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Plant economics spectrum governs leaf nitrogen and phosphorus resorption in subtropical transitional forests

Boyu Ma¹, Jielin Ge^{1*}, Changming Zhao¹, Wenting Xu¹, Kai Xu¹ and Zongqiang Xie^{1,2}

Abstract

Background Leaf nitrogen (N) and phosphorus (P) resorption is a fundamental adaptation strategy for plant nutrient conservation. However, the relative roles that environmental factors and plant functional traits play in regulating N and P resorption remain largely unclear, and little is known about the underlying mechanism of plant functional traits affecting nutrient resorption. Here, we measured leaf N and P resorption and 13 plant functional traits of leaf, petiole, and twig for 101 representative broad-leaved tree species in our target subtropical transitional forests. We integrated these multiple functional traits into the plant economics spectrum (PES). We further explored whether and how elevation-related environmental factors and these functional traits collectively control leaf N and P resorption.

Results We found that deciduous and evergreen trees exhibited highly diversified PES strategies, tending to be acquisitive and conservative, respectively. The effects of PES, rather than of environmental factors, dominated leaf N and P resorption patterns along the elevational gradient. Specifically, the photosynthesis and nutrient recourse utilization axis positively affected N and P resorption for both deciduous and evergreen trees, whereas the structural and functional investment axis positively affected leaf N and P resorption for evergreen species only. Specific leaf area and green leaf nutrient concentrations were the most influential traits driving leaf N and P resorption.

Conclusions Our study simultaneously elucidated the relative contributions of environmental factors and plant functional traits to leaf N and P resorption by including more representative tree species than previous studies, expanding our understanding beyond the relatively well-studied tropical and temperate forests. We highlight that prioritizing the fundamental role of traits related to leaf resource capture and defense contributes to the monitoring and modeling of leaf nutrient resorption. Therefore, we need to integrate PES effects on leaf nutrient resorption into the current nutrient cycling model framework to better advance our general understanding of the consequences of shifting tree species composition for nutrient cycles across diverse forests.

Keywords Elevational gradient, Leaf habit, Nutrient cycling, Nutrient resorption, Plant functional trait, Trait coordination

Introduction

Nutrient resorption is the process by which plant withdraws nutrients from senescing tissues before litterfall and thus is recognized as an adaptation strategy for plant nutrient conservation [1–4]. This process prolongs nutrient mean residence time, which enables plants to depend less on current nutrient uptake capacity to mitigate the nutrient limitation of plant production, thereby

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enhancing overall nutrient use efficiency and improving plant fitness in natural ecosystems [5–7]. Nutrient resorption represents a fundamental pathway of nutrient recycling in forest ecosystems, especially for nitrogen (N) and phosphorus (P), which are heavily involved in plant physiological processes and are integral components in many metabolic compounds, such as proteins and Ribonucleic Acid (RNA) [8, 9]. Plant N and P resorption is estimated to provide an average of 31% and 40% of the annual plant N and P requirements for forests globally, respectively [10]. Nutrient resorption efficiency (RE) and nutrient resorption proficiency (RP) have been well-recognized as complementary metrics of leaf nutrient resorption [3, 5, 11]. For leaves, RE indicates the proportion of nutrients that were resorbed before the abscission of green leaves, and RP represents the lowest nutrient concentration in the senescent leaves, which is considered to be the biochemical limit of resorption [5]. Therefore, conducting a quantitative analysis of leaf N and P resorption is necessary for gaining a better understanding of nutrient utilization and adaptation strategies of tree species and of how to simulate the nutrient cycling process of forest ecosystems.

Decades of research have illustrated environmental conditions (including climate and edaphic properties) and plant functional traits as predominant controls over leaf N and P resorption [2, 4, 12]. However, their relative roles in the leaf N and P resorption process are still elusive. Previous studies have revealed that N resorption efficiency (NRE) decreased as mean annual temperature (MAT) and mean annual precipitation (MAP) increased, while P resorption efficiency (PRE) followed opposite trends [12]. However, other studies have suggested that both NRE and PRE decreased as MAT and MAP increased [2, 3]. Because our current understanding of such associations between leaf N and P resorption and climate is primarily derived from data-integration studies at the global and regional scales, these inconsistent conclusions may be attributed to the diverse species compositions in the respective study areas.

Soil nutrient availability is another major environmental driver of leaf N and P resorption [2, 6]. It is recognized as a key factor that mediates the impact of climate on leaf N and P resorption [7, 13]. However, there is still an ongoing debate as to whether and how N and P resorption relates directly to soil nutrient availability. One possible reason is that the relative costs of resorbing N and P back into live tissues from senescing ones, instead of uptaking new N and P from the soil, remain largely uncertain. Particularly, nutrient constraints on plant growth and productivity transition from P limitation at low latitudes to N limitation at high latitudes [4, 14, 15], leading plants to trade off different nutrient acquisition

strategies depending on soil nutrient availability in tropical versus temperate regions. Furthermore, our nuanced understanding of nutrient availability and utilization in subtropical transitional forests remains unclear, seriously hindering a more general understanding of N and P resorption.

In addition to the above-mentioned environmental controls, plant functional traits are also the intrinsic biotic factors affecting N and P resorption. Current studies on leaf N and P resorption of different tree species mainly focus on leaf habits (i.e., deciduous and evergreen). Previous studies have demonstrated that evergreen tree species in tropical forests had higher NRE and PRE than deciduous counterparts [2, 16], but the NRE of evergreen trees was seemingly lower, and the PRE showed no significant difference in temperate forests [17, 18]. However, patterns and controls of nutrient resorption in subtropical transitional forests between tropical and temperate forests remain relatively unclear. These unexplained mechanisms call for the urgent need to link functional traits closely related to leaf habit to leaf N and P resorption, such as specific leaf area (SLA), leaf dry matter content (LDMC), and green leaf N and P concentrations [19, 20].

The analysis of individual functional traits can contribute to identifying specific traits that influence N and P resorption. In some cases, however, a certain plant trait may have reached its physiological threshold, rendering it insufficient for mitigating increasing environmental stress [21–23]. Under such circumstances, these different combinations of intercorrelating physiological and morphological traits led to the construction of trait coordination networks [24, 25]. Quantifying trait network patterns across leaf habits is essential for understanding the diversity of plant form and function, as well as for identifying the main drivers of ecological processes such as leaf nutrient resorption [25, 26]. The key traits related to leaf N and P economics could reflect trait-based adaptive strategies [27]. The differences between trait networks of deciduous and evergreen trees can characterize their respective manners of acquiring N and P resources [26, 28].

In recent decades, the plant economics spectrum (PES) has been proposed as a method to reflect the pervasive trade-offs and coordination in plant nutrient utilization by using the components and coordination relationships of trait networks to integrate a unified concept across plant taxonomy and growth forms [19, 29]. By integrating multivariate functional traits into PES, ecological trade-offs may become apparent, thus facilitating predictions of some important ecosystem processes such as nutrient resorption [21, 30]. Nonetheless, current studies examining the association between N and P resorption and PES

have produced inconsistent patterns, or even uncoupled relationships [6, 27, 31]. This phenomenon may be mainly attributed to particular adaptation strategies for each PES trait associated with N and P economics under environmental selection, forming multiple counteracting pathways affecting resorption processes [31]. Species with similar or opposite strategies converge or diverge along the axis of trait variation according to PES. Deciduous trees tend to adopt an acquisitive strategy, whereas evergreen trees tend to exhibit a conservative strategy [19, 28]. Furthermore, there have been significant advances in our understanding of PES for plant functional traits related to N and P economics at different spatial and biological scales [20, 31], but quantitative studies on how PES drives N and P resorption in leaves are still lacking [20, 27]. Therefore, we expected that PES well describe a trait *syndrome of leaf habits* that is closely associated with N and P resorption.

To date, although the individual effects of environmental factors and plant functional traits on leaf N and P resorption have been well documented, their relative roles at different scales remain largely unclear [2, 16, 32]. Global-scale studies have revealed that MAT and MAP significantly affect leaf N and P resorption, regional-scale studies have demonstrated that soil nutrient availability and leaf life span are dominant factors controlling leaf N and P resorption, but local-scale studies have indicated that leaf N and P resorption are tightly linked with tree species composition and plant functional traits [6, 12, 16, 32]. More critically, different spatial scales are usually accompanied by multiple differences in environmental conditions and clear distinct tree species compositions, which complicates the issue of dominant factors for nutrient resorption, and further hinders our robust understanding of regulatory mechanisms of plant nutrient resorption strategies in these diverse environments [23, 32, 33]. These aforementioned substantial complexity and uncertainty call for simultaneous studies on plant functional traits under continuous, wide-ranging environmental conditions. Elevational gradient precisely provides a continuously changing environment and bridges the extensive gaps in tree species composition and environmental isolation with its gradual change, is thus an ideal platform for exploring how plant functional traits and environmental controls over nutrient resorption simultaneously [34, 35].

In this study, we have investigated and quantified relationships between plant functional traits and leaf N and P resorption of broad-leaved tree species along an elevational gradient to get a more nuanced understanding of the drivers of nutrient resorption in subtropical China. To this end, we attempted to test the following hypotheses: (a) leaf habits directly explain more variations in leaf

N and P resorption of broad-leaved tree species than elevation, meaning that N and P resorption should be more strongly controlled by morphological and physiological trait combinations than by climate and soil conditions associated with elevational gradients; (b) deciduous and evergreen trees differentiate along an integrated PES, arraying on the acquisitive side and the conservative side, respectively; (c) PES is strongly coupled with N and P resorption, and these mediating associations can be largely attributed to one or more crucial traits.

Materials and methods

Study area

This study was carried out on the southern slope of Shennongjia Mountain (31°19′4″ N, 110°29′44″ E), northwest of Hubei Province, in central China. The region belongs to the transition zone between the (sub-) tropical and temperate climates and is an important biodiversity hotspot in China and globally. The mean annual temperature of this area is 10.6 °C, and annual precipitation ranges from 1306 to 1722 mm. The dominant soil classes are mountain yellow–brown soil and mountain brown soil, with a typical subtropical forest vegetation of deciduous and evergreen broad-leaved mixed forest [36].

Experimental design and field sampling

We conducted a field forest inventory on the southern slope of Shennongjia Mountain in July 2019 to identify common broad-leaved tree species that occurred with high frequency. We set up six sampling sites at intervals of 200 m from 800 to 1800 m above sea level (Fig. 1). We sequentially sampled all of the common representative broad-leaved tree species identified through pre-inventory on six sites (± 20 m elevation) and previous studies [37, 38]. For each site, we followed similar previous studies to sample [26, 31]. Specifically, we treated an individual mature tree as a sampling unit, with three repeat units for each tree species, at least 15 m apart between each two sampling units. Overall, we sampled 101 broad-leaved species, belonging to 33 families and 60 genera and formed 205 elevation-species combinations. The identification of tree species was based on taxonomic expertise, and the nomenclature followed the Flora of China [39], and all selected tree species were classified as evergreen ($n=43$) or deciduous ($n=58$) according to their leaf habit. Detailed sampling information is shown in Table S1.

We took the tree height as the selection criteria to identify mature and healthy individual trees as sampling units, referring to the Flora of China [39]. All sampling units are labeled to ensure the source of the mature leaf samples corresponds to that of the senescent leaf samples. In July and August of 2019 and 2020, we collected

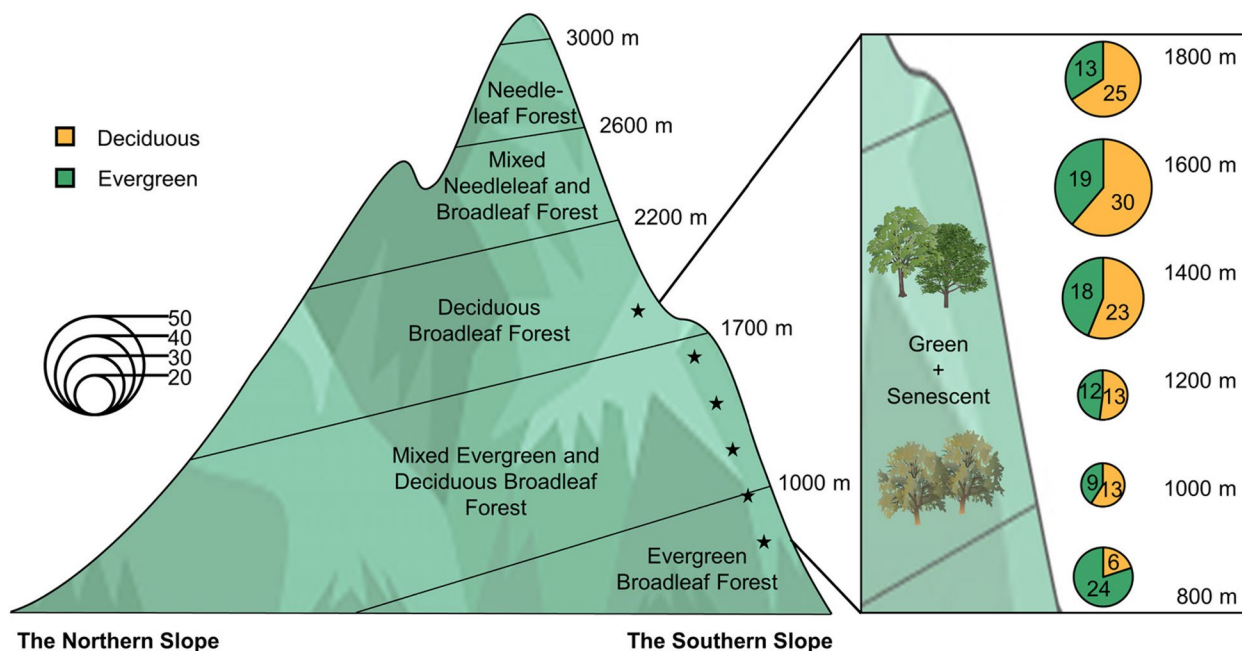


Fig. 1 Sampling diagram of broad-leaved tree species on the southern slope of Shennongjia Mountain. Asterisks represent the six sampling transects along the elevational gradient. The size of the pie chart represents the total number of tree species as shown in the left-most concentric circle, and the labels in the pie charts represent the numbers of deciduous and evergreen tree species sampled at each elevation. The background of the mountain was designed by pch.vector, Freepik (<http://www.freepik.com/>). Tree illustrations are from Tracey Saxby, Dylan Taillie, Kim Kraeer, and Lucy Van Essen-Fishman, Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagelibrary/>)

30–50 undamaged, relatively large, and fully expanded fresh mature leaf samples from the different canopy positions of each sampling unit, and we cut off representative twigs from each sample. We wore gloves during sampling to minimize sample contamination. Based on the previous field investigation experience in our target subtropical forests and literature records [40, 41], the peak period of leaf abscission for deciduous tree species is October and November in autumn, and that of evergreen tree species is October and November in autumn or April and May in spring. Therefore, in October and November of 2019 and 2020, we collected senescent leaves of all deciduous trees and partial evergreen trees, and the remaining senescent leaves of evergreen trees were collected in April and May 2020 to ensure that all senescent leaf samples were from the peak period of leaf abscission. We collected yellowed senescent leaves by shaking trees or picking up newly fallen leaves on the ground to avoid nutrient leaching from partly decomposed leaf litter on the forest floor, which could lead to an underestimation of leaf N and P concentrations [22, 42].

Measurement of plant functional traits

Here, we selected and determined 13 fundamental traits of fresh leaves according to previous standard protocols

[43–45] (Table S2). Mature fresh leaf samples were stored in sealed plastic bags immediately after collection in the field, and they were kept cool until being brought to the laboratory. On the day of sampling, we selected 3 intact fresh leaves from each sampling unit, separating the petioles for the following physical trait measurements [42, 46]. We then dried the remaining leaves in the oven at 65 °C for 48 h for subsequent chemical analysis [36, 46]. For each leaf subsample, we measured the relative content of Chlorophyll (SPAD) using a hand-held portable chlorophyll meter (SPAD-502), which was repeated at least three times for each leaf to avoid the possible impacts of leaf thickness and hair coats on SPAD. Leaf thickness (LT, mm) was quantified with a vernier caliper, and care was taken to avoid the main veins. Leaf samples were scanned by a leaf area meter (CI-203, USA) to determine leaf area (LA, cm²). The leaf subsamples were then weighed to determine the leaf fresh mass, and then they were dried in the oven at 65 °C for 48 h to constant mass to determine the leaf dry mass [36, 46]. This data was then used to calculate specific leaf area (SLA, leaf area/leaf dry mass, cm² g⁻¹) and leaf dry matter content (LDMC, leaf dry mass/leaf fresh mass). The length (PL, mm) and width (PW, mm) of each leaf sample petiole were measured by a vernier caliper. The twig dry matter

content (TDMC) of each tree was calculated using the same method as the leaf. Then twig wood density (TWD, g cm^{-3}) was calculated using the drainage method [47].

On the day of sampling, fresh and senescent leaves were dried in the oven at 65 °C for 48 h to constant mass [36, 46], and then they were ground with a laboratory mill for analysis of chemical elements. The leaf carbon (C) and N concentrations per unit mass for fresh green leaves (C_{gr}, N_{gr}, mg g^{-1}) and senescent leaves (C_{sen}, N_{sen}, mg g^{-1}) were determined by an element analyzer (vario EL cube CHNOS Elemental Analyzer, Elementar Analysensysteme GmbH, Hanau, Germany). We also calculated the ratio of leaf C to N concentrations (CN_{gr}) to serve as an indicator trait. The leaf P concentration per unit mass for fresh leaves (P_{gr}, mg g^{-1}) and senescent leaves (P_{sen}, mg g^{-1}) were determined using inductively-coupled plasma spectrometry after digestion of samples in HNO₃ (iCAP 6300 ICP-OES Spectrometer, Thermo Fisher, USA). More details are provided in Table S2.

Measurement of environmental factors

We measured a total of 11 environmental factors in this study (Table S3). At each elevation site, we used HOBO Onset microclimatic recorders (Onset Computer Corporation, USA) to measure actual microclimatic variables. These included air temperature (AT, °C), soil temperature (ST, °C), and soil moisture (SM, %). At each level, we selected five 2 m × 2 m plots with high frequencies of sampled trees and collected soil samples at a depth of 0–10 cm [18]. Visible plant materials and stones were removed from all soil samples. Next, the soil samples were air-dried at room temperature and either passed through a 100-mesh sieve for subsequent chemical analysis or frozen at –20 °C prior to microbiological assay. Soil total N concentration (SN, mg g^{-1}) was measured using the Kjeldahl method after digesting samples with H₂SO₄, and available N concentration (SNA, mg g^{-1}) was determined using the diffusion method after alkaline hydrolysis. Soil total P concentration (SP, mg g^{-1}) was quantified after wet digestion with concentrated HF and HClO₄, and soil available P concentration (SPA, mg g^{-1}) was determined in NaHCO₃ extraction, using the molybdenum antimony resistance colorimetry method. Soil organic C concentration (SOC, mg g^{-1}) was measured by titrimetry after oxidation with a mixture of potassium dichromate and sulfuric acid. Soil pH was measured using a pH electrode (PB-10, Sartorius, Germany) in a soil–water suspension (soil: water = 1:2.5 [v/w]). Soil microbial biomass C and N concentration (MBC, MBN, mg g^{-1}) were quantified using chloroform fumigation (multi N/C 3100, TOC/TNb analyzer, Analytik-Jena AG, Germany). The specific and detailed experimental procedures can be found in Protocols for Standard Biological Observation

and Measurement in Terrestrial Ecosystems [46]. More data details are provided in Table S3.

Nutrient resorption calculation

We used two fundamental and complementary metrics to quantify nutrient resorption: resorption efficiency (RE, %) and resorption proficiency (RP, mg g^{-1}) [2, 6]. RE was calculated as the ratio of the difference in nutrient concentrations between green and senescent leaves to green leaf nutrient concentrations. Considering the mass loss that occurs during leaf senescence, we used a mass loss correction factor (MLCF, 0.78 for evergreen broad-leaved tree species and 0.784 for deciduous broad-leaved tree species) to correct nutrient concentrations in senescent leaves [3]. RP was measured as the nutrient concentration in senescent leaves, with low litter nutrient concentrations corresponding to high RP and vice versa [5]. At each elevational site, we calculated the average value of each trait and nutrient resorption for each species.

Data analysis

We checked the data for normality and log-transformed it to improve the linearity of the relationships if necessary before conducting the analysis. To explore the effects of leaf habit and elevation on RE and RP, we used a two-way analysis of variance (ANOVA) followed by *t*-tests and Tukey's *post-hoc* test. To explore the relative importance of environmental factors and plant functional traits on leaf N and P resorption, we have added variance partition analysis. Based on the Pearson correlation, we further examined the intercorrelation of environmental factors and the relationships between individual environmental factors and nutrient resorption using Mantel's test in the VEGAN package [48]. In the VEGAN package we also then performed redundancy analysis (RDA) to test overall associations between environmental factors and nutrient resorption [48].

Since tree species phylogeny may influence the process of nutrient resorption [5], we used the V.PHYLOMAKER package [49], based on the published phylogenetic trees as background trees, to extract the common target nodes through tree species names and generated our target phylogenetic trees. The PLANTLIST package [50] was used to match the same canonical family, genus, and species information as the V.PHYLOMAKER package. We used Blomberg's *K* value and Pagel's λ value to evaluate the phylogenetic signal on each plant trait using the PICANTE and PHYTOOLS packages [51, 52]. A large *K* value and λ value with $p < 0.05$ indicated conservatism for a trait. We described plant functional trait coordination networks according to statistically significant Pearson correlations among traits and illustrated them using the IGRAPH package [53]. We adopted two indicators

to characterize the centrality of networks: D (degree, the number of adjacent edges for each vertex) and D_w (the sum of the edge weights of the adjacent edges for each vertex) [54].

To integrate these interrelated traits into PES, we performed a principal component analysis (PCA) using the basic function ‘prcomp’. Corresponding illustrations were made in the GGPILOT package [55]. To evaluate the difference in functional traits across leaf habits, we compared the trait scores of the first two axes (PC1 and PC2) between deciduous and evergreen trees using t -tests. Furthermore, to assess and compare the directions and strengths of principal components on N and P resorption across leaf habits, we conducted linear mixed effect models (LMMs) with tree species as random factors and the PC1 and PC2 scores as fixed effects using the LME4 package [56]. LMMs were used to deal with elevation-species pseudo-replication. To better identify and quantify which traits or trait combinations varied in relation to N and P resorption, we re-applied the similar LMMs with tree species as random factors and the 13 functional traits mentioned above as fixed effects to evaluate the role of each single trait. We removed the variables with the variance inflation factor (VIF) value >10 to avoid the potential multicollinearity of the models. These were visualized using the GGPILOT2 package [57]. All analyses and illustrations were performed in R 4.0.3 [58].

Results

Patterns of leaf N and P resorption across elevations and leaf habits

The overall NRE and PRE of broad-leaved trees were 39.65% and 50.76%, respectively. NRE was significantly higher in deciduous trees than in evergreen trees ($p < 0.05$, Fig. 2), but PRE displayed no significant difference across leaf habits ($p > 0.05$, Fig. 2). Mean leaf litter N and P concentrations of broad-leaved trees were 13.08 mg g^{-1} and 0.74 mg g^{-1} , respectively, generally higher than the threshold of incomplete resorption proposed by Killingbeck [5], indicating low N and P resorption proficiency (NRP and PRP). Moreover, deciduous trees exhibited higher N and P concentrations in senescent leaves than did evergreen trees, which suggests that deciduous trees have lower resorption proficiency ($p < 0.05$, Fig. 2). By contrast, NRE, NRP, PRE, and PRP were all insignificantly associated with elevation ($p > 0.05$, Table 1, Fig. S1). Furthermore, when considering the interaction of elevation and leaf habit, we found no significant relationship between NRE, NRP, and the interaction, but PRE and PRP were significantly affected by the interaction (Table 1).

Environmental effects on leaf N and P resorption

We found that environmental factors only explained 0.9% of the variation of leaf N and P resorption, while plant functional traits explained 13.8% of that, indicating that the relative effects of environmental factors are much weaker than plant functional traits (Fig. S2). In addition, the RDA results revealed that environmental factors played a minor role in N and P resorption along

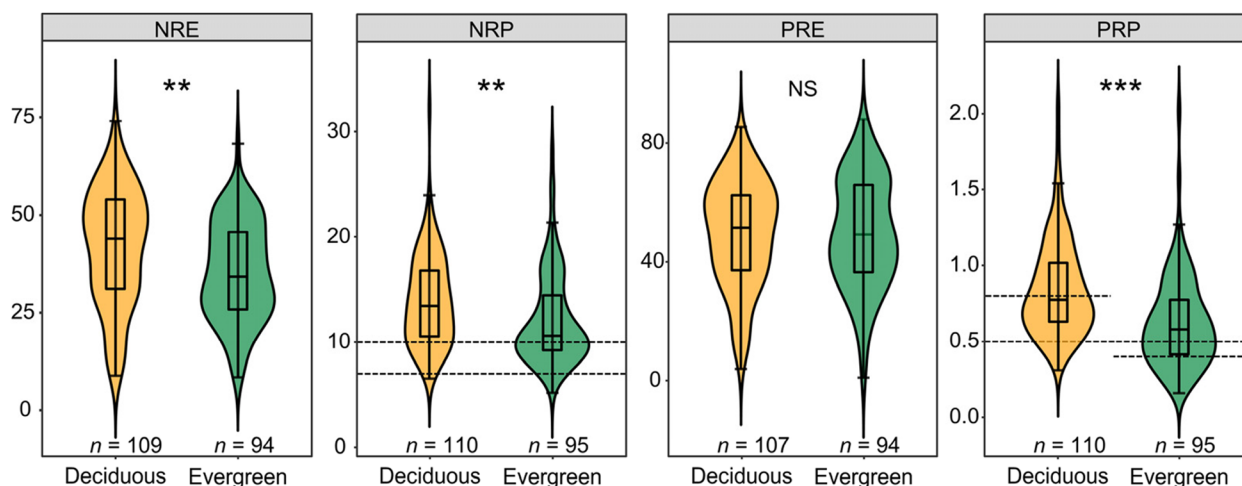


Fig. 2 N and P resorption efficiency (RE) and proficiency (RP) across leaf habits. Asterisks indicate significant differences between evergreen and deciduous tree species (** $p < 0.01$, *** $p < 0.001$), and NS indicates no significant difference. The dotted lines represent the thresholds for incomplete ($N > 10 \text{ mg g}^{-1}$, $P > 0.5 \text{ mg g}^{-1}$ for evergreen tree species, $P > 0.8 \text{ mg g}^{-1}$ for deciduous tree species) and complete ($N < 7 \text{ mg g}^{-1}$, $P < 0.4 \text{ mg g}^{-1}$ for evergreen tree species, $P < 0.5 \text{ mg g}^{-1}$ for deciduous tree species) resorption, as defined by Killingbeck (1996)

Table 1 Results of two-way ANOVA for elevation and leaf habit effects on N and P resorption efficiency and proficiency

Variable	Source of variation	Df	SS	% SS	F value	P value
NRE	Elevation	5	1456	3.60	1.551	0.176
	Leaf habit	1	1883	4.66	10.030	0.002
	Elevation × Leaf habit	5	1251	3.09	1.333	0.252
NRP	Elevation	5	87.2	2.21	0.922	0.468
	Leaf habit	1	133.8	3.39	7.073	0.008
	Elevation × Leaf habit	5	73.6	1.86	0.778	0.567
PRE	Elevation	5	1980	3.06	1.270	0.278
	Leaf habit	1	0	0.00	0.000	0.994
	Elevation × Leaf habit	5	3810	5.89	2.445	0.036
PRP	Elevation	5	0.6506	3.00	1.410	0.222
	Leaf habit	1	2.1425	9.88	23.220	<0.001
	Elevation × Leaf habit	5	1.0752	4.96	2.331	0.044

Df Degrees of freedom, SS Sum of squares, %SS percentage of sum of squares, NRE Nitrogen resorption efficiency, PRE Phosphorus resorption efficiency, NRP Nitrogen resorption proficiency, PRP Phosphorus resorption proficiency

the elevational gradient. Environmental factors merely contributed 4.19% ($R^2=4.19\%$, Fig. S3) of variation in N and P resorption. Furthermore, Mantel's test suggested that individual environmental factors do not significantly control N and P resorption ($p>0.05$, $r<0.2$, Fig. 3). Given the minor effects of the environmental factors, we mainly focused on the roles of plant functional traits in N and P resorption below analysis.

Associations between traits and leaf N and P resorption

We first constructed a phylogeny tree of our targeted tree species to assess phylogenetic affiliation (Fig. S4) and found that plant functional traits did not exhibit relatively high degrees of phylogenetic signal, with Blomberg's K value ranging from 0.142 (SPAD) to 0.374 (TDMC) and Pagel's λ value ranging from 0.082 (LA) to 0.787 (Cgr) (Table S4). This implied preference towards random trait evolution, with evolutionary patterns of traits likely to be influenced by non-phylogeny. Most of the plant functional traits correlated significantly with one another ($p<0.05$, Fig. 4). For all trait networks, SLA exhibited the highest connectedness, followed by PL, TDMC, and green leaf nutrient concentrations. The trait networks of deciduous trees displayed higher transitivity than those of evergreen trees (Table S5).

Given the close associations among traits, we performed PCA and found that PES could predict variation in N and P resorption well (Fig. 5 and Fig. 6). PC1 and PC2 explained 34.2% and 17.2% of trait variation, respectively. The 10 plant functional traits besides PW, TDMC, and Cgr all contributed significantly to PC1 ($p<0.05$, Table S6). Along the PC1 axis, traits representing a conservative resource utilization strategy (SPAD, LDMC, LT, TWD, and CNgr) occupied the right end, while traits

representing an acquisitive strategy (LA, SLA, PL, Ngr, and Pgr) were on the left. PC2 correlated significantly and positively with LA, LT, and PW, which represented a conservative strategy of tree structure and defense, and negatively with LDMC, TDMC, and TWD, which related to an acquisitive strategy of photosynthesis and nutrient supply. Most evergreen trees were distributed on the conservative side, while most deciduous species clustered on the acquisitive side ($p<0.05$, Fig. 5).

The PC1 axis exerted significant negative effects on NRE, NRP, PRE, and PRP for both deciduous and evergreen trees ($p<0.05$, Fig. 6), except that NRE of evergreen trees was not significantly affected. The PC2 axis showed no obvious impact on deciduous trees, while it positively affected NRE and negatively affected NRP and PRP of evergreen species ($p<0.05$, Fig. 6). For both deciduous and evergreen trees, SLA, N, and P concentrations in green leaves explained N and P resorption the most (Fig. 7).

Discussion

Here, we have mainly focused on leaf N and P resorption for more representative species along an elevational gradient than in past studies [22, 23, 35], considering environmental factors and plant functional traits simultaneously to explore their roles. Our field observations confirmed previous modeling predictions of N and P limitation that our target subtropical forest is potentially less nutrient-limited [14]. We found large differences in leaf N and P resorption as a result of various functional trait combinations derived from leaf habit of tree species, rather than diverse environmental conditions along the elevational gradient. The highly diversified strategies of nutrient use and conservation

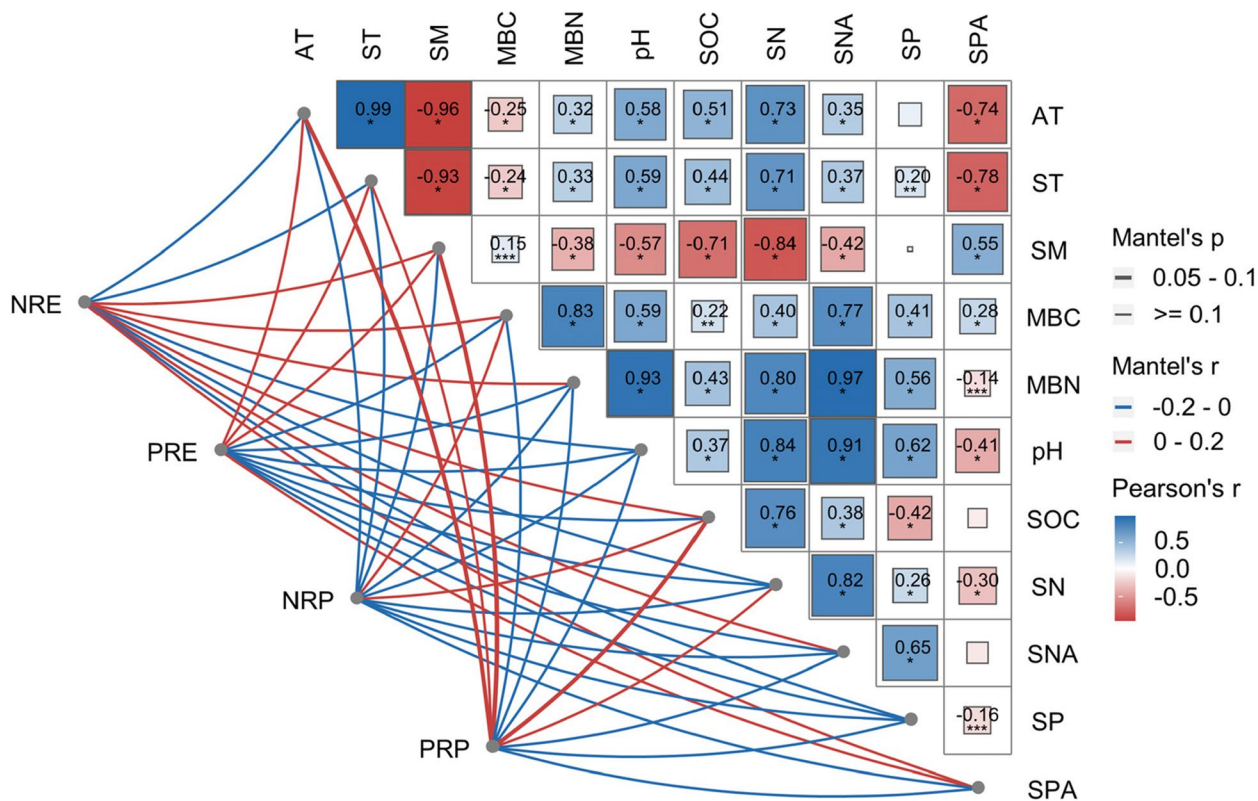


Fig. 3 Environmental factors play a minor role in nutrient resorption. Correlation between environmental factors and their effects on N and P resorption. Asterisks indicate the significance of effects among environmental factors (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). The edge color (r -size) corresponds to the coefficients between resorption characteristics and environmental variables. Edge width denotes the statistical significance (p -value) between each trait and environmental variable. AT, Air temperature; ST, Soil temperature; SM, Soil moisture; MBC, Soil microbial biomass carbon content; MBN, Soil microbial biomass nitrogen content; pH, Soil pH; SOC, Soil organic carbon content; SNA, Soil available nitrogen content; SP, Soil total phosphorus content; SPA, Soil available phosphorus content

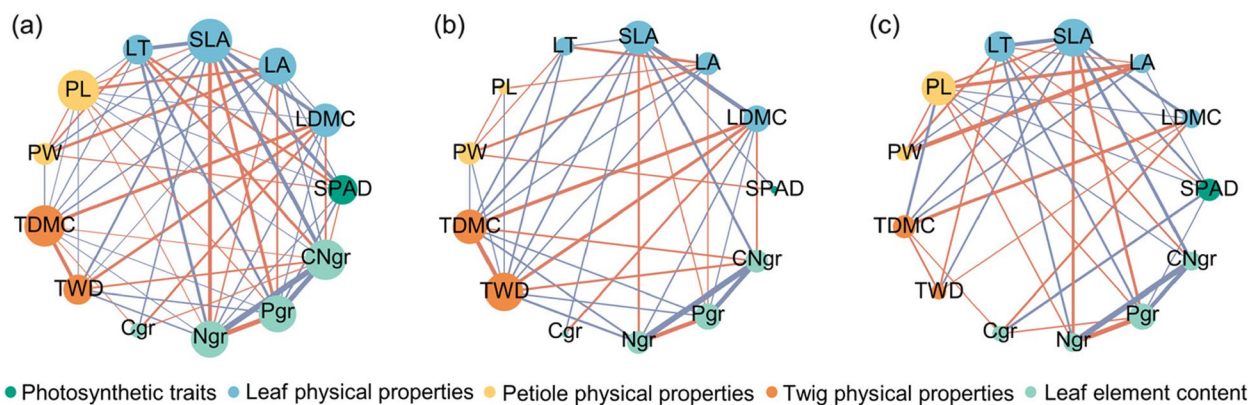


Fig. 4 Trait correlation networks of broad-leaved trees for (a) all, (b) deciduous, and (c) evergreen tree species. Traits in the network were represented as vertices and their correlations as the edges linking them. Different node colors represent different types of plant organs or tissues. Node size denotes the degree of connectedness. Red and blue edges represent positive and negative correlations ($p < 0.05$), respectively. SPAD, Chlorophyll relative content; LDMC, Leaf dry matter content; LA, Leaf area; SLA, Specific leaf area; LT, Leaf thickness; PL, Petiole length; PW, Petiole width; TDMC, Twig dry matter content; TWD, Twig wood density; Cgr, Carbon concentration in green leaves; Ngr, Nitrogen concentration in green leaves; Pgr, Phosphorus concentration in green leaves; CNgr, The ratio of carbon to nitrogen in green leaves

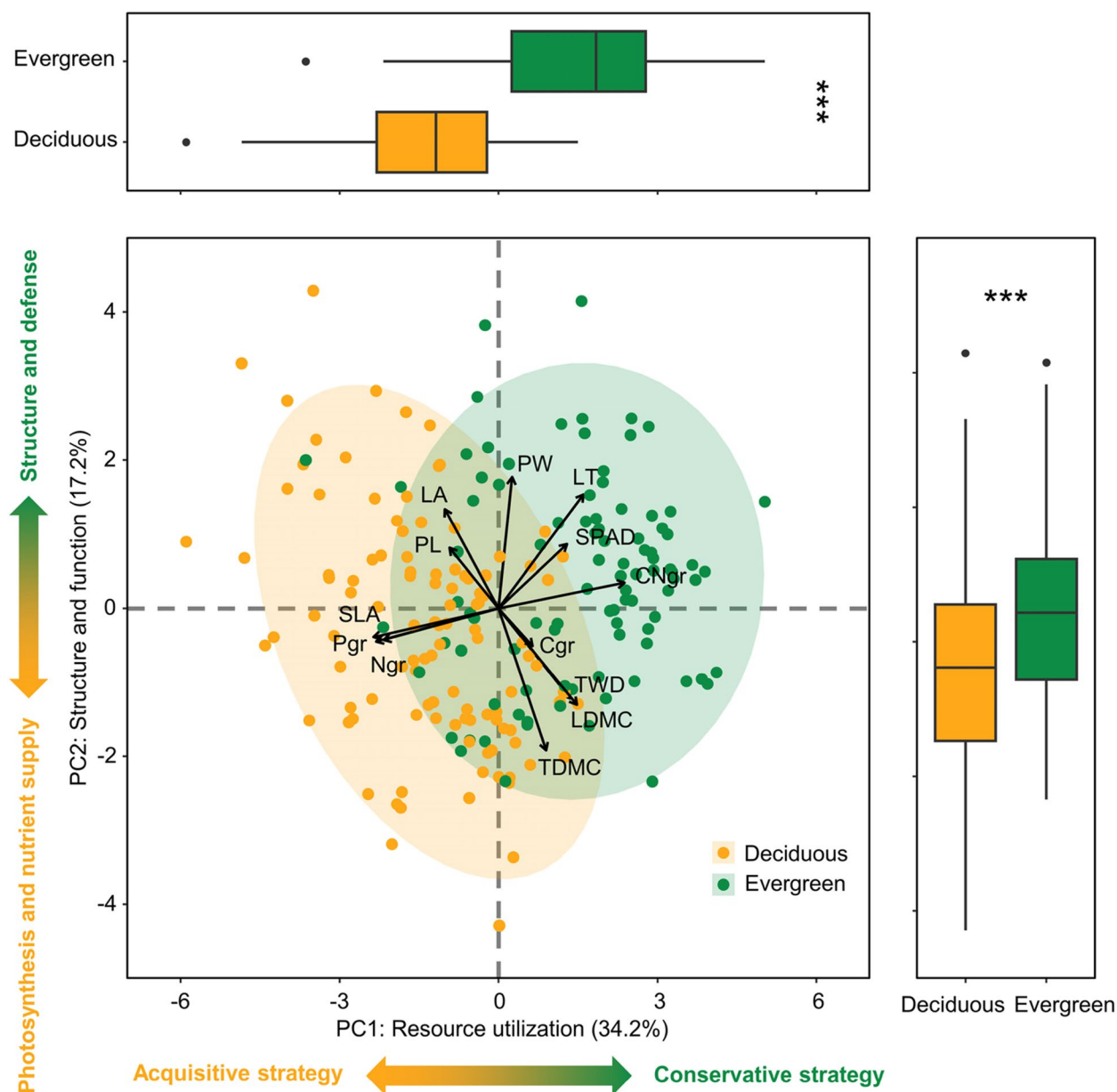


Fig. 5 Principal component analysis (PCA) of 13 plant functional traits. The confidence ellipses are drawn at the 90% level. The boxplots at the upper and right margins illustrate the differences in the distributions of tree species across leaf habits along the first and second PCA axes. Asterisks indicate significant differences between evergreen and deciduous trees ($***p < 0.001$). Abbreviations for plant functional traits are provided in Fig. 4

in deciduous and evergreen trees (i.e., acquisitive and conservative strategies, respectively) led to pronounced divergence in leaf N and P resorption. These findings clearly highlight the urgent need to recognize that distinct controls of nutrient cycling dominate at different scales and suggest that biogeochemical cycle models should incorporate multiple traits and their coordination rather than just including individual traits.

Deciduous tree species tend to resorb N and P more effectively but less proficiently than evergreen counterparts

We found that deciduous trees resorbed N more effectively than evergreen counterparts, but there was only a slight difference in resorbing P of trees (Fig. 2), which was similar to findings in previous studies from Aert [11] and Tang et al. [59], but contradictory to global-scale

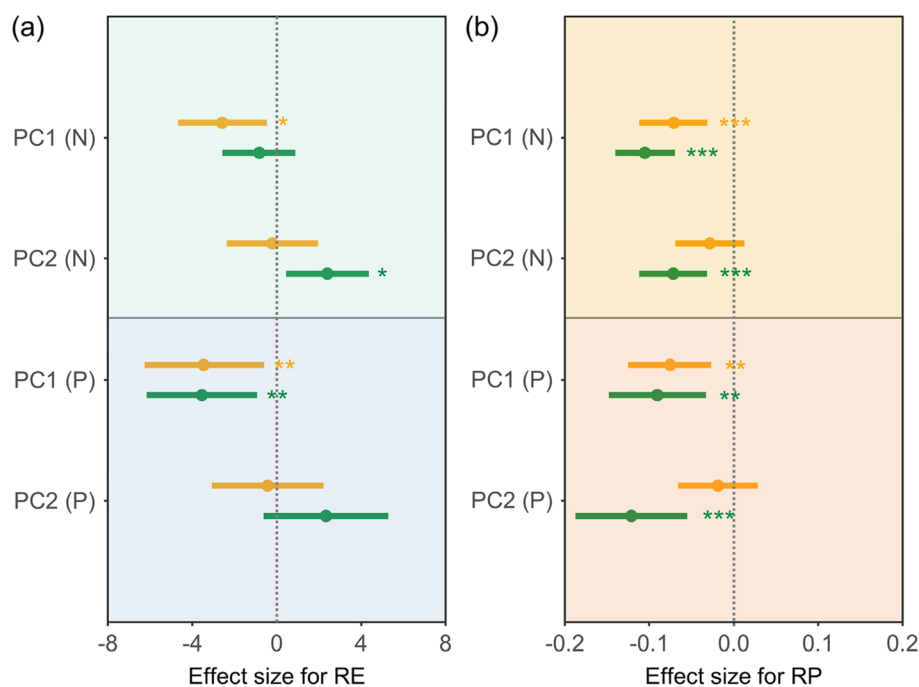


Fig. 6 The effect size of the first (PC1: photosynthesis and nutrient resource utilization) and second (PC2: structural and functional investment) principal components of 13 plant functional traits of evergreen and deciduous trees on leaf N and P **(a)** resorption efficiency (RE) and **(b)** resorption proficiency (RP) in linear mixed effect models. The horizontal error bars show the 95% confidence intervals of the fixed effect size from linear mixed effect models. Asterisks indicate the significance of the effects of PC1 and PC2 on RE and RP (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Yellow and green represent deciduous and evergreen trees, respectively

findings by Yuan and Chen [12] and Vergutz et al. [3]. Different from insignificant differences in NRP and PRP between deciduous and evergreen trees [59, 60], our study demonstrated that deciduous trees were less proficient in resorbing N and P than evergreen trees (Fig. 2), concurred with Aerts [11]. On one hand, this may be derived from the observation that mature leaf N and P exhibited much higher concentrations in deciduous trees ($N_{gr} = 18.67 \text{ mg g}^{-1}$, $P_{gr} = 1.39 \text{ mg g}^{-1}$) compared to evergreen trees ($N_{gr} = 14.16 \text{ mg g}^{-1}$, $P_{gr} = 1.01 \text{ mg g}^{-1}$) in our study. Consequently, leaf litter N and P concentrations, as the final products reflecting the nutrient status of mature fresh leaves after resorption, are likely to display significant differences. Moreover, the leaves of deciduous tree species are typically composed of more soluble compounds, such as proteins and carbohydrates [61, 62]. These compounds break down more easily thus achieving more efficient nutrient resorption for deciduous tree species. In contrast, the leaves of evergreen tree species typically contain more insoluble structural compounds such as cellulose and lignin, hindering leaf nutrient resorption for evergreen species [61, 63].

On the other hand, this could be attributed to the fact that leaf N and P resorption between deciduous and evergreen trees varied with leaf longevity and duration of leaf

abscission [2, 6, 64]. Deciduous trees, characterized by frequent leaf abscission and annual new leaf regeneration, tend to allocate more nutrients to facilitate faster growth and exhibit higher leaf production within their comparatively shorter growing seasons [65, 66]. Additionally, owing to their shorter abscission period and lower temperatures during the abscission season, the reaction time and activity of the decomposing enzymes for leaves may be insufficient, resulting in diminished soil nutrient availability and necessitating enhanced nutrient resorption to sustain growth and productivity [22]. In contrast, evergreen trees grow slowly and have long leaf lifespans, they develop adaptation strategies with low nutrient requirements to tolerate disadvantageous climatic and nutritional conditions, by maximizing the growth period and minimizing nutrient loss [6, 17]. Overall, due to the variable functional traits and nutrient strategies, N and P resorption varied across leaf habits [28, 67].

More notably, the strict classification of tree species into deciduous and evergreen could obscure important ecological variations in traits within each leaf habit, and the prominent distinction across leaf habits is essentially the result of a combination of many plant functional traits [64, 67, 68]. Therefore, considering the effect of leaf habit, a classification indicator only may be not enough,

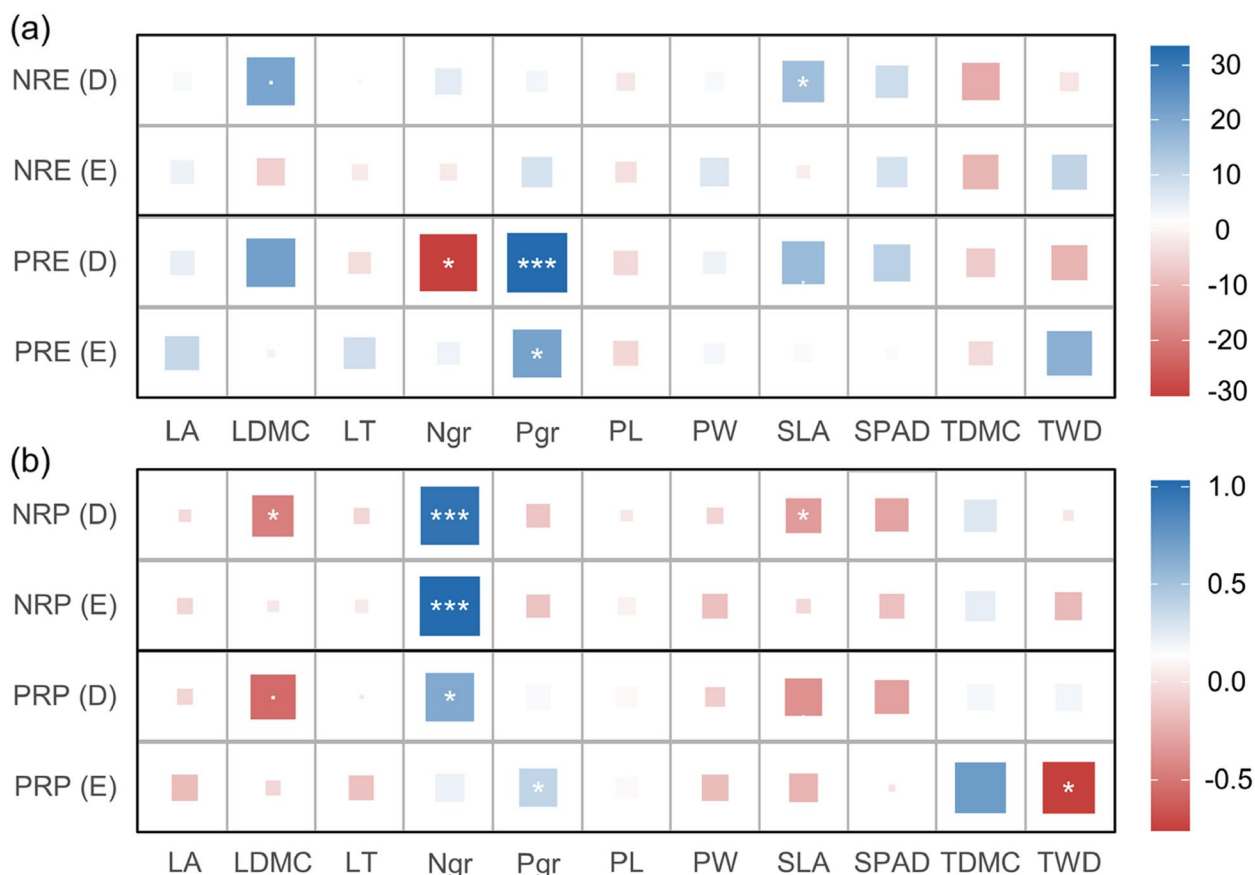


Fig. 7 Effects of plant functional traits of deciduous (D) and evergreen (E) trees on leaf N and P **(a)** resorption efficiency (RE) and **(b)** resorption proficiency (RP) in linear mixed effect models. The color and size shown indicate the direction and strength of the coefficients from linear mixed effect models. Asterisks indicate the significance of the effects of PC1 and PC2 on RE and RP ($p < 0.01$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$). Abbreviations for plant functional traits are provided in Fig. 4

further analyses on the relationship between plant functional traits and N and P resorption are necessary.

Dominant effects of PES on leaf N and P resorption

We found no clear phylogenetic signal of plant functional traits, which aligns with the point that the role of phylogeny was negligible when specific traits were considered [31, 69]. Other studies have also revealed that N and P resorption are not affected by phylogeny [70]. Therefore, we posit that the associations between plant functional traits and nutrient resorption in this study were phylogenetically independent. The strong associations of plant functional traits suggest that the evolution of traits is intimately linked [19, 29]. Trade-off strategies of resource acquisition and investment are defined as the trait combination form, that is, PES. One major dimension of our PES (PC1) represented photosynthesis and nutrient resource utilization, with a gradient of acquisitive strategy to conservative strategy running from left to right. The other dimension (PC2) reflected the structural

and functional investment, with a gradient of investment preferences for photosynthesis and nutrient acquisition and for tree growth and structural conservation from bottom to top (Fig. 5). Evergreen and deciduous trees here were mainly distributed in the upper right and lower left parts of the PCA, respectively, which suggested that each leaf habit had obvious preferences for plant functional trait combinations along with nutrient strategies [67]. The findings support our hypothesis that deciduous and evergreen trees differentiate along an integrated PES, arraying on the acquisitive side and the conservative side, respectively.

Plant functional trait networks and PES approaches could be particularly useful in considering complex and dynamic processes such as nutrient resorption [20, 31, 45]. We did find significant correlations between PES and resorption for both N and P in our subtropical forest, thus supporting our hypothesis that trait coordination taken along with multi-trait variation on the PCA axes collectively determine trade-offs in nutrient resource

utilization patterns. Remarkably, photosynthetic and nutrient resource utilization capacity positively affected N and P resorption for both deciduous and evergreen trees, whereas structure and defense investments only positively affected N and P resorption for evergreen trees ($p < 0.05$, Fig. 6). The differences in strategies between deciduous and evergreen trees is understandable, as they differ in phenology, leaf lifespan, and nutrient use efficiency [17, 68]. Deciduous trees are fast-growing species with cheaper tissue investments and rapid resource returns, but evergreen trees are slow-growing species with expensive tissue investments and slower resource returns on that investment [6, 66]. Deciduous species have an acquisitive strategy, and they accordingly have stronger nutrient resorption efficiency and weaker nutrient resorption proficiency. Deciduous trees use N and P exploitatively and have higher carbon assimilation and transpiration rates, which can improve photosynthetic efficiency and fix nutrients in a short period to enable rapid growth. Thus, deciduous trees are characterized by high SLA, high green leaf N, and P concentration, as well as by cheap but plentiful tissue expenditures (i.e., higher PL and LA) [26, 66]. Conversely, evergreen species adopt a conservative strategy, and so their N and P resorption process is relatively weak. Evergreen trees consume N and P economically, but they allocate expensive resources to build tissue with thick laminas and high tissue densities (i.e., high LT, LDMC, and TWD) to withstand physical and mechanical damage. Meanwhile, they slow growth to preserve nutrients, and they have higher SPAD and CNgr to reduce metabolic costs [26, 71, 72].

While the fundamental role of SLA and green leaf nutrients in mediating N or P resorption has been increasingly recognized, their explicit roles remain to be explored [21, 45, 73]. Here, we found that SLA and green leaf nutrient concentrations are the traits most affecting leaf N and P resorption, matching previous studies that SLA underlined the role of functional traits on leaf N and P utilization [21, 45, 74]. On one hand, while trait correlation networks varied with leaf habit, these traits had markedly higher values of centrality for both deciduous and evergreen trees. On the other hand, they were the most important components of PC1 and PC2 axes. Additionally, in the multivariate linear mixed effects models, SLA, Ngr, and Pgr had significant effects on N and P resorption (Fig. 6). These findings collectively suggested that plant functional traits related to leaf resource capture and defense play dominant roles in mediating the trait coordination of N and P economics. Specifically, we found that SLA, Ngr, and Pgr correlated positively with N and P resorption efficiency and senescent leaf N and P concentrations, which agreed with previous studies [3, 45, 74]. Here, we assumed that in our targeted subtropical

forests, evergreen trees showed an adaptive response to low resource availability, and deciduous trees adapted to reduce water loss during winter periods. Evergreen trees produce leaves with a long lifespan that exhibit a slow metabolism, low SLA, and low nutrient concentrations. Relative to evergreen trees, deciduous trees produce short-lived leaves that exhibit traits related to rapid metabolism, i.e., high SLA and high nutrient concentrations. This further accounts for the higher nutrient resorption efficiency of deciduous trees. Finally, we found the notable phenomenon that individual traits displayed a weaker relationship with nutrient resorption than did PES, which suggests that plant functional traits operate in a coordinated manner to produce divergent mechanisms for nutrient utilization under different nutrient conditions. This finding underscores the importance of considering multiple trait dimensions, rather than individual traits one at a time.

Subordinate role of environmental factors in leaf N and P resorption

Both efficiency and proficiency of N and P resorption showed no significant association with elevation, and only PRE and PRP exhibited marginally significant differences when considering the interaction of elevation and leaf habit (Table 1, Fig. S1). Variance partition analysis also demonstrated that environmental factors were less important than plant functional traits in driving variation of leaf N and P resorption (Fig. S2). These findings aligned with our hypothesis that in our target subtropical forests, elevation-related environmental factors directly explain less variations in leaf N and P resorption of broad-leaved tree species than leaf habits-related plant functional traits. Mantel's test and RDA further verified the negligible effects of environmental factors, including microclimates and soil nutrients, on leaf N and P resorption (Fig. 3, Fig. S3). Broad-scale studies have indicated that N and P resorption is closely related to soil nutrient availability [6, 18, 75]. At first sight, these seem to imply that tree species from nutrient-poor environments resorb nutrients more efficiently, with the important caveat that study species came from habitats differing widely in climate and soil. These tree species have undergone different environmental selection and genetic adaptation processes, thus tree species adaptation and acclimation are accompanying [35, 76]. There has been compelling evidence that plant functional traits are more likely to reflect plant nutrient utilization strategies and thus directly explain more to the variation in leaf N and P resorption than climate and soil along elevational gradients [22, 59, 77].

Therefore, we confirm our first hypothesis and argue that environmental factors play a minor direct role in N

and P resorption along elevational gradients. In other words, trees alter their N and P resorption along elevational gradients due to changes in tree species composition, essentially by changing plant trait combinations. Notably, similar to previous studies, we sampled only 0–10 cm of topsoil, which, although sufficient in the majority of cases [18], may weaken the importance of soil properties in leaf nutrient resorption. Therefore, it could be useful to sample deeper soil to improve our understanding of soil properties on nutrient resorption in further studies. Moreover, previous studies indicated that the abundance of trees with conservative strategies, which have lower nutrient resorption efficiency, increases at high altitudes in response to the low temperatures that hamper nutrient mineralization by slowing soil microbial activities [20, 62, 73]. This finding highlights that nutrient resorption is not merely a process but a plant nutrient utilization for adapting to diverse environments. Consequently, future research should pay more attention to the trade-offs of above- and below-ground nutrient acquisition pathways when exploring plant trait-resorption linkage to advance our understanding of nutrient cycling in forest ecosystems.

Conclusions

By collecting a greater number of representative tree species than in previous studies, we have simultaneously elucidated the relative contributions of environmental factors and plant functional traits to N and P resorption along an elevational gradient in the subtropical region. We found lower leaf N and P resorption in the subtropical transitional forest than previously assumed, expanding our current knowledge of leaf N and P resorption beyond the relatively well-studied tropical and temperate forests. Deciduous species tend to resorb nutrients more effectively but less proficiently than evergreen counterparts for both N and P. These imply highly diversified nutrient conservation strategies across leaf habits, with evergreen trees preferring conservative strategies that invest in growth and structure and deciduous trees preferring acquisitive strategies for photosynthetic and nutrient resources. Our work further highlighted the overriding role of plant functional traits in the transitional subtropical forest, and that incorporating PES, especially SLA and green leaf nutrient concentrations, into the monitoring and modeling of leaf nutrient resorption could notably improve our understanding of species-driven nutrient cycling. These findings underscored the potential importance of plant functional trait coordination and thus call for these PES effects on leaf nutrient resorption to be more explicitly incorporated into a current nutrient cycling model framework to better forecast the consequences of shifting tree species composition for

biogeochemical cycles in forest ecosystems since nutrient resorption has been commonly involved in many biogeochemical models.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12870-024-05484-9>.

Supplementary Material 1

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Authors' contributions

BM, JG, and ZX conceived and designed the study. BM and JG conducted the fieldwork and lab experiments with contributions from CZ, WX, KX, and ZX. BM conducted the data analyses. BM and JG led the writing of the manuscript. All authors contributed substantially to the final writing.

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Availability of data and materials

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

The collection of leaf samples was permitted by Xingshan County Forestry Bureau, Yichang, Hubei Province, China. We declare that this study complies with the guidelines and legislation of the People's Republic of China, the IUCN Policy Statement on Research Involving Species at Risk of Extinction, and the Convention on the Trade in Endangered Species of Wild Fauna and Flora.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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