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RESEARCH ARTICLE

Global change progressively increases foliar nitrogen–phosphorus ratios in China's subtropical forests

Yuan Lai[1,2] | Songbo Tang[1,3] | Hans Lambers[4] | Peter Hietz[5] | Wenguang Tang[6] | Frank S. Gilliam[7] | Xiankai Lu[1] | Xianzhen Luo[1] | Yutong Lin[1] | Shu Wang[1,2] | Feiyan Zeng[1] | Qi Wang[8] | Yuanwen Kuang[1,2]

[1]Guangdong Provincial Key Laboratory of Applied Botany and Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

[2]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China

[3]School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

[4]School of Biological Sciences, University of Western Australia, Perth, Western Australia, Australia

[5]Institute of Botany, University of Natural Resources and Life Sciences, Vienna, Austria

[6]School of Geography, University of Leeds, Leeds, UK

[7]Department of Earth and Environmental Sciences, University of West Florida, Pensacola, Florida, USA

[8]National-Regional Joint Engineering Research Center for Soil Pollution Control and Remediation in South China, Guangdong Key Laboratory of Integrated Agro-Environmental Pollution Control and Management, Institute of Eco-Environmental and Soil Sciences, Guangdong Academy of Sciences, Guangzhou, China

Correspondence

Qi Wang, National-Regional Joint Engineering Research Center for Soil Pollution Control and Remediation in South China, Guangdong Key Laboratory of Integrated Agro-Environmental Pollution Control and Management, Institute of Eco-Environmental and Soil Sciences, Guangdong Academy of Sciences, Guangzhou, China.
Email: jenniferqi520@gmail.com

Yuanwen Kuang, Guangdong Provincial Key Laboratory of Applied Botany and Key Laboratory of Vegetation, Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China.
Email: kuangyw@scbg.ac.cn

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Abstract

Globally increased nitrogen (N) to phosphorus (P) ratios (N/P) affect the structure and functioning of terrestrial ecosystems, but few studies have addressed the variation of foliar N/P over time in subtropical forests. Foliar N/P indicates N versus P limitation in terrestrial ecosystems. Quantifying long-term dynamics of foliar N/P and their potential drivers is crucial for predicting nutrient status and functioning in forest ecosystems under global change. We detected temporal trends of foliar N/P, quantitatively estimated their potential drivers and their interaction between plant types (evergreen vs. deciduous and trees vs. shrubs), using 1811 herbarium specimens of 12 widely distributed species collected during 1920–2010 across China's subtropical forests. We found significant decreases in foliar P concentrations (23.1%) and increases in foliar N/P (21.2%). Foliar N/P increased more in evergreen species (22.9%) than in deciduous species (16.9%). Changes in atmospheric CO_2 concentrations (P_{CO_2}), atmospheric N deposition and mean annual temperature (MAT) dominantly contributed to the increased foliar N/P of evergreen species, while P_{CO_2}, MAT, and vapor pressure deficit, to that of deciduous species. Under future Shared Socioeconomic Pathway (SSP) scenarios, increasing MAT and P_{CO_2} would continuously increase more foliar N/P in deciduous species than in evergreen species, with more 12.9%, 17.7%, and 19.4% versus 6.1%, 7.9%, and 8.9% of magnitudes under the scenarios of SSP1-2.6, SSP3-7.0, and SSP5-8.5, respectively. The results suggest that global change has intensified and

Yuan Lai and Songbo Tang should be considered joint first author.

will progressively aggravate N–P imbalance, further altering community composition and ecosystem functioning of subtropical forests.

KEYWORDS
foliar N:P ratios, global change, herbarium specimens, N–P imbalance, subtropical forests

1 | INTRODUCTION

Nitrogen (N) and phosphorus (P) are important components of proteins and nucleic acids, respectively (Sterner & Elser, 2002). Nitrogen is closely associated with photosynthesis, plant productivity, and litter decomposition, and P is strongly associated with protein synthesis, genetic material, energy transfer, and cell structure (Elser et al., 2010; Lambers, 2022; Sterner & Elser, 2002). They are essential nutrients affecting the metabolism, growth and development of plants (Elser et al., 2010; Turner et al., 2018), and thereby the composition, structure, and functioning of terrestrial ecosystems (Elser et al., 2007; Fernández-Martínez et al., 2020; Tang et al., 2018). Through growth and metabolism, plants couple N and P and other essential elements in relatively constrained ratios (Elser et al., 1996). Excess or deficiency of either N or P results in limitation of growth by N or P, adversely affecting plant growth and ecosystem productivity (Peñuelas & Sardans, 2022; Sterner & Elser, 2002). Foliar N and P ratios (N/P) have frequently been used to evaluate the N versus P limitation of primary productivity in different ecosystems (Güsewell, 2004; Tessier & Raynal, 2003). For example, a foliar $N/P<10$ or >20 suggests that plant growth and ecosystem productivity are limited by N or P, respectively (Güsewell, 2004). Quantifying temporal variation in foliar N/P is important to predict the dynamics of nutrient status, productivity, and carbon (C) storage in terrestrial ecosystems under the impacts of global change (Güsewell, 2004) and human activities (Peñuelas et al., 2013).

Global change, including elevated partial pressure of atmospheric CO_2 (P_{CO_2}), climate change, and increasing atmospheric N deposition (N_{dep}), has been accelerating at global or regional scales (Ackerman et al., 2019; Coumou & Rahmstorf, 2012; IPCC, 2014; Liu, Zhang, et al., 2013) which has led to alteration of N/P with severe consequences for ecosystems functioning (Peñuelas & Sardans, 2022). For instance, elevated P_{CO_2} may stimulate plant growth, resulting in changes in foliar N/P (Loladze, 2002); changes in temperature and rainfall could alter plant P availability via affecting soil P mineralization and dissolution (Dijkstra et al., 2012; Lie et al., 2022); rising vapor pressure deficit (VPD) caused by global warming might increase foliar N/P through restraining P demand of plants due to reduced photosynthesis under stomatal closure (Grossiord et al., 2020; Lihavainen et al., 2016); high precipitation and low potential evapotranspiration (PET) accompanied by high N_{dep} might increase the formation of non-labile P in acidic soils, thus decreasing foliar P concentration ([P]) and increasing N/P (Lin et al., 2022; Meier & Leuschner, 2014). Moreover, high N_{dep} may enhance the uptake of N (Sardans et al., 2017) or rhizosphere phosphatase activity (Marklein & Houlton, 2012), thus altering foliar N/P. Most previous studies looked at the effects of experiments or global change with specific drivers on foliar multi-element stoichiometry (Elser et al., 2010; Tian et al., 2019; Yue et al., 2017), but few investigated if this is actually happening and what the real drivers are on foliar N/P.

The sensitivity of plants to global change differs by leaf habit (i.e., evergreen and deciduous) and growth form (i.e., trees and shrubs) associated with their different leaf traits and growth rates (Way & Oren, 2010; Wright et al., 2005). For example, at the global scale, elevated P_{CO_2} increase water-use efficiency more strongly in evergreen species than in deciduous species (Niinemets et al., 2011; Soh et al., 2019); at the regional scale, trees and shrubs growing in natural habitats respond differently to global climate changes, with shrubs being less sensitive than trees to climatic warming because shrubs are more likely to be influenced by microclimate, topography, and soil temperature (Gazol & Camarero, 2012). The divergent responses among plant functional types to global change can also be reflected in nutrient allocation and utilization (Chen et al., 2013), with evergreen species having lower N-resorption efficiency but higher P-resorption efficiency than deciduous species (He et al., 2020). The faster foliar lifespan and higher growth rate of deciduous species than those of evergreen species result in higher foliar [N] and [P] of the former (Chen et al., 2013). Furthermore, foliar [N], [P], and N/P differ among plant species and are linked to phylogeny and environment and their interactions as evidenced by foliar elemental compositions of trees at a global scale (Sardans et al., 2021). The plant N and P stoichiometric characteristics have been extensively studied, but it is unclear whether there are differences in temporal dynamics among plant functional types under global change.

While the variation and drivers of foliar N/P have been studied at spatial scales (Vallicrosa et al., 2022) and by manipulative experiments (Liu, Huang, et al., 2013), few have addressed temporal changes driven by global change, with some exceptions in European forests based on long-term monitoring, which reported increases in foliar N/P over the past three decades (Jonard et al., 2015; Peñuelas et al., 2020; Talkner et al., 2015). However, only individual factors, that is, elevated P_{CO_2}, increasing N_{dep} and climate change, were considered as possible drivers of foliar N/P in those European studies. In fact, the variation of foliar N/P may involve complex interactions of multiple environmental factors, similar to those identified on water stress-gross primary production relationships of forests (Vallicrosa et al., 2022; Wang et al., 2022). In recent decades, Europe has seen a decline in N_{dep} (Ackerman et al., 2019), whereas elsewhere (e.g., subtropical forests in China) N_{dep} still increases in parallel with elevated P_{CO_2} (IPCC, 2014; Liu, Zhang, et al., 2013). Therefore, temporal trends and in the main drivers of foliar N/P likely differ between regions and biomes. In contrast to some temperate regions, studies about the interactions between global change and temporal trends of foliar N/P are rarely conducted in subtropical regions because of a lack of reliable long-term records (Bauters et al., 2020). Herbarium specimens provide an opportunity to obtain long-term series of foliar N/P (Bauters et al., 2020; Huang et al., 2016). Recently, we found that foliar [N] of forest species across subtropical China did not change over the last century (Tang et al., 2022), but it is not clear whether their foliar N/P changed. Revealing the temporal variation in foliar N/P and their climatic drivers would help to understand the past and predict future dynamics of forest growth, structure, and productivity and can provide key parameters to develop empirical models to scale the responses of forest ecosystems to global change (Tang et al., 2018).

Subtropical forests in China are subjected to global warming, shifting precipitation regime (Zhou et al., 2011), and increasing N_{dep} (Du et al., 2016). A combination of these and possibly other drivers affect plant nutrient stoichiometry (Tang et al., 2022) and ecosystem processes (Zheng et al., 2022). Given that CO_2 effects stimulate forests growth globally (Wang et al., 2020) and that regional N_{dep} did not increase foliar [N] in subtropical China (Tang et al., 2022), we hypothesized that (1) foliar N/P in subtropical forests increased during the period of 1920–2010, similar to patterns in temperate forests over past 3 decades (Jonard et al., 2015; Peñuelas et al., 2020; Talkner et al., 2015); (2) the change rate and their major drivers differed among plant functional types (i.e., leaf habit and growth form) because of their divergent responses to environmental factors (Gazol & Camarero, 2012; Niinemets et al., 2011; Soh et al., 2019); (3) major drivers will interact in their effect on foliar N/P, similar to on water stress-gross primary production relationships of forest (Wang et al., 2022). To analyze a complex dataset, we adopted a state-of-the-art machine learning local interpretation algorithm, the TreeExplainer-based Shapley additive explanation (TreeSHAP) approach (Lundberg et al., 2020), to identify the temporal variation in foliar N/P of 12 widely distributed species across subtropical forests of China (18–34° N, 97–122° E; Figure 1). Our objectives were to quantitatively estimate the major drivers and their interaction effects on foliar N/P from 1920 to 2010 and to predict the change in foliar N/P under future Shared Socioeconomic Pathways (SSP) scenarios. Testing the hypotheses and predicting the future foliar N/P will inform trends in N and P status as well as the structure and functioning of forest ecosystems under global change.

2 | MATERIALS AND METHODS

2.1 | Specimen collection

Herbarium specimens in this study were collected during 1920–2010 and were obtained from the Herbarium of South China Botanical Garden, Chinese Academy of Sciences (http://herbarium.scbg.cas.cn/). The selected specimens comprised 12 species (Table S1) that are widely distributed in natural broadleaved forests of subtropical China (18°–34° N, 97°–122° E). The 12 species with sampling time and sampling site (i.e., latitude, longitude, and altitude) were divided into plant functional types based on leaf habit (deciduous and evergreen) and growth form (shrubs and trees). To guarantee the reliability of sampling and analysis, only mature leaves were cut from specimens without any liquid or glue treatment. For each species, at least three specimens were selected per decade. Samples within each 0.1° latitude and longitude were assigned to the same sampling site (Craine et al., 2018). A total of 1811 specimens spanning 90 years were collected from 444 sites in subtropical China (Table S2; Figure 1).

2.2 | Foliar nutrients and environmental factors

The leaves were dried at 65°C to constant weight (72 h) and ground to powder. Foliar [P] ($g\,kg^{-1}$) was determined by the

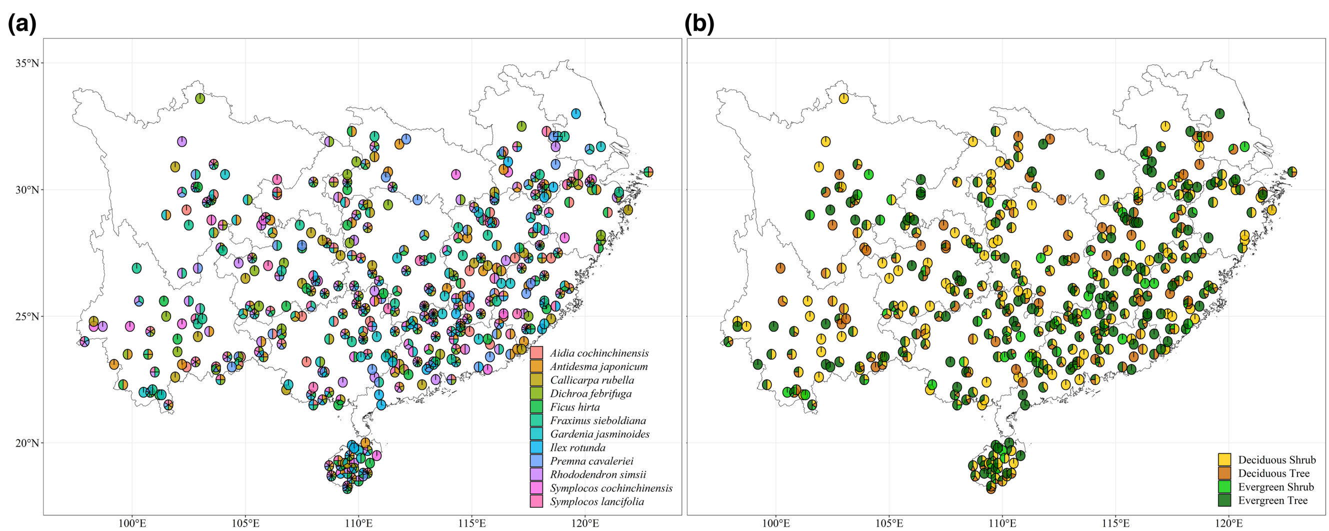

FIGURE 1 Sampling sites of 12 widely distributed species (a) and their functional types (b) in subtropical forests of China. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

molybdenum–antimony colorimetric method after the powder was digested with nitric acid and perchloric acid (Dong, 1996). Foliar [N] ($g\,kg^{-1}$) was obtained from our recent study (Tang et al., 2022). The measurement for each sample was performed in triplicate with the relative deviation <5% (Dong, 1996). Foliar N/P values were then calculated as the ratios of foliar [N] to [P] on a dry mass basis.

Ten common environmental factors (Table S3), that is, partial pressure of atmospheric CO_2 (P_{CO_2}), mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality (TS), precipitation seasonality (PS), annual maximum temperature (T_{max}), annual minimum temperature (T_{min}), potential evapotranspiration (PET), vapor pressure deficit (VPD), and atmospheric nitrogen deposition (N_{dep}), were obtained from the following sources. [CO_2] during 1920–2010 were downloaded from NASA GISS (https://data.giss.nasa.gov/modelforce/ghgases/). Since CO_2 availability depends on air partial pressure, rather than on concentration of CO_2, P_{CO_2} was calculated using elevation and [CO_2] of sampling site (Tang et al., 2022) to explore the effects of elevated atmospheric [CO_2] on foliar N/P. Maximum and minimum monthly temperature and mean monthly precipitation across the sampling sites were extracted from Peng et al. (2019) with ~0.5′ resolution and were used to calculate MAT, MAP, T_{max}, T_{min}, TS, and PS. TS and PS were calculated from the standard deviation of monthly values (Tang et al., 2022). PET and vapor pressure (VAP) were obtained from Climate Research Unit (CRU) TS v.3.26 with ~0.5′ resolution (Harris et al., 2014). VPD was calculated by VAP and monthly temperature (Grossiord et al., 2020). N_{dep} (dry and wet deposition of NO_y and NH_x) in subtropical China was derived from data (for 1850, 1960, 1970, 1980, 1990, 1997–2013) of Wang et al. (2017) via linear interpolation.

2.3 | Statistical analyses

We used linear regression to test the temporal variation in foliar N/P for all specimens and different plant types (leaf habit, growth form) as well as the individual species. Given the intrinsic properties of ratios, foliar N/P values were log-transformed to ensure robust and reproducible results (Isles, 2020). Bootstrap regressions were used to test whether there were differences in the slopes of time trends among functional types. First, a total of 1000 times bootstrapping was applied to generate the sub-databases for each functional type with "*bootstrap*" function in "*modelr*" R package (Wei et al., 2019; Wickham, 2022). Then, we calculated the regression slopes (annual change rates) of foliar N/P versus the time of the sub-databases. After obtaining the slopes of all sub-databases, we used Kruskal–Wallis test to obtain the differences in temporal trends among functional types with "*Kruskal*" function in "*agricolae*" R package (https://cran.r-project.org/package=agricolae).

We used five machine learning models to predict foliar N/P of plant functional types via environmental factors (Table S4). Among the models, random forest (RF) model performed relatively the best, following by eXtreme Gradient Boosting (XGB) and Stochastic Gradient Boosting (SGB) model. The root mean square error (RMSE) values in the testing sets were 6.34–8.06 for RF, 7.50–9.61 for XGB, 6.25–8.35 for SGB, respectively, in different plant functional types; and the R^2 of regressions between predicted and observed values for RF (ranging from 0.60 to 0.89) were much higher than those for XGB (ranging from 0.18 to 0.54) and SGB (ranging from 0.16 to 0.47). Therefore, RF model was used to determine the relative importance of environmental factors on foliar N/P for each plant functional type. In RF model, the "n_estimators," "min_sample_split," "min_samples_leaf," and "max_features" were set as 500, 2, 1, and 1, respectively. K-fold cross-validation is a robust technique for data splitting. It can leverage information in small data sets by combining the results of K rounds of different training, validation and test splits of the same dataset as explained by Lever et al. (2016). In this study, we used tenfold cross-validation and split the dataset into training, validation, and test sets. Specifically, for $K=10$, we created 10 balanced 60%/20%/20% training, validation, and test sets and averaged the test R^2 scores from each round. Test set and cross-validation approaches can help to reduce overfitting and produce a model that performs well on new data. RF model was established with the "sklearn" Python package (https://github.com/scikit-learn/scikit-learn).

TreeSHAP method based on game theory can provide local explanations for predictions by machine learning models (Lundberg et al., 2020; Lundberg & Lee, 2017), for example, RF and XGB models (Hou et al., 2022; Wang et al., 2022), and directly capture non-linear interactive effects by calculating the marginal contribution of features to model outputs. The explanation is based on the concept of Shapley values from co-operative game theory, which assigns a fair contribution to each player in a coalition game. SHAP values determine the contribution of each feature to the prediction, considering both direct effect and interaction with other features. We used TreeSHAP method to examine the total effects (SHAP values), main effects (SHAP main values, independent effects of the factors) and interactive effects between two environmental factors (SHAP interaction values) (Wang et al., 2022). To obtain an overview of which features are most important for a model, we plotted the SHAP values of every feature for every sample. The plot sorted features by the sum of SHAP value magnitudes over all samples and used SHAP values to show the distribution of the impacts each feature had on the model output (Lundberg et al., 2020). Different colors represent the feature values (red high, blue low). Features with positive SHAP values positively affected foliar N/P, while those with negative values had negative effects on foliar N/P. The magnitude is a measure of how strong the effect is (Lundberg et al., 2020). We also took the mean absolute value of the SHAP values for each feature to obtain a standard bar plot (produces stacked bars for multi-class outputs). All SHAP values for each environmental factor were averaged as the mean absolute SHAP value to quantify the overall impact of the environmental factors on the foliar N/P and ranked in a descending order.

In the present study, the SHAP value of each observation and interactive SHAP values between two environmental factors were estimated based on the RF models through the "*shap*" Python package (https://github.com/slundberg/shap). The mean SHAP value of each factor or interaction between two environmental factors was estimated from the average of the absolute SHAP values of all observations (Lundberg et al., 2020; Lundberg & Lee, 2017).

Temperature and P_{CO_2} increases are common features under the future three Shared Socioeconomic Pathway (SSP) scenarios (Tollefson, 2020) as well as key variables affecting plant eco-physiological processes (Lukac et al., 2010; Way & Oren, 2010). Therefore, we took MAT and P_{CO_2} as important global change factors into account in this study to predict future foliar N/P during 2081–2100 under future SSP scenarios and to compare with the predictions based on RF model during the baseline period (1970–2000). Three future SSP scenarios were involved in this study: (1) SSP1-2.6, taking the sustainable road with low challenges to mitigation and adaptation; (2) SSP3-7.0, taking the rocky road with high challenges to mitigation and adaptation; (3) SSP5-8.5, taking the highway with high challenges to mitigation, low challenges to adaptation (Riahi et al., 2017). Since the number size of the measured data was small during 1970–2000 (about 200) at sampling site scale, which may inadequately represent the entire subtropical regions in China, bringing incommensurability between the measured foliar N/P during 1970–2000 and predicted foliar during 2081–2100. We thus predicted foliar N/P at the regional scale during 1970–2000 using the trained random forest models based on our dataset. MAT, T_{max}, T_{min}, MAP, VAP (to calculate VPD), PET, PS, and TS used to predict foliar N/P were calculated from monthly values of CRU TS4.05 (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.05/), [CO_2] were produced by averaging historical data (346 ppm) for the period of 1970–2000, and N_{dep} (dry and wet deposition) were extracted from MIROC-ES2L output prepared for CMIP6 (https://aims2.llnl.gov/search). Then, we predicted the foliar N/P of each plant functional type during 2015–2100 under each scenario using the same models. Except for MAT and P_{CO_2}, which were replaced by the value under each scenario during 2015–2100, all environmental factors were the same as the period of 1970–2000. Finally, we calculated the changing magnitudes of foliar N/P based on their values during 1970–2000 and 2081–2100. The differences in changes of foliar N/P among plant functional types were tested by one-way ANOVA and Tukey's HSD post hoc tests.

The RF and TreeSHAP algorithm were performed in Python software (version 3.10.7), and the other statistical analyses were conducted in R software (R version 4.0.2; R Development Core Team; https: //www.r-project.org/). Significant level was set at $p<.05$.

3 | RESULTS

3.1 | Temporal variation in foliar N/P and [P]

Foliar N/P increased and foliar [P] decreased significantly for the period of 1920–2010. Overall, foliar N/P of all samples increased 21.2%, from 18.9 ± 6.8 in the 1920s to 22.9 ± 8.5 in the 2000s (Figure 2a; Table S5). Foliar [P] of all samples decreased 23.1%, from $1.3 \pm 0.8\,\mathrm{g\,kg^{-1}}$ in the 1920s to $1.0 \pm 0.6\,\mathrm{g\,kg^{-1}}$ in the 2000s (Figure S1a; Table S5). At the species level, foliar N/P increased (either significantly or non-significantly) for all species over the past 90 years and foliar [P] decreased in 10 species and increased in the other two during 1920–2010 (Figures S2 and S3).

The changing rates of both foliar N/P and [P] differed significantly between leaf habits (Figure 2b; Figure S1b) and across plant functional types (Figure 2c; Figure S1c). Foliar N/P increased more in evergreen species (22.9%) than in deciduous species (16.9%) (Figure 2d,e; Table S5). The rate of increase in evergreen species was higher than that in deciduous species (Figure 2b,d,e); evergreen shrubs increased faster than evergreen trees, deciduous shrubs, and deciduous trees (Figure 2c–e). Foliar [P] decreased significantly in deciduous species (20.0%) but did not significantly in evergreen species (Figure S1d,e; Table S5). In addition, foliar [P] of deciduous shrubs decreased significantly (Figure S1d), in comparison with the non-significant decline in evergreen or deciduous trees and evergreen shrubs ($p>.05$, Figure S1d,e).

3.2 | Drivers of temporal changes in foliar N/P

Drivers of temporal changes in foliar N/P were divergent among plant functional types. For deciduous species, MAT, P_{CO_2}, and VPD were the top three drivers of foliar N/P changes, and their mean SHAP absolute values were 1.400, 0.852, and 0.530, respectively (Figure 3a,b). The impact ranges of MAT (from −3.867 to 5.717) and P_{CO_2} (from −3.847 to 5.868) were the largest (Figure 3a). For evergreen species, P_{CO_2}, N_{dep}, and MAT ranked top three among the environmental factors affecting foliar N/P, with their mean SHAP absolute values being 0.779, 0.608, and 0.548, respectively (Figure 3c,d). The higher mean absolute SHAP value and the larger impact range of SHAP values indicate the greater influence of the factor on foliar N/P; the distribution of SHAP value with a long trail to the left or right indicates that the factor has strong negative or positive effect on foliar N/P, respectively. The SHAP values of MAT and P_{CO_2} showed a wide range with a long right tail indicating larger contribution from higher MAT and P_{CO_2}. Thereinto, MAT and P_{CO_2} with high feature values (in red), primarily on the right side of the zero SHAP value, and positively influenced foliar N/P of both deciduous and evergreen species (Figure 3a,c); in contrast, VPD negatively affected foliar N/P of deciduous species (Figure 3a).

Considering the significant differences in foliar N/P between growth forms (Figure 2d,e), we further explored the drivers of the temporal changes in shrubs and trees (Figure S4). P_{CO_2} and MAT were the two major factors driving foliar N/P of both deciduous shrubs (Figure S4a,b) and deciduous trees (Figure S4e,f). PS, T_{max}, and MAP were the main drivers of foliar N/P of evergreen shrubs, and their mean absolute SHAP values (1.584, 0.991, and 0.825, respectively) were higher than those of the top three factors, that is, N_{dep}, MAT and P_{CO_2} (0.711, 0.593, and 0.577, respectively), affecting foliar N/P of evergreen trees (Figure S4c,d,g,h). The mean SHAP absolute values across the 10 environmental factors among plant functional types indicated that these factors explained more changes in foliar N/P of evergreen shrubs than those of deciduous shrubs, deciduous trees, and evergreen trees, with the SHAP values being 1.388, 1.128, 0.531, and 0.459, respectively (Figure S4).

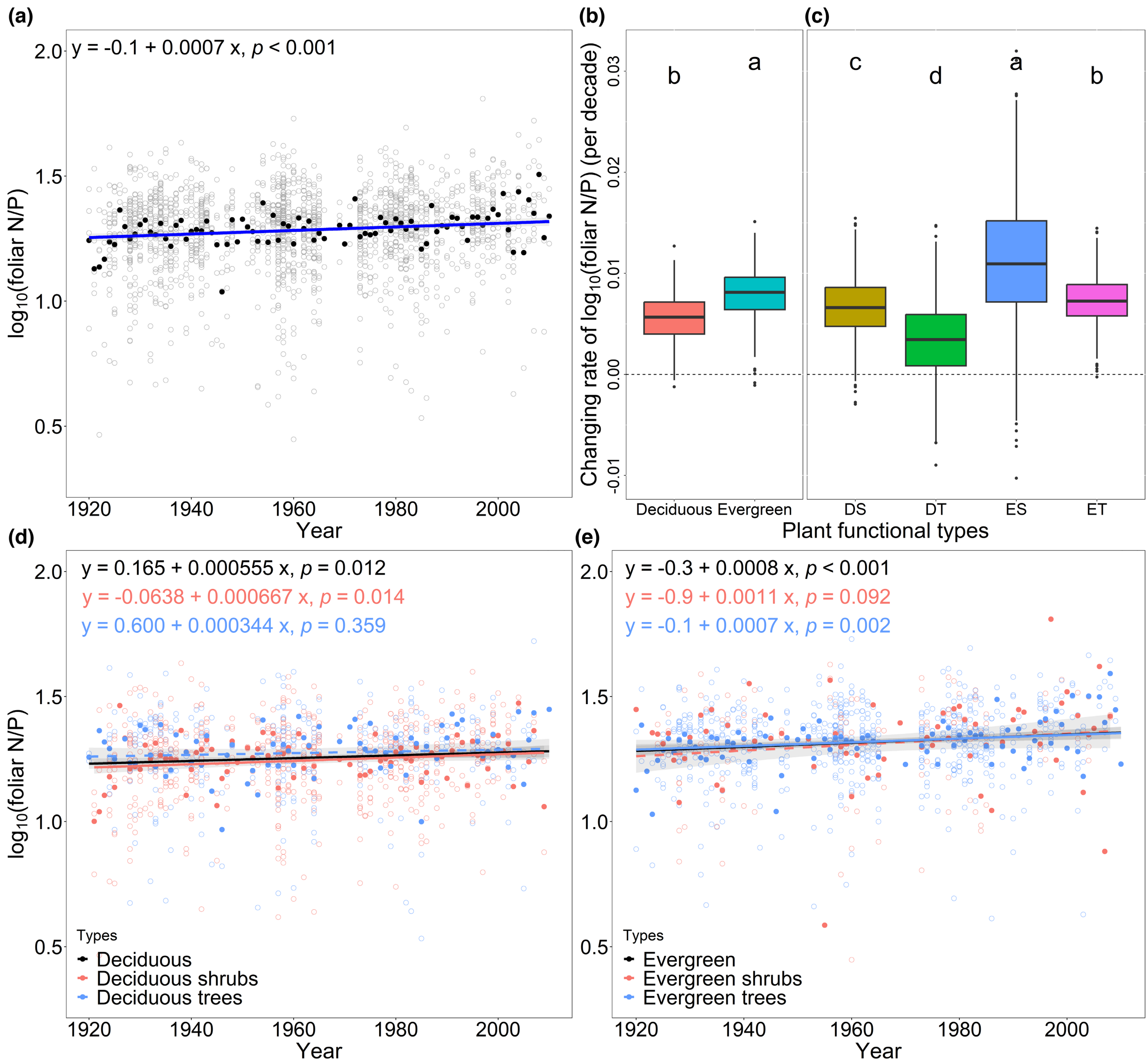

FIGURE 2 Temporal trends (a, d, e) of log-transformed foliar nitrogen to phosphorus ratios (N/P) for all samples and between different leaf habits (deciduous, evergreen) and growth forms (shrub, tree) during 1920–2010, and the changing rates (the bootstrapped regression slopes) of log-transformed foliar N/P between leaf habits (b) and among plant functional types (c). Symbols are individual samples (transparent dots) and averaged values for each year (non-transparent dots). Parameters at top-left corners are equations and *p*-values of the fitting lines on individual samples with 95% interval confidence (shaded area). The solid and dashed lines show significant and non-significant correlations, respectively, at $p < .05$. Different lowercase letters indicate significant differences among plant functional types at $p < .05$. DS, deciduous shrubs; DT, deciduous trees; ES, evergreen shrubs; ET, evergreen trees.

3.3 | Main and interactive effects of environmental factors on foliar N/P

The environmental factors showed main but not interactive effects on variations in foliar N/P (Figure S5), and the main effects differed among plant functional types (Figure 4; Figures S6 and S7). The plot of SHAP main effect values depict how a given variable impacts the foliar N/P of every sample (each dot), namely, how its independent effect on foliar N/P changes along its feature values. The SHAP main value of P_{CO_2} increased with increasing P_{CO_2}, indicating the positive effects of P_{CO_2} on foliar N/P (Figure 4a,b; Figures S6a,b and S7a,b). N_{dep} showed positive effects on foliar N/P of evergreen species (Figure 4d; Figure S7c,d) and deciduous shrubs (Figure S6c), but negative effects on N/P of deciduous trees (Figure 4c; Figure S6d), during the periods with relatively high N_{dep} (ca. >10 kg N ha^{-1} year^{-1}). The main effects of MAT on foliar N/P of deciduous as well as evergreen species and two functional types (deciduous shrubs and evergreen trees) were similar to those of P_{CO_2} (i.e., shifted from negative to positive) (Figure 4e,f; Figures S6e and S7f). The main effects of MAT on foliar N/P of

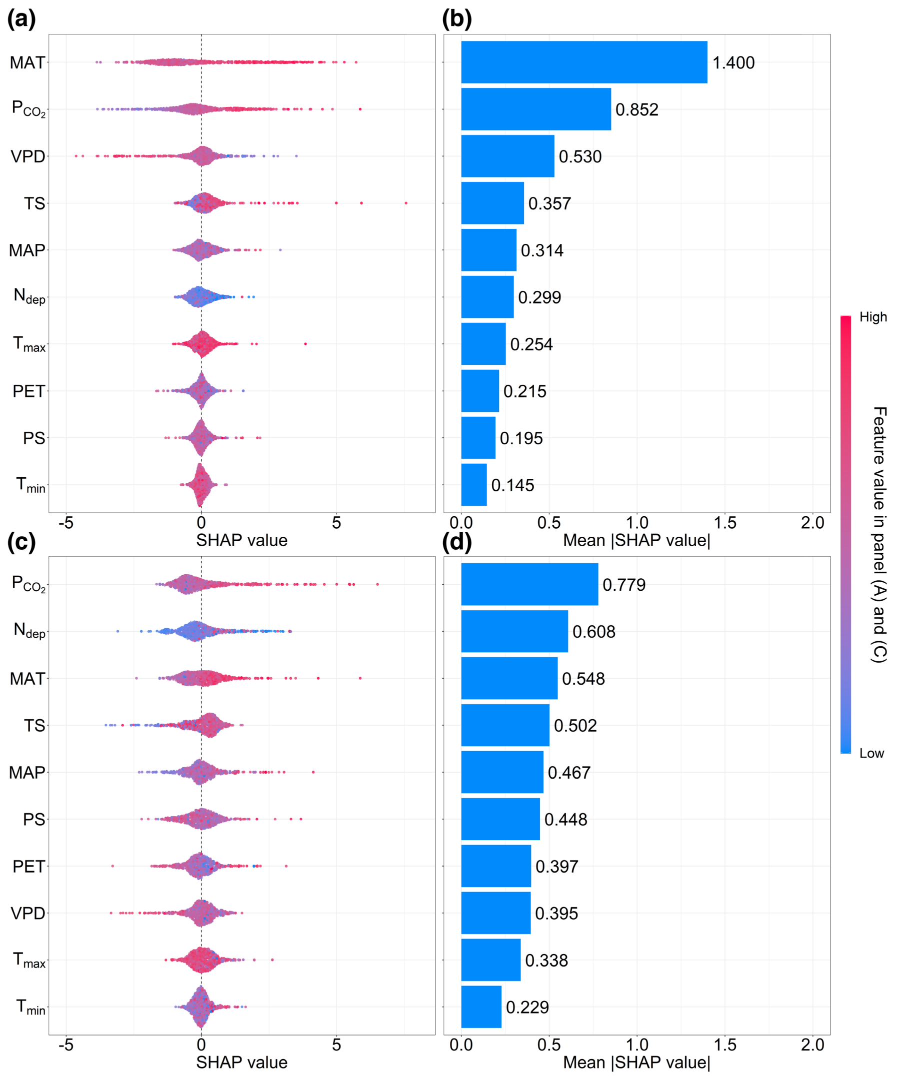

FIGURE 3 Total effects of environmental factors on foliar nitrogen to phosphorus ratios (N/P) for deciduous (a, b) and evergreen (c, d) species shown by summary plots of SHAP values and bar plot of the mean absolute SHAP values. MAP, mean annual precipitation; MAT, mean annual temperature; N_{dep}, atmospheric nitrogen deposition; P_{CO_2}, partial pressure of atmospheric CO_2; PET, potential evapotranspiration; PS, precipitation seasonality; T_{max}, annual maximum temperature; T_{min}, annual minimum temperature; TS, temperature seasonality; VPD, vapor pressure deficit.

evergreen shrubs shifted from negative to positive with the temperature threshold of 18°C (Figure S7e), and the negative main effects of MAT on foliar N/P of deciduous trees were found when temperature ranged from 14°C to 20°C (Figure S6f).

The SHAP main values of the factors associated with temperature and precipitation, for example, TS, T_{max}, T_{min}, MAP, PS, PET, displayed non-linear changes between leaf habits and across plant functional types (Figure 3g–r; Figures S6g–r and S7g–r). Specially, the main effects of PS on foliar N/P of evergreen shrubs shifted from positive to negative, with positive impact on foliar N/P under low PS and negative impact on foliar N/P under high PS (Figure S7k), while the opposite trend (shifted from negative to positive) was observed in the main SHAP values of T_{max} (Figure S7m). MAP with high feature values were primarily above the zero main SHAP value (Figure S7g), indicating their positive effects on foliar N/P of evergreen shrubs. The SHAP main effect values of VPD decreased with increasing VPD in both leaf habits (deciduous and evergreen species; Figure 3s,t), suggesting that the negative effects of VPD on foliar N/P increased as the atmosphere became drier. The same patterns occurred in shrubs and trees within deciduous species (Figure S6s,t), but not within evergreen species (Figure S7s,t).

3.4 | Future changes in foliar N/P

In predictions under future SSP scenarios with MAT and P_{CO_2} being taken into consideration, foliar N/P would be 6.1%–26.0% higher during 2081–2100 compared with 1970–2000 (Table 1). The increasing rates would be dependent on the SSP scenarios with the sustainable emission scenario (SSP1-2.6) always being the lowest (Figure 5), and the increasing magnitudes would also differ significantly between leaf habits (Figure S8a,c,e) and among plant functional types (Figure S8b,d,f). Deciduous species would increase more than evergreen species (Figure S8a,c,e), with greater changes, 12.9%, 17.7%, and 19.4% versus 6.1%, 7.9%, and 8.9%, under the scenarios of SS1-2.6, SSP3-7.0, and SSP5-8.5, respectively (Table 1). Between growth forms, the increasing magnitudes of trees' foliar N/P would always be larger than those of shrubs' foliar N/P (Figure S8b,d,f). However, deciduous species would still exhibit lower foliar N/P than evergreen species (Table 1), with deciduous shrubs having the smallest ratios (19.7, 20.4, and 20.7) among the plant functional types under SSP1-2.6, SSP3-7.0, and SSP5-8.5 scenarios (Table 1).

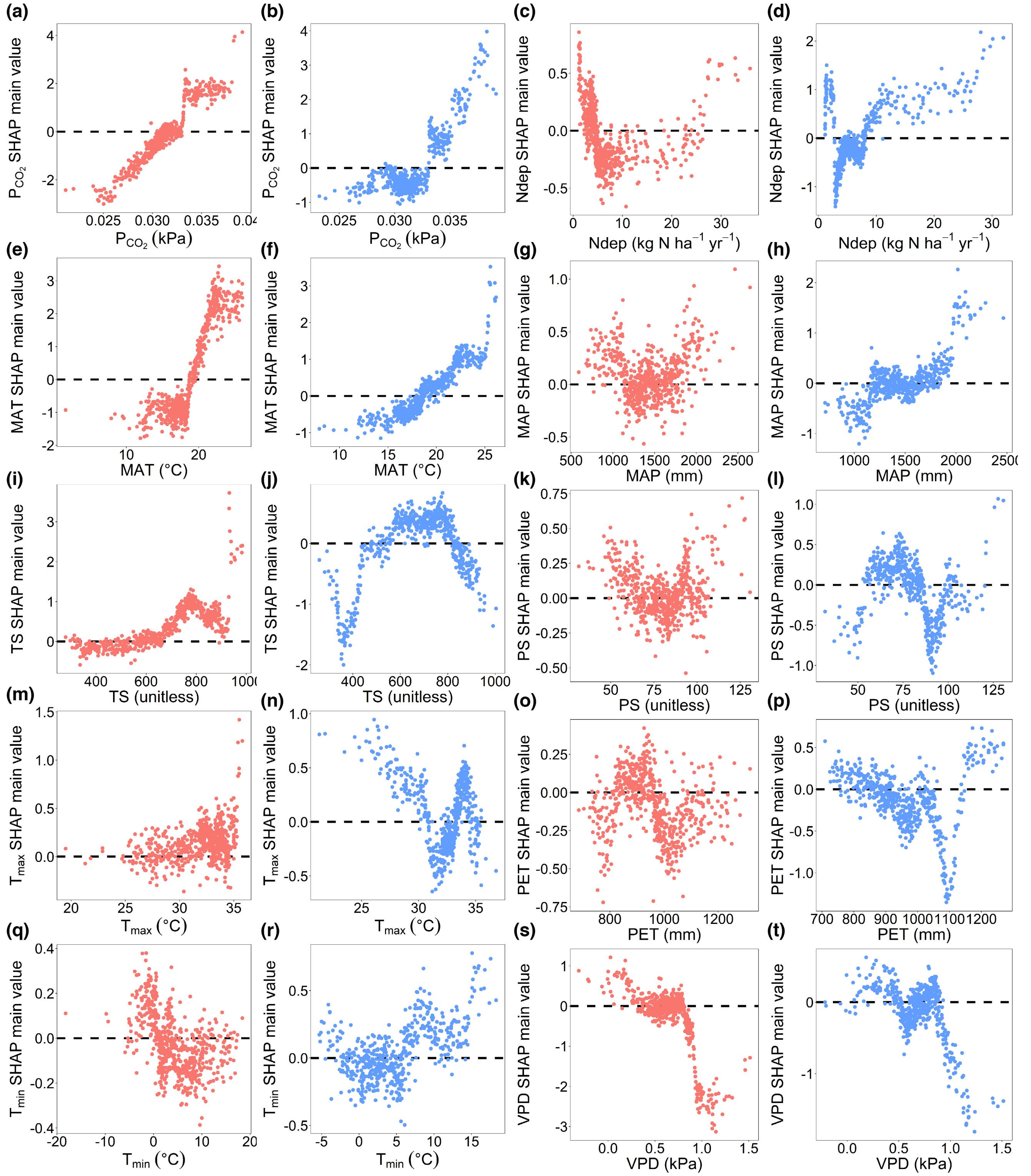

FIGURE 4 SHAP main effect values of major factors (a–t) on foliar nitrogen to phosphorus ratios (N/P) of deciduous (red dots) and evergreen species (blue dots). MAP, mean annual precipitation; MAT, mean annual temperature; N_{dep}, atmospheric nitrogen deposition; P_{CO_2}, partial pressure of atmospheric CO_2; PET, potential evapotranspiration; PS, precipitation seasonality; T_{max}, annual maximum temperature; T_{min}, annual minimum temperature; TS, temperature seasonality; VPD, vapor pressure deficit.

4 | DISCUSSION

We collected 1811 specimens of 12 widely distributed species, covering different plant functional types (deciduous and evergreen species, shrubs, and trees), to establish reliable long-term dynamics and driving factors of foliar N/P in subtropical forests of China. There was a significant generalized increase in foliar N/P among plant functional types over the past 90 years. However, the increasing rates

TABLE 1 Foliar nitrogen and phosphorus ratios (N/P) of different plant functional types during 2081–2100 under three future Shared Socioeconomic Pathway scenarios (SSP1-2.6, SSP3-7.0, SSP5-8.5) in which mean annual temperature and partial pressure of atmospheric CO_2 was taken into consideration. The increasing magnitudes (IM, %) of foliar N/P were calculated by comparing with the predicted foliar N/P during 1970–2000 using random forest model. Values are means ± standard deviations.

	2081–2100						
Functional type	**SSP1-2.6**	**IM (%)**	**SSP3-7.0**	**IM (%)**	**SSP5-8.5**	**IM (%)**	**1970–2000**
Deciduous species	21.0 ± 2.4	12.9	21.9 ± 1.4	17.7	22.2 ± 1.5	19.4	18.6 ± 2.5
Evergreen species	22.7 ± 1.5	6.1	23.1 ± 1.3	7.9	23.3 ± 1.3	8.9	21.4 ± 1.7
Deciduous shrubs	19.7 ± 2.2	8.8	20.4 ± 1.3	18.2	20.7 ± 1.3	14.4	18.1 ± 2.5
Deciduous trees	23.7 ± 2.8	18.5	24.9 ± 1.7	24.5	25.2 ± 1.7	26.0	20.0 ± 2.1
Evergreen shrubs	24.3 ± 1.8	7.5	24.8 ± 1.5	9.7	24.9 ± 1.4	10.2	22.6 ± 2.0
Evergreen trees	23.4 ± 1.9	9.9	24.1 ± 1.4	13.1	24.5 ± 1.5	15.0	21.3 ± 1.5

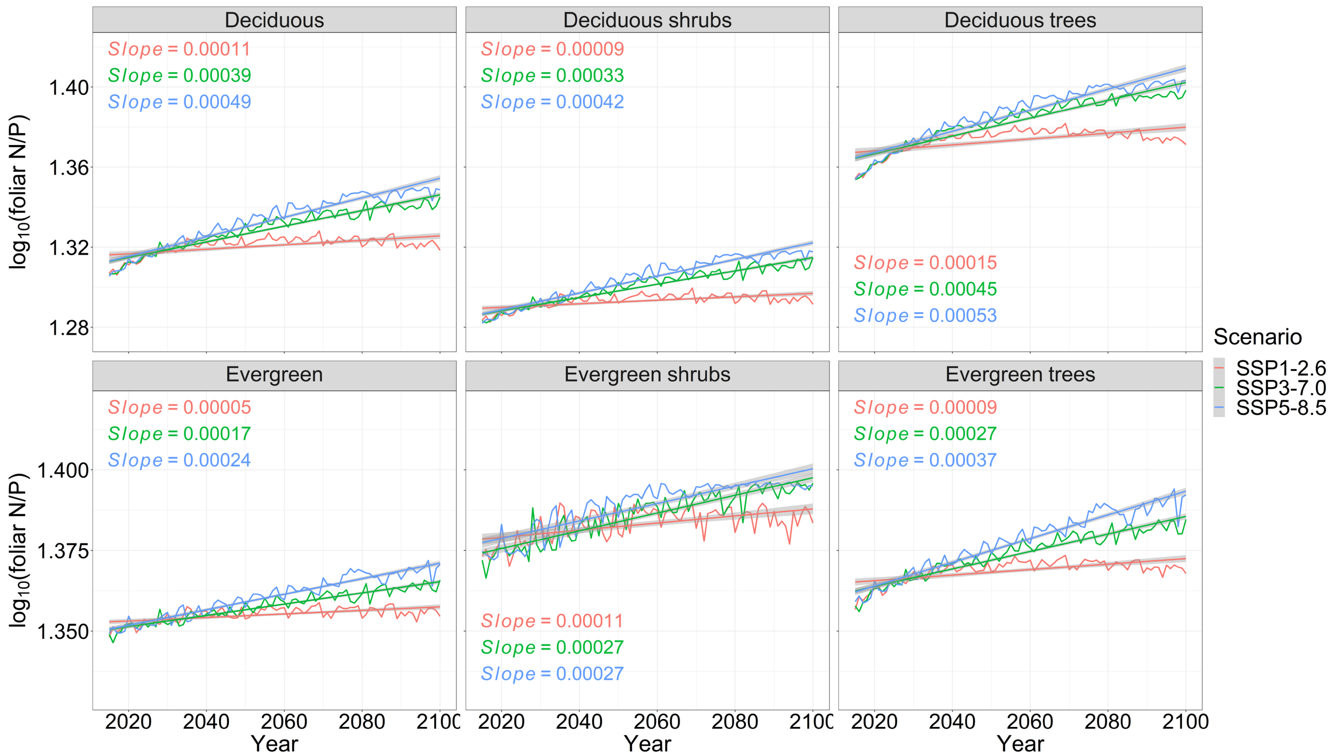

FIGURE 5 Temporal trends of log-transformed foliar nitrogen to phosphorus ratios (N/P) in different leaf habits and plant functional types from 2015 to 2100 under three future Shared Socioeconomic Pathways scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5) with mean annual temperature and partial pressure of atmospheric CO_2 being taken into consideration.

differed between evergreen and deciduous species in leaf habits and between shrubs and trees species in growth forms. Specifically, evergreen species, in particular evergreen shrubs, increased foliar N/P faster than deciduous species. We also identified different environmental factors driving foliar N/P among plant functional types. The environmental factors involved in this study explain the variation of foliar N/P in the studied subtropical forests well and provide a preliminary exploration to scientifically assess the dynamics of foliar N/P under global change.

As hypothesized, the significant increases in foliar N/P over a long-term period (past 90 years) in this study (Figure 2a) were similar to the trends in European forests over a short-term period (past 10–30 years) supported by a forest monitoring program (the International Co-operative Program on Assessment and Monitoring of Air Pollution Effects on Forests) (Jonard et al., 2015; Peñuelas et al., 2020; Talkner et al., 2015) and to the ones in a limited study in China's subtropical forest over only 3 years (1955, 1978, 2014) close to urban center (Huang et al., 2016). In contrast, herbarium specimens from African tropical forests which were subjected to high N deposition did not exhibit changes in foliar N/P over three different periods (1935–1938, 1951–1953, 2012–2013), possibly due to external P inputs leading to increases in leaf [P] (Bauters et al., 2020).

According to plant N versus P limitation theory (Güsewell, 2004), the increase in foliar N/P from 18.9 ± 6.8 to 22.9 ± 8.5 over the past nine decades, in particular the high foliar N/P (>20) after the 1990s (Table S5) in this study indicates that there is progressive N–P imbalance in China's subtropical forests and forest species are shifting toward increasing P limitation.

Foliar N/P of both evergreen and deciduous species (Table S5) in this study are much higher than the average in a global dataset (11.8) (Reich & Oleksyn, 2004), but unlike the close foliar N/P between evergreen and deciduous species (13.4 vs. 13.9) worldwide (Aerts, 1996). Furthermore, foliar N/P of evergreen species was much higher than that of deciduous species in our study (e.g., 25.2 vs. 20.7 in the 2000s; Table S5). The faster rate of increase of evergreen species than of deciduous species (Figure 2) suggests differential dynamics of foliar N/P between leaf habits with different chemical characteristics (Table S5). Foliar [N] and [P] and their ratios reflect the strategies of plants to resource acquisition and allocation as well as the effect of environment on N and P uptake and allocation (Elser et al., 2010). The results imply aggravated P limitation in subtropical forests and more intense N–P imbalance in evergreen species than in deciduous species, which agree with Zhang et al. (2005) and meet the strategy that deciduous species quickly return investment of nutrients in leaves, with short life span, high nutrient concentrations, and fast mass-based photosynthetic rates (Wright et al., 2004, 2005). Consequently, deciduous species may have greater resistance to P limitation associated with greater growth capacity than evergreen species do in subtropical forests under the impacts of global change.

Environmental factors driving variation in foliar N/P indeed differed among plant functional types (Figure 3; Figure S4). Inconsistently with our hypothesis, the major drivers showed little interaction on foliar N/P (Figure S5), similar to those on terrestrial C:N:P stoichiometry (Yue et al., 2017). The increasing P_{CO_2} and MAT were identified as the determinants affecting foliar N/P of deciduous species during 1920–2010 in subtropical forests, which is consistent with the findings in Mediterranean and temperate forests (Peñuelas et al., 2020). The impacts of P_{CO_2} and MAT on foliar nutrients are probably dependent on the differential responses of nutrient demand and supply (Tian et al., 2019). As a result of CO_2 fertilization, plant growth increases the nutrient demand (Tian et al., 2019). However, unlike foliar [N] which might be supplemented by high N deposition in subtropical forest (Tang et al., 2022), there is little P deposition, so availability depends on soil storage and recycling. The low plant-available soil P in subtropical China (Zhang et al., 2005), coupled with the decrease imposed by rising MAT (Hou et al., 2018), further aggravated plant N–P imbalance. An increase in temperature is usually accompanied by increase in VPD (Grossiord et al., 2020; Tang et al., 2022), but VPD showed negative effects on foliar N/P (Figure S6), which might be associated with the promotion of inorganic phosphate and organic P compounds from the soil solution to the root surfaces under the enhanced transpiration from rising VPD (Cernusak et al., 2011; Grossiord et al., 2020).

Foliar N/P of evergreen species was affected not only by P_{CO_2} and MAT, but also by N_{dep} (Figure 3). However, N_{dep} was the determinant of foliar N/P in trees rather than in shrubs (Figure S4), suggesting that foliar nutrients status in evergreen trees might be susceptible to increasing N deposition. This result is supported by the faster maximum photosynthetic rate of shrubs than that of trees under high N deposition in a subtropical forest (Zhang et al., 2023), suggesting greater plasticity of shrubs than trees in response to N_{dep}. Interestingly, N_{dep} had differential effects on foliar N/P between evergreen (positive, Figure S7d) and deciduous (negative, Figure S6d) trees, implying that evergreen trees are more likely to be negatively affected by P limitation than deciduous trees under increasing N deposition. The divergent responses of foliar N/P between evergreen and deciduous trees to N_{dep} may be the result of resource-conserving strategy of evergreen trees, as evidenced by their lower foliar [N], slower photosynthetic rates and longer leaf span (Warren & Adams, 2004). Given their longer leaf life span (Wright et al., 2005), evergreen trees might demand more N and P than deciduous trees especially under CO_2 fertilization (Tian et al., 2019). The negative effect of high N_{dep} on foliar N/P of deciduous trees in this study was surprising and might be ascribed to the accelerated P-cycling by increasing N_{dep} (Marklein & Houlton, 2012). Most deciduous species across the northeastern United States acquire sufficient P to counterbalance the increases in N availability under high levels of N_{dep}, leading to an increased foliar [P] and declined foliar N/P (Crowley et al., 2012). Deciduous trees may release more phosphatases under increasing N deposition and stimulate P mineralization, leading to lower N/P than evergreen trees (Chen et al., 2020; Keeler et al., 2009). The divergent responses of foliar N/P of different plant functional types to N_{dep} in this study suggest a progressive N–P imbalance in China's subtropical forest species and greater susceptibility to P limitation for evergreen trees under increasing N deposition.

Notably, evergreen shrubs increased foliar N/P with the fastest rate (Figure 2c–e) among plant functional types in the period of 1920–2010. Considering the largest impact range of SHAP values across the 10 environmental factors on evergreen shrubs (Figure S4), we inferred evergreen shrubs were most significantly influenced by global change. The variables relating to precipitation and temperature, that is, PS, T_{max}, MAP, MAT, and TS, ranked top among the factors (Figure S4). Excess or frequent precipitation may decline plant photosynthesis and decrease P uptake as shown by the positive effects of high MAP and low PS (Figure S7g,k) on foliar N/P, which is supported by the greater foliar N/P at moist compared with dry sites in temperate forests (Meier & Leuschner, 2014) and in wet than in dry seasons in tropical rain forests (Townsend et al., 2007). Although warming might stimulate plant uptake to P (Lie et al., 2022), abnormal TS can disrupt plant nutrient uptake (Lukac et al., 2010). In addition, extreme temperatures influence not only nutrient absorption via altering transpiration, photosynthesis, and respiration but also nutrient availability via changing enzyme activity and microbial mineralization (Rennenberg et al., 2006). Likewise, high T_{max} and MAT (Figure S7e,m) may inhibit P uptake by reducing plant physiological activities, leading to increase in foliar N/P. Therefore, the extremes and seasonality of temperature and precipitation should be taken into account when clarifying the impacts of environmental changes on plant nutrient demand and absorption (Lukac et al., 2010).

We predicted that foliar N/P would increase but with deciduous species having greater magnitudes than evergreen species under all three future SSP scenarios of MAT and P_{CO_2} (Figure S8a,c,e). The results imply that the variation in foliar N and P status between deciduous and evergreen species would be asynchronous under global warming and increasing P_{CO_2}. The higher foliar N/P of evergreens species than that of deciduous species implies more intense N–P imbalance would occur in evergreen species during 2081–2100 (Table 1). If global warming as a result of increasing P_{CO_2} continues, deciduous species may gain an advantage over evergreen species to maintain relatively favorable foliar N and P status, but this depends on adequate water availability. Compared with evergreen species, stem hydraulic conductivities of deciduous species are larger when sufficient water is available; however, evergreen species with small xylem vessels constrain assimilation when water is not limiting (Bowman & Prior, 2005; Eamus et al., 2000). Given the capacity of foliar stoichiometric homeostasis to predict plant species dominance, temporal stability, and responses to global change (Yu et al., 2015), the smallest increases in foliar N/P of deciduous shrubs (Table 1) at least implies that deciduous shrubs have greater plasticity than the other plant functional types under future global warming. The divergent shifts in foliar N/P among plant functional types may alter forest community composition and forest productivity, consequently decreasing the C sink of subtropical forest ecosystems (Wieder et al., 2015). Encouragingly, the lowest increases in foliar N/P suggests that it will more benefit plants to maintain foliar stoichiometric homeostasis under the sustainable emission scenario (SSP1-2.6, Figure 5).

Although the present study detected the dynamics of foliar N/P, identified their driving factors, and preliminarily predicted variation in foliar N/P in subtropical forests, more research is needed to determine the generality of the patterns, the mechanisms underlying the dynamics and where the limit or saturation of this dynamics is. Clarification of plant physiological and soil ecological process involved in environmental changes from the perspective of different plant functional types can further provide a basis for the maintenance of plant diversity and forest functioning under future global change.

AUTHOR CONTRIBUTIONS

Yuan Lai: Formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Songbo Tang:** Formal analysis; investigation; methodology; visualization; writing – review and editing. **Hans Lambers:** Writing – review and editing. **Peter Hietz:** Writing – review and editing. **Wenguang Tang:** Writing – review and editing. **Frank S. Gilliam:** Writing – review and editing. **Xiankai Lu:** Writing – review and editing. **Xianzhen Luo:** Investigation; writing – review and editing. **Yutong Lin:** Investigation. **Shu Wang:** Investigation. **Feiyan Zeng:** Resources. **Qi Wang:** Formal analysis; methodology; visualization; writing – review and editing. **Yuanwen Kuang:** Conceptualization; funding acquisition; investigation; project administration; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://doi.org/10.5061/dryad.dncjsxm56.

ORCID

Yuan Lai https://orcid.org/0000-0002-9332-2652
Songbo Tang https://orcid.org/0000-0001-9334-8089
Hans Lambers https://orcid.org/0000-0002-4118-2272
Peter Hietz https://orcid.org/0000-0002-0458-6593
Wenguang Tang https://orcid.org/0000-0003-1673-2364
Frank S. Gilliam https://orcid.org/0000-0002-5525-0766
Xiankai Lu https://orcid.org/0000-0001-7720-6048
Xianzhen Luo https://orcid.org/0000-0002-6629-9063
Yutong Lin https://orcid.org/0000-0001-6816-8422
Qi Wang https://orcid.org/0000-0002-1954-197X
Yuanwen Kuang https://orcid.org/0000-0003-0627-9519

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