





## ARTICLE

# Patterns and controls of foliar nutrient stoichiometry and flexibility across United States forests

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## Abstract

Plant element stoichiometry and stoichiometric flexibility strongly regulate ecosystem responses to global change. Here, we tested three potential mechanistic drivers (climate, soil nutrients, and plant taxonomy) of both using paired foliar and soil nutrient data from terrestrial forested National Ecological Observatory Network sites across the USA. We found that broad patterns of foliar nitrogen (N) and foliar phosphorus (P) are explained by different mechanisms. Plant taxonomy was an important control over all foliar nutrient stoichiometries and concentrations, especially foliar N, which was dominantly related to taxonomy and did not vary across climate or soil gradients. Despite a lack of site-level correlations between N and environment variables, foliar N exhibited intraspecific flexibility, with numerous species-specific correlations between foliar N and various environmental factors, demonstrating the variable spatial and temporal scales on which foliar chemistry and stoichiometric flexibility can manifest. In addition to plant taxonomy, foliar P and N:P ratios were also linked to soil nutrient status (extractable P) and climate, especially actual evapotranspiration rates. Our findings highlight the myriad factors that influence foliar chemistry and show that broad patterns cannot be explained by a single consistent mechanism. Furthermore, differing controls over foliar N versus P suggests that each may be sensitive to global change drivers on distinct spatial and temporal scales, potentially resulting in altered ecosystem N:P ratios that have implications for processes ranging from productivity to carbon sequestration.

## KEYWORDS

climate, element ratios, National Ecological Observatory Network (NEON), nitrogen, phosphorus, plant taxonomy, stoichiometric flexibility

## INTRODUCTION

Plant element stoichiometry, specifically the relative tissue contents of carbon (C), nitrogen (N), and phosphorus (P), influences foundational ecosystem

properties such as C and nutrient-use efficiency, net primary production (NPP), and decomposition rates, among other processes (Blanes et al., 2013; Güsewell, 2004; Koerselman & Meuleman, 1996; Manzoni et al., 2012; Peng et al., 2017; Richardson et al., 2005).

Foliar stoichiometry is influenced by resource availability, climate conditions, plant growth form, taxonomy, and evolved nutrient-use strategies, all of which can be relevant at different biological scales ranging from individual plants to entire ecosystems (Ågren, 2008; McGroddy et al., 2004; Sardans et al., 2011; Sardans & Peñuelas, 2014). Yet, the extent to which plant stoichiometry is fixed versus flexible, and the spatial and temporal scales at which stoichiometric flexibility may manifest, are not well understood.

Ultimately, stoichiometric flexibility—the ability of organisms to adjust the proportions of elements in their tissues as resource availability shifts—underpins ecosystem responses to global changes, especially those that alter the availability of resources such as N and CO<sub>2</sub> (Sistla & Schimel, 2012). In particular, stoichiometric flexibility represents plants' ability to modify their tissue chemistry to better adapt to their resource environment. Reflecting this critical importance, the magnitude of foliar stoichiometric flexibility strongly influences projected terrestrial C cycle responses to climate change (Meyerholt & Zaehle, 2015; Zhu et al., 2020). Thus, understanding the drivers of plant C:N:P stoichiometry and stoichiometric flexibility, and the temporal and spatial scales at which they are relevant, is a crucial endeavor. While stoichiometry of all plant tissues (e.g., leaves, wood, and roots) has potentially important implications for ecosystem function, foliage is likely to be especially relevant given its short turnover time, large nutrient pool size, and direct relationship with multiple key aspects of physiological activity.

Numerous analyses have identified patterns in global foliar chemistry. On average, foliar N and P concentrations tend to increase with increasing latitude (e.g., from the tropics to the polar regions) (Han et al., 2005; McGroddy et al., 2004; Reich & Oleksyn, 2004). Average foliar P concentrations typically increase more than N concentrations, leading to a relative decrease in foliar N:P from low to high latitudes. Several hypotheses have been proposed to explain these patterns. First, global-scale patterns of foliar chemistry may be driven by plant physiological responses to climate, particularly temperature. In relatively cold, high-latitude sites, declining enzymatic efficiency requires increased investment into N- and P-rich compounds in plant foliage to support metabolism (Kerkhoff et al., 2005; Reich & Oleksyn, 2004). Evidence for this hypothesis, known as the “Temperature Physiology Hypothesis,” includes correlations between temperature and foliar P at the global scale (Reich & Oleksyn, 2004). Furthermore, temperature-adjusted growth rates of mangrove trees across tropical and temperate regions (27° N to 36° S) correlate with site mean annual temperature, suggesting that plants may scale up growth rates in colder climates with shorter growing seasons, presumably requiring higher

concentrations of tissue N and P (Kerkhoff et al., 2005; Lovelock et al., 2007).

Although the “Temperature Physiology Hypothesis” can explain global patterns of foliar nutrient concentrations, it does not correctly predict patterns of foliar nutrient stoichiometry. Due to relatively greater P requirements in plants with higher growth rates, the “Temperature Physiology Hypothesis” predicts declines in leaf N:P ratios with decreasing latitude, the opposite of observed patterns (Reich & Oleksyn, 2004). Incorporating precipitation into this hypothesis can help to explain patterns of foliar N:P stoichiometry. Meta-analyses of manipulative experiments show that foliar N:P is inversely related to rainfall (Yuan & Chen, 2015; Yue et al., 2017), perhaps reflecting relatively high ecosystem N losses (Alvarez-Clare & Mack, 2011; Schuur & Matson, 2001). Similarly, C:nutrient ratios declined with increasing rainfall over a climate gradient in the Mediterranean (Sardans et al., 2011). Because of the potential role of precipitation in addition to temperature in influencing foliar stoichiometry, hereafter we refer to this hypothesis as the “Climate Physiology Hypothesis.”

Next, foliar chemistry patterns may reflect broad patterns in soil resource availability. Low-latitude (tropical) soils tend to be relatively highly weathered (Palm et al., 2007), thus low in P relative to temperate forest soils (Reed et al., 2011; Walker & Syers, 1976), which could explain both the relative decline in foliar P and increase in N:P in tropical versus high-latitude ecosystems (McGroddy et al., 2004; Reich & Oleksyn, 2004; Richardson et al., 2005). This explanation, hereafter referred to as the “Soil Nutrient Hypothesis,” has been supported by a meta-analysis comparing leaf traits to soil nutrients and climate variables, which found that soil N and P availabilities were better predictors of leaf traits, especially leaf nutrient concentrations, than climate (Ordoñez et al., 2009). Furthermore, P limitation—as indicated by P use efficiency, foliar P resorption, and the N:P of resorption—declines with increasing latitude (Lovelock et al., 2007; McGroddy et al., 2004; Reed et al., 2012; Vitousek, 1982). Manipulative experiments and natural gradient studies also provide support for the “Soil Nutrient Hypothesis.” Numerous fertilization experiments have shown that foliar N and P increase (and C:nutrient ratios decrease) in response to fertilization with the corresponding nutrients (Ostertag & DiManno, 2016; Sistla et al., 2015; Vitousek, 1998; Yang et al., 2011; Yuan & Chen, 2015; Yue et al., 2017). Correlations between soil and foliar nutrients have also been observed across natural gradients of soil nutrient availability, with weaker effects of increased soil nutrients on foliar N compared with foliar P (Massmann et al., 2021; Perakis & Sinkhorn, 2011; Richardson et al., 2005).





Species-specific patterns in leaf physical (e.g., specific leaf area) and chemical traits have been noted in numerous studies (Adams et al., 2016; He et al., 2010; Wright et al., 2004), reflecting differing evolutionary strategies of plant resource investment. These taxonomic (e.g., plant family, genus, and species) controls over foliar stoichiometry are captured in a third hypothesis, the “Species Composition Hypothesis.” Within a particular biogeochemical environment, coexisting plant species often exhibit contrasting foliar stoichiometry (Sardans & Peñuelas, 2014), potentially reflecting different plant resource economic strategies. Plant species also differ in their degree of foliar stoichiometric flexibility in response to changes in nutrient availability (Yu et al., 2011). Globally, the broad decline in foliar N:P with increasing latitude noted in Reich and Oleksyn (2004) is not observed uniformly in all plant families, indicating a role of plant taxonomy in controlling tissue chemistry response to environmental conditions (Tian et al., 2019). Across the tropics, foliar N is most strongly explained by plant taxonomy, rather than soil chemistry or climate (Asner et al., 2014; Townsend et al., 2007). However, the relative importance of taxonomy compared with environmental factors, namely climate and soil properties, in controlling foliar chemistry is not well understood. Reich and Oleksyn (2004) concluded that variation in the biogeography of plant species types and traits only played a small role in global patterns of foliar N and P. Additionally, closely related species can exhibit divergent stoichiometries, and respond differently to environmental conditions (Yang et al., 2015). While tissue chemistry across climate and soil gradients does appear to be influenced by plant taxonomy, it may be more strongly controlled by soil resource availability (Hogan et al., 2021; Richardson et al., 2005), suggesting hierarchical controls over foliar stoichiometry that could vary across spatial and temporal scales.

Previous research suggests three plausible mechanisms of control over foliar stoichiometry patterns: climate, soil nutrients, and plant taxonomy. These mechanisms are not necessarily mutually exclusive, and interactions among them may be important. For example, plant species that produce tissue with lower concentrations of N and P may be evolutionarily selected for in environments with relatively low nutrient availability due to a growth advantage (Kerkhoff et al., 2005; Sardans & Peñuelas, 2014), suggesting an interaction between taxonomic and edaphic controls. Studies that have tested multiple mechanisms at once tend to find evidence supporting multiple hypotheses. A study in a New Zealand temperate rainforest toposequence found that both soil chemistry and shifts in plant community composition across sites contributed to variation in foliar

N:P ratios (Richardson et al., 2005). Similarly, a meta-analysis found significant interactions between climate and soil nutrient variables in influencing foliar traits, including foliar chemistry (Ordoñez et al., 2009), suggesting that multiple mechanisms may be responsible for observed gradients in foliar chemistry and stoichiometry.

Despite the possibility that multiple interacting mechanisms could influence broad patterns of foliar chemistry, the relative importance of these three controls across different spatial and temporal scales is not well understood. This partially arises from the rarity of paired observations of foliar and soil chemistry. Furthermore, temperature and soil nutrient resources tend to covary, with warm, wet tropical ecosystems having relatively nutrient-poor soils compared with cool, dry temperate and boreal ecosystems. This relationship makes it difficult to differentiate the effects of soil nutrients from the effects of climate when soil nutrients are not directly measured and are instead inferred from latitude and ecosystem type. Also, integrating knowledge from global-scale analyses with results of regional and manipulative studies is challenging, especially because stoichiometric flexibility can manifest on multiple scales ranging from individual plants to entire ecosystems (Sistla & Schimel, 2012). Thus, the mechanisms governing foliar stoichiometry at different levels of biological organization remain unclear.

The recent establishment of the National Ecological Observatory Network (NEON), a set of long-term ecological research sites spanning a broad range of ecosystem types across the United States, provides an opportunity to test these hypotheses, because NEON collects paired foliar chemistry and soil nutrient data (total N, extractable N and P, and N mineralization rates) across a wide range of climatic conditions (Hinckley et al., 2016). Furthermore, the presence of common plant species across multiple NEON sites provides an opportunity to examine intraspecific flexibility in foliar chemistry. Together, these data allow us to explore controls over foliar stoichiometry at both a site and species level in the context of these three previously established hypotheses.

## MATERIALS AND METHODS

### Data collection

Foliar and soil chemistry data from all NEON forested terrestrial sites were obtained from the NEON data portal in January 2021 (National Ecological Observatory Network [NEON], 2021a, 2021b, 2021c). Sites represented a wide variety of biomes from tropical rainforests to boreal forests and were located between 18° N and 68° N



latitude (Appendix S1: Figure S1, Table S1). Altogether, 1076 foliar chemistry (C, N, and P concentration) samples representing 164 woody and herbaceous plant species at 47 terrestrial sites were accessed from the “Plant foliar traits” data product (DP1.10026.001). Foliar data were obtained from one collection bout per site conducted during the typical period of peak greenness at each site between 2016 and 2019. Within NEON sites, foliar samples were collected from plots within the NEON eddy flux tower airshed as well as plots distributed across the landscape. The number of plots sampled per foliar sample collection bout ranged from 5 to 22, with an average of 15 plots sampled per foliar collection. Foliar samples were collected as described in the NEON Terrestrial Observatory System Science Design for Terrestrial Biogeochemistry (Hinckley et al., 2016). In this design, woody plants were selected for sampling in order to provide a representative sample of canopy coverage. In plots with herbaceous plants present, foliage was collected via clip strips, with multiple species represented in a single foliage sample. The number of species sampled within a plot ranged from 1 to 6, with an average of 1.9 species sampled per plot. The number of foliar samples collected per plot ranged from 1 to 6, with an average of 2.2 foliar samples collected per plot.

Bulk soil C, total N, and extractable inorganic N (ammonium  $[\text{NH}_4^+] + [\text{NO}_3^-]$  concentrations, and net N mineralization rates) from soil samples 0 to 30 cm depth were accessed from the “Soil physical and chemical properties, periodic” data product (DP1.10086.001). Periodic soil collection data represent three sets of soil cores per plot, with up to 10 plots sampled per site, with one to two sampling bouts conducted per site between 2014 and 2019. Bulk soil P from 0 to 30 cm depth data was not collected during the periodic sampling bouts, so extractable P data were instead accessed from the “Soil physical and chemical properties, distributed initial characterization” data product (DP1.10047.001). Soil initial characterization data were obtained from one soil pit per plot, with 10–34 plots sampled per site. Because the presence and relative depths of soil organic and mineral horizons varied both within and among sites, we chose to analyze bulk soil data from 0 to 30 cm depth in order to estimate nutrient pools potentially available to plants, as has been done in similar studies (Ordoñez et al., 2009).

In the NEON experimental design, soil and foliar chemistry collections were not necessarily co-located within a site. In order to maximize usable, representative data, we used all soil and foliar data available within a site, including foliar data collected from plots lacking soil data and vice versa. Overall, out of 483 total plots, both soil and foliar samples were collected in 284 plots. Within a site, the number of plots with both soil and foliar data

collected ranged from 1 to 11, with an average of 8.9 plots having both soil and foliar data within a site. We discarded NEON foliar and soil chemistry data that did not meet NEON’s quality assurance standards, and calculated mean values for laboratory technical replicates.

Mean annual temperature (MAT) and precipitation (MAP) at each site were included in the NEON site metadata. Actual evapotranspiration (AET) and aboveground NPP data for each site were accessed using the EarthData APPEARS tool. Although eddy flux towers are installed at all NEON sites, fully processed flux-based gross primary productivity (GPP) and NPP data are not currently available; hence MODIS NPP values were used instead. Briefly, MODIS AET is calculated using the Penman–Monteith equation with meteorological and vegetation property data as inputs (Mu et al., 2011; Running et al., 2021). MODIS NPP is estimated by subtracting maintenance respiration estimates from remotely sensed absorbed photosynthetically active radiation with a biome-specific conversion efficiency parameter (Running et al., 2015). Site AET and NPP values used in this analysis represent the average of annual MODIS values from 2005 to 2020.

## Statistical analyses

To analyze the effect of among-site differences in climate and soil chemistry on foliar stoichiometry (testing the “Climate Physiology Hypothesis and the Soil Nutrient Hypothesis,” respectively), average values of foliar chemistry (N concentration [%], P concentration [%], N:P ratio, C:N ratio, and C:P ratio) were calculated for each site. Arithmetic means were calculated for foliar nutrient concentrations, while geometric means were calculated for stoichiometric ratios, in order to reduce bias (Isles, 2020). Because the NEON sample collection methodology took canopy coverage into account, we did not perform any further weighting of foliar chemistry data. We then used simple linear regressions to test the effects of climate and/or soil variables of interest (latitude [°], MAT [°C], MAP [mm/year], AET [mm/year], NPP [ $\text{kg C m}^{-2} \text{ year}^{-1}$ ], total soil N concentration [%], soil N mineralization rate [ $\mu\text{g N g}^{-1} \text{ dry soil day}^{-1}$ ], and soil extractable P concentration [ $\text{mg P kg}^{-1} \text{ soil}$ ]).

To determine the relative importance of site conditions versus plant taxonomy in driving foliar traits (testing the “Species Composition Hypothesis” against the other two), nested mixed linear models were constructed using all foliar data points. Site and nested family, genus, and species (i.e., taxonomy) were both treated as random effects, and variance was partitioned between site and taxonomic effects (Asner et al., 2014).





To determine the relative importance of climate and soil variables on foliar N, P, C:N, N:P, and C:P ratios (testing the “Climate Physiology Hypothesis and the Soil Resource Hypothesis”), we used a random forest modeling approach in which thousands of correlation trees were used as a basis for ensemble predictions (Pal, 2005). Each foliar chemistry variable was independently modeled with the same site-averaged climate and soil variables as above used as predictor variables. Random forest models were run for 10,000 iterations—the minimum number of iterations yielding stable results between model runs—using the *party* R package (Hothorn et al., 2006; Hothorn & Zeileis, 2015). Variable importance was determined by the mean decrease in accuracy resulting from the exclusion of each predictor variable, adjusting for correlations between predictor variables (Strobl et al., 2008).

To examine the sensitivity of foliar chemistry to environmental gradients at the species level, we quantified variation in foliar chemistry within individual plant species present at five or more sites; these included: *Acer rubrum*, *Quercus alba*, *Quercus rubra*, *Liriodendron tulipifera*, and *Liquidambar styraciflua*. The *n* of each species-site combination ranged from 2 to 12. We used a one-way ANOVA for each foliar chemistry variable and species combination, with site as the dependent variable. If the ANOVA results indicated significant among-site differences in a trait within a species, we performed simple linear regressions on the foliar chemistry data within each species against the same climate and soil variables noted above.

## RESULTS

Sites were located between 18° N and 68° N latitude and experienced a wide range in environmental conditions (Appendix S1: Figure S1, Table S2). Mean annual temperature ranged from −4 to 25°C and MAP ranged from 177 to 2685 mm/year. Mean AET ranged from 129.9 to 1672.2 mm/year, and mean annual NPP ranged from 0.1 to 1.6 kg C m<sup>−2</sup> year<sup>−1</sup>. Sites also exhibited a wide range in soil nutrient availability (Appendix S1: Table S3). Soil C concentrations ranged from 0.2% to 29.7%, soil N concentrations ranged from 0.03% to 1.48%, C:N ratios ranged from 5.4 to 34.1 (mass: mass), N mineralization rates ranged from 0.01 to 1.04 μg N g<sup>−1</sup> soil day<sup>−1</sup>, and soil extractable P contents ranged from 2.86 to 123.19 mg P kg<sup>−1</sup> soil (all values for 0–30 cm depth).

Across the NEON sites, site-averaged foliar N ranged from 0.85% to 3.01% and foliar C:N ratios ranged from 14.5 to 52.3. Neither site-averaged foliar N nor C:N ratios exhibited a significant latitudinal pattern (Figure 1a,b).

Site-averaged foliar P ranged from 0.07% to 0.34% and increased significantly with increasing latitude (Figure 1c). Site-averaged foliar C:P ratios ranged from 124 to 904 and N:P ratios ranged from 5.6 to 24.1; both were significantly negatively correlated with latitude (Figure 1d,e).

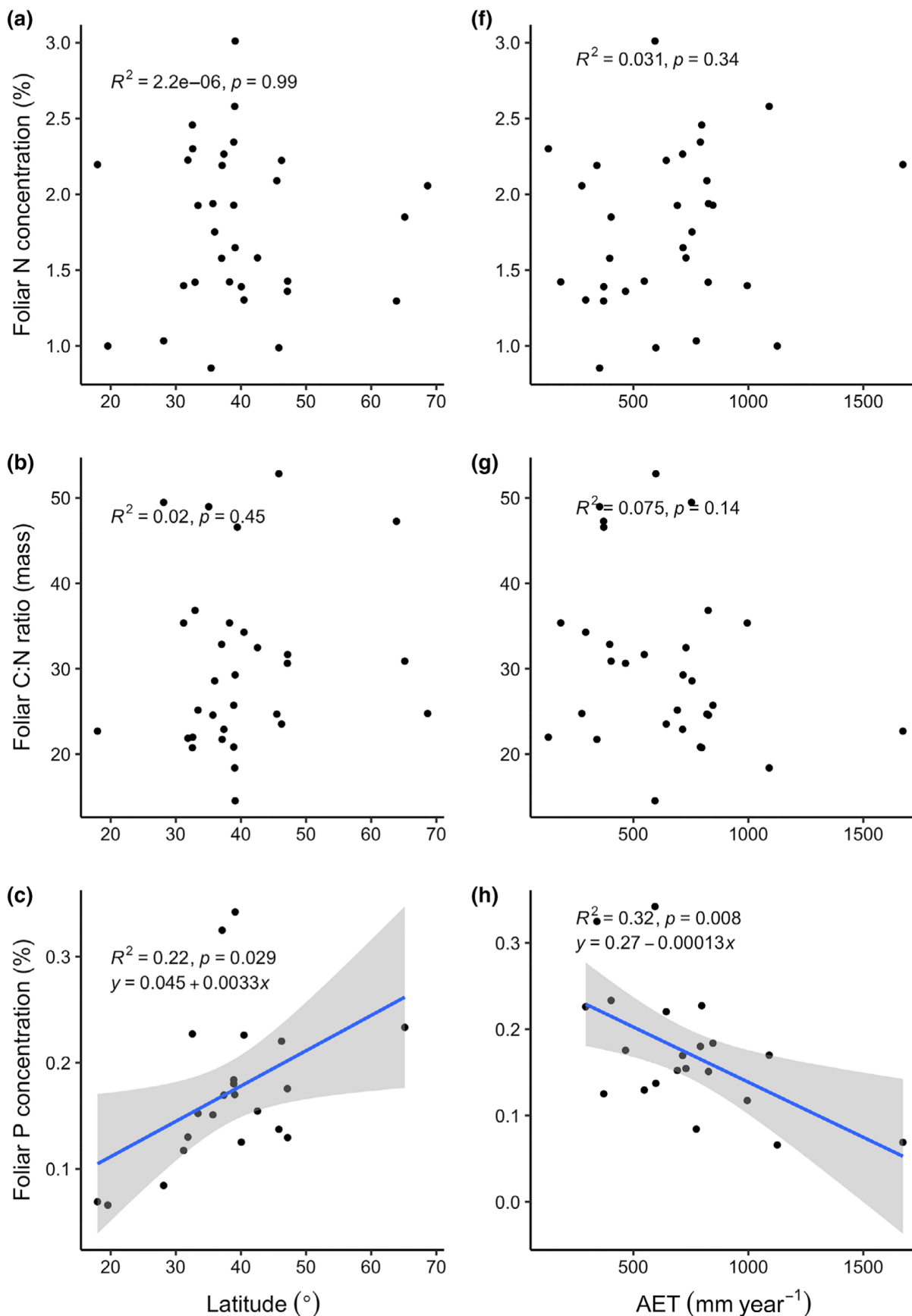
Site-averaged foliar P concentrations were negatively correlated with AET (Figure 1h; Table 1), NPP, MAP, and soil N concentration, and positively correlated with soil extractable P (Figure 2b). Site-averaged foliar N:P was positively correlated with AET (Figure 1j), NPP, MAT, soil N concentration, and soil N mineralization rate (Figure 2c), and negatively correlated with soil extractable P (Figure 2d). Site-averaged foliar C:N was negatively correlated with soil N mineralization rate. Site-averaged foliar C:P was positively correlated with AET (Figure 1i), NPP, MAP, soil N concentration, and negatively correlated with soil extractable P (Table 1).

The nested random effects mixed model approach to variance partitioning revealed that across all foliar samples, taxonomy (family, genus, and species as a nested random effect) was related to the largest proportion of the variance in foliar N, P, C:N, and C:P ratios (55%–69%; Figure 3; Appendix S1: Table S4), but not foliar N:P ratios. Taxonomy generally was related to a greater share of the variance for N traits compared with P traits. However, foliar N:P variance was not strongly related to either taxonomy or site, but was instead mainly related to model residuals (Figure 3).

We then used random forest modeling followed by variance importance analysis to determine whether specific environmental variables were related to among-site differences in all foliar chemistry data points (i.e., not site-averaged). The environmental variable most strongly related to foliar N and C:N was soil N mineralization rate (Figure 4a,b). Soil extractable P and AET were the independent variables most strongly related to foliar P and N:P (Figure 4c), and MAP was the independent variable most strongly related to foliar C:P (Figure 4d). Similarly, the independent variable most strongly related to foliar N:P was AET (Figure 4e). In general, climate variables tended to be most strongly related to P, N:P, and C:P, consistent with the results of our site-level linear regressions. By contrast, although site-averaged foliar N and C:N were largely not correlated with soil chemistry, our random forest modeling analyses indicated that soil variables were related to foliar N and C:N in individual plants.

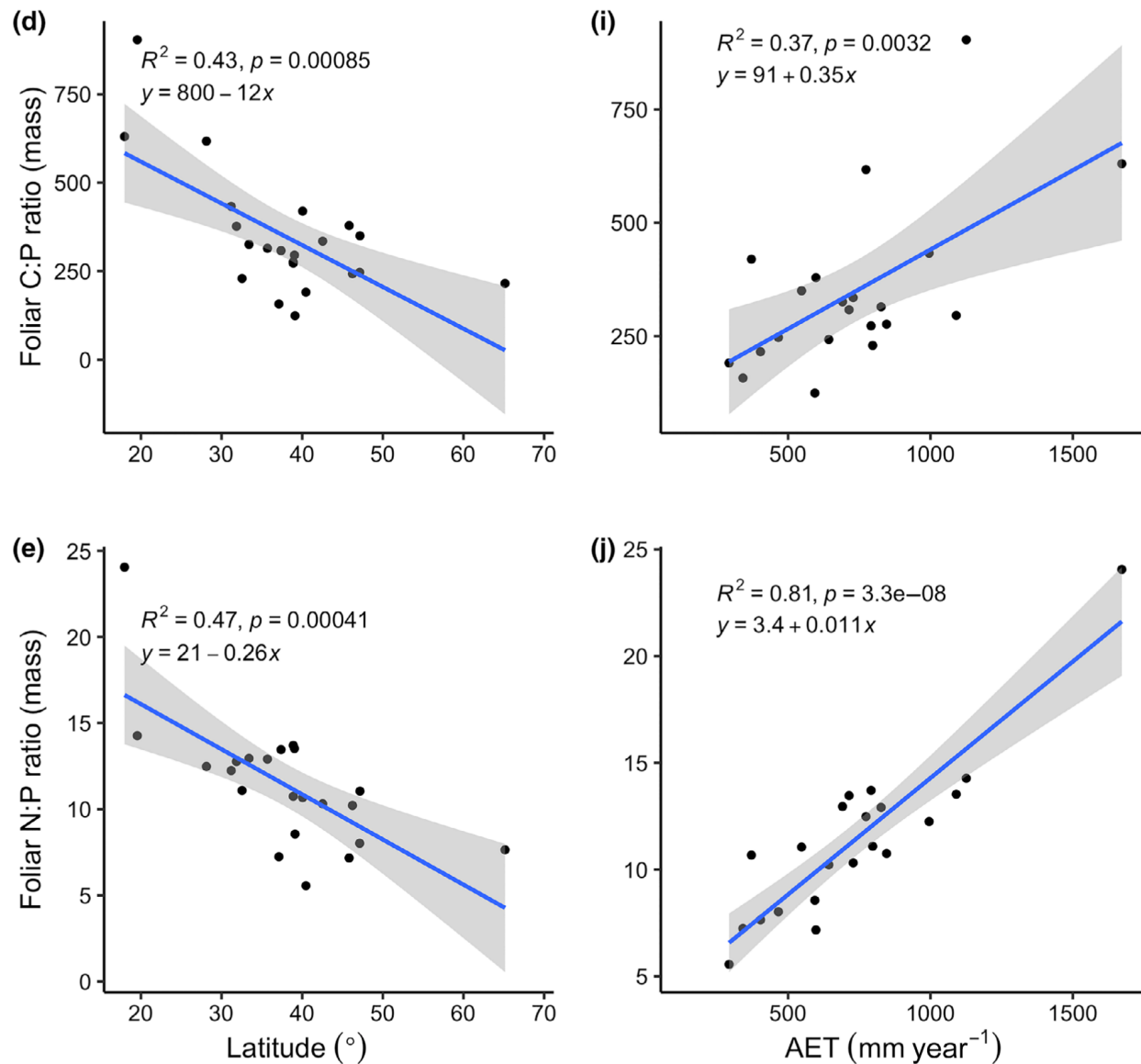
To examine intraspecific flexibility in foliar chemistry, we focused on five widely distributed tree species: *Acer rubrum*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Quercus alba*, and *Quercus rubra*. Within individual tree species, foliar N exhibited significant within-site and





**FIGURE 1** Site-averaged foliar N concentration (a, f), C:N ratio (b, g), P concentration (c, h), C:P ratio (d, i), and N:P ratio (e, j) plotted against latitude (left column) and actual evapotranspiration rates (AET) (right column). Blue lines represent statistically significant simple linear regressions and gray shading represents the 95% confidence intervals. Regression equations,  $R^2$  values, and  $p$ -values were calculated using simple linear regression.





**FIGURE 1** (Continued)

among-site variability (Figure 5). Individual species exhibited up to a two-fold range in foliar N value within a single site, and all species studied displayed significantly different foliar N and C:N values among sites (Appendix S1: Table S5). Furthermore, despite the lack of correlation between site-averaged foliar N and latitude or any climate or soil variables, some patterns were detected at a species-specific level (Appendix S1: Tables S6–S10). There were significant negative correlations between evapotranspiration and foliar N concentration in *A. rubrum*, *L. styraciflua*, *L. tulipifera*, and *Q. alba*, and significant positive correlations between soil N mineralization rates and foliar N in *L. tulipifera* and *Q. alba*. Interestingly, there was a negative correlation between soil N mineralization rates and foliar N in *L. styraciflua*. There were also significant negative correlations between soil extractable P and foliar N in *L. styraciflua*,

*L. tulipifera*, and *Q. rubra*. By contrast, intraspecific foliar P and C:P did not differ significantly among sites (Appendix S1: Table S5), although within-site intraspecific foliar P varied by as much as three-fold (Appendix S1: Figure S2). Foliar N:P ratio was only significantly different among sites in *L. tulipifera* (Appendix S1: Table S5).

## DISCUSSION

We tested three possible mechanisms to explain large-scale variation in plant foliar chemistry: the “Climate Physiology Hypothesis,” the “Soil Nutrient Hypothesis,” and the “Species Composition Hypothesis.” Our results show that different mechanisms exert control over among-site patterns of foliar N versus foliar P, with



**TABLE 1** Simple linear regression statistics showing correlations between site-average foliar chemistry (foliar N, P, N:P, C:N, and C:P ratios) and site environmental conditions.

		Independent variable								
								Soil N mineralization rate	Soil extractable P	NPP
Foliar trait	Statistic	Latitude	AET	MAT	MAP	Soil N	Soil C			
Foliar N	$R^2$	0	0.03	0.02	0.05	0	0.01	0.04	0.03	0
	$p$ -value	0.994	0.343	0.464	0.24	0.826	0.51	0.269	0.33	0.773
	Slope	...	...	...	...	...	...	...	...	...
Foliar C:N	$R^2$	0.02	0.07	0.04	0.03	0.01	0	<b>0.16</b>	0	0
	$p$ -value	0.452	0.144	0.282	0.379	0.611	0.736	<b>0.035</b>	0.793	0.753
	Slope	...	...	...	...	...	...	<b>−16.39</b>	...	...
Foliar P	$R^2$	<b>0.22</b>	<b>0.32</b>	0.05	<b>0.27</b>	<b>0.19</b>	0.13	0.08	<b>0.31</b>	<b>0.32</b>
	$p$ -value	<b>0.029</b>	<b>0.008</b>	0.295	<b>0.013</b>	<b>0.044</b>	0.097	0.233	<b>0.007</b>	<b>0.007</b>
	Slope	<b>0.003</b>	<b>−0.0001</b>	...	<b>−0.0001</b>	<b>−0.08</b>	...	...	<b>0.001</b>	<b>−0.13</b>
Foliar C:P	$R^2$	<b>0.43</b>	<b>0.37</b>	0.11	<b>0.42</b>	<b>0.38</b>	<b>0.3</b>	0.2	0.18	<b>0.49</b>
	$p$ -value	<b>0.001</b>	<b>0.003</b>	0.123	<b>0.001</b>	<b>0.002</b>	<b>0.008</b>	0.053	0.052	<b>&lt;0.001</b>
	Slope	<b>−11.8</b>	<b>0.35</b>	...	<b>0.19</b>	<b>277</b>	<b>11.62</b>	...	...	<b>402</b>
Foliar N:P	$R^2$	<b>0.47</b>	<b>0.81</b>	<b>0.35</b>	0.08	<b>0.26</b>	0.08	<b>0.41</b>	<b>0.22</b>	<b>0.5</b>
	$p$ -value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.004</b>	0.21	<b>0.016</b>	0.204	<b>0.003</b>	<b>0.028</b>	<b>&lt;0.001</b>
	Slope	<b>−0.26</b>	<b>0.01</b>	<b>0.32</b>	...	<b>4.82</b>	...	<b>8.3</b>	<b>−0.05</b>	<b>8.62</b>

Note: Statistically significant correlations ( $p < 0.05$ ) are shown in bold text. Slopes are only shown for statistically significant regressions.

Abbreviations: AET, actual evapotranspiration rates; MAP, mean annual precipitation; MAT, mean annual temperature; NPP, net primary production.

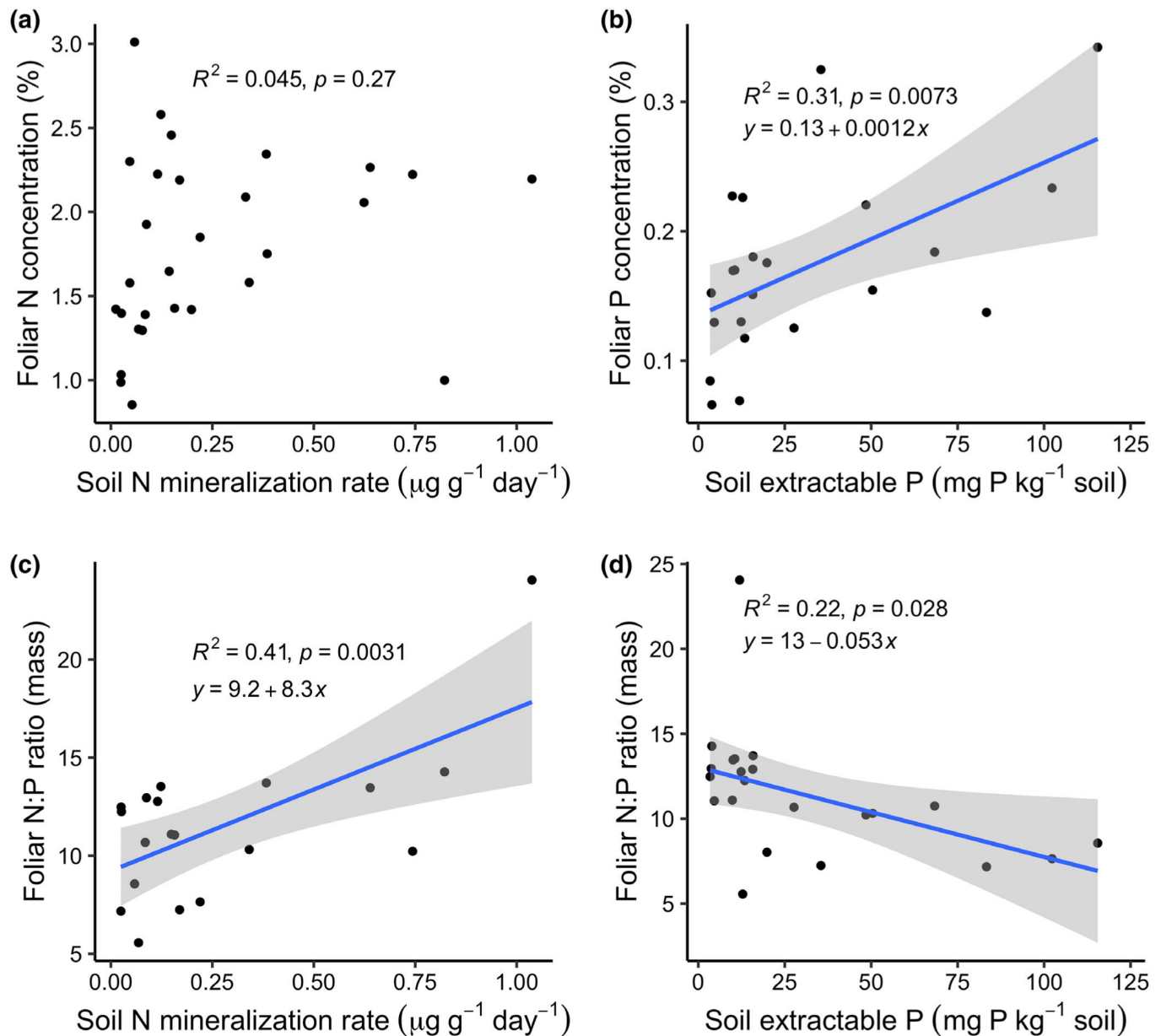
important implications for how plants may respond to global change. Overall, plant taxonomy explained the most variance in foliar nutrient concentrations and stoichiometries. In addition to taxonomy, site-level foliar P and N:P ratios were also correlated with soil nutrient status and climate, while site-level foliar N and C:N ratios were not correlated with soil nutrient or climate variables. The strong relationship between plant taxonomy and foliar N and C:N ratios (Figure 3; Appendix S1: Table S4) is consistent with previous studies showing dominant taxonomic constraints over foliar N in the tropics (Asner et al., 2014; Townsend et al., 2007). Our study sites encompass a much wider range in temperature, precipitation, and soil nutrient conditions, yet site-averaged foliar N concentrations were not correlated with any of these site variables (Table 1). Thus, patterns of foliar N across the entire dataset appear to be most consistent with the “Species Composition Hypothesis.”

Plant taxonomy was related to about half of the variation in nonaveraged foliar P, but soil nutrient concentrations and climate were also important explanatory variables (Figure 3; Appendix S1: Table S4). Site-averaged foliar P was positively correlated with site-averaged soil extractable P (Figure 2b), lending support to the “Soil Nutrient Hypothesis.” Correlations between foliar P and soil P have previously been noted in ecosystem-scale

studies (Alvarez-Clare & Mack, 2011; Hidaka & Kitayama, 2011; Parfitt et al., 2005), and within systems across species (Reed et al., 2008), and foliar P often increases in response to P fertilization (Ostertag, 2010; Ostertag & DiManno, 2016). Previous global analyses have indirectly linked foliar P (and N:P) to soil P via the “Substrate Age Hypothesis,” which postulates that foliar P declines in the unglaciated tropics due to the presence of highly weathered soils with relatively low rock-derived nutrient contents (Chadwick et al., 1999; Crews et al., 1995; Vitousek et al., 1995). However, most studies conducted at such scales have not included direct measurements of soil P concentration, but instead have relied on the generally observed decline in soil P availability from high latitudes to the tropics (Cross & Schlesinger, 1995; Walker & Syers, 1976; Yang et al., 2013). The only global-scale meta-analysis of which we are aware that previously compared the effect of soil nutrients versus climate on leaf traits was limited by relatively few soil P measurements (Ordoñez et al., 2009).

Our results also showed that AET and soil P are equally well correlated with site-averaged foliar P concentrations (Figures 1 and 2). However, AET is a stronger correlate of site-averaged foliar N:P ratios than is soil P (Figures 1 and 2), suggesting that global-scale patterns in foliar P are likely to be not solely driven by variation in



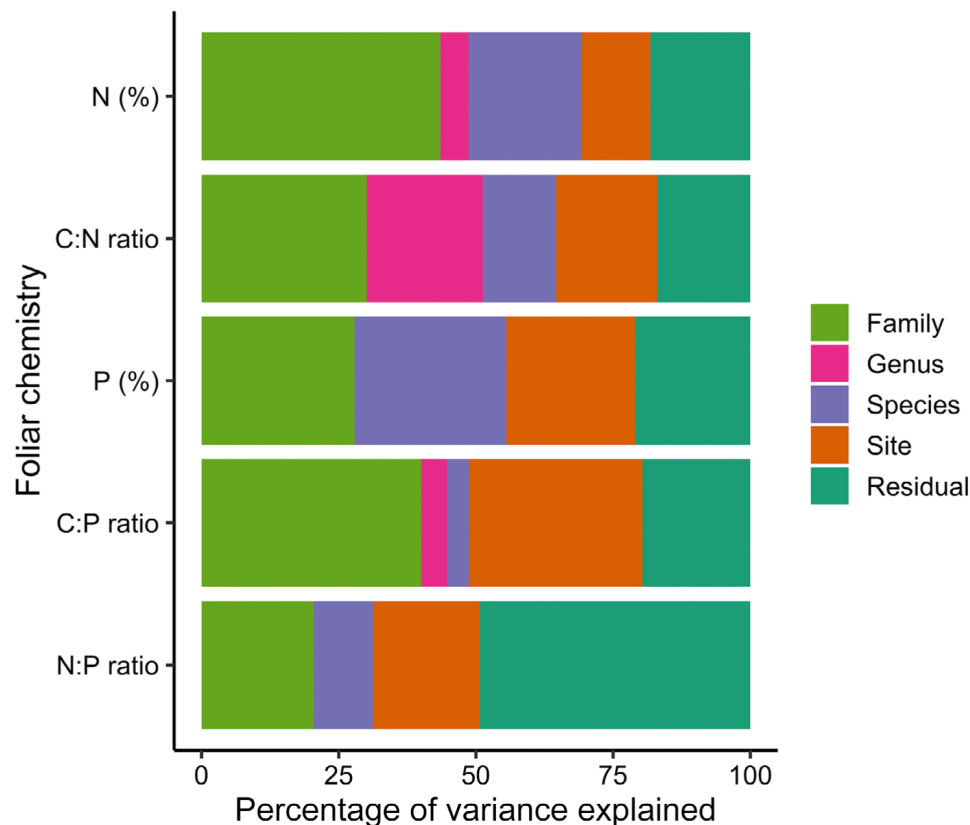


**FIGURE 2** (a) Site-averaged foliar N plotted against soil N mineralization rate; (b) foliar P plotted against soil extractable P concentration; (c) foliar N:P plotted against soil N mineralization rate and (d) soil extractable P concentration. Blue lines represent statistically significant simple linear regressions and gray shading represents the 95% confidence intervals. Regression equations,  $R^2$  values, and  $p$ -values were calculated using simple linear regression.

soil P content between temperate and tropical regions. Instead, climate appears to influence foliar P and N:P independently of soil P availability, potentially via increased plant growth rates and nutrient demand in tropical climates, supporting the “Climate Physiology Hypothesis.” These results contrast with those of a previous global-scale meta-analysis which found that soil fertility explained more variance in foliar chemistry than climate (Ordoñez et al., 2009). This is likely because their study examined MAT and MAP as climate variables, but not AET, which integrates both energy and water availability (Fisher et al., 2011). By making use of a large

dataset of paired soil and foliar P measurements from a wide range of biomes, our study reveals multiple interacting mechanisms that may drive global patterns of foliar P.

Overall, our site-averaged data suggest that broad patterns of foliar N and foliar P are explained by different mechanisms. While foliar N and P are both strongly constrained by plant taxonomy (family, genus, and species), consistent with the “Species Composition Hypothesis” (Figure 3), foliar P is also strongly linked to environmental variables, supporting both the “Soil Nutrient” and the “Climate Physiology Hypotheses.”



**FIGURE 3** Variance partitioning between site and taxonomic effects for each foliar chemistry variable (foliar N, P, C:N, N:P, and C:P). Variance partitioning was calculated using a nested random effects model with two random effects: (1) site and (2) family, genus, and species as a nested variable.

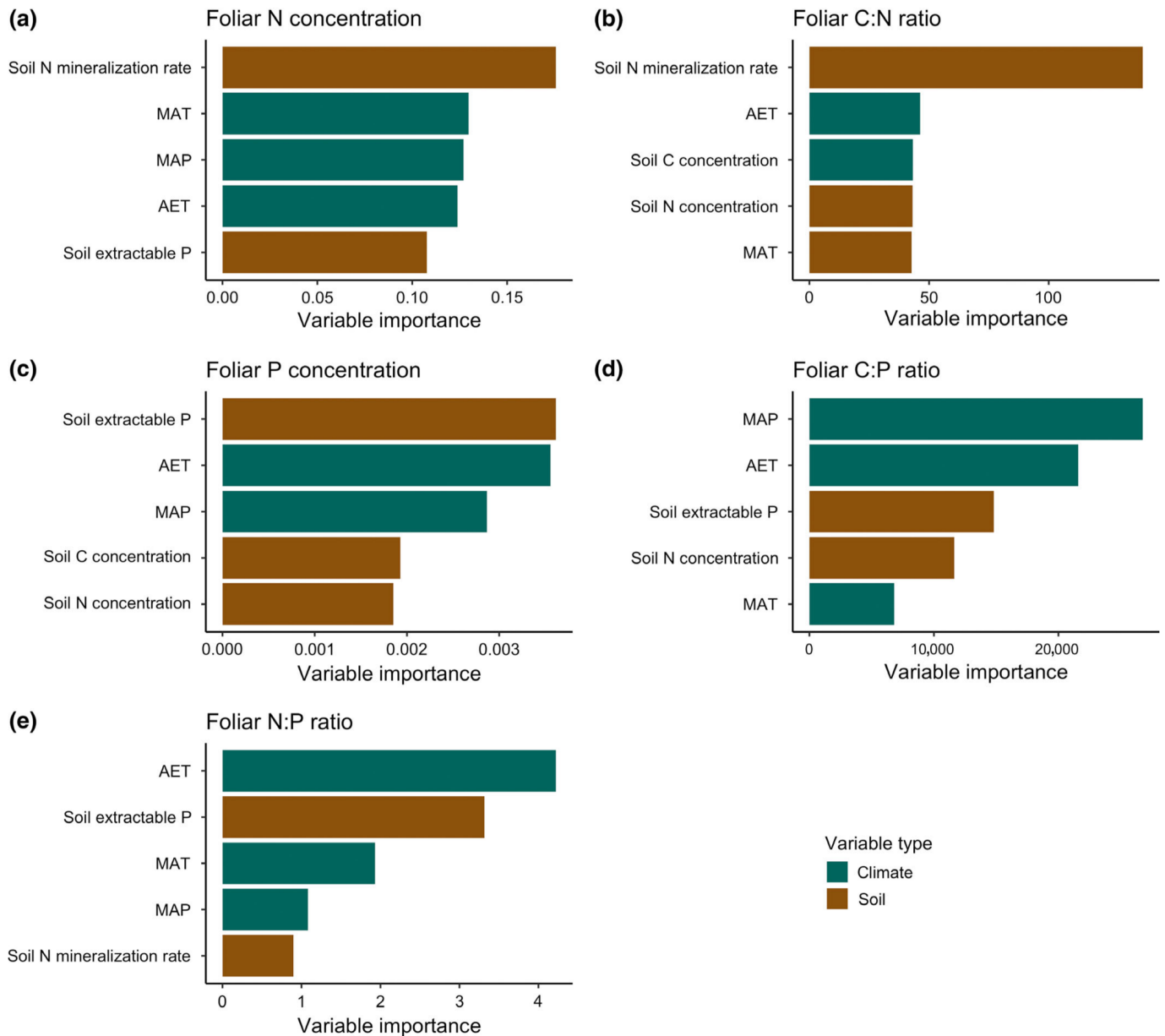
Our findings highlight the myriad factors that influence foliar chemistry and suggest that broad patterns of foliar chemistry cannot be explained by just one mechanism (Lovelock et al., 2007). These differential controls over foliar nutrient concentrations have potentially important implications on the stoichiometric plasticity of ecosystems in response to global change drivers. If foliar N is largely driven by plant taxonomy, substantial changes to foliar chemistry on an ecosystem scale may require shifts in plant community composition. Conversely, our study suggests that foliar P is more strongly related than N to local environmental conditions, which may occur more rapidly via changes in tissue nutrient allocation in individual organisms. As a result, foliar N may shift more slowly than P in response to global changes (e.g., N deposition, warming, drought), leading to altered ecosystem N:P ratios, as has been observed in long-term fertilization research in the northeastern USA (Gonzales & Yanai, 2019), and other laboratory- and field-based manipulative studies (Xu et al., 2020; Yuan & Chen, 2015).

Across the NEON sites, which span diverse biomes from tropical rainforests to boreal forests, site-averaged foliar N and P concentrations and N:P ratios encompassed the full range of previously observed global values (Reich & Oleksyn, 2004). The latitudinal patterns

in foliar P and N:P mirror findings from previous global-scale meta-analyses, which showed an increase in foliar P concentration and a decline in N:P ratios with increasing latitude (McGroddy et al., 2004; Reich & Oleksyn, 2004). However, while previous meta-analyses have also shown relative increases in foliar N with latitude (although weaker than the increase in foliar P), we did not observe this pattern across the NEON terrestrial sites. This may reflect the more limited geographic extent of the NEON sites versus those analyzed in previous, global-scale meta-analyses. However, the ranges of MAT and MAP at sites in our dataset are comparable with the ranges observed in global-scale studies (Ordoñez et al., 2009; Reich & Oleksyn, 2004).

Nitrogen and P are often thought to limit global NPP (Du et al., 2020; Elser et al., 2007; Hou et al., 2020; LeBauer & Treseder, 2008), and foliar nutrient stoichiometry is frequently used as an indicator of nutrient limitation (Güsewell, 2004). However, we found no correlation between NPP and site-averaged foliar N, a negative correlation between NPP and site-averaged foliar P, and a positive correlation between NPP and site-averaged foliar C:P and N:P ratios (Table 1). This is not entirely surprising, given that foliar nutrient concentrations have previously been observed to be significantly lower

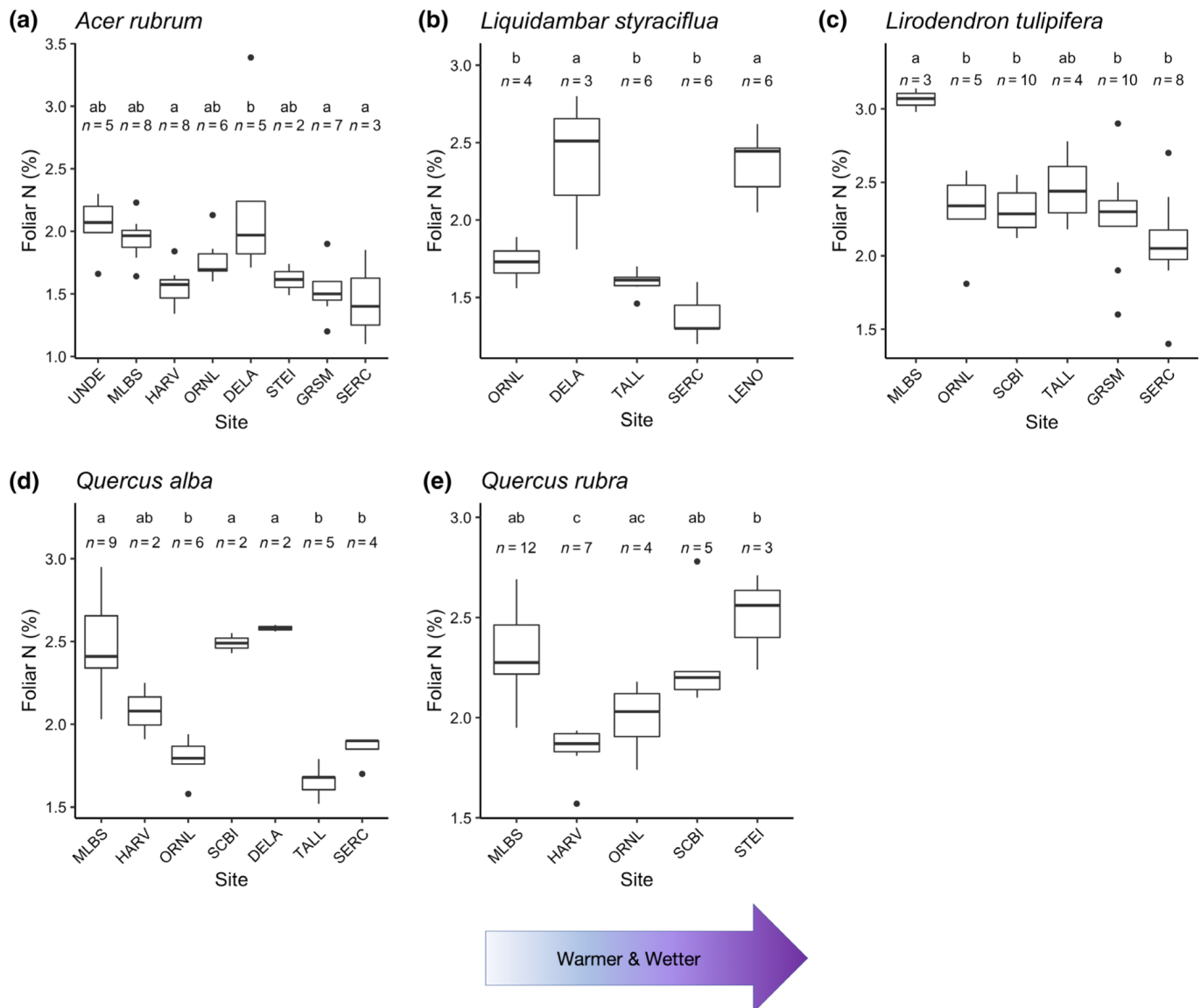




**FIGURE 4** Relative importance of climate (green bars) and soil (brown bars) variables in explaining: (a) foliar N; (b) C:N; (c) P; (d) C:P; and (e) N:P. Each foliar chemistry variable was independently modeled with the same climate and soil variables as above, and used as predictor variables in random forest models run for 1000 iterations. Variable importance was determined by the mean decrease in accuracy resulting from the exclusion of each predictor variable, adjusting for correlations between predictor variables. AET, actual evapotranspiration rates; MAP, mean annual precipitation; MAT, mean annual temperature.

(and C:nutrient ratios significantly higher) in tropical forests versus temperate and boreal ecosystems (McGroddy et al., 2004; Ordoñez et al., 2009; Reich & Oleksyn, 2004), yet tropical ecosystems account for more than a third of global NPP (Roy et al., 2001). In addition to nutrient availability, NPP is influenced by growing season length, incoming solar radiation, leaf area index, soil water availability, plant carbon allocation, and numerous other factors. The decoupling of NPP and foliar nutrient concentrations provides evidence that rather than indicating a limitation to productivity, flexible foliar stoichiometry

may allow plants to remain productive even in relatively nutrient-poor environments (Massmann et al., 2021). Site NPP was positively correlated with average site N mineralization rates (Appendix S1: Figure S3), suggesting that NPP may be constrained by nutrients, but this is not necessarily reflected in foliar nutrient concentrations, as has been demonstrated in tropical fertilization experiments (Alvarez-Clare & Mack, 2015). Overall, our findings suggest that ecosystem-level stoichiometric flexibility—particularly in N:P and C:P ratios—may be an important mechanism by which productivity is



**FIGURE 5** Boxplots showing foliar N concentrations in: (a) *Acer rubrum*; (b) *Liquidambar styraciflua*; (c) *Liriodendron tulipifera*; (d) *Quercus alba*; and (e) *Quercus rubra* across NEON sites. The band in the middle of each box represents the median foliar N concentration and top and bottom of the box represent the first and third quartiles, respectively. Whiskers indicate the maximum and minimum values (excluding outliers). Outliers are represented by closed circles. Sites on the x-axis are arranged in order of increasing actual evapotranspiration rates (AET). Site name acronyms are explained in Appendix S1: Table S1. Different lowercase letters above boxes indicate significant differences in foliar N values among sites, based on a one-way ANOVA with site as the factor and Tukey's honestly significant difference post hoc test. The number of samples per species per site is indicated below the significance letters.

maintained in putatively nutrient-limited ecosystems. Future studies may be able to test this using flux tower GPP estimates from NEON sites when those data become available.

### Implications of stoichiometric flexibility across biological scales

Stoichiometric flexibility can manifest on multiple scales ranging from individual plant tissues to whole ecosystems

(Sistla & Schimel, 2012). While our site-averaged regressions provide insight into whole-ecosystem patterns of plant stoichiometry, we also examined plant foliar nutrient concentrations and stoichiometry at the species level. We found significant intraspecific variation in foliar chemistry. Although most of that variation was unexplained, we did find species-specific correlations between environmental conditions and foliar chemistry. For several of the species examined, foliar N varied significantly among sites and was correlated with one or multiple climate or soil variables (Appendix S1: Tables S6–S10). Patterns were



species specific. For example, *A. rubrum* foliar N was only correlated with AET (Appendix S1: Table S6), and weakly so, while *L. styraciflua* foliar N was strongly correlated with MAT, MAP, AET, soil N mineralization rate, and extractable P (Appendix S1: Table S7).

The species-specific patterns of foliar N across environmental gradients highlight differing biological scales of variation between foliar N and foliar P. While variation in foliar P across environmental gradients is apparent at the site level (Figures 1 and 2)—presumably reflecting the sensitivity of foliar P to environmental drivers in many plant species—relationships between environmental variables and foliar N are much more taxonomically constrained (Appendix S1: Tables S6–S10). Species-specific variation in foliar N stands in contrast with the site-averaged data, which showed no variation in foliar N across latitudes and no correlation between foliar N and any environmental variables. This pattern of species-specific flexibility in foliar N suggests that site-averaged data mask intraspecific flexibility in foliar N (Figure 5), as has been seen in other studies (Dybziński et al., 2013), and demonstrates the variable spatial and temporal scales on which stoichiometric flexibility can manifest.

Our findings highlight the key role of plant community composition in shaping ecosystem-level patterns of foliar chemistry. Precipitation and soil nutrients are strong predictors of plant species distribution (Condit et al., 2013), and the presence of species specialized for particular conditions seems to allow plant communities to maintain productivity, even when soil nutrients are relatively scarce (Turner et al., 2018). Such shifts in plant community composition across climate and soil resource gradients are likely to also influence community-level foliar stoichiometry (Massmann et al., 2021). Thus, our data suggest that disturbances that shift community composition (e.g., land-use history, climate change) may also have strong effects on foliar chemistry, particularly foliar N.

## Implications for models and conclusions

Land models are increasingly incorporating flexible foliar stoichiometry schemes, with the goal of improving model representation of ecosystem dynamics (Fisher et al., 2019; Meyerholt & Zaehle, 2015; Zhu et al., 2020). However, the best way to represent stoichiometric flexibility and coupled biogeochemical cycles in models remains unclear (Rastetter, 2011; Wieder et al., 2015). Resolving these uncertainties is critical for constraining the trajectory of terrestrial ecosystem responses to climate change and elevated CO<sub>2</sub> (Caldararu et al., 2020; Kovenock et al., 2021).

Our results illustrate several robust correlations between frequently modeled environmental variables and foliar nutrient concentrations and stoichiometries that could be used to inform model development.

We found a strong correlation between AET and site-averaged foliar N:P ratios, a relationship that could be used to constrain modeled leaf stoichiometry. Furthermore, our analyses showed large variation in foliar chemistry within and among sites, and that a large proportion of the taxonomic variation in foliar chemistry occurred at the family level (Figure 3). These results are consistent with findings from the tropics, where taxonomic variation is thought to largely be driven by N-fixing taxa (Asner et al., 2014). Symbiotic N-fixing plant taxa were largely absent from our dataset, suggesting that taxonomic control over foliar N may be more widespread than previously noted. These observations underscore the limitations of the standard parameterization of foliar chemistry by plant functional types in models, which neglects important variation in foliar stoichiometry at regional to global scales (Butler et al., 2017; Vallicrosa et al., 2021). We emphasize that the timescales over which foliar stoichiometric flexibility can respond and potentially overcome nutrient limitation under climate change also remains poorly resolved, but that addressing this uncertainty is critical to improving both the understanding and predictions of ecosystem responses to global change.

Flexibility in foliar nutrient concentrations and stoichiometries plays a key role in the plant response to global change by allowing plants to maintain biomass and growth rates despite possible declines in nutrient availability (Sistla & Schimel, 2012). As such, the degree of flexibility in plant tissue stoichiometry will be a powerful lever for projected terrestrial C sequestration through the next century (Meyerholt & Zaehle, 2015; Zhu et al., 2020). Our study demonstrates different proportional controls of the dominant mechanisms driving variation in foliar N and P stoichiometry, with key implications for future experimental and modeling studies. The specific physiological mechanisms behind N versus P variation can influence the spatial and temporal scales of foliar chemistry shifts in response to global change. Understanding the physiological mechanisms that drive foliar chemistry variation (e.g., individual adaptation to a change in resource availability versus shifts in plant community composition) is of critical importance, and can be tested in both experimental and observational frameworks. Our findings underscore how interactions among climate, soil nutrients, and plant taxonomy are likely to influence foliar stoichiometry in ways that may ultimately constrain (or enhance) vegetation responses to global change drivers.



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## CONFLICT OF INTEREST

The authors declare no conflict of interest.


## DATA AVAILABILITY STATEMENT

Data analyzed in this study are publicly available via the National Ecological Observatory Network data repository and were derived from the following data products: NEON (National Ecological Observatory Network), Plant foliar traits (DP1.10026.001), <https://data.neonscience.org> (accessed November 11, 2020); NEON (National Ecological Observatory Network), Soil physical and chemical properties, periodic (DP1.10086.001), <https://data.neonscience.org> (accessed November 13, 2020); NEON (National Ecological Observatory Network), Soil physical and chemical properties, distributed initial characterization (DP1.10047.001), <https://data.neonscience.org> (accessed December 2, 2020). Code to reproduce the analyses and figures (Dynarski, 2022) is available in Zenodo at <https://doi.org/10.5281/zenodo.7111945>.

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## REFERENCES

- Adams, M. A., T. L. Turnbull, J. I. Sprent, and N. Buchmann. 2016. "Legumes Are Different: Leaf Nitrogen, Photosynthesis, and Water Use Efficiency." *PNAS* 113: 4098–103.
- Ågren, G. I. 2008. "Stoichiometry and Nutrition of Plant Growth in Natural Communities." *Annual Review of Ecology, Evolution, and Systematics* 39: 153–70.
- Alvarez-Clare, S., and M. C. Mack. 2011. "Influence of Precipitation on Soil and Foliar Nutrients across Nine Costa Rican Forests." *Biotropica* 43: 433–41.
- Alvarez-Clare, S., and M. C. Mack. 2015. "Do Foliar, Litter, and Root Nitrogen and Phosphorus Concentrations Reflect Nutrient Limitation in a Lowland Tropical Wet Forest?" *PLoS One* 10: e0123796.
- Asner, G. P., R. E. Martin, R. Tupayachi, C. B. Anderson, F. Sinca, L. Carranza-Jiménez, and P. Martinez. 2014. "Amazonian Functional Diversity from Forest Canopy Chemical Assembly." *Proceedings of the National Academy of Sciences of the United States of America* 111: 5604–9.
- Blanes, M. C., B. Viñeola, J. Merino, and J. A. Carreira. 2013. "Nutritional Status of Abies Pinsapo Forests along a Nitrogen Deposition Gradient: Do C/N/P Stoichiometric Shifts Modify Photosynthetic Nutrient Use Efficiency?" *Oecologia* 171: 797–808.
- Butler, E. E., A. Datta, H. Flores-Moreno, M. Chen, K. R. Wythers, F. Fazayeli, A. Banerjee, et al. 2017. "Mapping Local and Global Variability in Plant Trait Distributions." *PNAS* 114: E10937–46.
- Caldararu, S., T. Thum, L. Yu, and S. Zaehle. 2020. "Whole-Plant Optimality Predicts Changes in Leaf Nitrogen under Variable CO<sub>2</sub> and Nutrient Availability." *New Phytologist* 225: 2331–46.
- Chadwick, O. A., L. A. Derry, P. M. Vitousek, B. J. Huebert, and L. O. Hedin. 1999. "Changing Sources of Nutrients during Four Million Years of Ecosystem Development." *Nature* 397: 491–7.
- Condit, R., B. M. J. Engelbrecht, D. Pino, R. Pérez, and B. L. Turner. 2013. "Species Distributions in Response to Individual Soil Nutrients and Seasonal Drought across a Community of Tropical Trees." *PNAS* 110: 5064–8.
- Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, A. Darrell, D. Mueller-Dombois, and P. M. Vitousek. 1995. "Changes in Soil Phosphorus Fractions and Ecosystem Dynamics across a Long Chronosequence in Hawaii." *Ecology* 76: 1407–24.
- Cross, A. F., and W. H. Schlesinger. 1995. "A Literature Review and Evaluation of the Hedley Fractionation: Applications to the Biogeochemical Cycle of Soil Phosphorus in Natural Ecosystems." *Geoderma* 64: 197–214.
- Du, E., C. Terrer, A. F. A. Pellegrini, A. Ahlström, C. J. van Lissa, X. Zhao, N. Xia, X. Wu, and R. B. Jackson. 2020. "Global Patterns of Terrestrial Nitrogen and Phosphorus Limitation." *Nature Geoscience* 13: 221–6.
- Dybzinski, R., C. E. Farrior, S. Ollinger, and S. W. Pacala. 2013. "Interspecific Vs Intraspecific Patterns in Leaf Nitrogen of Forest Trees across Nitrogen Availability Gradients." *New Phytologist* 200(1): 112–21.
- Dynarski, K. A. 2022. "biogeokaty/neon\_stoich\_flex\_ms: Initial release (v1.0)." Zenodo. <https://doi.org/10.5281/zenodo.7111945>.
- Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. "Global Analysis of Nitrogen and Phosphorus Limitation of Primary Producers in Freshwater, Marine and Terrestrial Ecosystems." *Ecology Letters* 10: 1135–42.
- Fisher, J. B., R. J. Whittaker, and Y. Malhi. 2011. "ET come home: potential evapotranspiration in geographical ecology." *Global Ecology and Biogeography* 20: 1–18.
- Fisher, R. A., W. R. Wieder, B. M. Sanderson, C. D. Koven, K. W. Oleson, C. Xu, J. B. Fisher, M. Shi, A. P. Walker, and





- D. M. Lawrence. 2019. "Parametric Controls on Vegetation Responses to Biogeochemical Forcing in the CLM5." *Journal of Advances in Modeling Earth Systems* 11: 2879–95.
- Gonzales, K., and R. Yanai. 2019. "Nitrogen–Phosphorous Interactions in Young Northern Hardwoods Indicate P Limitation: Foliar Concentrations and Resorption in a Factorial N by P Addition Experiment." *Oecologia* 189: 829–40.
- Güsewell, S. 2004. "N: P Ratios in Terrestrial Plants: Variation and Functional Significance." *New Phytologist* 164: 243–66.
- Han, W., J. Fang, D. Guo, and Y. Zhang. 2005. "Leaf Nitrogen and Phosphorus Stoichiometry across 753 Terrestrial Plant Species in China." *New Phytologist* 168: 377–85.
- He, J.-S., X. Wang, B. Schmid, D. F. B. Flynn, X. Li, P. B. Reich, and J. Fang. 2010. "Taxonomic Identity, Phylogeny, Climate and Soil Fertility as Drivers of Leaf Traits across Chinese Grassland Biomes." *Journal of Plant Research* 123: 551–61.
- Hidaka, A., and K. Kitayama. 2011. "Allocation of Foliar Phosphorus Fractions and Leaf Traits of Tropical Tree Species in Response to Decreased Soil Phosphorus Availability on Mount Kinabalu, Borneo." *Journal of Ecology* 99: 849–57.
- Hinckley, E.-L. S., G. B. Bonan, G. J. Bowen, B. P. Colman, P. A. Duffy, C. L. Goodale, B. Z. Houlton, et al. 2016. "The Soil and Plant Biogeochemistry Sampling Design for the National Ecological Observatory Network." *Ecosphere* 7: e01234.
- Hogan, J. A., O. J. Valverde-Barrantes, W. Tang, Q. Ding, H. Xu, and C. Baraloto. 2021. "Evidence of Elemental Homeostasis in Fine Root and Leaf Tissues of Saplings across a Fertility Gradient in Tropical Montane Forest in Hainan, China." *Plant and Soil* 460: 625–46.
- Hothorn, T., K. Hornik, and A. Zeileis. 2006. "Unbiased Recursive Partitioning: A Conditional Inference Framework." *Journal of Computational and Graphical Statistics* 15: 651–74.
- Hothorn, T., and A. Zeileis. 2015. "Partykit: A Modular Toolkit for Recursive Partytioning in R." *Journal of Machine Learning Research* 16: 3905–9.
- Hou, E., Y. Luo, Y. Kuang, C. Chen, X. Lu, L. Jiang, X. Luo, and D. Wen. 2020. "Global Meta-Analysis Shows Pervasive Phosphorus Limitation of Aboveground Plant Production in Natural Terrestrial Ecosystems." *Nature Communications* 11: 637.
- Isles, P. D. F. 2020. "The Misuse of Ratios in Ecological Stoichiometry." *Ecology* 101: e03153.
- Kerkhoff, A. J., B. J. Enquist, J. J. Elser, and W. F. Fagan. 2005. "Plant Allometry, Stoichiometry and the Temperature-Dependence of Primary Productivity." *Global Ecology and Biogeography* 14: 585–98.
- Koerselman, W., and A. F. M. Meuleman. 1996. "The Vegetation N: P Ratio: A New Tool to Detect the Nature of Nutrient Limitation." *The Journal of Applied Ecology* 33: 1441.
- Kovenock, M., C. D. Koven, R. G. Knox, R. A. Fisher, and A. L. S. Swann. 2021. "Leaf Trait Plasticity Alters Competitive Ability and Functioning of Simulated Tropical Trees in Response to Elevated Carbon Dioxide." *Global Biogeochemical Cycles* 35: e2020GB006807.
- LeBauer, D. S., and K. K. Treseder. 2008. "Nitrogen Limitation of Net Primary Productivity in Terrestrial Ecosystems Is Globally Distributed." *Ecology* 89: 371–9.
- Lovelock, C. E., I. C. Feller, M. C. Ball, J. Ellis, and B. Sorrell. 2007. "Testing the Growth Rate Vs. Geochemical Hypothesis for Latitudinal Variation in Plant Nutrients." *Ecology Letters* 10: 1154–63.
- Manzoni, S., P. Taylor, A. Richter, A. Porporato, and G. I. Ågren. 2012. "Environmental and Stoichiometric Controls on Microbial Carbon-Use Efficiency in Soils." *New Phytologist* 196: 79–91.
- Massmann, A., M. A. Cavaleri, S. F. Oberbauer, P. C. Olivas, and S. Porder. 2021. "Foliar Stoichiometry Is Marginally Sensitive to Soil Phosphorus across a Lowland Tropical Rainforest." *Ecosystems* 25: 61–74.
- McGroddy, M. E., T. Daufresne, and L. O. Hedin. 2004. "Scaling of C:N:P Stoichiometry IN Forests Worldwide: Implications of Terrestrial Redfield-Type Ratios." *Ecology* 85: 2390–401.
- Meyerholt, J., and S. Zaehle. 2015. "The Role of Stoichiometric Flexibility in Modelling Forest Ecosystem Responses to Nitrogen Fertilization." *New Phytologist* 208: 1042–55.
- Mu, Q., M. Zhao, and S. W. Running. 2011. "Improvements to a MODIS Global Terrestrial Evapotranspiration Algorithm." *Remote Sensing of Environment* 115: 1781–800.
- National Ecological Observatory Network (NEON). 2021a. "Plant Foliar Traits (DP1.10026.001)." <https://data.neonscience.org> (accessed November 11, 2020).
- National Ecological Observatory Network (NEON). 2021b. "Soil Physical and Chemical Properties, Distributed Initial Characterization (DP1.10047.001)." <https://data.neonscience.org> (accessed December 2, 2020).
- National Ecological Observatory Network (NEON). 2021c. "Soil Physical and Chemical Properties, Periodic (DP1.10086.001)." <https://data.neonscience.org> (accessed November 13, 2020).
- Ordoñez, J. C., P. M. V. Bodegom, J.-P. M. Witte, I. J. Wright, P. B. Reich, and R. Aerts. 2009. "A Global Study of Relationships between Leaf Traits, Climate and Soil Measures of Nutrient Fertility." *Global Ecology and Biogeography* 18: 137–49.
- Ostertag, R. 2010. "Foliar Nitrogen and Phosphorus Accumulation Responses after Fertilization: An Example from Nutrient-Limited Hawaiian Forests." *Plant and Soil* 334: 85–98.
- Ostertag, R., and N. M. DiManno. 2016. "Detecting Terrestrial Nutrient Limitation: A Global Meta-Analysis of Foliar Nutrient Concentrations after Fertilization." *Frontiers in Earth Science* 4: 23.
- Pal, M. 2005. "Random Forest Classifier for Remote Sensing Classification." *International Journal of Remote Sensing* 26: 217–22.
- Palm, C., P. Sanchez, S. Ahamed, and A. Awiti. 2007. "Soils: A Contemporary Perspective." *Annual Review of Environment and Resources* 32: 99–129.
- Parfitt, R. L., D. J. Ross, D. A. Coomes, S. J. Richardson, M. C. Smale, and R. A. Dahlgren. 2005. "N and P in New Zealand Soil Chronosequences and Relationships with Foliar N and P." *Biogeochemistry* 75: 305–28.
- Peng, Y., F. Li, G. Zhou, K. Fang, D. Zhang, C. Li, G. Yang, G. Wang, J. Wang, and Y. Yang. 2017. "Linkages of Plant Stoichiometry to Ecosystem Production and Carbon Fluxes with Increasing Nitrogen Inputs in an Alpine Steppe." *Global Change Biology* 23: 5249–59.
- Perakis, S. S., and E. R. Sinkhorn. 2011. "Biogeochemistry of a Temperate Forest Nitrogen Gradient." *Ecology* 92: 1481–91.
- Rastetter, E. B. 2011. "Modeling Coupled Biogeochemical Cycles." *Frontiers in Ecology and the Environment* 9: 68–73.
- Reed, S. C., C. C. Cleveland, and A. R. Townsend. 2008. "Tree Species Control Rates of Free-Living Nitrogen Fixation in a Tropical Rainforest." *Ecology* 89: 2924–34.





- Reed, S. C., A. R. Townsend, E. a. Davidson, and C. C. Cleveland. 2012. "Stoichiometric Patterns in Foliar Nutrient Resorption across Multiple Scales." *New Phytologist* 196: 173–80.
- Reed, S. C., A. R. Townsend, P. G. Taylor, and C. C. Cleveland. 2011. "Phosphorus Cycling in Tropical Forests Growing on Highly Weathered Soils." In *Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling, Soil Biology*, edited by E. Bütemann, A. Oberson, and E. Frossard, 339–69. Berlin, Heidelberg: Springer.
- Reich, P. B., and J. Oleksyn. 2004. "Global Patterns of Plant Leaf N and P in Relation to Temperature and Latitude." *Proceedings of the National Academy of Sciences* 101: 11001–6.
- Richardson, S. J., D. A. Peltzer, R. B. Allen, and M. S. McGlone. 2005. "Resorption Proficiency along a Chronosequence: Responses among Communities and within Species." *Ecology* 86: 20–5.
- Roy, J., B. Saugier, and H. A. Mooney. 2001. *Terrestrial Global Productivity*. Cambridge, MA: Academic Press.
- Running, S. W., Q. Mu, and M. Zhao. 2015. *MOD17A3H MODIS/Terra Gross Primary Productivity Yearly L4 Global 500 m SIN Grid*. NASA LP DAAC. <http://doi.org/10.5067/MODIS/MOD17A3H.006>.
- Running, S. W., Q. Mu, and M. Zhao. 2021. *MODIS/Terra Net Evapotranspiration 8-Day L4 Global 500 m SIN Grid V061*. NASA EOSDIS Land Processes DAAC. <https://doi.org/10.5067/MODIS/MOD16A2.061>.
- Sardans, J., and J. Peñuelas. 2014. "Climate and Taxonomy Underlie Different Elemental Concentrations and Stoichiometries of Forest Species: The Optimum "Biogeochemical Niche"." *Plant Ecology* 215: 441–55.
- Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2011. "Factors Affecting Nutrient Concentration and Stoichiometry of Forest Trees in Catalonia (NE Spain)." *Forest Ecology and Management* 262: 2024–34.
- Schuur, E., and P. Matson. 2001. "Net Primary Productivity and Nutrient Cycling across a Mesic to Wet Precipitation Gradient in Hawaiian Montane Forest." *Oecologia* 128: 431–42.
- Sistla, S. A., A. P. Appling, A. M. Lewandowska, B. N. Taylor, and A. A. Wolf. 2015. "Stoichiometric Flexibility in Response to Fertilization along Gradients of Environmental and Organismal Nutrient Richness." *Oikos* 124: 949–59.
- Sistla, S. A., and J. P. Schimel. 2012. "Stoichiometric Flexibility as a Regulator of Carbon and Nutrient Cycling in Terrestrial Ecosystems under Change." *New Phytologist* 196: 68–78.
- Strobl, C., A.-L. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. "Conditional Variable Importance for Random Forests." *BMC Bioinformatics* 9: 307.
- Tian, D., Z. Yan, S. Ma, Y. Ding, Y. Luo, Y. Chen, E. Du, et al. 2019. "Family-Level Leaf Nitrogen and Phosphorus Stoichiometry of Global Terrestrial Plants." *Science China. Life Sciences* 62: 1047–57.
- Townsend, A. R., C. C. Cleveland, G. P. Asner, and M. M. Bustamante. 2007. "Controls Over Foliar N:P Ratios IN Tropical Rain Forests." *Ecology* 88: 107–18.
- Turner, B. L., T. Brenes-Arguedas, and R. Condit. 2018. "Pervasive Phosphorus Limitation of Tree Species but Not Communities in Tropical Forests." *Nature* 555: 367–70.
- Vallicrosa, H., J. Sardans, J. Maspons, P. Zuccarini, M. Fernández-Martínez, M. Bauters, D. S. Goll, et al. 2021. "Global Maps and Factors Driving Forest Foliar Elemental Composition: The Importance of Evolutionary History." *New Phytologist* 233: 169–81.
- Vitousek, P. 1982. "Nutrient Cycling and Nutrient Use Efficiency." *The American Naturalist* 119: 553–72.
- Vitousek, P. M. 1998. "Foliar and Litter Nutrients, Nutrient Resorption, and Decomposition in Hawaiian *Metrosideros Polymorpha*." *Ecosystems* 1: 401–7.
- Vitousek, P. M., D. R. Turner, and K. Kitayama. 1995. "Foliar Nutrients during Long-Term Soil Development in Hawaiian Montane Rain Forest." *Ecology* 76: 712–20.
- Walker, T. W., and J. K. Syers. 1976. "The Fate of Phosphorus during Pedogenesis." *Geoderma* 15: 1–19.
- Wieder, W. R., C. C. Cleveland, W. K. Smith, and K. Todd-Brown. 2015. "Future Productivity and Carbon Storage Limited by Terrestrial Nutrient Availability." *Nature Geoscience* 8: 441–4.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428(6985). <https://doi.org/10.1038/nature02403>.
- Xu, S., J. Sardans, J. Zhang, and J. Peñuelas. 2020. "Variations in Foliar Carbon:Nitrogen and Nitrogen:Phosphorus Ratios under Global Change: A Meta-Analysis of Experimental Field Studies." *Scientific Reports* 10: 12156.
- Yang, X., Z. Huang, K. Zhang, and J. H. C. Cornelissen. 2015. "C:N:P Stoichiometry of *Artemisia* species and Close Relatives across Northern China: Unravelling Effects of Climate, Soil and Taxonomy." *Journal of Ecology* 103: 1020–31.
- Yang, X., W. M. Post, P. E. Thornton, and A. Jain. 2013. "The Distribution of Soil Phosphorus for Global Biogeochemical Modeling." *Biogeosciences* 10: 2525–37.
- Yang, Y., Y. Luo, M. Lu, C. Schädel, and W. Han. 2011. "Terrestrial C:N Stoichiometry in Response to Elevated CO<sub>2</sub> and N Addition: A Synthesis of Two Meta-Analyses." *Plant and Soil* 343: 393–400.
- Yu, Q., J. J. Elser, N. He, H. Wu, Q. Chen, G. Zhang, and X. Han. 2011. "Stoichiometric Homeostasis of Vascular Plants in the Inner Mongolia Grassland." *Oecologia* 166: 1–10.
- Yuan, Z. Y., and H. Y. H. Chen. 2015. "Decoupling of Nitrogen and Phosphorus in Terrestrial Plants Associated with Global Changes." *Nature Climate Change* 5: 465–9.
- Yue, K., D. A. Fornara, W. Yang, Y. Peng, Z. Li, F. Wu, and C. Peng. 2017. "Effects of Three Global Change Drivers on Terrestrial C:N:P Stoichiometry: A Global Synthesis." *Global Change Biology* 23: 2450–63.
- Zhu, Q., W. J. Riley, C. M. Iversen, and J. Kattge. 2020. "Assessing Impacts of Plant Stoichiometric Traits on Terrestrial Ecosystem Carbon Accumulation Using the E3SM Land Model." *Journal of Advances in Modeling Earth Systems* 12: e2019MS001841.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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