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Soil phosphorus drives plant trait variations in a mature subtropical forest

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Abstract

Earth system models are implementing soil phosphorus dynamic and plant functional traits to predict functional changes in global forests. However, the linkage between soil phosphorus and plant traits lacks empirical evidence, especially in mature forests. Here, we examined the soil phosphorus constraint on plant functional traits in a mature subtropical forest based on observations of 9943 individuals from 90 species in a 5-ha forest dynamic plot and 405 individuals from 15 species in an adjacent 10-year nutrient-addition experiment. We first confirmed a pervasive phosphorus limitation on subtropical tree growth based on leaf N:P ratios. Then, we found that soil phosphorus dominated multidimensional trait variations in the 5-ha forest dynamic plot. Soil phosphorus content explained 44% and 53% of the variance in the traits defining the main functional space across species and communities, respectively. Lastly, we found much stronger phosphorus effects on most plant functional traits than nitrogen at both species and community levels in the 10-year nutrient-addition experiment. This study provides evidence for the consistent pattern of soil phosphorus constraint on plant trait variations between the species and community levels in a mature evergreen broadleaf forest in the East Asian monsoon region. These findings shed light on the predominant role of soil phosphorus on plant functional trait variations in mature subtropical forests, providing new insights for models to incorporate soil phosphorus constraint in predicting future vegetation dynamics.

KEYWORDS
nutrient addition, plant functional traits, soil phosphorus constraint, species and community traits, subtropical forest

1 | INTRODUCTION

Plant functional traits are crucial features that modulate plant performance via influencing growth, survivorship, and reproduction (Díaz et al., 2016; Wright et al., 2004). Plant traits largely determine community assembly and the multiple functioning of ecosystems, such as biomass production and carbon storage (Migliavacca et al., 2021; van der Plas et al., 2020). Thus, our ability to understand and predict ecosystem function largely depends on quantifying plant trait distributions and their responses to environmental drivers (Kovenock & Swann, 2018). Climatic drivers shape and shift functional traits and ecological strategies across broad biogeographical gradients (Wieczynsk et al., 2019). However, plant functional traits at fine-grained communities are usually predominantly driven by local soil nutrient levels rather than large-scale climate variables (Bruelheide et al., 2018; Simpson et al., 2016). In addition, there is growing recognition that nutrient addition has become one of the most pervasive drivers shaping species composition, and thereby ecosystem functional changes (Seabloom et al., 2021). Therefore, understanding the relationship between soil nutrients and plant functional traits is crucial for predicting the dynamics of species-rich ecosystems such as mature forests.

Soil phosphorus (P) is tightly related to plant growth and ecosystem productivity (Crous et al., 2017). A recent global analysis has suggested a wide distribution of P limitation on terrestrial plant growth and biomass production, especially in tropical and subtropical ecosystems (Du et al., 2020). The P limitation can even constrain the response of terrestrial carbon uptake to climate change (Terrer et al., 2019). Thus, there is a growing demand to couple the P cycle with vegetation dynamics in Earth system models (ESMs) (Reed et al., 2015). Besides incorporating P cycling, many ESMs are improving the representation of global vegetation dynamics based on plant functional traits (Berzaghi et al., 2020; Franklin et al., 2020). Those traits-based developments of ESMs commonly take advantage of the empirical trait-environment relationships and trait-trait covariance for representing different ecological strategies (Cui et al., 2020; Xia et al., 2017; Yang et al., 2015). However, as the global pattern and magnitude of soil P constraint on plant traits remain inadequately understood, the implementations of the P cycle and plant functional traits are generally decoupled in ESMs.

The relationship between plant traits and soil nutrients indicates a trade-off between growth rate and nutrient conservation (Reich et al., 1992; Wright et al., 2004; Xu et al., 2020). When soil P availability is not limiting, plant species tend to have higher specific leaf area (SLA), leaf nutrient concentration, and metabolic rate (Reich, 2014). Global patterns of traits-soil nutrient relationship have been studied extensively (Maire et al., 2015; Ordoñez et al., 2009). However, it remains unclear whether soil P availability pervasively limits the variation in different plant functional traits in those P-limited ecosystems. Several methods are available to estimate nutrient constraint, including nutrient-addition experiments (Chen et al., 2020; Hou et al., 2021), spatial trait–soil nutrient relationships (Maire et al., 2015), and thresholds of leaf nitrogen to phosphorus (N:P) ratios (Du et al., 2020; Güsewell, 2004). Nutrient-addition experiment is one of the most direct ways to examine nutrient constraints and can provide comparable effect sizes for different levels of nutrient treatments (Firn et al., 2019; Xia & Wan, 2008). On the local scale, spatial analyses on the covariance between plant traits and their controlling factors could also infer the limiting roles of soil nutrients on plant trait variations (Reichstein et al., 2014). In addition, the leaf N:P ratio is a widely used simple indicator for identifying plant nutrient limitations on plant growth and biomass production (Yan et al., 2017). Applying the above methods can reveal multiple lines of evidence for the role of soil P in regulating plant trait variations in a specific ecosystem.

Nearly 71% of the subtropical forests locate in China and adjacent countries (Figure 1; Corlett & Hughes, 2015). Mature subtropical forests in China are characterized by highly diverse plant trait composition (Liu et al., 2018), and trait variations are critical for their ecosystem functions, such as primary productivity (Cui et al., 2019). A growing body of research has suggested that soil P rather than N limits plant growth and biomass production in subtropical forests (Li et al., 2018; Qiao et al., 2020; Wang et al., 2019). For example, a global meta-analysis shows that the magnitude of P limitation on plant production is more significant in tropical and subtropical forests than in other regions (Hou et al., 2020). In addition, recent global change has significantly altered soil P concentration in subtropical China, and the P limitation over subtropical forests is projected to be more severe (Yu et al., 2018). These studies underscore the urgent need to incorporate

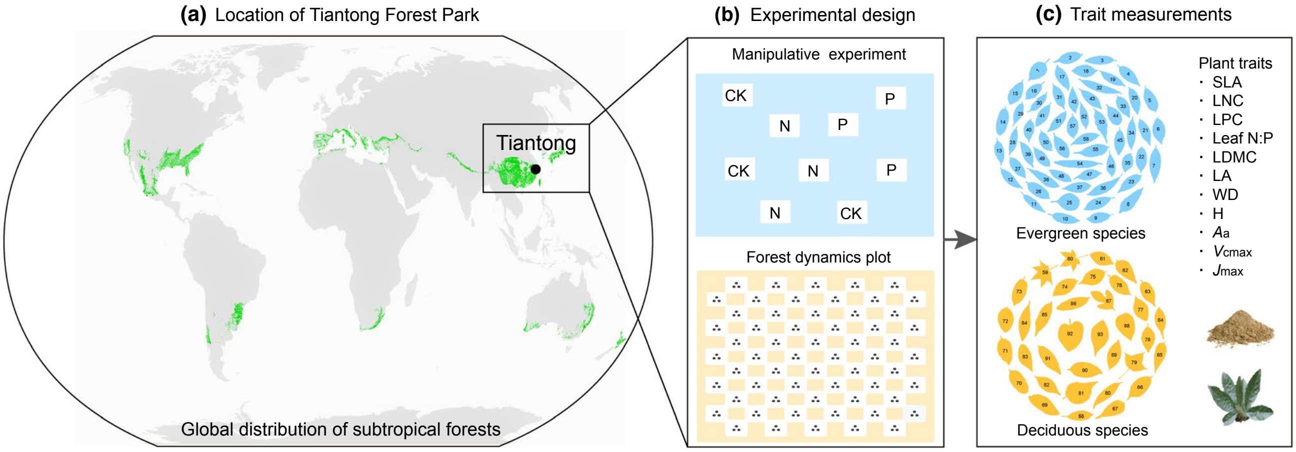

FIGURE 1 The location of Tiantong Forest Park and study design. (a) Global distribution of subtropical forests (FAO, 2020. Global Forest Resources Assessment, 2020. Rome). (b) Design of nutrient-addition experiment and survey of 60 subplots in the 5-ha forest dynamic plot. Treatments in nutrient-addition experiment include control (CK), N addition (N), and P addition (P). The black scatters are soil sampling sites in 60 subplots of the 5-ha forest dynamic plot. (c) Graphical summary of the total 58 evergreen species and 35 deciduous species (Table S1). The measured plant traits include specific leaf area (SLA), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), leaf nitrogen to phosphorus ratio (leaf N:P), leaf dry matter content (LDMC), leaf area (LA), wood density (WD), maximum plant height (H), maximum photosynthetic rate (*A*a), maximum rate of carboxylation (*V*cmax), and maximum rate of electron transport (*J*max)

nutrient supply limitations into future ecological predictions (Dantas de Paula et al., 2021). However, it remains unclear whether soil P also drives the variations of plant functional traits from species to community level in the mature subtropical forests.

This study hypothesizes that soil P plays a critical role in regulating the variations of plant functional traits in mature subtropical forests. On the global scale, the imbalanced atmospheric N and P deposition (Peñuelas et al., 2012) can aggravate soil P limitation on plant growth (Li et al., 2016; Zhu et al., 2016). Recent studies suggest a strong soil P constraint on leaf traits, especially leaf nutrient concentration, in various terrestrial ecosystems (Firn et al., 2019; Mayor et al., 2014; Yang, 2018). In this study, we applied multiple approaches in a mature tropical forest to test the hypothesis of soil P constraint on plant trait variations on the species and community levels. We first estimated the soil P limitation on different plant species based on their leaf N:P ratios. Then, we investigated the role of soil P in shaping spatial trait covariations in a 5-ha forest dynamic plot. Lastly, we directly quantified the magnitude of soil P constraint on plant functional traits and the pervasiveness of P constraint across species and communities in a 10-year nutrient-addition experiment. This study examines whether soil P is a critical factor in limiting variations of multiple plant functional traits in a mature subtropical forest.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was conducted in the Zhejiang Tiantong Forest Ecosystem National Observation and Research Station (29°48′N, 121°47′E), which is located in Eastern China. This area is characterized as a subtropical evergreen broadleaf forest, with the mean annual temperature as 17°C and annual precipitation as 1600 mm. The dominant species in this subtropical forest include *Schima superba*, *Castanopsis fargesii*, *Choerospondias axiliaris*, and *Machilus leptophylla* (Ali & Yan, 2017). This study used two approaches to test soil P constraint on plant functional traits: experimental evidence based on 405 individuals from 15 species in a 10-year field nutrient-addition experiment and spatial analysis according to 9943 individuals from 90 species in a 5-ha forest dynamic plot (Figure 1).

2.2 | The 5-ha forest plot and trait measurements

The 5-ha forest dynamic plot was located adjacent to the nutrient-addition experiment and was divided into 60 (20 × 20 m) subplots. All the individuals with the stem diameter at breast height ≥1 cm were tagged, geo-referenced, and identified to species level. A total of 9943 individuals belonging to 90 species were recorded. We then measured plant functional traits and environmental factors for the 60 subplots to test the plant trait covariations and their underlying environmental drivers (Figure 1). Plant traits related to the resource economics spectrum and competitive ability were measured, including SLA ($cm^2\ g^{-1}$), leaf N concentration (LNC, $g\ kg^{-1}$), leaf P concentration (LPC, $g\ kg^{-1}$), leaf N:P ratio, leaf dry matter content (LDMC, $mg\ g^{-1}$), leaf area (LA, cm^2), maximum plant height (H, m), and wood density (WD, $g\ cm^{-3}$). The trait LA, SLA, and LDMC for each individual in the 60 subplots were measured. For leaf nutrient traits and WD, measurements were taken for seven randomly-selected mature trees for each species. The maximum plant height was compiled from the Chinese flora data set. The measured soil environmental variables include soil organic carbon (SOC, $g\ kg^{-1}$), total nitrogen (TN, $g\ kg^{-1}$) and total phosphorus (TP, $g\ kg^{-1}$), soil temperature (ST, °C), soil moisture (SM, %), slope (°), pH, and elevation (Elev, m). Overall, the mean plant traits of 90 species and the soil environmental variables of 60 subplots were collected from the 5-ha forest dynamic plot.

2.3 | Nutrient-addition experiment and trait measurements

The nutrient-addition experiment was conducted in nine 20 m × 20 m plots of the station (Zheng et al., 2017), with three treatments and three replicates per treatment (control: 0 kg N $ha^{-1}\ yr^{-1}$; N addition: 100 kg N $ha^{-1}\ yr^{-1}$; P addition: 50 kg P $ha^{-1}\ yr^{-1}$). From January 2011, fertilizer was applied monthly over the litter layer. The control plots received equivalent water to avoid differences in throughfall among different treatments. Leaf physiological and morphological traits are sensitive to indicate the responses (e.g., acclimation, adaptation, and species turnover) of plants to nutrient addition. Therefore, eight leaf functional traits in 405 individuals belonging to 15 species were measured in 2020. The sampled species accounted for 90% of the total basal area per plot. Three individuals were sampled for each species in each plot. To avoid the effects of both light and height, the sampling positions for the same species should be at the same height. If the sample size of a species was less than three in a plot, we took repeated random samples from the same individual. Three branches at the top of the canopy for each individual were randomly selected for measurements of leaf traits following standard protocols. The final sampled leaf traits included SLA ($cm^2\ g^{-1}$), LA (cm^2), LNC ($g\ kg^{-1}$), LPC ($g\ kg^{-1}$), leaf N:P ratio, maximum photosynthetic rate (A_a, $\mu mol\ m^{-2}\ s^{-1}$), maximum rate of carboxylation (V_{cmax}, $\mu mol\ m^{-2}\ s^{-1}$), and maximum rate of electron transport (J_{max}, $\mu mol\ m^{-2}\ s^{-1}$). The soil properties and plant community characteristics for each plot were simultaneously examined.

2.4 | Quantification of community-level functional traits

Each functional trait is scaled up from species level to community level by considering the relative basal area for different species (Garnier et al., 2004). The up-scaling equation is:

$$CWM_{j,k} = \sum_{i=1}^{nk} p_{i,k} x_{i,j}$$

where nk is the number of species sampled in plot k, $p_{i,k}$ is the relative basal area of species i in plot k, and $x_{i,j}$ is the mean value of species i for trait j. We calculated the community-level trait from species-level data for each trait in the 60 subplots of the 5-ha plot and the 9 plots in the nutrient-addition experiment.

2.5 | Quantification of the optimum environmental conditions for each species

To determine the optimum environmental conditions for each species in the 5-ha forest dynamic plot, we computed the kernel density estimate for all species simultaneously with respect to the environmental factor (Figure S1). The kernel density estimator is

$$\hat{f}_h(x) = \frac{1}{n}\sum_{i=1}^{n} K_h(x - x_i) = \frac{1}{nh}\sum_{i=1}^{n} K\left(\frac{x - x_i}{h}\right)$$

where $K(\bullet)$ is the kernel (a non-negative function that integrates to one and has mean zero) and $h > 0$ is a smoothing parameter called the bandwidth. A kernel with subscript h is called the scaled kernel and defined as $K_h(x) = 1/h\,K(x/h)$. We used the kernel density estimate to compute the optimum environmental conditions for each species (i.e., the value of the environmental factors where the species attains its highest probability of occurrence) (Laughlin et al., 2021). These optimum environmental conditions for each species were used to detect the major environmental drivers for explaining the multidimensional trait variations at the species level as well as the bivariate relationships between functional traits and soil nutrients across species.

2.6 | Statistical analysis

Principal component analysis (PCA) was used to test the multivariate covariant relationships of plant functional traits across species and communities. The PCA allows us to reduce a multidimensional trait space to its first two principal trait axes (Trait PC1 and PC2). Then, we identified the primary soil drivers of multidimensional trait variation by calculating the relative importance of each soil variable in explaining the geographical patterns of trait PC1 and PC2. Relative importance is defined as the proportionate contribution of each predictor to R^2 in multiple regression, considering both its unique contribution and contribution when combined with other variables (Johnson, 2000). PCA was performed using the prcomp function, and relative importance was quantified using the "*relweights*" function in R version 3.5.3 (R Core Team, 2015).

Furthermore, bivariate relationships between functional traits and soil nutrients across species and communities were calculated using the lm function in R. Response surface analysis was conducted to show the relationships between soil TN and TP versus plant functional traits by fitting first-order (linear) functions using package rsm in R (Lenth, 2009). The multiway factorial ANOVA in SPSS (SPSS Inc. Ver.16, USA) was used to test the main and interactive effects of N, P, and functional groups on plant functional traits. The mean effect sizes of nutrient addition on plant functional traits were defined and graphed as the percentage changes of trait values in the treatment plot compared with the control plot.

3 | RESULTS

3.1 | Phosphorus limitation of subtropical species inferred from leaf N:P ratio

In total, we measured plant functional traits of 9943 individuals belonging to 90 species in the 5-ha forest dynamic plot and 405 individuals belonging to 15 species from the 10-year nutrient-addition experiment (Figure 2). In the 5-ha forest dynamic plot, the measured plant traits including SLA (133.25 ± 32.03 $\text{cm}^2\ \text{g}^{-1}$), LA (19.93 ± 25.62 cm^2), leaf N:P (32.84 ± 9.12), LPC (0.54 ± 0.13 g kg^{-1}), LNC (16.87 ± 2.79 g kg^{-1}), WD (0.54 ± 0.08 g cm^{-3}), H (11.44 ± 6.18 m) and LDMC (401.73 ± 45.54 mg g^{-1}). For the 10-year nutrient-addition experiment, the measured plant traits including SLA (98.01 ± 22.02 $\text{cm}^2\ \text{g}^{-1}$), LA (14.57 ± 8.35 cm^2), leaf N:P (31.10 ± 13.00), LPC (0.51 ± 0.18 g kg^{-1}), LNC (14.16 ± 2.43 g kg^{-1}), A_a (6.17 ± 1.78 μmol $\text{m}^{-2}\ \text{s}^{-1}$), V_{cmax} (36.72 ± 16.73 μmol $\text{m}^{-2}\ \text{s}^{-1}$) and J_{max} (57.93 ± 26.28 μmol $\text{m}^{-2}\ \text{s}^{-1}$).

The leaf N:P ratio has been proposed as a simple alternative indicator to detect plant nutrient limitation among these measured plant traits. For the 90 species in the 5-ha forest dynamic plot, the averaged leaf N:P ratio was 31.08 ± 13.03, ranging from 13.61 in *Symplocos lancifolia* to 94.61 in *Ilex buergeri* (Figure 3a). For different leaf habits, evergreen species had lower leaf N and P concentrations than deciduous species ($p < .01$), while there was no significant difference in leaf N:P ratio among functional groups ($p > .05$, Figure S2). Among the 15 species from the nutrient-addition experiment, leaf N:P ratios varied from 22.00 in *Castanopsis carlesii* to 75.67 in *Cyclobalanopsis stewardiana*, with the mean value as 43.10 ± 17.23 (Figure 3b). More than 90% of the subtropical species were limited by P, with leaf N:P ratios larger than 20:1.

3.2 | Predominant role of soil phosphorus in spatial trait covariations

In the 5-ha forest plot, the PCA detected two principal trait axes for explaining the multidimensional trait variations (Figure 4). These two principal trait axes respectively accounted for 55.5% (PC1 = 36.2%, PC2 = 19.3%) and 77.2% (PC1 = 57.5%, PC2 = 19.7%) of total multidimensional trait variation across species and communities. At the species level, trait PC1 aligns most strongly with the variations in SLA (0.27) and LNC (0.27), whereas trait PC2 aligns with leaf N:P (0.51) and LPC (−0.32) (Figure 4a).

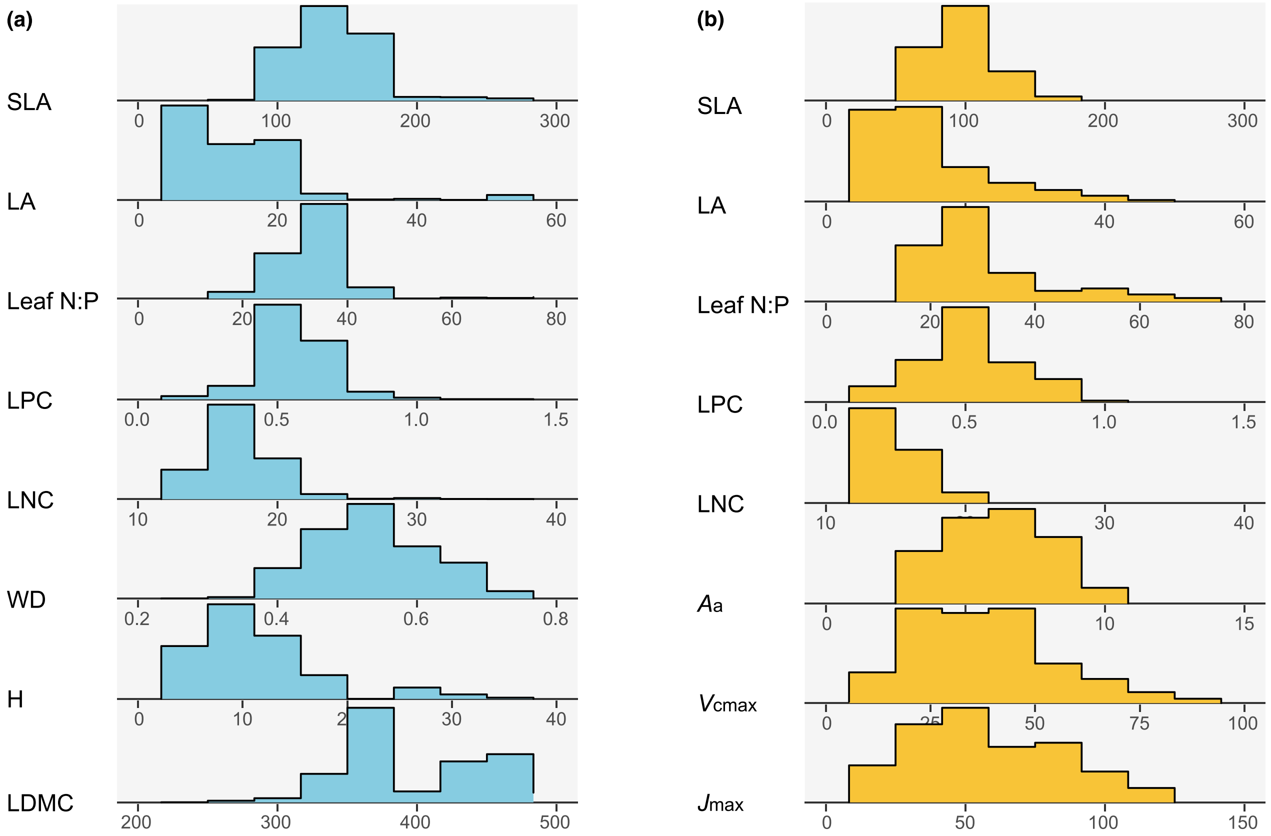

FIGURE 2 Variations of plant functional traits for 9943 individuals in the 5-ha forest dynamic plot (a) and 405 individuals from the 10-year nutrient-addition experiment (b)

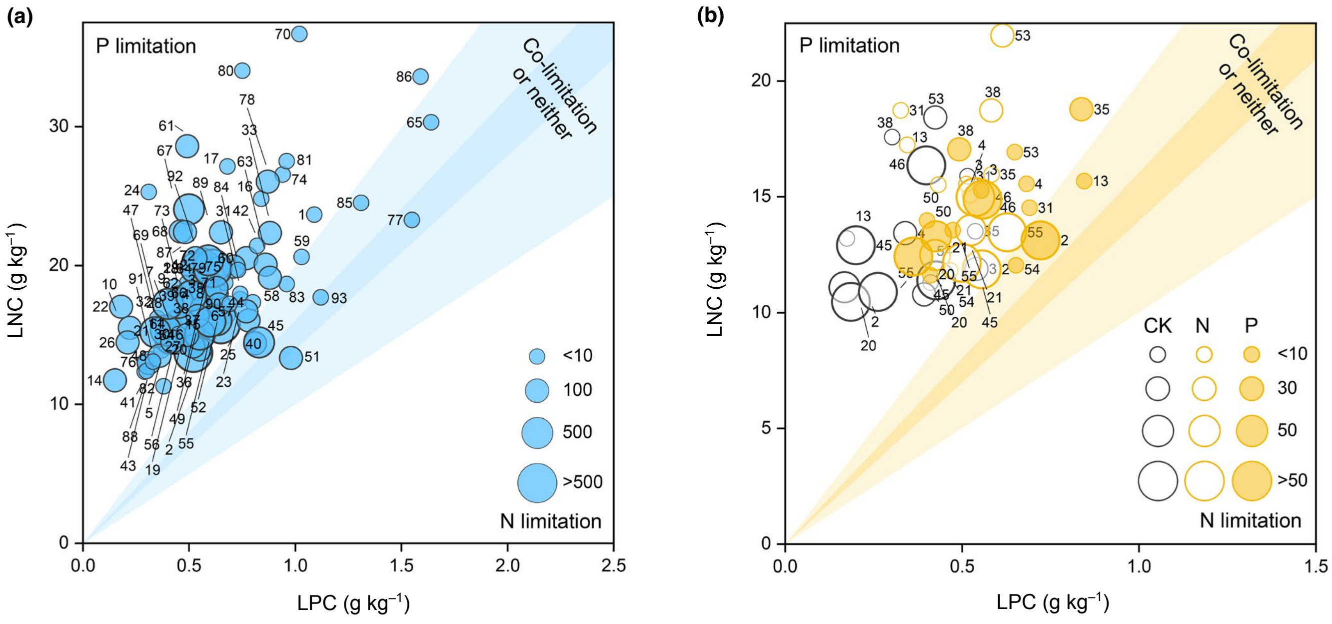

FIGURE 3 Leaf N:P ratios of 90 species in the 5-ha forest dynamic plot (a) and 15 species from different nutrient treatments (b). The size of the circle indicates the species abundance. Label for the circle corresponds to the serial number of species in Table S1 (evergreen species:1–58; deciduous species: 59–93). The blue shadings show two widely used leaf N:P thresholds for determining nutrient limitations: 14:1 versus 16:1 from Koerselman and Meuleman (1996), 10:1 versus 20:1 from Güsewell (2004)

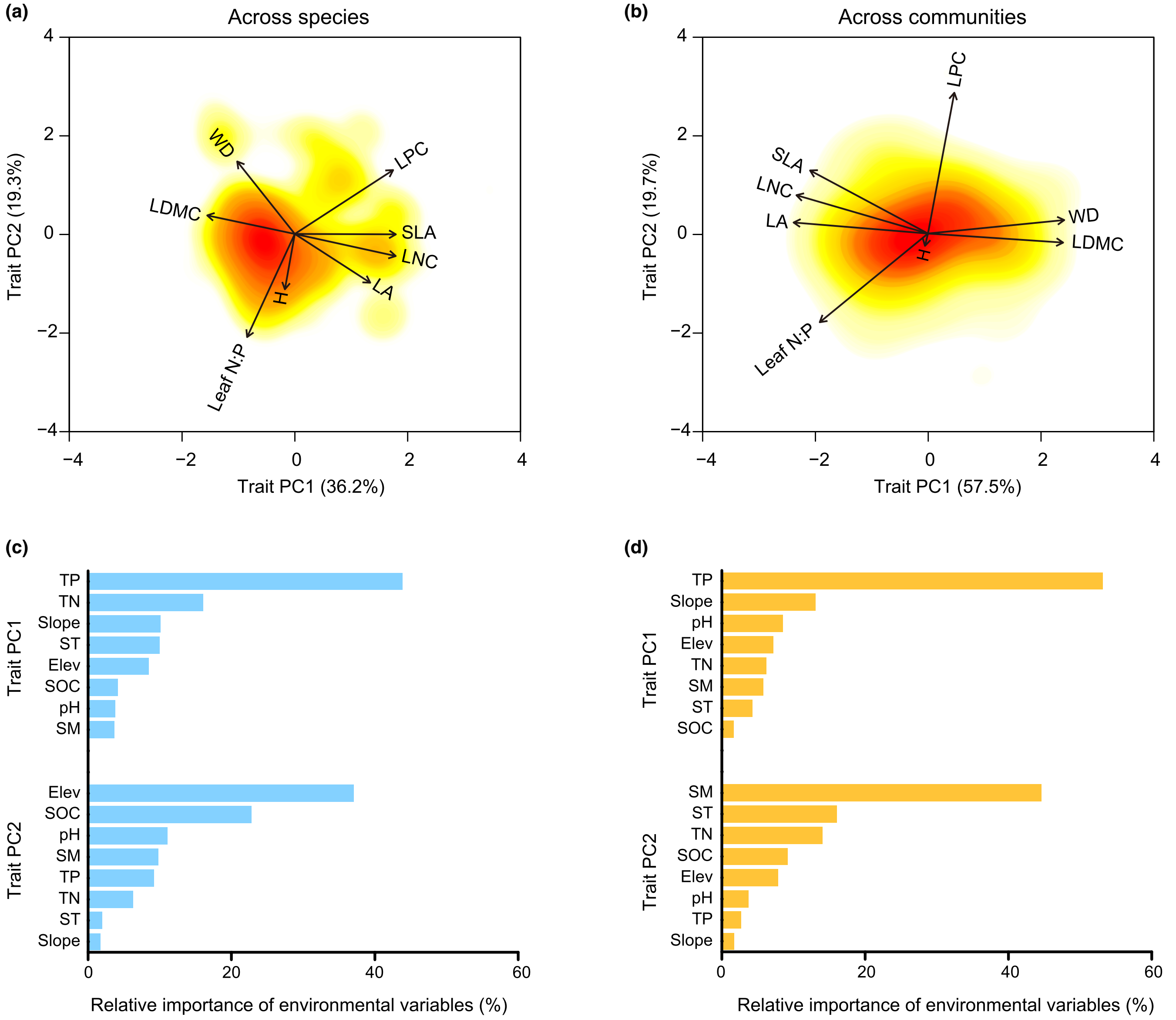

FIGURE 4 The first two principal component axes of trait space across species and communities and the strength of their correlations with each environmental factor. (a, b) The first two principal trait axes (traits PC1 and PC2) across species and communities. Solid arrows indicate the direction and weighing of vectors representing the eight plant traits. The red regions represent the occurrence probability of species or community from highest (red) to lowest (white) in the trait space defined by PC1 and PC2. (c, d) Relative contributions of environmental variables in driving spatial patterns of the first two principal trait axes

At the community level, trait PC1 aligns with WD (0.43), LDMC (0.43), LA (−0.43) and LNC (−0.42), while trait PC2 aligns with LPC (0.77) and leaf N:P (−0.48) (Figure 4b). We further identified the primary environmental drivers of multidimensional trait variation by calculating their relative contributions in driving the first two principal trait axes. At the species level, the trait PC1 was primarily determined by soil TP (44%) and soil TN (16%), whereas the trait PC2 was associated with elevation (37%) and soil organic carbon (23%) (Figure 4c). At the community level, the trait PC1 was most strongly related to soil TP (53%) and slope (13%), whereas trait PC2 was associated with soil moisture (45%) and soil temperature (16%) (Figure 4d).

Linear regressions showed bivariate relationships between functional traits and soil nutrients across species and communities. At the species level, soil TP were significantly correlated with SLA ($r = 0.40$, $p < .001$), LPC ($r = 0.22$, $p < .05$), LNC ($r = 0.26$, $p < .01$) and LDMC ($r = -0.22$, $p < .05$), whereas only SLA ($r = 0.30$, $p < .01$) and LNC ($r = 0.25$, $p < .05$) showed significantly relationship with soil TN (Figure S3a and c). At the community level, soil TN only significantly affected H ($r = 0.37$, $p < .001$; Figure S3b). By comparison, SLA ($r = 0.41$, $p < .001$), LA ($r = 0.40$, $p < .001$), LNC ($r = 0.51$, $p < .001$) and leaf N:P ($r = 0.38$, $p < .001$) were positively related to soil P, whereas WD ($r = -0.56$, $p < .001$) and LDMC ($r = -0.47$, $p < .001$) decreased along soil P gradient (Figure S3d).

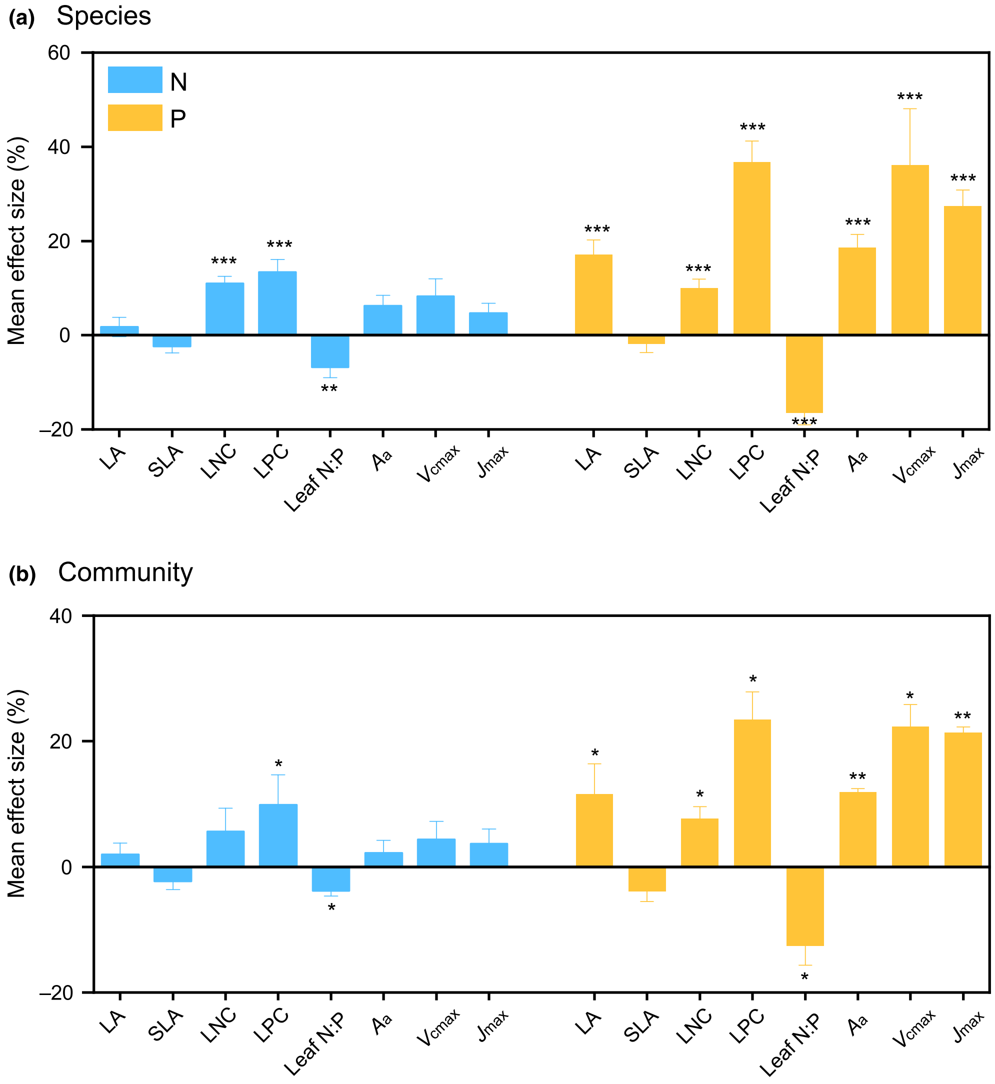

FIGURE 5 The mean effect sizes of N and P addition on plant functional traits at species (a) and community (b) levels. Error bar denotes SE between species and communities. The significance of effect sizes: $^*p < .05$; $^{**}p < .01$; $^{***}p < .001$

3.3 | Experimental evidence for phosphorus constraint on plant functional traits

Furthermore, the nutrient-addition experiment provided direct evidence for the differential responses of plant functional traits to N and P addition. At the species level, significant main effects on seven of the eight leaf traits were found under P addition (all $p < .001$), whereas N addition only changed leaf nutrient traits ($p < .001$ for LNC, $p < .001$ for LPC, and $p < .01$ for leaf N:P, Table S2). The significant species × nutrient addition interaction showed that the magnitude of soil P constraint differs among plant species. Among the eight leaf traits, leaf P concentration was most sensitive to nutrient addition, with the mean effect sizes as 13.40% and 36.71% under N and P addition, respectively (Figure 5a). At the community level, N addition significantly increased LPC by 9.89% and decreased leaf N:P by 3.80% ($p < .05$) but showed nonsignificant effects on other six leaf traits (all $p > .05$). By comparison, P addition significantly affected LA (11.60%, $p < .05$), LNC (7.66%, $p < .05$), LPC (23.42%, $p < .05$), leaf N:P (−12.57%, $p < .05$), A_a (11.89%, $p < .01$), V_{cmax} (21.13%, $p < .05$) and J_{max} (20.17%, $p < .01$) (Figure 5b and Table S3).

4 | DISCUSSION

Many studies have highlighted the importance of soil N limitation on ecosystem productivity and carbon sequestration in subtropical forests (Lu et al., 2021; Xia et al., 2013; Yu et al., 2014). However, this study shows a predominant role of soil P in driving plant trait variations in a mature subtropical forest. According to the two widely used N:P thresholds for determining nutrient limitations, 91% of the subtropical species are strongly limited by P, with leaf N:P ratios larger than 20:1 (Figure 3). In addition, analyses from the 5-ha forest dynamic plot suggest that soil P is a stronger predictor for spatial covariations of plant functional traits than soil N (Figure 4).

Furthermore, results from the 10-year nutrient-addition experiment directly proves that the mean effect sizes of P addition on plant functional traits are larger than N addition (Figure 5). These multiple lines of evidence together suggest a substantial soil P constraint on the variations of plant functional traits in the mature subtropical forests.

Our analyses also demonstrate a more important role of soil P in driving plant trait variations than microclimatic conditions (soil temperature and soil moisture), topographic factors (elevation and slope), and other soil environmental variables (SOC and pH) (Figure 4). The importance of soil P in regulating functional trait shifts is receiving increasing attention and could be further confirmed by recent advances. For example, an analysis based on a global trait data set has proven that soil variables (soil pH and available P) are stronger predictors of leaf photosynthetic traits than climatic variables (Maire et al., 2015). Another study across subtropical forests suggests that the explanatory power of soil total P for shifts in functional traits is much higher than topography (Huang et al., 2021). To the best of our knowledge, our study is the first to provide empirical evidence for the predominant role of soil P on multiple plant trait variations both at the species and communities levels. According to the paradigm of P limitation (Dalling et al., 2016), a large fraction of P in tropical soils may be in the microbial and litter pools. Plants could cope with low P availability through increases in P resorption efficiency. Indeed, we found that long-term P addition significantly increased P concentration in the plant, soil, and litter pools (Figure S4). However, P resorption efficiency was weakly influenced by the increased P availability, further supporting that plant P limitation was not improved even under P addition. In addition, the magnitude of the P constraint also depends on the pretreatment soil P levels (Firn et al., 2019; Hou et al., 2021). Considering the continuous decrease in soil total P concentration across all soil depths during the past 60 years in subtropical China (Yu et al., 2018), we suggest that the intensity of soil P constraint on functional traits may increase in the near future.

Recent researches suggest that the imbalanced atmospheric N and P deposition is expected to alter terrestrial nutrient availability and aggravate P limitation in subtropical regions (Peñuelas et al., 2012; Zhu et al., 2016). However, we know much less about the effect of N deposition on the P constraint of plant trait variations. This study showed that the 10-year N addition enhanced LPC and caused a significant decrease in leaf N:P ratio (Figure 4). The decreased leaf N:P ratio indicates that P limitation for subtropical species is partly alleviated under long-term N addition. Several possible biochemical mechanisms may explain why plant P uptake benefits from N addition. First, a high N supply could increase soil phosphatase activity or initiate root branching and hence stimulate the plant capacity for P acquisition during the initial stage (Marklein & Houlton, 2012; Pasley et al., 2019). Second, the stimulation of N addition to soil phosphatase activity would diminish over time, thereby alleviating N-induced changes in soil available P or total P content (Figure S5). A recent meta-analysis supports the above mechanism, showing that long-term N loading does not affect soil P content and phosphatase activity but alleviates P limitation by initially stimulating soil phosphatase activity (Chen et al., 2020).

Our study also reveals a consistent pattern of soil P constraint on plant trait variations between the species and community levels. Firstly, the P addition altered the same seven traits on the species and community level, and the most responsive traits were LPC and V_{cmax} (Figure 5). Such a similar response pattern could result from the limited changes in species composition. According to the importance value index of dominant species, species composition of this mature subtropical forest was not affected by long-term nutrient addition, except for the importance value of *Rhododendron ovatum* was slightly increased under P addition (Figure S6). Conversely, the species-specific P constraint could not translate into the community level if species distributions dramatically vary along soil P gradient (Turner et al., 2018). Secondly, we demonstrate similar spatial trait covariances along soil P gradient between species and communities across 60 survey subplots in the 5-ha forest dynamic plot. Species with higher SLA, LNC, and LPC were more prevalent in soils with high P content, while species with higher LDMC were more common in low P soil (Figure S3c). Likewise, plant communities in soils with high P content were characterized by higher SLA, LA, LNC, and leaf N:P, whereas plant communities with higher WD and LDMC tended to dominate in low P soils (Figure S3d). These results reveal the dominant role of soil P in driving species-specific trait responses and community trait assembly in mature subtropical forests.

Although this study applies multiple approaches to illustrate the linkage between soil phosphorus and plant traits, several limitations deserve further discussion. First, in general, plant-available N and P cannot be substituted entirely by soil total N and P, with most soil nutrients being in insoluble forms that are unavailable to plants. Soil nutrient available to plants is also tightly coupled with the deposition of labile P via litter inputs. Here, the significant positive relationships between soil total nutrient and litter nutrient further strengthen the representativeness of total soil nutrients to available nutrients in this forest (Figure S7). Second, many leaf anatomical and physiological traits can be affected by both light and height of the foliage (Cavaleri et al., 2010). More efforts should be made to explore the vertical trends of plant traits in subtropical forests, which have long been theorized to affect forest productivity. Third, some recent studies suggest that many cations (e.g., boron, calcium, potassium, and zinc) could affect N:P ratio due to luxury consumption or dilution of N or P (Dalling et al., 2016). Therefore, the effects of other cations should be considered in the future evaluation of plant nutrient limitations. Fourth, several methods have been developed to scale-up traits across species to the community level (Garnier et al., 2004; Massmann et al., 2022), which may produce different community-level traits and affect the final response patterns. In this study, we detected that results from two different scaling methods both support the stronger P-addition effects on leaf traits than N in this subtropical forest (Figure S8).

In conclusion, our findings underline the critical role of soil nutrients in regulating plant trait variations and thereby constraining ecosystem function in mature subtropical forests. We found that the soil P dynamics could cause substantial changes in functional traits, which is currently under-represented in most large-scale biogeochemical models (Luo et al., 2015; Piao et al., 2020; Reed et al., 2015). Many recent studies have recommended trait-based approaches for including environment-driven trait variations to improve vegetation dynamics modeling (Cui et al., 2019; Verheijen et al., 2015; Yang et al., 2015). This study also shows that the field observations of plant trait variability from the species to community level can improve the understanding of plant-soil interactions on the ecosystem scale. We recommend incorporating P constraint on plant trait variations as a critical step toward predicting vegetation dynamics and ecosystem changes in subtropical forests.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

EC and JX devised and conducted the analysis. EY and ZZ provided critical suggestions on the method and results. All authors contributed to the writing and revising of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.19207899.v1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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