



# The scaling of leaf nitrogen and phosphorus along a phosphorus availability gradient in a subtropical forest

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**Abstract** Allometric scaling of leaf nitrogen (N) and phosphorus (P) provides information on species adaptation to resource availability and nutrient limitation of primary production. Studies examining how plant functional traits vary spatially have historically used global datasets, which may blur variation at local scale and thus some of the key drivers. Global studies have observed leaf N–P scaling exponents varied across different functional groups, latitudinal zones, ecoregions, and sites. However, whether these trends are consistent in a local habitat is still unclear. Here, we capitalized on a soil P availability gradient

in subtropical China to examine scaling exponents of leaf N–P. We investigated 21 woody species at P-rich and P-poor sites for two consecutive years and estimated scaling exponents of leaf N–P across P-type sites, leaf ages, plant functional types, and phylogeny. The exponents varied across the abovementioned levels from 0.356 to 0.699. Averaged across all plant species, the exponent of 0.612 was a departure from the global average of  $2/3$  (0.66) and  $3/4$  (0.75). Two types of P-sites did not affect N–P exponents of deciduous-broadleaved trees and evergreen conifers. Our findings indicated that leaf N–P scaling exponents significantly differed within plant functional types and highlighted the resource availability in shaping nutrient cycling and evolutionary processes at local scales.

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## Introduction

Nitrogen (N) and phosphorus (P) are key macronutrients in plants supporting growth through both structural and energy-producing parts. Nitrogen is an important component of amino acids (the building blocks of proteins), chlorophyll, and the molecule responsible for photosynthesis. Phosphorus is a critical part of ATP, the energy-carrying molecule used to drive photosynthesis and plant growth (Elser et al. 1996; Güsewell 2004). These two elements are tightly linked and are important parameters in stoichiometric plant growth models (Agren 2004; Niklas et al. 2005). Plants invest disproportional N vs. P due to the difference in physiological growth strategies and varying soil environments, as observed at both local and global scales (Lambers et al. 2008; Townsend et al. 2007). Hence, there is a scaling relationship between leaf N and P concentration which is quantified via slope ( $\alpha$ , scaling exponent) and intercept ( $\beta$ , coefficient) on a log–log scale, based on the function  $N = \beta P^\alpha$  (Kerkhoff et al. 2005; Reich et al. 2010). The “Growth Rate Hypothesis” (Sterner & Elser 2002) posited that higher proportional P in rRNA concentration in plants correlates to higher growth rates. Two earlier studies claimed that the scaling relationship of N vs. P concentration in plants follows a simple rule at global scales in that the scaling exponent converges around the value 0.66 (Wright et al. 2004) or 0.75 (Niklas et al. 2005). However, the underlying mechanisms behind these numeric laws are still not clear.

Evaluating the scaling relationship between N and P at the global scale may overwrite important variations at the local scale that may arise due to variations in nutrient availability or community composition (Kerkhoff et al. 2006; Tian et al. 2017). Moreover, it is difficult to ascribe a mechanism behind the scaling relationship at the global scale because there are too many unconstrained variables. Global analyses also ignore the role of time and the plasticity of species. Global datasets and short-term nutrient addition experiments are not able to resolve whether the evolutionary history of a plant community is the main driver of scaling relationships under various resource

limitations. Therefore, case studies across various habitat and soil nutrient availability gradients are needed to explain the mechanisms behind the general exponent laws on a global scale.

In the following years after the general rules (0.66 and 0.75) were described, several studies developed and completed with larger datasets and quantified scaling factors as a narrower range (from 0.678 to 0.73). (Niklas 2006; Reich et al. 2010; Tian et al. 2017), but little effort has been directed toward determining the underlying mechanisms driving these observations. The acquisition and allocation of N and P in plants vary across geographical locations, soil nutrient status, major functional types, species, and family, and it is expected that scaling exponents of N and P will vary in tandem (Niklas and Cobb 2006; Zhang et al. 2012). For example, deciduous species have higher N and P concentrations than evergreen species to meet fast growth; conifers usually have lower N concentrations than broadleaved species. We expect that N and P scaling exponents will change between conifers and broadleaved species (evergreen and deciduous trees). Actually, a global analysis found conifers have the lowest N and N–P exponents, while no significant differences were found between deciduous and evergreen-broadleaved trees. However, one plant functional type may show a large difference in N and P concentrations in different ecosystems (e.g., temperate vs. tropical ecosystems). In this case, we expect to see a different role of plant functional types in shaping N–P exponents in our study area compared to a global study. Additionally, soil nutrient imbalance, particularly N and P, can also influence leaf N and P concentrations and thus N–P exponents. For instance, in a controlled nutrient addition experiment, Yan et al. (2018) found that the N–P scaling exponent decreased with the increasing levels of N addition, but increased with the increasing levels of P addition. Another community-level leaf N–P scaling exponent’s study showed that the scaling exponents declined with increasing growth rate, which highlighted the role of soil P availability. Here, we hypothesize that along with natural P gradient sites, leaf N–P scaling exponents may increase with soil P concentration and scaling exponents may vary significantly within plant functional types.

Other factors such as leaf age in evergreen trees and phylogeny may also play a role (Aerts 1995; Doust 1980). Generally, both N and P can be resorbed during

leaf senescence and with similar magnitude (Vergutz et al. 2012). However, a few case studies found that P concentration decreases disproportionately compared to N across the foliage life span (Achat et al. 2018). Based on the previous work, we hypothesized the scaling exponent of N vs. P in the current-year leaves would be smaller than that of 2-year-old leaves. Different from plant functional groups, phylogeny (species and family) indicates growth strategies in another way. For example, *Proteaceae* in P-poor tropical ecosystems usually have higher phosphorus use efficiency than other families (Lambers et al. 2012). In this study, as a widely distributed dominant family, whether or not *Fagaceae* have a significantly different N–P exponent than other families due to local adaptation is intriguing. At the species level, N–P exponents may have large ranges due to large differences in N and P concentrations and growth strategies. Pooled data have advantages to illustrate how species influence N–P exponents, excluding environmental factors; here, we would like to examine within a limited dataset, how N–P exponents vary in species and how sampling numbers may influence the results.

Subtropical soils are generally depleted in “rock-derived” elements such as P, calcium (Ca), and magnesium (Mg) due to strong weathering and leaching as well as efficient retention of P in biota (Vitousek et al. 2010; Walker & Syers 1976). However, soils developed on phosphate rock are rich in P, N, and other important nutrients (Wen et al. 2018). Hence, plants in subtropical areas may present different stoichiometric traits based on adaptations to various nutrient habitats (Townsend et al. 2007). However, the importance of plant functional types and phylogeny vs. environmental factors in shaping exponents might reflect the influence of local habitats. The central hypotheses in this study are that (1) in natural P gradient sites in subtropics, leaf N–P scaling exponents may increase with soil P concentration and scaling exponents may vary significantly within plant functional types. (2) Because P concentration decreases disproportionately compared to N across the foliage life span, the scaling exponent of N vs. P in current-year leaves would be smaller than that of 2-year-old leaves.

## Materials and methods

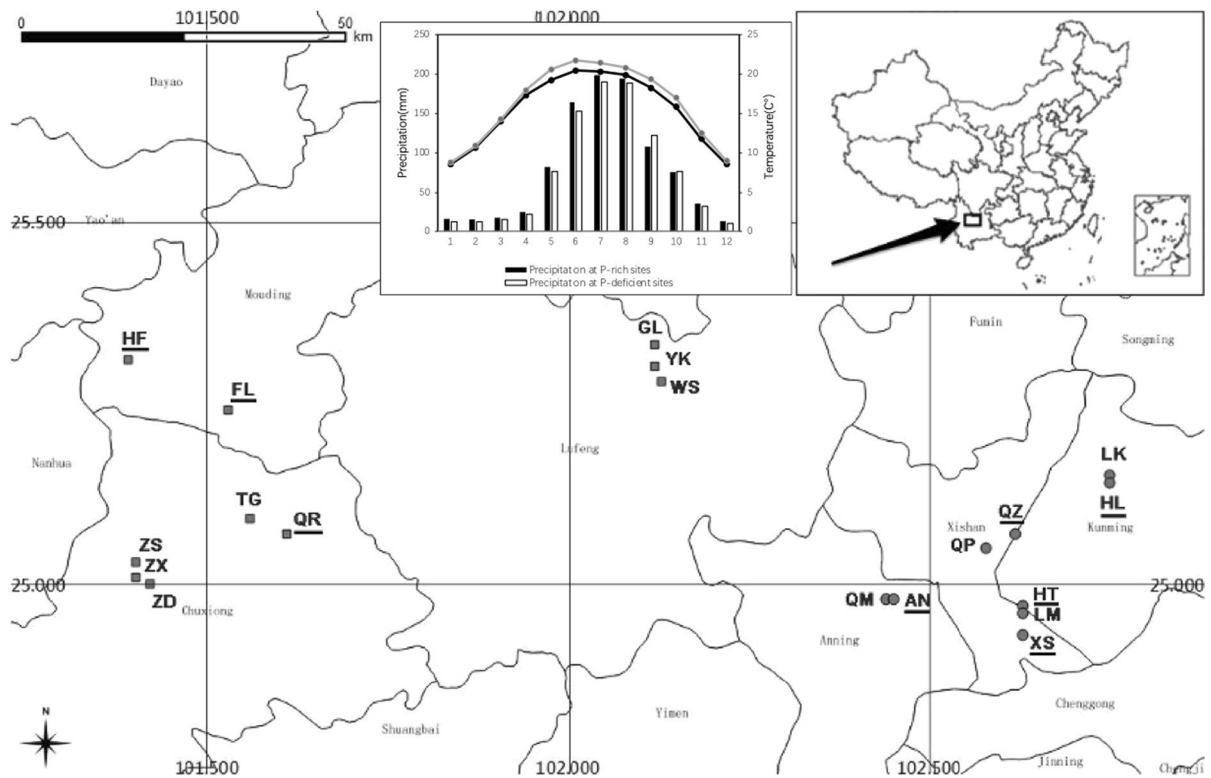
### Site description

The study region located at Yunnan–Guizhou Plateau (about 2000 m a.s.l.) in Yunnan Province, southwestern China. In this region, the phosphate rock developed randomly within non-phosphate rocks (Fig. 1). The concentration of  $P_2O_5$  in rocks at the P-rich site is about 0.89% at the P-rich site and 0.04% at the P-deficient site (Table S1). Ferralsols and Acrisols are primary soil types in this area, according to World Reference Base for Soil Resources (Group 2014). The climates are similar at the contrasting P-sites (Fig. 1). The zonal vegetation consists of semi-humid evergreen-broadleaved forests and warm temperate conifer forests, including evergreen-broadleaved trees (EB), evergreen conifers (EC), and deciduous-broadleaved trees (DB).

Nineteen sites were selected within the study area, including nine on P-rich sites (Kunming) and ten on P-deficient sites (Chuxiong county) (Fig. 1). At each site, three 20 × 20-m plots were set up (Table S2). In this region, the *Fagaceae* family dominated evergreen and deciduous broadleaf, including *Quercus variabilis*, *Q. acutissima*, and *Cyclobalanopsis glaucoides*. *Pinus yunnanensis* and *Keteleeria evelyniana* are primary species in conifers.

### Sampling

The leaf and soil samples were collected in August 2016 and 2017. Leaf samples were collected in the upper middle part of the south-facing crown of trees. Samples of full-expanded and medium-sized leaves were collected. For each species at each site, three to five samples were randomly collected (about 200 g per individual) from different healthy individuals and then mixed into one sample. For evergreen trees (EB and EC), we selected current-year leaves and 2-yr-old leaves as two separate samples. In total, we collected 495 leaf samples in two years, involving 21 species representing 8 families (Table S3). Four species were DB, 12 species were EB, and 5 were EC (Table S3). Additionally, nine topsoil samples (0–10 cm) and rock samples were collected per site (rock samples collected in nine sites) and mixed into one sample.



**Fig. 1** Locations of sampling sites in Yunnan Province, southwestern China. Squares and dots represent phosphorus (P)-rich sites and P-deficient sites, respectively. Site name underlined denotes sampling in 2016 and 2017 while not underlined denotes sampling in 2016. The inserted picture showed monthly mean air temperature and monthly precipitation from

1981 to 2010 at P-rich sites (including Kunming city and Anning county) and P-deficient sites (including Chuxiong city, Mouding, and Lufeng county; China Meteorological Administration). The complete name list of each site is given in Supplementary Table S2. The map is drawn using QGIS version 2.18

### Chemical analyses

We stored and transported samples to the laboratory in coolers immediately after collection. Fresh leaves were dried at 105 °C for 30 min and 60 °C for 48 h (Markert 1994). We put soil and rock samples in a window open room to air dry for one month to constant weight. After that, we ground and sieved samples through a 0.25-mm screen for total element determination and by hand through a 0.2-mm screen for other chemical analysis.

The soil and leaf samples were digested with trace metal-grade nitric acid and diluted with deionized water (Dahlquist and Knoll 1978). Total N concentrations were determined with an elemental analysis-stable isotope ratio mass spectrometer (Vario ELIII; Elementar, Germany). Total and available P concentrations were determined with a plasma optical

emission spectrometer (ICP-OES) (Iris Advantage 1000; Thermo Jarrell Ash, Franklin, MA). The contents of  $\text{NH}_4^+\text{-N}$  and  $\text{NO}_3^-\text{-N}$  were determined by Automated Discrete Analyzers (SmartChem 200; Alliance, France). Chemical compositions of rocks were determined with Sequential X-ray Fluorescence Spectrometer (XRF) (Ramsey et al., 1995). The concentrations of all elements were expressed as milligrams per gram of dry weight.

### Data analyses

The scaling relationships between leaf N and P concentrations in this study were described by a mathematical equation of the type  $N = \beta P^\alpha$ , linearized under the form  $\log(N) = \log(\beta) + \alpha \log(P)$  (Niklas 1994). Here, we defined X and Y as leaf P and N concentrations, respectively. The term  $\alpha$ —the slope of the

scaling relationship, is the allometric coefficient or rate of divergence, while the term  $\beta$  is the intercept or elevation of the relationship. The value of  $\beta$  indicates the differences independent of leaf P concentration when two regression lines share the common slope.

We conducted T tests to examine the differences in nutrient concentrations of soils and rocks between P-rich and P-poor sites. In this paper, we  $\log_{10}$  transformed the N and P concentration for all observations and then used reduced major axis (RMA) regression to determine the N vs. P scaling relationship (Warton et al. 2006). Confidence intervals for individual regression slopes followed (Pitman 1939). To answer whether the scaling component in subtropical China approaches 0.66 or 0.75 and whether regional differences are related to parent geology, plant functional types, phylogeny (species and family), and leafage, we used likelihood ratio tests to evaluate the heterogeneity of RMA regression exponents (Warton et al. 2006). Each exponent ( $\alpha$ ) was tested against the hypothesized value (general scaling exponent of leaf N vs. P concentration: 0.66 or 0.75 using the one-sample test. The calculation of RMA was conducted using “smatr” package (Warton et al. 2012). Additionally, a GLM was used to determine the relationship between soil, leaf traits, and the value of the scaling exponent. To determine whether leaf N and P concentrations and N:P ratios were affected by plant evolutionary history, we determined phylogenetic signals using Pagel’s  $\lambda$  (Pagel 1999). All the data analysis and drawing were conducted by R version 3.4 (R Development Core Team, 2018) and Datagraph 4.3 (Visual Data Tools, Inc, 2018, USA).

## Results

### Leaf N and P concentrations and N:P ratios at different levels

Concentrations of N and P in soils were higher at the P-rich sites than those at the P-poor soils (Table S4). Averaged across all plant species, leaf N and P concentrations were 14.08 and 1.12 mg g<sup>-1</sup>, respectively. However, at each level, significant differences were found in leaf N and P concentrations and N:P ratios (Table 1). For example, at soil P level, N and P concentrations are higher, while N:P mass ratio is lower at P-rich

sites, compared to P-deficient sites. At Plant functional types level, DB had the highest N and P concentrations, while EC and EB had the lowest N and P concentration, respectively. When considering the effects of both plant functional types and soil types, EC or DB did not show significantly different N and P concentrations at P-rich and P-poor sites, while EB at P-poor sites had higher N and P concentrations than at P-poor sites (Table 1).

### Scaling exponents of leaf N relative to P at different levels

Averaged across all the species, the scaling exponent was 0.612 (95% CI=0.516, 0.661) and a statistically significant departure from 0.66 to 0.75 ( $p < 0.001$ , Table 2). The scaling exponents differed significantly among the three functional types. EB showed the highest exponent (0.599), while the DB showed the lowest (0.356). The scaling exponent of DB and EC significantly differed from 0.66 to 0.75 ( $p < 0.001$ , Table 2). There were no significant differences between Ericaceae (0.471), Pinaceae (0.471), and Fagaceae (0.511) (Table 2, Fig. 1), or between Current-yr. leaves (0.551) and 2-yr-old leaves (0.575) (Table 2), or between P-rich (0.699) and P-poor (0.607) sites. EC or DB did not show significantly different exponents at P-rich and P-poor sites, while EB at P-rich sites (0.281) had lower exponents than at P-poor sites (0.627) (Table 2).

### Relationships between scaling exponents of leaf N relative to P and environmental factors

Soil nutrients, pH, and CEC did not significantly affect N–P scaling exponents in this study (Fig. 2). However, seemingly the trends of exponent variation along with soil factors contrast at DB and EC-dominated sites and other sites (Fig. 2). Leaf N and P concentrations affected exponent variations, particularly at functional types and species levels (Fig. 3). Wide leaf P and narrow leaf N concentration range led to lower N–P exponents of DB than the other two functional types, which may indicate different N or P accumulation of plants (Fig. 3). N–P scaling exponents significantly increased with the number of observations in this study indicating that the sampling number may greatly influence the estimation of leaf N–P scaling exponents (Fig. 3f). When the sample size was larger than 150, the N–P scaling exponents located between empirical values 0.66 and 0.75.

**Table 1** N and P concentrations and N:P mass ratio (mean  $\pm$  se) in leaves across different levels

Different levels		N concentration (mg g <sup>-1</sup> )	P concentration (mg g <sup>-1</sup> )	N:P mass ratio
All	All	14.08 $\pm$ 0.17	1.12 $\pm$ 0.02	14.82 $\pm$ 0.86
Natural soil P gradients	P-rich sites	15.92 $\pm$ 0.29***	1.41 $\pm$ 0.04***	12.26 $\pm$ 0.35***
	P-deficient sites	13.03 $\pm$ 0.19***	0.96 $\pm$ 0.02***	16.28 $\pm$ 1.33***
Plant functional types	Evergreen broadleaves (EB)	13.31 $\pm$ 0.23b	0.88 $\pm$ 0.03c	16.42 $\pm$ 0.40a
	Deciduous broadleaves (DB)	18.86 $\pm$ 0.29a	1.39 $\pm$ 0.06a	16.23 $\pm$ 0.86a
Functional types *	Evergreen conifers (EC)	12.30 $\pm$ 0.18c	1.16 $\pm$ 0.03b	13.10 $\pm$ 1.76a
P-sites	PEB	14.46 $\pm$ 0.30*	1.07 $\pm$ 0.05*	15.45 $\pm$ 0.34
	REB	13.28 $\pm$ 0.30*	0.94 $\pm$ 0.04*	15.78 $\pm$ 0.55
	PDB	18.41 $\pm$ 0.37	1.17 $\pm$ 0.04	18.19 $\pm$ 1.14
	RDB	17.04 $\pm$ 0.32	1.22 $\pm$ 0.05	16.45 $\pm$ 0.64
	PEC	12.48 $\pm$ 0.18	1.15 $\pm$ 0.02	13.34 $\pm$ 1.67
	REC	12.27 $\pm$ 0.18	1.15 $\pm$ 0.03	13.28 $\pm$ 1.86
Phylogeny (family, species $\geq$ 3)	Fagaceae	16.49 $\pm$ 0.26a	1.18 $\pm$ 0.04a	16.27 $\pm$ 0.54a
	Ericaceae	11.11 $\pm$ 0.45b	0.77 $\pm$ 0.06b	15.82 $\pm$ 0.89a
	Pinaceae	11.97 $\pm$ 0.16b	1.14 $\pm$ 0.03a	13.19 $\pm$ 1.93a
Leaf age (for evergreen trees)	Current-yr leaves	13.38 $\pm$ 0.20***	1.11 $\pm$ 0.03***	13.16 $\pm$ 0.33
	2-yr-old leaves	11.80 $\pm$ 0.22***	0.96 $\pm$ 0.03***	13.68 $\pm$ 0.43

Significant differences at each scale were tested by T test (Natural soil P gradients, functional types \*P-sites, and leaf age levels) or ANOVA (Other levels). At functional types \*P-sites level, significant differences were examined for each functional type at two types of P-sites. \*means significant differences between each variable at natural soil P gradients and leaf age levels, respectively. Different minuscules mean significant differences between variables at each level

\* $p < 0.05$ , \*\* $p < 0.01$  and \*\*\* $p < 0.001$

## Discussion

### Resource availability and composition effects at P-rich and P-poor sites

Our study examined the scaling exponents of leaf N concentration relative to P in subtropical China. We capitalized on a natural gradient in soil phosphorus concentrations to determine whether nutrient availability, phylogeny, and plant functional traits, influenced nutrient scaling relationships in plants. Our data partly rejected hypothesis 1 that leaf N–P scaling exponents may increase with soil P concentration, although we did see trends that the exponents increased with soil total and available P concentrations (Fig. 2). Although we hypothesized that leaf age influences N–P scaling exponents, we did not find significant differences between current-yr. leaves and 2-yr. leaves. This is consistent with other research between young-leaf and mature-leaf stages in *Arabidopsis thaliana* (Yan et al. 2018). We also did not find a statistically significant difference in exponents

between P-rich and P-deficient sites or between phylogenetic clades.

The scaling exponent was 0.612 for all of the data combined and thus a statistical departure from the previous estimated values of 0.66 and 0.75 (Reich et al. 2010; Tian et al. 2017). The exponent for all the data pooled in our study area was also lower than the exponent in tropical (0.651) biomes (Reich et al. 2010). However, at the leaf age, family, and plant functional type levels, we found distinct differences in the exponents, with a significant departure from general values 0.66 or 0.75 (Table 2). This result highlights how differing plant compositions developed from different resources and nutrient use strategies. A higher exponent at P-rich sites may indicate that N has a higher uptake rate in plants as compared to P-deficient sites, suggesting that higher N and P concentrations at P-rich sites maintain nutrient-rich ecosystems to provide plants with more resources (Table S4). The insignificant relationship at P-sites probably resulted from the local adaptation of species in an unfavorable environment, which amplifies or

**Table 2** Scaling of leaf N concentration in relation to leaf P concentration at different levels (P-sites, functional type, P-sites x functional type, and leafage for evergreen trees)

	Different levels	n	Exponent ( $\alpha$ ) with 95%CI	R <sup>2</sup>	Intercept ( $\beta$ )	Departure from 2/3	Departure from 3/4
	All	495	0.612 (0.566,0.661)	0.28	1.12	<0.001	<0.001
P-sites (soil nutrient status)	P-rich sites	180	0.699 (0.611,0.800) N	0.20	1.10	N	N
	P-deficient sites	315	0.607 (0.547,0.674) N	0.20	1.13	N	<0.001
Functional types	Evergreen broad-leaves (EB)	151	0.599 (0.530,0.677) a	0.46	1.16	N	<0.001
	Deciduous broad-leaves (DB)	111	0.356 (0.301,0.421) c	0.25	1.23	<0.001	<0.001
Functional types *	Evergreen conifers (EC)	233	0.522 (0.464,0.587) b	0.20	1.06	<0.001	<0.001
P-sites	PEB	116	0.627 (0.536,0.732)*	0.29	1.17	N	<0.05
	REB	35	0.281 (0.207,0.380)*	0.24	1.19	<0.001	<0.001
	PDB	61	0.345 (0.271,0.439) N	0.22	1.23	<0.001	<0.001
	RDB	50	0.403 (0.300,0.542) N	0.19	1.21	=0.01	<0.001
	PEC	138	0.505 (0.432,0.590) N	0.14	1.06	<0.001	<0.001
	REC	95	0.523 (0.431,0.635) N	0.11	1.07	<0.05	<0.001
Phylogeny (family, species $\geq 3$ )	Fagaceae	197	0.511 (0.458,0.570) a	0.45	1.19	<0.001	<0.001
	Ericaceae	25	0.471 (0.355,0.623) a	0.67	1.11	<0.05	<0.001
	Pinaceae	212	0.471 (0.417,0.533) a	0.19	1.06	<0.001	<0.001
Leaf age (for evergreen trees)	Current-yr. leaves	175	0.551 (0.481,0.631) N	0.19	1.14	<0.01	<0.001
	2-yr-old leaves	161	0.575(0.498,0.664) N	0.15	1.09	<0.05	<0.001

495 leaf samplings were collected in both 2016 and 2017. All the analyses were based on two-year data except for analysis at the leaf age level which used data in 2016. All RMA regressions were significant (likelihood ratio tests,  $p < 0.0001$ ). All equations were fit using the log–log version of the equation:  $N = \beta P^\alpha$ . Reduced major axis intercepts ( $\beta$ ), slopes (exponents,  $\alpha$ ) with 95% CI (confidence interval),  $R^2$ , and  $n$  (number of observations) were presented. Each exponent ( $\alpha$ ) was tested if equals a specific value (general scaling exponent of leaf N vs. P concentration: 2/3 or 3/4,  $H_0$ : slope not different from 2/3 or 3/4, N means not significant). At each level, the exponents ( $\alpha$ ) were examined by one-sample test or multiple comparisons (different minuscules denote significant difference at  $p < 0.05$ . N means not significant, \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ ). At functional types \* P-sites level, significant differences were examined for each functional type at two types of P-sites. PEB indicates EB at P-deficient sites, while REB means EB at P-rich sites

dampens resource heterogeneity (Urban et al. 2020), thus altering the original nutrient cycling pattern.

Previous studies have shown that geologically derived P variation in soils influenced soil pH, which manifested as nutrient-rich and -poor habitats (Wen

et al. 2018). We did not find significant relationships between N–P scaling exponents and soil P, which is different from the studies conducted on a global scale (Tian et al. 2017). Our results underscore that drivers may vary at local scales. Our previous studies have



**Fig. 2** Relationships between the N to P scaling exponents and soil variables at all sites. Different color dots denote different site types based on dominated plant functional types. DB

shown that variation in soil P concentration leads to variation in N content, mineral nutrient, and other functional traits (Ji et al. 2019, 2018; Wen et al. 2018). In our study, P-rich sites were developed from phosphate-rich bedrock and thus plants at this location have been exposed to higher P concentrations through their recent evolutionary history. In contrast, nitrogen concentration differences between sites are likely more recent due to elevated nitrogen deposition over the last ~150 years (Galloway et al. 2008). Long-term selection is able to develop morphological, physiological, or metabolic adaptations to the local environment, generating ecotypic differentiation in important functional traits (Savolainen et al. 2007). Phosphate-rich bedrock supported a local “favorable island” in P-poor subtropics and thus island plants adopted P-efficient strategies under local adaptation (Ji et al. 2019, 2018). This could lead to less sensitive variations in plant response to P compared to N availability. Additionally, the lack of a significant effect between the two sites reflected plant

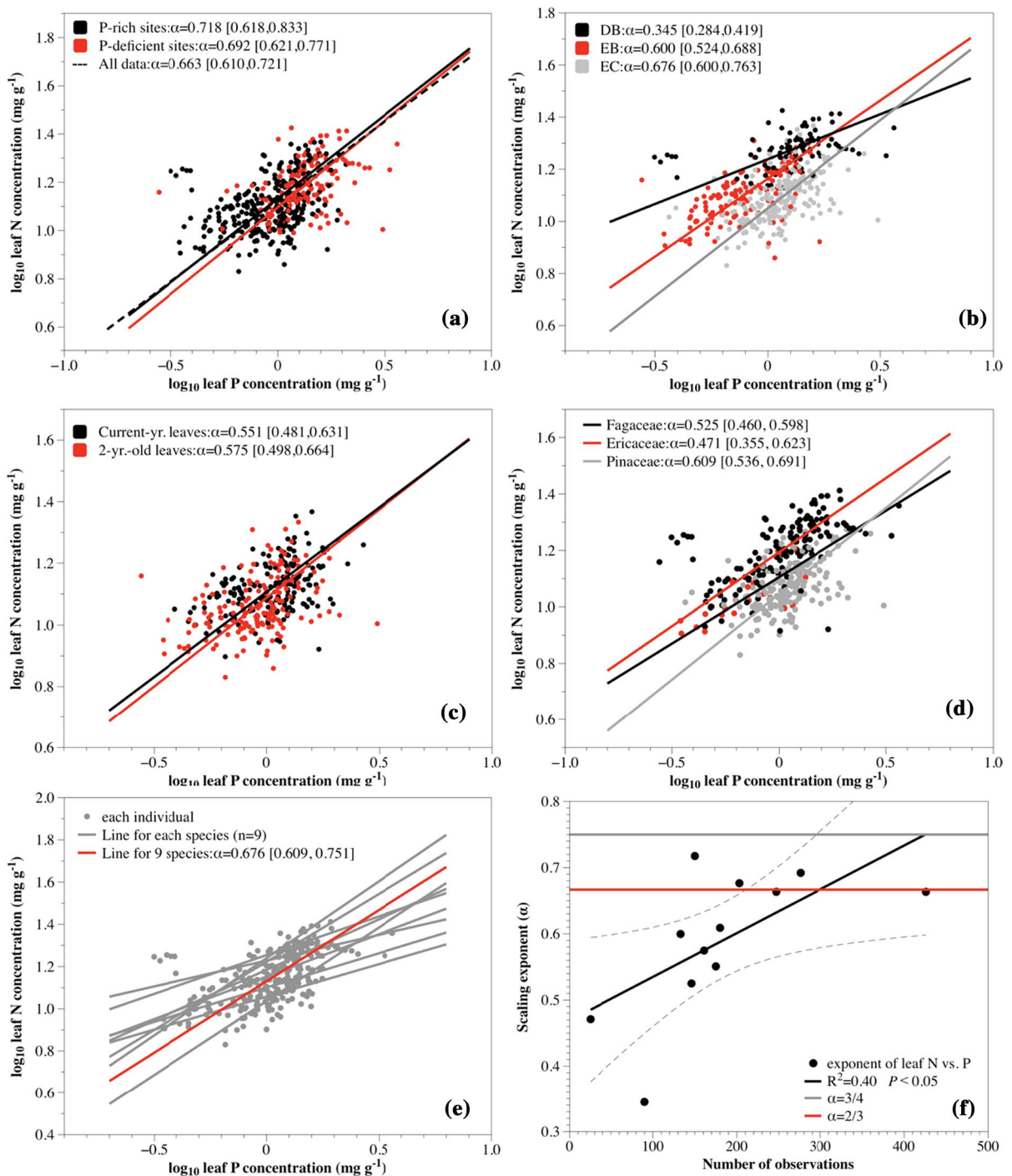
means deciduous-broadleaved trees; EB indicates evergreen-broadleaved trees; EC indicates evergreen conifers

composition variance based on timing and spatial distribution of resource acquisition. Community and ecosystem stability can potentially change when species have different sensitivities to environmental factors (Tilman & Downing 1994). We also found that the number of observations significantly influenced exponents (Fig. 3f). We have to admit that the limited dataset in the current study may not be sufficient to provide strong support in N–P exponent’s research; more case studies with large sampling are needed in future. Overall, our results suggest that local nutrient-rich habitats, compared to surrounding P-poor sites, improved soil conditions and plant performance, altered plant composition, and ecosystem process.

Plant functional types matter most at a local habitat scale

In this local scale study, plant functional types was more important than phylogeny in influencing leaf





**Fig. 3** Relationships between N–P exponents and leaf N and P concentrations at **a** site level, **b** plant functional group level, **c** leaf age level, **d** family level, **e** species level, and **f** the relationship between N–P exponents and number of observations. Species were used to calculate exponents at species level when samples were more than 10. We only used current-year leaf

samples to estimate N–P exponents for figures a, b, d, and e due to limited data for the 2-yr-old leaves. Scaling exponents ( $\alpha$ ) were calculated from the RMA regression between leaf N and leaf P concentrations and the lower and upper 95% confidence limits were presented in square brackets. All RMA regressions were significant (likelihood ratio tests,  $p < 0.05$ )

N-P scaling exponents. Inconsistent exponents among the three plant functional types suggest diversified growth strategies (Ågren & Weih 2012; Ji et al. 2018; Wen et al. 2018). DB showed the lowest exponent (0.356) in our study, and this exponent was significantly less than the previous value reported for DB (0.712) (Tian et al. 2017). Previous studies reported that DB had lower exponents than EB (Tian et al. 2017) and conifers (McGroddy et al. 2004). This is potentially due to the rapid growth rates of DB, which results in a greater P demand (Elser et al. 2003). The wide leaf P concentration range also supported this suspicion (Fig. 2) and indicated that plant species with faster P accumulation or potentially susceptible to P limitation may have low leaf N–P scaling exponents (Guo et al., 2020).

Admittedly, plant functional types are not completely free of phylogenetic influences (Kerkhoff et al. 2006). Scaling exponents at the phylogeny level are more linked to the inheritance from previous ancestors than present-day environments (Duckworth et al. 2000). Varying scaling exponents at the phylogeny level may indicate evolutionary effects for plant nutrient acquisition and accumulation strategies (Kerkhoff et al. 2006; Sardans et al. 2015). However, our study found that the three families shared similar scaling exponents but had distant phylogenetic clades. This can be explained by there were no phylogenetic signals in leaf N and P concentrations (Table S5); that is to say, phylogeny doesn't influence leaf N and P concentrations in the current study. The three families are dominant in this area and this suggests that within a local subtropical habitat, even across differing geologies, the dominant families adopted similar N and P acquisition strategies. In contrast, the plant functional type is a classification based on characteristics, such as life form (Raunkiaer 1934), function (deciduous or evergreen) (Dansereau 1951), leaf size, and shape (Dansereau 1951; Küchler and Zonneveld 2012). Evergreen trees are considered suitable in unfavorable conditions due to long leaf lifespans and low nutrient loss, while deciduous trees are reported to avoid environmental stresses through varied strategies, such as greater nutrient resorption efficiencies, higher nitrogen contents, and rates of photosynthesis, but lower water usage (Aerts 1995; Sobrado 1991; Wen et al. 2018). Plant functional types are believed to represent how plants adapted to varying environments and

thus link plant physiology and ecosystem functions (Díaz and Cabido 2001).

### Implications for tropical ecosystems

Generally, the richest and largest phosphorite deposits form in tropical and subtropical areas in the world where clay minerals and hydroxides are the end products of weathering and aluminum phosphates are formed (Cook & McElhinny 1979; Cook & Shergold 1984; Sheldon 1964). Soils developed on phosphorite bedrock are P-rich due to geochemical and biochemical processes (Cross & Schlesinger 1995; Walker & Syers 1976). Previous experiments in subtropical areas revealed that P and P-related traits were altered at P-rich sites (Wen et al. 2018; Yan et al. 2015). In this study, the N–P scaling exponents were different from both a global dataset (Tian et al. 2017) and controlled nutrient addition experiments (Zhang et al. 2018). This suggests that phosphorite bedrock in subtropics/tropics create a unique habitat where potentially ecological functions are varying, including nutrient uptake and use strategies in species (Ji et al. 2018), plant metabolic regulation (Ji et al. 2019), and even faster biogeochemical cycling (unpublished data).

### Supporting information

Additional Supporting Information may be found in the online version of this article.

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**Author contribution** CL and JW conceived the presented idea. JW, NS, HJ, BD, and MU conducted the field sampling. JW carried out the lab experiment and statistical analyses. JZ verified the analytical methods. JW wrote the manuscript draft. YL, JB, LM, HK, GL, and CL discussed the results and contributed to the final manuscript.

**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Not applicable.

**Consent to participate** Not applicable.

**Consent to Publish** Not applicable.

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