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RESEARCH ARTICLE

Tree species with conservative foliar nutrient status and strong phosphorus homeostasis are regionally abundant in subtropical forests

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Abstract

1. Foliar nitrogen (N) or phosphorus (P) status and their stoichiometric homeostasis are integral parts of the plant nutrient economy that determines the success of plant species in environments where N or P limits plant growth. Despite growing evidence for higher predictability of stoichiometric homeostasis of N (H_N) than that of P (H_P) on plant species abundance in temperate grasslands, no previous studies explicitly examined how foliar N and P status modulate the relationships between stoichiometric homeostasis and species distribution (regional species abundance) of woody plants, especially in P-limited (sub)tropical ecosystems. We hypothesized that species with a conservative foliar nutrient status but a higher H_P (but not H_N) would be regional abundant in P-limited forest.
2. We measured foliar N (LNC) and P (LPC) contents of 54 woody species, community composition and soil N and P contents across 94 forest plots in Chinese subtropical forests. Then we evaluated the species' levels of N and P stoichiometric homeostasis and their regional abundance to test our hypotheses.
3. H_N and H_P significantly increased with decreasing LNC and LPC. Foliar nutrient status positively correlated with the minimum values of both soil N and P contents, but only negatively associated with the maximum value of soil P content, indicating that conservative species can occupy a wider range of soil P- than N-based nutrient niche. Meanwhile, species abundance negatively correlated with LNC and LPC, and positively correlated with H_N and H_P. However, the structure equation model analysis showed that species abundance increased with decline of LNC but not yet with increased H_N. In contrast, species abundance enhanced with increased H_P and decreased LPC via H_P, rather than directly with a decline of LPC.
4. *Synthesis*. This study provides empirical evidence that species with conservative foliar nutrient status are more stable in terms of N and P stoichiometric homeostasis, and foliar N and P economy modulate species abundance distribution in different ways. Our results suggest that maintaining strong stoichiometric homeostasis

of leaf P, while maintaining conservative economy of N, is a key physiochemical mechanism for shaping species abundance distribution in P-limited forests.

KEYWORDS
Foliar nutrient status, N:P ratio, nutrient limitation, plant nutrient economy, soil nutrient gradient, species abundance, stoichiometric homeostasis

1 | INTRODUCTION

Nitrogen (N) and phosphorus (P) are essential elements for plant growth and metabolism, for instance as components of enzymes and other proteins, chlorophyll, nucleic acids, phospholipids in cell membranes and ATP in energy-demanding processes (Fernández-Martínez, 2022). Therefore, and because of their wide variability across spatial scales, they act as crucial chemical filters for sorting plant community assemblages (Peñuelas et al., 2019; Sardans et al., 2021). In terrestrial plant communities, low overall N and/or P availability and high temporal or spatial variability in availability are two important challenges to plants (Ågren et al., 2012; Güsewell, 2004). Whether and how different species meet these challenges through their plant nutrient economy matter to species' success in terms of growth and survival, and thereby their commonness or rarity (Aerts & Chapin, 2000; Eller & Oliveira, 2017; Elser et al., 2010). On the one hand, nutrient-conservative species with 'slow' resource management acclimatize to nutrient-poor soils by functioning at low foliar nutrient concentration, enabling them to survive and maintain growth, albeit slowly; while nutrient-acquisitive species with 'fast' strategy will suffer higher mortality when faced with nutrient shortage (Eller & Oliveira, 2017; Maracahipes et al., 2018; Power et al., 2011; Reich, 2014). On the other hand, some species maintain relatively stable foliar N and P compositions, that is, with great strength of stoichiometric homeostasis (H), which is crucial for their competitive success and abundance while being subjected to spatial or temporal variability in nutrient supply across habitats (Meunier et al., 2014; Yu et al., 2010).

Stoichiometric homeostatic regulation reflects underlying resource allocations for physiological and biochemical functions of plants and the degree of homeostasis may be highly relevant to fitness and to a species' ecological strategy (Meunier et al., 2014) and elementome plasticity (Fernández-Martínez et al., 2021). Species with strong stoichiometric homeostasis have the ability to maintain relatively constant nutrient concentrations or ratios when confronted with variation in the relative availabilities of these nutrients in their surroundings (e.g. soil; Sterner & Elser, 2002). Strong stoichiometric homeostasis may promote their competitive success and abundance in the face of soil nutrient variability (Meunier et al., 2014; Yu et al., 2010). Together, overall foliar nutrient levels along an axis from nutrient conservative to acquisitive strategy sensu (Aerts & Chapin, 2000; Reich, 2014) and stoichiometric homeostasis shape the presence/absence as well as the respective abundances of species within communities under specific environmental conditions (Peñuelas et al., 2019; Yu et al., 2011, 2015). Insightfully, recent research has demonstrated that plant species with strong homeostasis for N (high H_N) are more common and stable through time than low-H_N species in N-limited ecosystems (Fernández-Martínez et al., 2021; Sardans et al., 2012; Yu et al., 2010; Yu et al., 2015). These findings have greatly improved the theoretical and empirical foundation for the understanding of how the plant nutrient economy associates with species abundance distribution. However, the generality and adaptive value of different combinations of foliar nutrient levels and homeostasis across different ecosystems are still poorly understood.

Foliar nutrient status and stoichiometric homeostasis are integral parts of the plant nutrient economy that together may affect species abundance (Yu et al., 2015). Nutrient-poor soils select for (1) slow strategies species with conservative nutrient economy which can tolerate infertile soils or suppress nutrient supply to their surroundings for their own survival (Reich, 2014), and for (2) strong stoichiometric homeostasis species which have high competitiveness at poor nutrient supply and are more likely abundant and stable in the community across terrestrial ecosystems (Sardans et al., 2021; Yu et al., 2010). Therefore, we hypothesized (Figure 1) that, for growth-limiting elements in the soil, plants with conservative foliar nutrient economy and generally lower nutrient levels have stronger stoichiometric homeostasis than plants with acquisitive foliar nutrient economy (Hypothesis 1). Theoretically, stoichiometric homeostasis should reflect the ability of the species to achieve good fitness in diverse soil nutrient conditions (Meunier et al., 2014; Sterner & Elser, 2002). As such, while probably having low local abundance due to competition with acquisitive species in fertile soil, species with conservative foliar nutrient economy should be able to occupy a diverse array of habitats with a wide range of soil nutrient availabilities at the regional scale, explained by their strong ability to decouple foliar N levels from variation in soil nutrient supply (Figure 1a). However, in previous empirical and theoretical studies, how foliar nutrient status and stoichiometric homeostasis together determine species' abundance distribution (regional species abundance: the frequency of a given species across a given region, hereinafter referred to as species abundance) along soil nutrient availability gradients, has mostly been inferred rather than directly tested. Therefore, it still remains largely unclear how overall foliar nutrient level impacts the pattern of species-level stoichiometric homeostasis and, in turn, the distribution range along the gradient of soil nutrients. This knowledge is crucial for a clear picture of species abundance distribution through spatial variability or changes in soil nutrient availability.

The possible trade-off between foliar nutrient conservation in high-H species versus foliar nutrient acquisition in low-H species

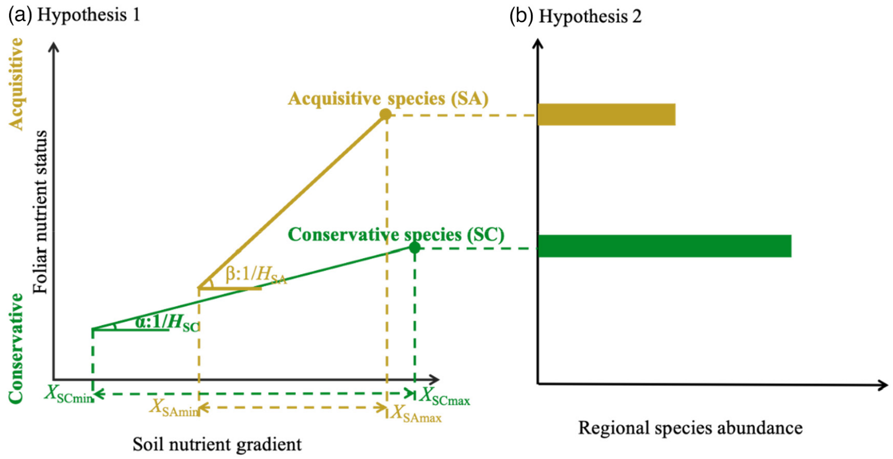

FIGURE 1 Conceptual model hypothesizing the relationship among foliar nutrient status, the strength of stoichiometric homeostasis (H) and species abundance. The x-axis illustrates soil nutrient gradient, at which X_{SAmin}, X_{SAmax}, X_{SCmin} and X_{SCmax} indicate the minimum and the maximum values of soil nutrient contents that nutrient-acquisitive species (SA) and nutrient-conservative species (SC) can occupy. The y-axis illustrates foliar nutrient status from conservative to acquisitive species. In panel (a), the slope of the green line (α) indicates the reciprocal of the strength of stoichiometric homeostasis (i.e. greater H_{SC}) for conservative species. The slope of the goldenrod line (β) indicates the reciprocal of the strength of stoichiometric homeostasis (i.e. lower H_{SA}) for acquisitive species. In panel (b), the length of the crosswise bar indicates regional species abundance (a given species' plot frequency across the Ningbo region) for conservative and acquisitive species respectively

is particularly important for predicting plant species commonness and rarity across regional communities, where N and/or P limits plant growth and is highly variable (Stahl et al., 2014; Sterner & Elser, 2002). Plant species that are adapted to low but highly variable soil nutrient availability (i.e. the nutrient-conservative, high H-species) can only manage slow growth but can sustain a strong position through both high nutrient use efficiency and great ability to maintain stable nutrient stoichiometry in these environments (Lambers & Poorter, 1992; Sterner & Elser, 2002). In contrast, where nutrients are plentiful, nutrient-acquisitive species with low H are faster growing (Frost et al., 2005; Yu et al., 2012). Thus, they may have higher local abundance but cannot adapt to low soil nutrient conditions. Correspondingly, we hypothesized further that nutrient-conservative, high-H species have higher frequency of occurrence (i.e. regional abundance) than those nutrient extravagant low-H species across regional natural communities where plant growth-limited N and/or P are highly variable (Hypothesis 2, Figure 1b).

There is ample evidence that plant growth is predominantly limited by N in most temperate, boreal and polar ecosystems, while it is limited by P in many subtropical and tropical ecosystems (Ågren et al., 2012; Huang et al., 2013; Reinhard et al., 2016; Turner et al., 2018; Vitousek et al., 2010; Yan et al., 2008) and generally in very old, strongly weathered soils (Lambers et al., 2008; Wardle et al., 2004). The strength of stoichiometric homeostasis of N and P on species abundance may differ between temperate and (sub)tropical regions. In previous empirical studies, involving a 2-year field P addition experiment and a large-scale survey in temperate grassland ecosystems, respectively, only H_N was significantly positively correlated with plant species abundance, while H_P was not significantly linked with species abundance (Yu et al., 2010, 2015). In a Tibetan alpine steppe, species abundance was not affected by either H_N or H_P (Wu & Wang, 2019). Surprisingly, hardly any research has focused on whether and how the strength of stoichiometric homeostasis of N and P is linked with woody species abundance. Based on the results for herbaceous plants, we predicted that stoichiometric homeostasis can also control woody species abundance. Specifically, in subtropical forests, where vegetation productivity tends to be primarily limited by P, we predicted that H_P controls species abundance more tightly than H_N across forest communities at the regional scale. Moreover, considering the trade-offs between foliar nutrient status and stoichiometric homeostasis in our hypothesis (1), we proposed an additional hypothesis (2) that nutrient-conservative species with high-H will have a wider distribution range (higher regional abundance) than nutrient extravagant low-H species. Since H_N is a better predictor of species abundance in N-deficient ecosystems, we hypothesize (3) that H_P plays a stronger role than H_N in determining species commonness and rarity across mostly P-limited forest communities.

In order to test our hypotheses, we quantified N and P contents in leaves of 54 woody species and their soils across 94 woody communities in subtropical China. Then we evaluated the species' levels of N and P stoichiometric homeostasis and their regional abundance to further test our hypotheses.

2 | MATERIALS AND METHODS

2.1 | Study region, forest plots and species abundance

This study was carried out in the Ningbo region, a coastal area in eastern China (28°51′–30°33′N, 120°55′–122°16′E, Figure S1). The landscape is a mixture of plains, basins and low hills (4–900 m a.s.l.), covering a total area of 9816 km^2. As a dominant landscape element, low hills are inlaid in a fragmented pattern on the plains. The regional topography is rugged and the dominant soil types are ferrasols (i.e. red clay soils; FAO 2014–2015) with pH of 4.4–5.1. Due to strong oxidization and leaching in the wet and humid climate, ferralsols are typically rich in iron and aluminium oxides, but poor in organic matter and soluble minerals, especially in phosphorus (Yan et al., 2013). The regional climate is subtropical, with hot and humid summers, and cool and dry winters. Mean annual temperature is 16.5°C and mean annual rainfall is 1440 mm.

Historically, the dominant vegetation type in the region was subtropical evergreen broadleaf forests (EBLFs), which had been extensively logged until the 1980s and had completely disappeared across the plains. The majority of the remaining intact or semi-intact EBLFs have been preserved in the hilly lands and are found in natural reserves, forest parks and around water reservoirs, where human disturbance levels are rather low. In recent decades, there has been widespread natural regeneration of forest vegetation. On the less fertile hillsides, the forests are often dominated by evergreen trees of the genera *Cyclobalanopsis*, *Castanopsis* and *Lithocarpus* (Fagaceae), *Cinnamomum* and *Machilus* (Lauraceae) and *Schima superba* (Theaceae) in the overstorey layer and evergreen species of the genera *Ilex*, *Symplocos* and *Camellia* in the understorey. In contrast, in the valley areas, mixed evergreen-deciduous broad-leaved forests prevail due to the fertile soils, and *Liquidambar formosana*, *Quercus acutissima* and *Cinnamomum camphora* are the dominant species.

From July to September of 2014 and 2015, we investigated woody communities from 94 EBLFs sites that had passed stand initiation stage and differed visibly in terms of species composition and soil organic matter depth. The contents of soil N and P, broadly represent soil N and P availability as evidenced by positive relationships between soil N or P content and above-ground biomass across these forests (see Figure S2, the data from 94 plots investigation, and the biomass value were calculated using allometric equation based on species density data of community survey). Soil N and P content varied 14-fold and 41-fold respectively with the different terrain features across the 94 EBLFs sites (see Results), thus representing a topography-mediated range of soil nutrient availability in the region. Additionally, we used SLA as an indirect positive indicator of soil nutrient availability (Ordonez et al., 2009), rate of plant biomass production (Lambers & Poorter, 1992) and position along the strategy axis from resource conservative to resource acquisitive (Wright et al., 2004).

In each site, we set-up a representative 20 m × 20 m plot for a detailed survey of the woody vegetation. A minimum distance of 50 m between adjacent plots was maintained to avoid spatial autocorrelation and pseudo-replication. In each plot, species identity was determined for all woody plants taller than 0.5 m, and then the presence/absence of a given species in each plot was estimated. Species richness per plot ranged from 8 to 47 (25 species on average), with a total of 176 species from 96 genera and 50 families across all sites. Stem density of our sampled sites ranged from 0.15 to 1.54 stems/m^2, and stem basal area on a ground area basis ranged from 39 to 2715 cm^2/m^2.

Since our interest in this study was to test how foliar N and P status and their stoichiometric homeostasis of woody plants affect regional species abundance distribution, we estimated the frequency across plots (i.e. number of plots/94) to indicate the regional abundance for a given species. Although we focused on species distribution, we found that more widely distributed species also had higher abundance and dominance in this subtropical forest (Figure S3).

2.2 | Measurements of foliar and soil N and P contents

To measure the site-specific foliar N and P contents, we collected species-specific leaf samples from at least three individual trees in each of the 94 plots. For singleton and doubleton species within a plot, we sampled two or three additional individuals nearby a plot to ensure an equal sample size for each species in a given site. On the field, we cut at least three branches from each individual plant at its canopy edge. On each branch, we selected 20 fully developed and healthy-looking leaves, which were immediately wrapped in a moist paper towel. Each sample was then stored in a sealed plastic bag and kept cool until brought back to the laboratory for measurement.

In the laboratory, 60 leaves from three branches were combined for a given individual plant and scanned using a leaf area meter (LI-3100C, Li-Cor) to determine the mean leaf area. Then leaf samples were dried at 75°C for 48 hr in an oven to determine leaf dry mass for calculating specific leaf area (SLA, leaf area per mass). Finally, the leaf samples were ground by using a laboratory mill and then passed through a 0.15 mm sieve for determining foliar N and P contents (LNC and LPC). The micro-Kjeldahl method was used to analyse leaf N and P contents (mg/g). Specifically, it was measured photometrically after samples had been digested with nitric acid (HNO_3) on a discrete autoanalyser (Smartchem 200, Alliance). Leaf N and P contents of a species for a given plot were mean values of the three individuals.

To characterize soil nutrient availability conditions of a plot, we used some of the most commonly used measures: soil total N and total P (see Figure S2 for their positive relationships with above-ground biomass production, implying that soil N and P contents scaled with their availability), which were measured in the majority of cases for the upper 20 cm of soil. Five soil samples were taken with a metal corer after removing the litter layer from randomly chosen locations in each plot, on the day of sampling plant leaves. In total, there were 470 samples (94 plots × 5 samples). In the laboratory, soil samples were air-dried in a ventilated room for 30 days. A subsample from each of the 470 air-dried samples was passed through a 0.5 mm sieve to analyse total N content, and another subsample was ground further to pass through a 0.25 mm mesh to analyse total P content on a discrete autoanalyser (Smartchem 200, Alliance, France). We used mean values of soil N or P contents from five locations within a plot to represent soil nutrient conditions of a given site.

2.3 | Calculation of stoichiometric homeostatic regulation coefficients and foliar N:P ratios across species

To test the extent to which foliar nutrient status correlates with regional variation in soil nutrient supply, 54 of 176 woody species that occurred in more than five plots (i.e. ensuring great variability of soil nutrient supply across sites), were selected for calculating stoichiometric homeostatic regulation coefficients, that is, the strength of stoichiometric homeostasis (H). We estimated the H_N for 45 and H_P for 36 of these species, because the other species had a strict homeostasis (H approaching infinity, p-value > 0.05 in the following regression equation). The homeostatic regulation coefficient was estimated according to Sterner and Elser (2002) as the Equation (1) below:

$$H = \frac{\log(x)}{\log(y) - \log(c)}, \quad (1)$$

where y is foliar N or P content, x is soil N or P content and c is a constant (according to regression analysis of the homeostatic model equation: $\log(y) = \log(c) + \log(x)/H$, $1/H$ is the slope of the log-linearized relationship). If H was negative, the absolute value was used.

In addition, we calculated mass-based N:P ratio for each of the 54 species to be an indirect indicator of whether plant productivity is more severely limited by P than N (or vice versa) in the studied subtropical region (Güsewell, 2004). Leaf N:P ratio >16 tends to indicate P limitation and <14 N limitation (Koerselman & Meuleman, 1996). The N:P ratio for each species was calculated across individuals among communities where a given species occurred.

2.4 | Statistical analysis

All data were log-10 transformed before analysis to improve normality of distributions and linearity of relationships. To test whether conservative species with low foliar nutrients are more stoichiometrically homeostatic (i.e. high homeostatic regulation coefficient), we used linear regression to fit the bivariate relationship between LNC and H_N and between LPC and H_P respectively. Furthermore, in order to examine whether conservative species can also grow in a wider range of soil nutrient supply than acquisitive species do at the regional scale, we conducted linear regressions for the cross-species patterns of foliar nutrient status against different percentiles of soil N and P contents. Thereto, we quantified foliar nutrient status by conducting a principal component analysis (PCA) of LNC and LPC across species. The first axis (PC1) accounted for 83.1% of total variation in foliar N and P contents (Figure S4), with lower PC1 score indicating more conservative and higher scores more acquisitive foliar nutrient status for a given species. Therefore, the species' PC1 scores were used in subsequent analyses to represent the foliar nutrient status across 54 species. Then box plots were constructed to represent soil nutrient values for forest plots where a given species occurred. Also, linear regressions were conducted between foliar nutrient status (PC1 score of each species) and the minimum value, the first quartile (Q1) value, the median value, the third quartile value (Q3), the maximum value of soil nutrient contents, respectively, which together represent the range of soil nutrient levels.

If foliar nutrient status was significantly positively associated with the minimum value of soil nutrient contents, we considered that conservative species were better adapted to nutrient-poor soils than acquisitive species. We expected that this pattern also matters to other relatively low values of soil nutrient contents such as the Q1 and median values. However, if foliar nutrient status is negatively related to the maximum value of soil nutrients, it could mean that conservative species can also grow better in nutrient-rich soils than acquisitive species. The combination of these two reverse patterns would thus indicate that nutrient-conservative species have a greater ability to acclimatize to a diverse array of soil nutrients (Figure 1a).

To test our hypotheses 2 and 3 (Figure 1), linear regression was employed also to examine bivariate relationships between species abundance (relative plot frequency) and each of the foliar nutrient contents (LNC and LPC) and H (H_N and H_P). In addition, we conducted linear regression between SLA and, respectively, foliar nutrient status (LNC, LPC and PC1 scores mentioned previously), H_N, H_P and species frequency. This analysis aimed to test whether this widely used alternative indicator of species' nutrient economic strategy can generally be associated with both stoichiometric homeostasis and regional species abundance.

Finally, to quantify whether (assuming P to be the main limiting nutrient,) LPC and H_P each played a stronger, direct or indirect role than LNC and H_N in determining species commonness and rarity across communities in the studied subtropical region, we fitted a full structural equation model (SEM) with LNC, LPC, H_N and H_P on species abundance distribution. Twenty-seven tree species were selected that meet all the requirements for SEM analysis. Mardia's multivariate normality test confirmed that the multivariate normality of our data ($K = 47.06$, $p = 0.08$) did not influence the estimated probabilities associated with Chi-square (Grace et al., 2016). The initial SEM contained all possible correlations among these variables and the final SEM was selected for each significant path based on the lowest Akaike information criterion (AIC) value and the p-value of each regression coefficient. We assessed the fit of the full model using a Chi-square test ($p > 0.05$), goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The standardized coefficients were used to compare direct effects across paths. We added the standardized direct and indirect effects from all the given exogenous variables to calculate their total effects on species abundance (Grace et al., 2016). All analyses were conducted in R software version 3.6.0 (R Core Team, 2019). We used the R package LAVAAN to estimate the SEM parameters (Rosseel, 2012).

3 | RESULTS

Across 54 species, foliar N content ranged from 11.50 ± 2.77 mg/g to 26.08 ± 9.58 mg/g, foliar P content ranged from 0.30 ± 0.16 mg/g to 1.05 ± 0.32 mg/g (Table S1), and foliar N:P ratio ranged from 16.69 ± 5.72 to 55.42 ± 20.73, that is, all species had N:P > 16, implying overall P limitation (Figure S5). The homeostatic value of H_N ranged from 0.69 to 9.76 (Table S2), while H_P ranged from 0.67 to 7.63 (Table S3). There was a larger variability in soil P than soil N, with soil N content ranging from 1.05 mg/g to 15.3 mg/g, and with soil P ranging from 0.14 mg/g to 1.64 mg/g (Table S4).

Foliar N and P contents negatively correlated with H_N and H_P respectively (Figure 2a,b). In addition, H_N and H_P negatively correlated with species abundance (Figure 2c,d). Also, LNC and LPC negatively correlated with species abundance (Figure 2e,f). Remarkably, SLA positively correlated with foliar nutrient status (LNC, LPC and PC1 scores), and negatively correlated with both H_N and H_P and species abundance (Figure S6).

Moreover, foliar nutrient status (PC1) positively correlated with the minimum and the third quartile values (Q3) of soil N contents (Figure 3a,b, Table 1), while positively correlated with the minimum and the first quartile values (Q1) but negatively correlated with the maximum value of soil P contents (Figure 3c,d; Table 1). Besides, there were significantly positive correlations between foliar nutrient status and the minimum soil N:P ratio and negative correlations between foliar nutrient status and the maximum value of soil N:P ratio (Figure S7; Table S5).

The SEM model yielded a good fit to the data, and accounted for 77% of the variation in regional species abundance (Figure 4; Table S6). LNC and LPC had negative direct effects on H_N and H_P respectively. LPC did not directly ($r = -0.27$, $p > 0.05$) but indirectly affect species abundance via decreasing H_P ($r = -0.18$, $p < 0.05$). In contrast, LNC had a significant negative direct effect on species abundance ($r = -0.41$, $p < 0.01$) but did not affect species abundance indirectly via H_N ($r = -0.03$, $p > 0.05$; Figure 4; Table S6). Interestingly, H_P had a significant positive effect on species abundance ($r = 0.37$, $p < 0.05$), but the direct effect of H_N on species abundance was non-significant ($r = 0.05$, $p > 0.05$; Figure 4; Table S6).

4 | DISCUSSION

This study has explicitly examined whether, across woody species, there is a continuum from nutrient-conservative, high-*H* species to nutrient-acquisitive, low-*H*; and whether such a pattern underpins the plant species commonness and rarity in P-limited subtropical

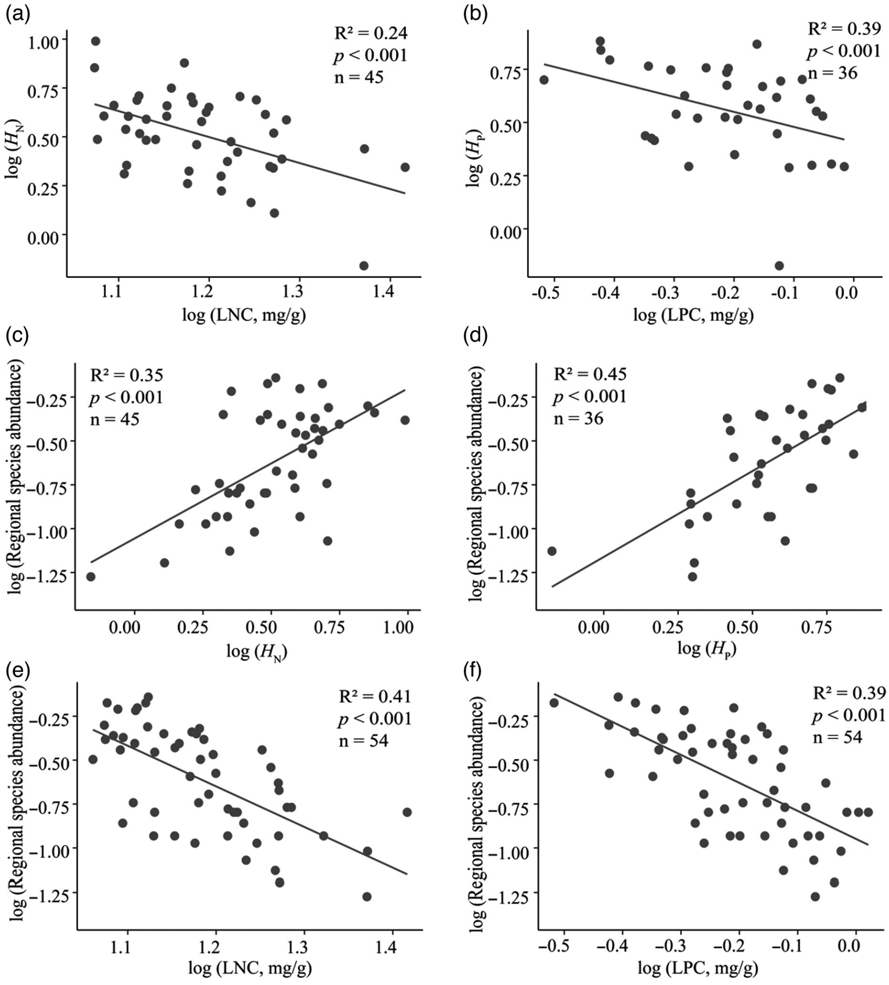

FIGURE 2 (a, b) Bivariate relationships between foliar N and P contents and strength of N and P stoichiometric homeostasis (H_N and H_P). (c, d) Bivariate relationships between strength of N and P stoichiometric homeostasis and regional species abundance. (e, f) Bivariate relationships between foliar N and P contents and regional species abundance. Coefficients of determination (adjust R^2), *p*-values and the number of species used for analysis (*n*) are given

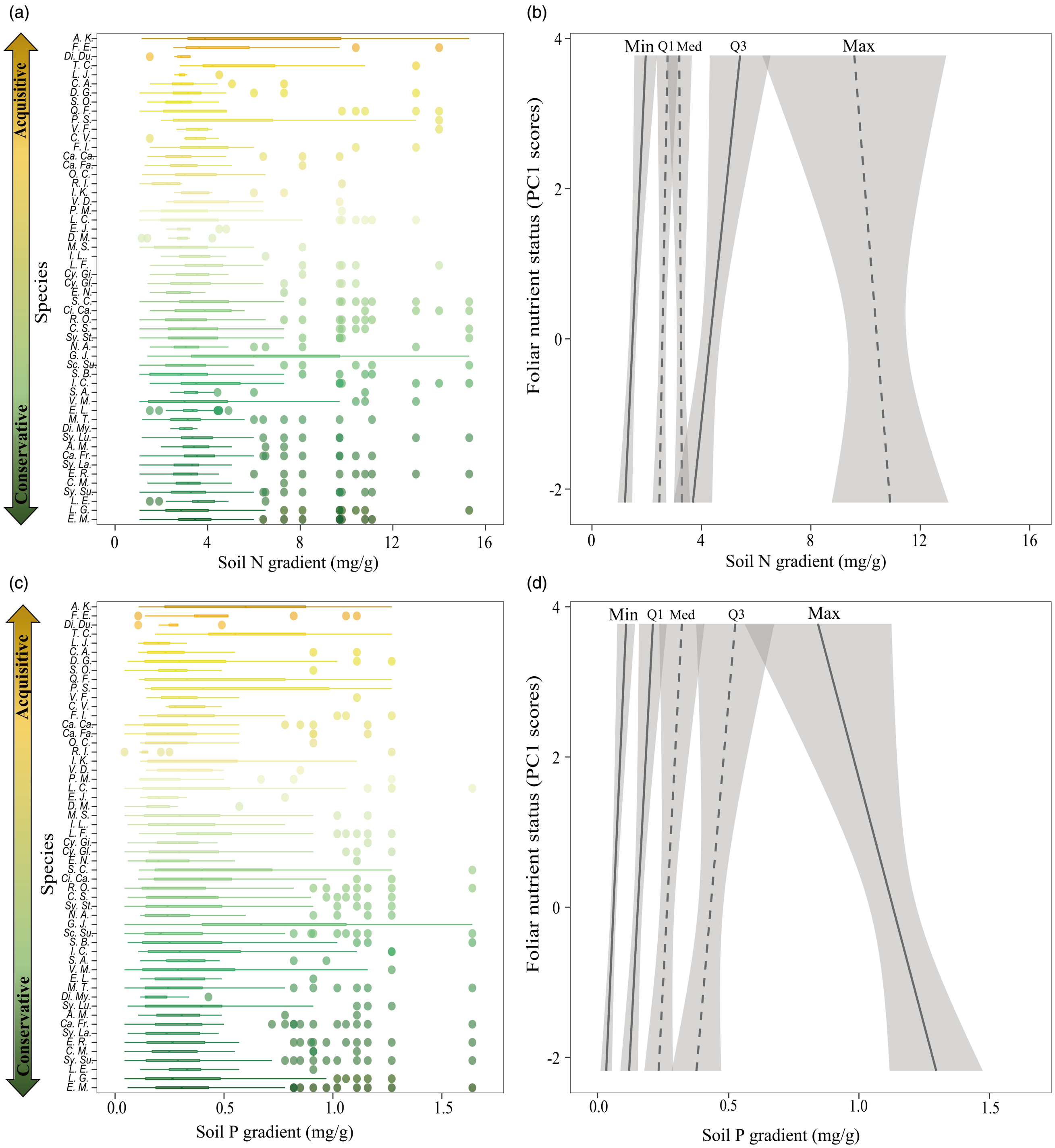

FIGURE 3 Woody species' nutrient economy strategy and their occurrence along soil nutrient gradients. (a) and (c) Box plots showing soil N and P contents, respectively, for forest plots where a given species occurred. The y-axis illustrates the rank of the 54 studied species along a gradient of foliar nutrient status. (b) and (d) The regression relationships between species' foliar nutrient status (from low nutrient level in conservative species at the bottom to high nutrient levels for acquisitive species at the top) and the soil N and P contents at which these species were found respectively. The regression was conducted separately for the minimum value (Min), first quartile (Q1) value, median value (Med), third quartile value (Q3) and maximum value (Max) of soil N and P contents. Foliar nutrient status was quantified as the scores of the first axis of a principal component analysis based on foliar N and P contents across species. Solid and dashed lines indicate the significant ($p < 0.05$) and non-significant ($p \geq 0.05$) regression relationship between soil nutrient content and foliar nutrient status respectively

TABLE 1 Estimated parameters of the linear regression relationships between foliar nutrient status (PC1 score of each species) and different percentiles of soil N and P contents

	Soil N			Soil P		
Independent variables	**Regression coefficient**	R^2_{adjusted}	p-value	**Regression coefficient**	R^2_{adjusted}	p-value
Minimum value (Min)	0.28	0.09	**0.02**	4.06	0.13	**<0.01**
First quartile value (Q1)	0.13	0.00	0.31	2.02	0.08	**0.03**
Median value (Med)	−0.03	0.00	0.78	0.80	0.02	0.17
Third quartile value (Q3)	0.09	0.06	**0.04**	0.44	0.01	0.19
Maximum value (Max)	−0.01	0.00	0.60	−0.36	0.06	**0.04**

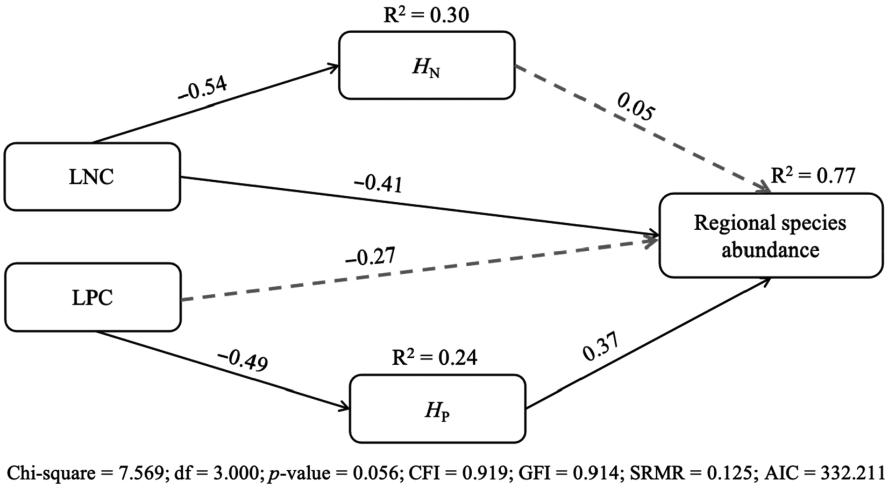

FIGURE 4 Structural equation model linking species abundance with strength of N and P stoichiometric homeostasis (H_N and H_P) and foliar nutrient status (LNC and LPC) across woody plant species in subtropical forests. For each path, the standardized regression coefficient is shown. Black solid lines indicate significant paths ($p < 0.05$), and grey dash lines are for non-significant paths ($p \geq 0.05$). R^2 indicates the total variation in an endogenous (dependent) explained by all exogenous (independent) variables

forest ecosystems. Indeed, we found negative relationships between foliar nutrient status and stoichiometric homeostasis for both N and P. This result supports our hypothesis 1 that plant species with conservative foliar nutrient status are higher in stoichiometric homeostasis than those species with acquisitive foliar nutrient status. Moreover, consistent with our hypothesis 2, we found that species with low foliar N and P contents but strong stoichiometric homeostasis achieve high regional abundance, with which H_P playing a stronger role than H_N in determining the regional-scale species abundance distribution. These findings extend the test of the relationships between stoichiometric homeostasis and species abundance from herbaceous species in temperate grassland ecosystems (Dijkstra et al., 2012; Yu et al., 2011, 2015) to the woody plant species in subtropical forest ecosystems, where plant growth is generally limited by P, instead of N.

The negative relationships between foliar nutrient status and stoichiometric homeostasis indicate a plant nutrient economy trade-off (Elser et al., 2010; Yu et al., 2015). Similar to the S-strategy species, that is, stress-tolerant species in the CSR plant ecological strategy scheme (Grime, 1979), species capable of maintaining growth and survival in nutrient limited environments tend to be conservative in resource consumption through lowering foliar nutrients and improving nutrient use efficiency (Hayes et al., 2014; Wright & Westoby, 2003), as well as increasing elementome plasticity (Fernández-Martínez, 2022), thus maintaining stable stoichiometric homeostasis (Sterner & Elser, 2002; Yu et al., 2012). The reverse is true for fast growing species that are extravagant in nutrient consumption with high foliar nutrient contents at the expense of maintaining less stable stoichiometric homeostasis when nutrients are constantly available in large supply (Reich, 2014; Sterner & Elser, 2002). This foliar nutrient status associated patterns of species stoichiometric homeostasis should also be generalized to other leaf economic traits. We found that SLA, one of the key traits structuring the leaf economic spectrum and associated with foliar nutrient concentration (Wright et al., 2004), also traded off against both H_N and H_P (Figure S6d,e). As SLA is also negatively related to light supply for photosynthesis and carbon investments in structure and defence, these patterns also suggest that species with the degree of stoichiometric homeostasis is also related to the economy of other resources such as carbon and light (Reich, 2014). Such relationships will be an important topic for in-depth follow-up study.

The consequence of the trade-offs between foliar nutrient status and stoichiometric homeostasis on plant growth may depend on ecosystem type, especially soil nutrient-limitation type. Specifically, in the ecosystems where N is less available than P to plant growth, species with great foliar N conservativeness and stoichiometric homeostasis contribute much to their abundance distribution (Yu et al., 2010, 2015). Such pattern is reversed in our studied subtropical ecosystem where foliar N:P ratio ranged from 16.69 to 55.42 across species (i.e. consistently larger than

16), suggesting a pronounced P limitation for plant growth (Koerselman & Meuleman, 1996; Yan et al., 2010). Since P is more deficient and variable than N in this region (Table S4; Figure S5), plant species with conservative foliar nutrients should be advantaged in their growth by high H_P, rather than H_N. These contrasting patterns consistently suggest that, across different soil N and P compositions in specific ecosystems, possessing a high degree of stoichiometric homeostasis for the most deficient nutritional element is a viable strategy of plant species for alleviating nutrient stress (Hayes et al., 2014; Sterner & Elser, 2002). Understandably, during long-term strong oxidization, leaching and soil acidification in (sub)tropical region, soil P increasingly acts as a chemical filter to select species capable of maintaining relatively stable foliar P level rather than stable N level (Laliberte et al., 2014). Strong foliar nutrient conservativeness and stoichiometric homeostasis should be an important physiochemical mechanism driving species abundance distribution (Elser et al., 2010; Sardans et al., 2012; Yu et al., 2010). In this study, the bivariate regression analysis showed that species abundance enhanced with increases in both H_N and H_P. This result is partially consistent with the finding that species with high H_N but not yet high H_P are more dominant in temperate grasslands (Yu et al., 2012, 2015). More mechanistically, however, our SEM analysis showed that, although species with conservative foliar N had high H_N, these features did not improve their abundance. In contrast, there was a remarkable indirect impact of conservative foliar P status on species abundance via increased H_P. Our SEM results therefore suggest that, in a given ecosystem with given limitation of a particular nutritional element, foliar N and P status modulate the regional-scale species abundance distribution through different ways.

Soil nutrients that are less available to plant growth are more important for modulating species performance through strong stoichiometric homeostasis, but not yet other nutrients, even though they may be indicative of species abundance distribution such as N in this study. This can be evidenced by our results that foliar nutrient status was significantly positively correlated with the minimum values of soil N and P contents, but only negatively associated with the maximum value of soil P content (Figure 3; Table 1). The positive relationships between foliar nutrient status and the minimum values of soil N and P contents again support the view that conservative species are more successful than acquisitive species in nutrient-poor soils (Harpole et al., 2011; Hayes et al., 2014). In contrast, the negative relationship between foliar nutrient status and the maximum value of soil P content indicates that conservative species are also well adapted to P-rich soils. Together, these two contrasting patterns suggest that conservative species are more flexible than acquisitive species in their foliar nutrient economy, especially for P, to maintain foliar nutrient composition relatively stable regardless of spatial variation in soil P availability. Therefore, conservative species could occupy a broader range along the soil P-based than the N-based biogeochemical niche (Peñuelas et al., 2019), thereby increasing their regional abundance across P-limited subtropical forests. By contrast, it is not necessary to decouple foliar N levels from soil N through N stoichiometric homeostasis for plant species when N limiting is not severe for plant growth (Sterner & Elser, 2002). In line with the biogeochemical niche hypothesis (Peñuelas et al., 2019), such distinct stoichiometric strategies of woody plants suggest that species abundance distribution is jointly determined by soil chemical filters and elemental composition related evolutionary history of species (Fernández-Martínez et al., 2021; Sardans et al., 2021).

In conclusion, this study advances our understanding of how foliar nutrient status trades off with stoichiometric homeostasis across plant species, consequently influencing species commonness and rarity in subtropical forests where soil P is more critical than N to plant growth. Across these forests, P stoichiometric homeostasis was a key driver of species abundance distribution. Our findings highlight that the relative strength of stoichiometric homeostasis between N and P on local absence/presence and thus regional abundance distribution of plant species is ecosystem type specific, that is, the dominant control of stoichiometric homeostasis on species abundance distribution depends on which nutritional element is relatively less available than another for plant carbon assimilation. Maintaining strong stoichiometric homeostasis of deficient and variable P while maintaining conservative economy of N is a key physiochemical mechanism for shaping regional species abundance distribution in P-limited subtropical forests. Future studies should test whether these mechanisms as revealed here for subtropical forests also apply to other P-limited ecosystems in the world. Such knowledge is essential to establish a more complete picture of the physiochemical mechanisms underlying species abundance distribution and community assembly in the context of globally increasing N deposition, and its consequences via increasing P limitation.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

E.-R.Y. and H.C. designed and conceptualized the experiment; H.C., C.G., B.T., L.-T.Z., M.-S.X., B.-L.S., B.-Y.Y., W.-H.Y and Y.-C.Y. collected the data; H.C. and E.-R.Y. analysed the data and wrote the manuscript; H.C., J.H.C.C. and E.-R.Y.; revised and improved the manuscript. All authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

Data available from Dryad Digital Repository at http://doi.org/10.5061/dryad.fttdz08vm (Ci et al., 2022).

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