropical forests remain productive and are able to maintain high levels of diversity (Kitayama, 2005; Ouyang et al., 2021). Forest trees have evolved diverse strategies in response to P deficiency to acquire and/or efficiently use P, including biological (e.g., root and microbial) processes to increase the P availability in the soil (Lambers et al., 2008; Ushio et al., 2015; Wu et al.,

2019). Therefore, better understanding how forest tree species regulate soil P availability can improve our understanding of the mechanisms of tree species coexistence and productivity maintenance in tropical or subtropical forests.

The majority of tree species form mycorrhizal associations which are prevalent in the organic and mineral soil horizons. In this symbiotic relationship, trees receive mineral nutrients via their root system associated with mycorrhizal fungal hyphae, and in return, fungi receive carbohydrates assimilated via photosynthesis (van der Heijden et al., 2015). Two main types of mycorrhizal associations in forests are formed by arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi (Smith and Read, 2008; Brundrett and Tedersoo, 2018). Symbiotic associations with AM and ECM fungi are a crucial strategy to enhance P uptake by tree species (Smith and Read, 2008). Compared with AM fungi, ECM fungi displayed the unique ability to utilize a simple organic

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P (P_o) source in a pure culture experiment (Dighton, 1983; Sawyer et al., 2003), which suggests that they have the ability to produce and release enzymes related to hydrolysis of these compounds. A field study by Liu et al. (2018) also reported that tropical and subtropical ECM trees of the families Dipterocarpaceae, Fagaceae and Juglandaceae exhibited higher absorption efficiencies of soil P_o in comparison to AM trees. In contrast, AM fungi display an extraordinarily limited capacity for enzymatic degradation, and therefore primarily take up mineral P (P_i) (Talbot et al., 2008). ECM fungi can produce phosphomonoesterase (acid and alkaline phosphatase), phosphodiesterase and phytase (Burke et al., 2014) to promote the mineralization of P_o, which in turn liberates P_i for plant uptake (Read and Perez-Moreno, 2003; Treseder and Lennon, 2015). ECM fungi can also produce and release low-molecular-weight organic acids, including citric, malonic and oxalic acids (Wallander, 2000; Tuason and Arocena, 2009; Zhang et al., 2014), which in turn can augment the P availability from mineral-bound P_i sources (Hinsinger, 2001; Hodge, 2017). For instance, Wallander (2000) reported a positive relationship between the concentration of easily extractable P_i (Olsen-P) and the concentration of oxalate, as well as a negative correlation with pH in the rhizosphere soil samples from ECM trees. However, how and the degree to which trees and their associated mycorrhizal fungi regulating the soil P availability remain controversial.

Given the unique differences in nutrient acquisition strategies between AM and ECM fungi, Phillips et al. (2013) proposed a mycorrhizal associated nutrient economy (MANE) framework, which predicts that AM forests utilize an inorganic nutrient economy, whereas an organic nutrient economy occurs in ECM forests. Recently, a first field test developed from the MANE framework for the P cycle using temperate deciduous forest stands found that organic forms of P were more available in ECM soils than in AM soils (Rosling et al., 2016). However, both Phillips et al. (2013) and Rosling et al. (2016) make clear that their results may not be extrapolated beyond temperate forests. For example, studies in the tropics have provided some evidence against a fundamental difference in nitrogen (N) cycling between AM and ECM forests, as tropical forests, regardless of mycorrhizal types, are characterized by faster organic N mineralization rates due to their higher temperature and greater presence and higher activity of hydrolytic enzymes (Tedersoo et al., 2012; Andersen et al., 2017). Therefore, the applicability of the MANE framework in P cycle to forest ecosystems outside temperate region needs further verification. Moreover, previous experiments that examined the mycorrhizal effects on P cycling were conducted as comparisons between AM and ECM forests, providing support for patterns in AM-dominated versus ECM-dominated plots (Rosling et al., 2016). As various environmental factors, together with mycorrhizal tree abundance, vary between the two forest types, simple comparisons may not explain the mycorrhizal-mediated effects (Craig et al., 2018). For these reasons, a graph of the relative abundances of AM versus ECM trees (i.e., mycorrhizal gradient) can serve as an appropriate experimental foundation for assessing the mycorrhizal effects on biogeochemical processes (Jo et al., 2019).

In this study, we examined how the dominant mycorrhizal associations of different tree species influence P availability in the organic horizon and mineral topsoil along a natural mycorrhizal gradient in subtropical forests. We quantified the contents of four bioavailable P pools (soluble P, chelate-labile P, enzyme-labile organic P, and mineral occluded P) using the recently developed biologically-based P (BBP) extraction method (Deluca et al., 2015). Compared with the common soil P extraction method (e.g., Olsen P) and classical Hedley extraction method (Hedley et al., 1982), the BBP approach provides a simple P assessment regime using a combination of established extraction procedures to represent the P solubilized by the four primary plant P acquisition mechanisms: (1) root interception, (2) organic acid complexation/dissolution, (3) enzyme hydrolysis and (4) proton excretion induced acidification (Deluca et al., 2015; Wu et al., 2020). Aside from the bioavailable P pool sizes, we also assessed the proportional magnitudes of the P pool sizes (e.g., the chelate-labile P/enzyme-labile

organic P ratio). These are important because they indicate the relative effectiveness of different P acquisition strategies (Crain et al., 2018). The aims of this study were to test (i) whether the mycorrhizal associations of locally dominant trees explain the variation in bioavailable P; (ii) if and how mycorrhizal tree dominance regulate soil P availability. Given that ECM fungi can produce and release low-molecular-weight organic acids and hydrolyze enzymes, we hypothesized that the contents of the soil chelate-labile P and enzyme-labile organic P increases with the increasing ECM tree dominance.

2. Materials and methods

2.1. Site description and experiment design

This study was conducted at Dashanchong Forest Park (28° 23' 58" – 28° 24' 58" N, 113° 17' 46" – 113° 19' 08" E), Changsha County, Hunan Province, China. The park is characterized by a humid subtropical monsoon climate, with mean annual precipitation of 1416 mm and a mean annual temperature of 17.3 °C. The altitude ranges from 55 to 217 m above mean sea level. The soil is composed of well-drained clay loam red soil, and is classified as an Alliti-Udic Ferrosol, corresponding to Acrisol in the World Reference Base for Soil Resource ((IUSS Working Group WRB, 2015)). No human disturbance activities have been allowed in this park since the late 1950 s. Secondary forests have developed multiple plant communities at different stages of restoration and succession following decades of forest protection. These secondary forests are ideal for testing the influence of dominant mycorrhizal functional types on soil processes because they are well characterized (Ouyang et al., 2016), and exhibit similarities in their parent materials, climate and topography.

In October 2019, forty-five plots (10 m × 10 m) reflecting the natural gradient of secondary forest mycorrhiza were established. In each plot, trees were identified to species, diameter at breast height (DBH) was recorded, and the mycorrhizal associations of each tree species was determined (Brundrett and Kendrick, 1990; van der Heijden et al., 2015). The selected plots included the full existing gradient of tree mycorrhizal associations, which was determined by basal area (BA) of the tree species associated with either AM or ECM fungi. Plots across the gradients were identified as ECM-dominated (n = 15, ≥70 % ECM associated tree species), AM-dominated (n = 15, ≥70 % AM associated tree species), and mixed plots (n = 15, ECM trees constituted 30–70 % of the total BA) (Fig. S1 and Table S1). Tree species associated with ECM fungi in these forest plots included *Pinus massoniana*, *Lithocarpus glaber*, *Cyclobalanopsis glauca*, *Quercus fabri*. The dominant AM-associated tree species were *Choerospondias axillaris*, *Cunninghamia lanceolata*, *Elaeocarpus japonicas*, *Cinnamomum camphora*.

2.2. Sample collection

Leaf litterfall was collected monthly from December 2019 to November 2020 using a trap (1.0 m × 1.0 m × 0.25 m) installed in the middle of each plot. The collected samples were placed in cloth bags, transported to the laboratory, dried at 60 °C to a constant weight, and weighed. The annual litterfall biomass was considered as the total amount of litterfall in 12 months, and the litterfall quality (C/N ratio) was determined using an element analyzer.

Soil samples were collected in February, July, and November 2020. To eliminate edge effects, adjacent subplots were avoided as much as possible, and when edge effects could not be eliminated, 5-points mixed sampling method was used to mitigate edge effects. The five sampling points in this method included the center of the subplot and four points equidistant from the center to the corners of the plots. Using a 5-cm-diameter stainless steel soil corer, organic soil was sampled at a depth of 0–5 cm, and mineral soil was sampled at a depth of 5–15 cm. The samples from the same horizon were then combined and mixed thoroughly. Freshly-collected soil samples were frozen in polyethylene

bags and transported to the laboratory. Soil samples were sieved using a 2-mm mesh to homogenize the soil and remove roots, rocks, and woody debris. The sieved soil was then divided into three subsamples. One subsample was immediately weighed for analysis of soil moisture, one subsample was air-dried and sieved for physicochemical analyses, and one subsample was stored at 4 °C for analysis of bioavailable P concentrations, microbial biomass and acid phosphatase activity.

2.3. Sampling analysis

Soil moisture was determined by oven-drying the samples at 105 °C to constant weight. Soil pH was determined in a 1:2.5 (w/v) soil-to-water extract ratio on composite samples using a pH meter (FE20K, Mettler-Toledo Instrument Co., Ltd.). Soil organic carbon (SOC) and total nitrogen (TN) were measured on ground soils using $K_2Cr_2O_7-H_2SO_4$ oxidation and Kjeldahl methods, respectively. Soil mineral N (i.e., NH_4^+ and NO_3^-) was extracted with a 2 M KCl solution and measured using an Autoanalyzer III continuous flow analyzer. Total P (TP) was determined using the molybdenum blue colorimetric method at an 880 nm wavelength with an UV-vis spectrometer. Soil Olsen-P was extracted using 0.05 M HCl-0.25 M ($1/2H_2SO_4$) and was analyzed via the molybdenum blue colorimetric method. Soil microbial biomass C (MBC), N (MBN) and P (MBP) were determined in fresh soil using the chloroform fumigation extraction method (Brookes et al., 1982). Soil acid phosphatase (ACP) activity was determined using the 4-methylumbelliferone (MUB)-linked substrate method (Deng et al., 2016).

The four soil bioavailable P pools were measured using the biologically-based P (BBP) method according to DeLuca et al (2015). The four bioavailable phosphorus forms are extracted with four extractants respectively, where soluble P ($CaCl_2$ -P) was assessed using a 10 mM $CaCl_2$ solution; chelate-labile P (citric-P) using a 10 mM citric acid solution; enzyme-labile organic P (enzyme-P) using a final concentration of 0.02 enzyme units mL^{-1} solution mixed with phosphatase and phytase; and mineral occluded P (HCl-P) using a 1 M HCl solution. Briefly, the method included four steps as follows: (1) the fresh soil (0.5 g) sample was weighed into four 15-mL centrifuge tubes, and 10 mL of $CaCl_2$, citric acid, enzyme mixture, and HCl were added into the four centrifuge tubes, respectively; (2) each centrifuge tube was shaken for 3 h on a reciprocal shaker at 180 rpm; (3) 1 mL of the mixture was extracted from a depth of 2/3 of the centrifuge tube into a 1.5 mL centrifuge tube and was separated for 1 min (10000 rpm, 25 °C) to obtain a supernatant containing four bioavailable P; (4) Citric-P extracts were diluted tenfold, and HCl-P extracts were diluted twentyfold. The $CaCl_2$ -P and enzyme-P extracts were not diluted. All extracts were determined by malachite green method at 630 nm (Tsutomu, 1991) using a Multiskan Spectrum.

2.4. Statistical analysis

Prior to statistical analysis, season averages (mean value for February, July and November) were generated for each plot to remove effects of seasonal variation and missing values. Differences in the soil variables (e.g., bioavailable P) across the mycorrhizal gradient were evaluated using single liner regression with ECM tree dominance (by basal area) as the predictor and the bioavailable P variables as response variables. To examine the relative sizes of P pools from the BBP fractions, mean pool sizes from the AM- or ECM-dominated samples were divided by one another (e.g., citric-P mean/ $CaCl_2$ -P mean) to obtain the ratios among pools. Uncertainty for these ratios was estimated by generating 95 % bootstrap confidence intervals (Efron, 1987). Differences in ratios between the plots dominated by AM- and ECM-dominated examined using one-way ANOVA with Tukey's HSD test.

To test the hypothesis that mycorrhizal dominated tree types could be closely related to bioavailable P dynamics, ordinary least squares (OLS) multiple regression was used to identify the mycorrhizal gradient-bioavailable P relationships after accounting for confounding

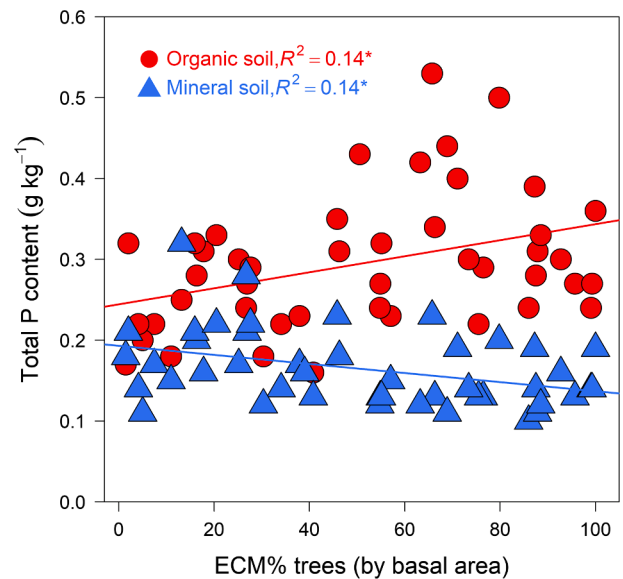


Fig. 1. The relationship between ectomycorrhizal (ECM) tree dominance and total P content in the organic (red circle) and mineral (blue triangle) soils. Each point represents the seasonal averages (February, July and November 2020) in each plot ($n = 45$). Only significant fitted lines are shown: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

environmental variables, such as tree productivity, species richness and edaphic variables. All variables were standardized (average = 0 and SD = 1) before the OLS multiple regression analysis. Akaike's information criteria (AIC) was used to identify the best OLS model, as implemented in the R package "MASS" (version 7.3–51.4). The variance inflation factor (VIF) was calculated for each of the OLS multiple regression models using the R package "CAR" (version 3.0–10). A threshold criterion of $VIF < 3$ was used to select appropriate variables in the best multiple regression model and to remove highly correlated variables (Chen et al., 2019).

Structural equation models (SEMs; Grace, 2006) were constructed based on the results of our path analyses to evaluate the direct and indirect relationships between the four forms of bioavailable P as well as the factors mentioned above. Goodness of fit for the SEMs model were evaluated with (1) a Chi-square test (χ^2 ; where the model has a good fit when $0 \leq \chi^2/df \leq 2$ and $0.05 < P \leq 1.00$), and (2) the root mean square error of approximation (RMSEA; where the model has a good fit when $0 \leq RMSEA \leq 0.05$ and $0.10 < P \leq 1.00$) (Schermelleh-Engel et al., 2003). These analyses were conducted using the AMOS 23.0 software package (IBM SPSS, Chicago, IL, USA).

3. Results

3.1. Soil P pools across the mycorrhizal gradient

Total P contents increased linearly with increasing ECM tree dominance in the case of the organic soil, while a decreasing trend was observed in the mineral soil (Fig. 1). The average content of total P was $0.29 g kg^{-1}$ in the organic soil and $0.16 g kg^{-1}$ in the mineral soil. Contents of $CaCl_2$ -P, citric-P, and HCl-P in both the organic and mineral soils increased with ECM tree dominance (Fig. 2). However, the enzyme-P contents for both soil horizons were not affected by tree mycorrhizal type (Fig. 2c). In the mineral soil, $CaCl_2$ -P ($0.26 mg kg^{-1}$), citric-P ($10.9 mg kg^{-1}$) and HCl-P ($82.1 mg kg^{-1}$) contents in ECM-dominated plots were 1.1, 2.9 and 1.2-times higher than those of the AM-dominated plots, respectively. The four forms of soil bioavailable P were significantly correlated with soil Olsen P in the case of both organic soil and mineral soil ($p < 0.05$), respectively, except for enzyme-P in mineral soil

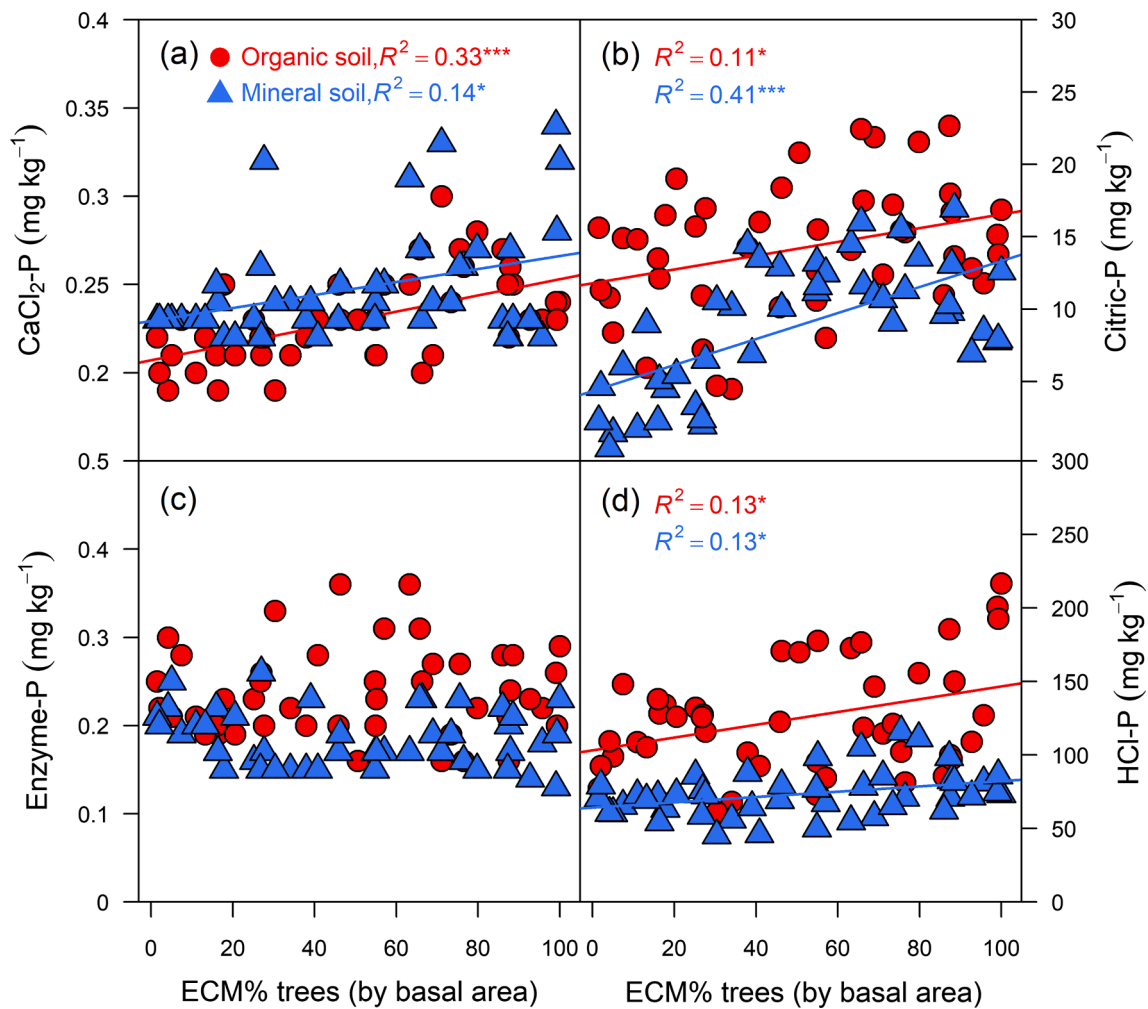


Fig. 2. The relationship between ectomycorrhizal (ECM) tree dominance and soil $\text{CaCl}_2\text{-P}$ (a), Citric-P (b), Enzyme-P (c) and HCl-P (d) contents. Each point represents the seasonal averages (February, July and November 2020) in each plot ($n = 45$). Only significant fitted lines are shown: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(Fig. S2).

3.2. Soil biologically based P fractions ratio

Results of the paired bootstrap statistical analysis for bioavailable P content by individual sample, mycorrhizal types and extractant showed that the citric-P and HCl-P pools were larger than both the $\text{CaCl}_2\text{-P}$ and enzyme-P pools (Table 1). In the organic soil, the ratios of citric-P/ $\text{CaCl}_2\text{-P}$, enzyme-P/ $\text{CaCl}_2\text{-P}$, HCl-P/ $\text{CaCl}_2\text{-P}$, HCl-P/citric-P and HCl-P/enzyme-P displayed no significant difference between AM- and ECM-dominated plots. However, soil citric-P/enzyme-P in ECM-dominated plots was 1.3-times higher ($p < 0.05$) than that of the AM-dominated plots. In the mineral soil, tree mycorrhizal types significantly altered the ratio of citric-P/ $\text{CaCl}_2\text{-P}$, citric-P/enzyme-P, HCl-P/citric-P and HCl-P/enzyme-P. Specially, the ratio of citric-P/enzyme-P in ECM-dominated plots was 3.0-times higher than that of the AM-dominated plots, while the ratio of HCl-P/citric-P in the AM-dominated plots was 4.1-times higher than in the ECM-dominated plots.

3.3. Effects of ECM tree dominance on soil bioavailable P pools

Results from the best OLS multiple regression model (the model with the highest R^2_{adj} and lowest AIC) indicated that the ECM tree dominance (by basal area, abbreviated as ECM% trees) was consistently among the best predictors of bioavailable P content after accounting for other plant and soil factors (Table 2). Specifically, $\text{CaCl}_2\text{-P}$ in organic soil was most

effectively predicted by ECM% trees, which explained 31.0 % of the variation. For citric-P contents, the combination of ECM% trees and MBC explained 22.0 % of the variation in the organic soil, while ECM% trees, SOC, and soil N/P ratio were the best predictors of the variation in mineral soil (52.8 % explained variation). ECM% trees and SOC were the main factors of HCl-P content in both the organic soil (26.8 % explained variation) and the mineral soil (29.7 % explained variation).

The SEMs for the organic soil further illustrated how ECM tree dominance affected soil bioavailable P, which was mainly through modifying litter quality, soil pH, soil moisture, SOC and microbial biomass (Fig. 3). These factors together accounted for 47 %, 56 %, and 50 % of the variation in $\text{CaCl}_2\text{-P}$, citric-P, and HCl-P content, respectively.

4. Discussion

4.1. Effects of mycorrhizal types on soil bioavailable P pools

In this study, the linkages between mycorrhizal tree dominance and soil bioavailable P pools were examined using a natural gradient of mycorrhizal associations in a subtropical forest where AM and ECM trees co-occur under the same parent soil and climate conditions. Evidence from previous studies suggests that trees associating with AM and ECM fungi have distinct effects on ecosystem-level C and N cycling (Philips et al., 2013; Lin et al., 2017). Our study provides evidence that these associations also result in plot-level differences in soil total P

Table 1

Results of the paired bootstrap analysis for soil biologically based P fractions ratio under mycorrhizal tree dominance.

Comparison	Mycorrhizal type	Effectiveness Ratio	Lower 95 % CI	Upper 95 % CI
Organic soil				
Citric-P/CaCl ₂ -P	AM-dominated	60.3 ± 4.36a	52.4	68.6
	ECM-dominated	62.6 ± 3.61a	56.4	68.9
Enzyme-P/CaCl ₂ -P	AM-dominated	1.07 ± 0.05a	0.98	1.17
	ECM-dominated	0.90 ± 0.05a	0.80	0.99
HCl-P/CaCl ₂ -P	AM-dominated	552 ± 22.09a	509	595
	ECM-dominated	548 ± 50.91a	453	644
Citric-P/Enzyme-P	AM-dominated	58.2 ± 5.26b	48.7	68.8
	ECM-dominated	72.8 ± 5.92a	60.4	85.2
HCl-P/Citric-P	AM-dominated	10.0 ± 0.95a	8.51	11.8
	ECM-dominated	8.88 ± 0.74a	7.59	10.26
HCl-P/Enzyme-P	AM-dominated	528 ± 28.16a	475	583
	ECM-dominated	616 ± 48.28a	531	710
Mineral soil				
Citric-P/CaCl ₂ -P	AM-dominated	15.9 ± 2.54b	11.3	20.90
	ECM-dominated	42.5 ± 3.30a	36.7	48.90
Enzyme-P/CaCl ₂ -P	AM-dominated	0.84 ± 0.05a	0.74	0.94
	ECM-dominated	0.71 ± 0.04a	0.63	0.79
HCl-P/CaCl ₂ -P	AM-dominated	292 ± 11.91a	271	315
	ECM-dominated	320 ± 18.77a	289	355
Citric-P/Enzyme-P	AM-dominated	20.3 ± 3.34b	15.0	25.7
	ECM-dominated	60.7 ± 3.82a	54.3	67.7
HCl-P/Citric-P	AM-dominated	32.5 ± 9.88a	19.7	51.0
	ECM-dominated	7.86 ± 0.47b	7.04	8.70
HCl-P/Enzyme-P	AM-dominated	358 ± 18.51b	328	392
	ECM-dominated	467 ± 32.32a	408	543

Note: Different lower case letters are significantly different between AM-dominated and ECM-dominated plots ($p < 0.05$).

content and P bioavailability (Fig. 1 and Fig. 2). However, inconsistent with the MANE framework which was demonstrated mainly in temperate forests, we found no differences in enzyme-labile organic P in AM and ECM plots, along with higher soil bioavailable inorganic P in ECM plots than in AM plots (Fig. 2). These finding may be mainly due to: 1) in subtropical acidic soils, P is mainly bound to Al and Fe oxides, and as a result, the supply of P to plants is mainly controlled by adsorption/desorption processes (Sanyal and Datta, 1991); 2) ECM fungi can weather minerals by releasing low-molecular-weight organic chelators and hydrogen ions to increase P availability, while AM fungi cannot (Taylor et al., 2009; Zhang et al., 2014; Hodge, 2017; Tedersoo et al., 2019); 3) the pathway of P acquisition in AM fungi is based primarily on their high-affinity uptake system and fast translocation to plants (Smith and Smith, 2011), which may explain the consistently low levels of soil soluble P in AM-dominated plots.

The relative effectiveness ratios of different biological mechanisms assessed by the BBP method have been previously shown to reflect soil P supply ability and P acquisition strategies (Crain et al., 2018). In this study, the ratios of citric-P/CaCl₂-P and HCl-P/CaCl₂-P were both greater than 1 (Table 1), indicating that acid excretion into the soil may be an effective P acquisition strategy for plants, aside from absorbing CaCl₂-P in soil pore water. The ratio of citric-P/enzyme-P was also greater than 1, indicating that organic acids may have greater potential to release P than phosphatase and phytase, and ECM trees display higher potential than AM trees (Zhang et al., 2014). Interestingly, Deluca et al (2015) observed that the P content in the phosphatase extractable pool

Table 2

Summary of the best ordinary least squares (OLS) multiple linear regression models for the effects of biotic and abiotic factors on bioavailable P in the organic and mineral soil.

Variable	Estimate	SE	t-value	p-value	VIF
Organic soil					
CaCl ₂ -P: $df = 43$; $R_{adj}^2 = 0.310$; $SE_{resid} = 0.830$; $F = 20.81$; $AIC = -14.77$					
ECM% trees	0.571	0.125	4.561	<0.001	1.000
Citric -P: $df = 42$; $R_{adj}^2 = 0.220$; $SE_{resid} = 0.903$; $F = 5.93$; $AIC = -8.47$					
ECM% trees	0.487	0.150	3.243	0.002	1.213
MBC	0.362	0.150	2.41	0.020	1.213
Enzyme-P: $df = 42$; $R_{adj}^2 = 0.155$; $SE_{resid} = 0.93$; $F = 5.02$; $AIC = -3.32$					
Litter biomass	0.288	0.139	2.077	0.044	1.001
ACP activity	0.324	0.139	2.338	0.024	1.001
HCl-P: $df = 42$; $R_{adj}^2 = 0.268$; $SE_{resid} = 0.856$; $F = 9.06$; $AIC = -11.14$					
ECM% trees	0.268	0.132	2.027	0.049	1.054
SOC	0.422	0.132	3.186	0.003	1.054
Mineral soil					
CaCl ₂ -P: $df = 42$; $R_{adj}^2 = 0.218$; $SE_{resid} = 0.884$; $F = 7.13$; $AIC = -8.17$					
Litter biomass	0.332	0.136	2.445	0.019	1.037
ACP activity	-0.447	0.136	-3.291	0.002	1.037
Citric -P: $df = 45$; $R_{adj}^2 = 0.528$; $SE_{resid} = 0.687$; $F = 18.92$; $AIC = -32.99$					
ECM% trees	0.611	0.104	5.898	<0.001	1.092
SOC	0.302	0.105	2.890	0.006	1.111
Soil N/P ratio	0.271	0.104	2.608	0.012	1.101
Enzyme-P: $df = 42$; $R_{adj}^2 = 0.166$; $SE_{resid} = 0.913$; $F = 5.38$; $AIC = -5.27$					
Tree richness	-0.377	0.145	-2.604	0.012	1.106
ACP activity	0.392	0.145	2.703	0.010	1.106
HCl-P: $df = 42$; $R_{adj}^2 = 0.297$; $SE_{resid} = 0.839$; $F = 10.27$; $AIC = -12.93$					
ECM% trees	0.442	0.129	3.441	0.001	1.034
SOC	0.453	0.129	3.522	0.001	1.034

was about twice that of the citric acid extractable pool, while we observed the opposite relationship. The ratio of HCl-P/citric-P in AM-dominated plots was the highest, which indicated that Pi in AM soils was more strongly occluded, and weak organic acid alone was not sufficient to release P from soil matrix. Collectively, our findings provide a field test suggesting that the MANE framework may not be fully applicable in subtropical forests.

4.2. Mechanisms underlying mycorrhizal association effect on soil P pools

We observed that total P content increased with ECM tree dominance in the organic soil while a decreasing trend was observed in the mineral soil (Fig. 1). This finding may be attributed to the fact that ECM trees generally produce leaf litter with lower quality (i.e., higher C/N ratio) which leads to greater accumulation of recalcitrant organic matter in surface soils compared to AM trees (Phillips et al., 2013; Midgley et al., 2015). The leaf litterfall collected over one year suggested that there was no difference in annual litterfall biomass, but the litter C/N ratio increased with increasing of ECM tree dominance (Fig. S3). On the other hand, the total P content decreased with ECM tree dominance in the mineral soil, likely because the mobilization of P (increase of soluble P) accelerated soil removal via plant uptake. Moreover, ECM fungi have been shown to significantly increase the volume of soil occupied by fine roots through the production of massive hyphae, which broadens the range of P uptake by ECM trees (Smith and Read, 2008).

Understanding the underlying mechanisms leading to changes of soil bioavailable P pools across the gradient of ECM tree dominance is incredibly important. In this study, ECM tree dominance was positively and directly associated with soil CaCl₂-P, citric-P and HCl-P, but not enzyme-P (Fig. 2). This suggests that ECM trees can more efficiently obtain P_i compared to AM trees through organic acid complexation and acidification rather than producing more phosphatase for P_o mineralization. Our results showed that there were no significant differences in acid phosphatase activity across the mycorrhizal gradient (Fig. S4b). Similarly, a study in a tropical montane forest also observed comparable phosphatase activity between AM and ECM trees (Steidinger et al., 2015). The SEMs implemented here provide powerful evidence that

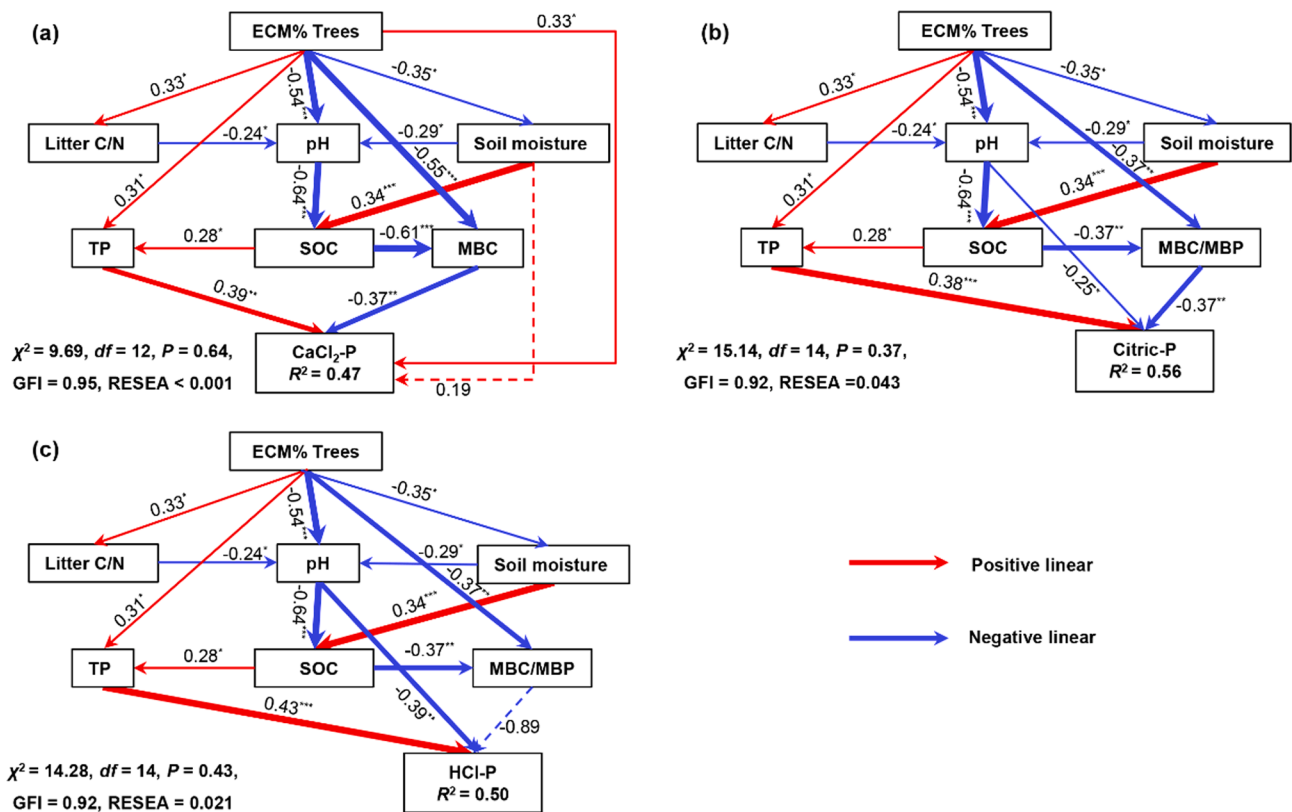


Fig. 3. Structural equation models showing how ectomycorrhizal (ECM) tree dominance and edaphic factors regulate soil CaCl₂-P (a), citric-P (b), enzyme-P (c) and HCl-P (d) in the organic soil. Numbers in the arrows indicate the standardized path coefficients, with the arrow thickness proportional to the strength of the path coefficients (**p* < 0.05, ***p* < 0.01, ****p* < 0.001). *R*² denotes the proportion of variance explained. The chi-square test (χ^2), degree of freedom (*df*), goodness-of-fit index (GFI), and root-mean-square error of approximation (RMSEA) are listed on the model.

ECM tree dominance mediated P bioavailability by altering soil properties and microbial biomass (Fig. 3). Previous work has shown that recalcitrant leaf litter and ample organic acid exudation can lead to relatively stronger soil acidification (i.e., lower pH) in ECM forests (Cheeke et al., 2017; Tedersoo et al., 2019). We indeed found that soil pH decreased with increasing ECM tree dominance (Fig. S4a). In this way, soil acidification can promote the dissolution of insoluble P and desorption of adsorbed P on the surface of Al or Fe oxides (Plassard et al., 2011; Wu et al., 2019). Under this circumstance, our results illustrated that a strong positive correlation between pH and HCl-P, and also citric-P (Fig. S5). Consequently, the depleted CaCl₂-P can be replenished by releasing P into soil solution from citric-P and HCl-P pools in ECM forests.

Our results are also in line with the emerging view that soil microbial biomass play an important role in driving P cycling, as we have shown that MBC/P was negatively correlated with CaCl₂-P, citric-P and HCl-P content (Fig. 3 and Fig. S6). In our study, the microbial biomass P (MBP) constitutes a significant component of total soil P, which was higher than citric-P content and comparable with HCl-P content. It is evident that microorganisms effectively compete with plants for available P and therefore represent a significant pool of immobilized P that is temporarily unavailable to plants (Rosling et al., 2016). However, over the longer term, all microbial biomass P is potentially available to plants which suggests that immobilization of P within biomass is an important mechanism for regulating the supply of P (Richardson and Simpson, 2011). Given the importance of plant-soil microbe interactions in governing nutrient cycling (Wu et al., 2019), an integrated analysis of the linkages among tree mycorrhizal type, soil microbial community composition, and soil P cycling processes is worthy of future research.

4.3. Implications

The present study provides evidence that differences in soil P bioavailability between AM and ECM forests, which enables a better understanding of potential relationships between tree mycorrhizal associations and P biogeochemistry processes. By focusing on evergreen broadleaf forests, we avoid confounding ECM dominance with leaf habit as far as possible. Nonetheless, as with many previous studies (Lin et al., 2017; Craig et al., 2018), our analyses cannot fully separate effects of mycorrhizal type from effects of other functional traits of tree species. Therefore, our study implied that the importance of considering both the mycorrhizal type and plant traits together in future studies.

Understanding the degree to which mycorrhiza mediate the effects of forest tree composition on soil P bioavailability is of great importance for sustainable forest management. Our findings indicate that the ECM trees could effectively acquire P_i in response to P deficiency in subtropical soils, as ECM soils tend to possess a larger bioavailable P pool. This finding improves our understanding of why some ECM trees (e.g., *Pinus massoniana*) have colonized subtropical P-limited soils as pioneer species and why some ECM trees (e.g., *Lithocarpus glaber* and *Cyclobalanopsis glauca*) have evolved as the dominant species in climax communities. Moreover, the ability of ECM trees to promote P availability in soils has an ecologically important role in fostering the coexistence of tree species in subtropical forests. This suggest that in practices of afforestation or in restoration of degraded forests, it is potentially to consider mixed AM with ECM tree species for enhancing ecosystem productivity and stability.

5. Conclusions

Soil P bioavailability was examined across a natural mycorrhizal

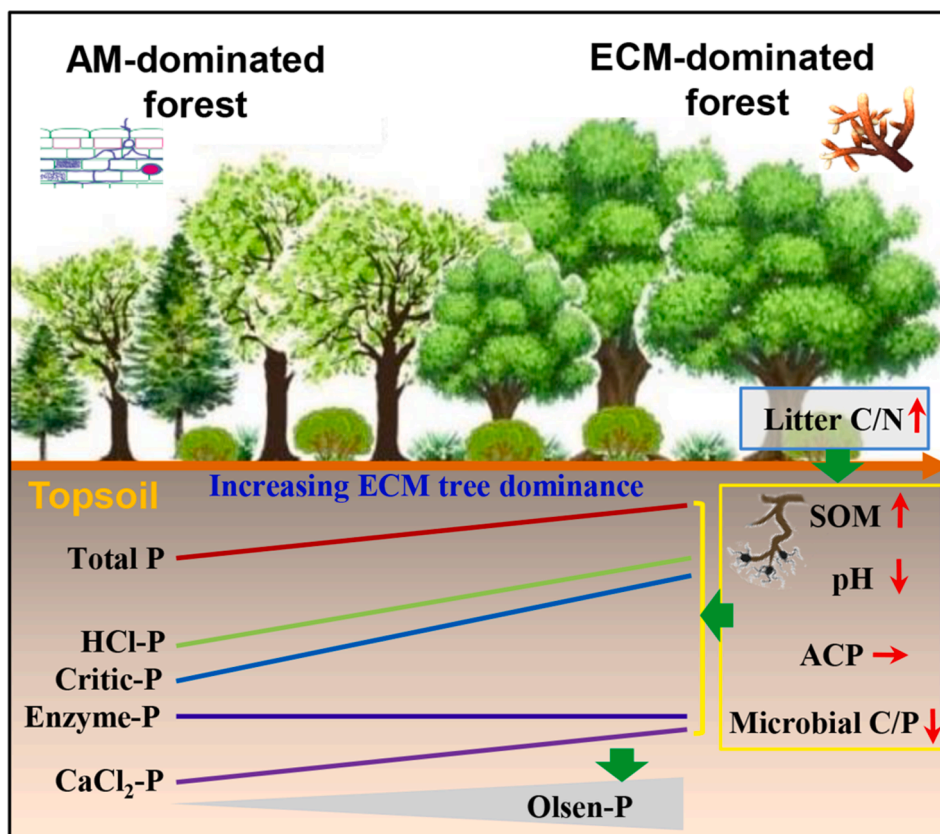


Fig. 4. Conceptual diagram illustrate the effects of tree mycorrhizal types on topsoil bioavailable P in subtropical forests. SOM and ACP represent soil organic matter and acid phosphatase, respectively.

gradient within a subtropical forest site where AM and ECM trees co-occurred. Our results showed that trees associated with AM and ECM fungi displayed different soil P supply abilities and P acquisition strategies. Contents of $\text{CaCl}_2\text{-P}$, citrate-P and HCl-P but not enzyme-P increased with ECM tree dominance (Fig. 4). Specially, ECM-dominated forest soils exhibited markedly higher (1.2–2.9 times) citrate-P and HCl-P than AM-dominated forests did, indicating that ECM trees can effectively acquire P_i in subtropical soils. Acid phosphatase, which is involved in the acquisition of P_o , had similar activity between AM and ECM forests. Annual leaf litterfall input was similar in the quantity, but the quality (i.e., litter C/N ratio) increased with ECM tree dominance. Results from the SEM showed that increasing ECM tree dominance increased litter C/N ratio, SOC and soil moisture, but decreased pH and microbial biomass C/P, all of them critically in mediating P bioavailability. Overall, these findings provide the evidence that tree mycorrhizal associations affect soil P bioavailability.

CRediT authorship contribution statement

Xiaoxu Qi: Investigation, Visualization, Writing-original draft. **Liang Chen:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing-review&editing. **Jing-ao Zhu:** Investigation. **Zhen Li:** Investigation. **Huimin Lei:** Investigation. **Qi Shen:** Investigation. **Huili Wu:** Writing-review & editing. **Shuai Ouyang:** Writing-review & editing. **Yelin Zeng:** Writing-review & editing. **Yangting Hu:** Writing-review & editing. **Wenhua Xiang:** Supervision, Validation, Writing-review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions

L.C. conceived the ideas and designed methodology; X.Q., L.C., J.Z., Z.L., H.L., H.W., S.O., Y.Z. and Y.H. performed experiments, conducted fieldwork, and collected and analysed the data; X.Q. and L.C. led the writing of the manuscript. W.X. contributed significantly to revisions. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120435>.

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