Dynarski Katherine A (Orcid ID: 0000-0001-5101-9666)
Soper Fiona M. (Orcid ID: 0000-0002-9910-9377)
Cleveland Cory C. (Orcid ID: 0000-0002-8804-4248)

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

Katherine A. Dynarski[1], Fiona M. Soper[2], Sasha C. Reed[3], William R. Wieder[4, 5], Cory C. Cleveland[1]

[1] Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT, USA
[2] Department of Biology and Bieler School of Environment, McGill University, Montréal, QC, Canada
[3] U.S. Geological Survey, Southwest Biological Science Center, Moab, UT, USA
[4] Climate and Global Dynamics Laboratory, National Center for Atmospheric Research, Boulder, CO, USA
[5] Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder CO, USA

Corresponding author: Katherine A. Dynarski. E-mail: katy.dynarski@gmail.com

Present Address for Katherine A. Dynarski: Franklin County Natural Resources Conservation District, St. Albans, VT, USA)

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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 U.S. 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 (AET). 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.

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 (Koerselman & Meuleman 1996; Güsewell 2004; Richardson *et al.* 2005; Manzoni *et al.* 2012; Blanes *et al.* 2013; Peng *et al.* 2017). 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 (McGroddy *et al.* 2004; Ågren 2008; 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_2 (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) (McGroddy *et al.* 2004; Reich & Oleksyn 2004; Han *et al.* 2005). 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 (Reich & Oleksyn 2004; Kerkhoff *et al.* 2005). 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 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 (Schuur & Matson 2001; Alvarez-Clare & Mack 2011). 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 (Walker & Syers 1976; Reed *et al.* 2011), 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 availability 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 (Vitousek 1982; McGroddy *et al.* 2004; Lovelock *et al.* 2007; Reed *et al.* 2012). 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 (Vitousek 1998; Yang *et al.* 2011;

Sistla *et al.* 2015; Yuan & Chen 2015; Ostertag & DiManno 2016; 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 to foliar P (Richardson *et al.* 2005; Perakis & Sinkhorn 2011; Massmann *et al.* 2021).

Species-specific patterns in leaf physical (*e.g.,* specific leaf area) and chemical traits have been noted in numerous studies (Wright *et al.* 2004; He *et al.* 2010; Adams *et al.* 2016), 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 (Townsend *et al.* 2007; Asner *et al.* 2014). However, the relative importance of taxonomy compared to 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 (Richardson *et al.* 2005; Hogan *et al.* 2021), 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 to 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, c, b). 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: Fig. S1, Appendix S1: Table S1). Altogether, 1,076 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 2016-2019. 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 5-22, 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 1-6, with an average of 1.9 species sampled per plot. The number of foliar samples collected per plot ranged from 1-6, with an average of 2.2 foliar samples collected per plot.

Bulk soil C, total N, and extractable inorganic N (ammonium [NH_4^+] + [NO_3^-] concentrations, and net N mineralization rates) from soil samples 0-30 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 2014-2019. Bulk soil P from 0-30 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 0-30cm depth in order to estimate nutrient pools potentially available to plants, as has been done in similar studies (Ordoñez *et al.* 2008).

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 1-11, 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 & Zhao 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 2005-2020.

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 y^{-1}], AET [mm y^{-1}], NPP [kg C m^{-2} y^{-1}], total soil N concentration [%], soil N mineralization rate [µg N g^{-1} dry soil d^{-1}], and soil extractable P concentration [mg P kg^{-1} 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 are 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 10000 iterations – the minimum number of iterations yielding stable results between model runs – using the *partykit* 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 2-12. 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: Fig. S1, Appendix S1: Table S2). Mean annual temperature ranged from -4°C to 25°C and MAP ranged from 177 to 2685 mm y^{-1}. Mean AET ranged from 129.9 to 1672.2 mm y^{-1}, and mean annual NPP ranged from 0.1 to 1.6 kg C m^{-2} y^{-1}.

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^{-1} soil day^{-1}, and soil extractable P contents ranged from 2.86 to 123.19 mg P kg^{-1} 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 (Fig. 1A & B). Site-averaged foliar P ranged from 0.07% to 0.34% and increased significantly with increasing latitude (Fig. 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 (Fig. 1D & E).

Site-averaged foliar P concentrations were negatively correlated with AET (Fig. 1H, Table 1), NPP, MAP, and soil N concentration, and positively correlated with soil extractable P (Fig. 2B). Site-averaged foliar N:P was positively correlated with AET (Fig. 1J), NPP, MAT, soil N concentration, and soil N mineralization rate (Fig. 2C), and negatively correlated with soil extractable P (Fig. 2D). Site-averaged foliar C:N was negatively correlated with soil N mineralization rate. Site-averaged foliar C:P was positively correlated with AET (Fig. 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%, Fig. 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 to P traits. However, foliar N:P variance was not strongly related to either taxonomy or site, but was instead mainly related to model residuals (Fig. 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 (Fig 4A & B). Soil extractable P and AET were the independent variables most strongly related to foliar P and N:P (Fig. 4C), and MAP was the independent variable most strongly related to foliar C:P (Fig. 4D). Similarly, the independent variable most strongly related to foliar N:P was AET (Fig. 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, though 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 among-site variability (Fig. 5). Individual species exhibited up to a 2-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: Table 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 3-fold (Appendix S1: Fig. 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 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 (Fig. 3, Appendix S1: Table S4) is consistent with previous studies showing dominant taxonomic constraints over foliar N in the tropics (Townsend *et al.* 2007; Asner *et al.* 2014). 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 non-averaged foliar P, but soil nutrient concentrations and climate were also important explanatory variables (Fig. 3, Appendix S1: Table S4). Site-averaged foliar P was positively correlated with site-averaged soil extractable P (Fig. 2B), lending support to the *Soil Nutrient Hypothesis*. Correlations between foliar P and soil P have previously been noted in ecosystem-scale studies (Parfitt *et al.* 2005; Alvarez-Clare & Mack 2011; Hidaka & Kitayama 2011), 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 (Crews *et al.* 1995; Vitousek *et al.* 1995; Chadwick *et al.* 1999). 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 (Walker & Syers 1976; Cross & Schlesinger 1995; 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 show that AET and soil P are equally well-correlated with site-averaged foliar P concentrations (Figs. 1 & 2). However, AET is a stronger correlate of site-averaged foliar N:P ratios than is soil P (Figs. 1 & 2), suggesting that global-scale patterns in foliar P are likely not solely driven by variation in 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* (Table 2), foliar P is also strongly linked to environmental variables, supporting both the *Soil Nutrient* and the *Climate Physiology Hypotheses*. 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. On the other hand, 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 United States (Gonzales & Yanai 2019), and other lab- and field-based manipulative studies (Yuan & Chen 2015; Xu *et al.* 2020).

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 (though 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 range of MAT and MAP at sites in our dataset are comparable to the range observed in global scale studies (Reich & Oleksyn 2004; Ordoñez *et al.* 2009).

Nitrogen and P are often thought to limit global NPP (Elser *et al.* 2007; LeBauer & Treseder 2008; Du *et al.* 2020; Hou *et al.* 2020), 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 (and C:nutrient ratios significantly higher) in tropical forests versus temperate and boreal ecosystems (McGroddy *et al.* 2004; Reich & Oleksyn 2004; Ordoñez *et al.* 2009), 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: Fig. 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 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 intra-specific 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: Table 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 (Figs. 1, 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 to 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 (Fig. 5), as has been seen in other studies (Dybzinski *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 likely 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 (Meyerholt & Zaehle 2015; Fisher *et al.* 2019; 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_2 (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 show large variation in foliar chemistry within and among sites, and that a large proportion of the taxonomic variation in foliar chemistry occurs at the family level (Fig. 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 to and potentially overcome nutrient limitation under climate change also remains poorly resolved, but that addressing this uncertainty is critical to improve both the understanding and predictions of ecosystem responses to global change.

Flexibility in foliar nutrient concentrations and stoichiometries plays a key role in plant response to global change by allowing plants maintain biomass and growth rates despite possible declines in nutrient availability (Sistla & Schimel 2012). As such, the degree of flexibility in plant tissue stoichiometry is 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 likely influence foliar stoichiometry in ways that may ultimately constrain (or enhance) vegetation responses to global change drivers.

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Tables

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.

Foliar Trait	*Statistic*	*Independent Variable*								
		Latitude	AET	MAT	MAP	Soil N	Soil C	Soil N mineralization rate	Soil extractable P	NPP
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	**0.16**	0	0
	P-value	0.452	0.144	0.282	0.379	0.611	0.736	**0.035**	0.793	0.753
	slope	-	-	-	-	-	-	**-16.39**	-	-
Foliar P	R^2	**0.22**	**0.32**	0.05	**0.27**	**0.19**	0.13	0.08	**0.31**	**0.32**
	P-value	**0.029**	**0.008**	0.295	**0.013**	**0.044**	0.097	0.233	**0.007**	**0.007**
	slope	**0.003**	**-0.0001**	-	**-0.0001**	**-0.08**	-	-	**0.001**	**-0.13**
Foliar C:P	R^2	**0.43**	**0.37**	0.11	**0.42**	**0.38**	**0.3**	0.2	0.18	**0.49**
	P-value	**0.001**	**0.003**	0.123	**0.001**	**0.002**	**0.008**	0.053	0.052	**<0.001**
	slope	**-11.8**	**0.35**	-	**0.19**	**277**	**11.62**	-	-	**402**
Foliar N:P	R^2	**0.47**	**0.81**	**0.35**	0.08	**0.26**	0.08	**0.41**	**0.22**	**0.5**
	P-value	**<0.001**	**<0.001**	**0.004**	0.21	**0.016**	0.204	**0.003**	**0.028**	**<0.001**
	slope	**-0.26**	**0.01**	**0.32**	-	**4.82**	-	**8.3**	**-0.05**	**8.62**

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

Figure Legends

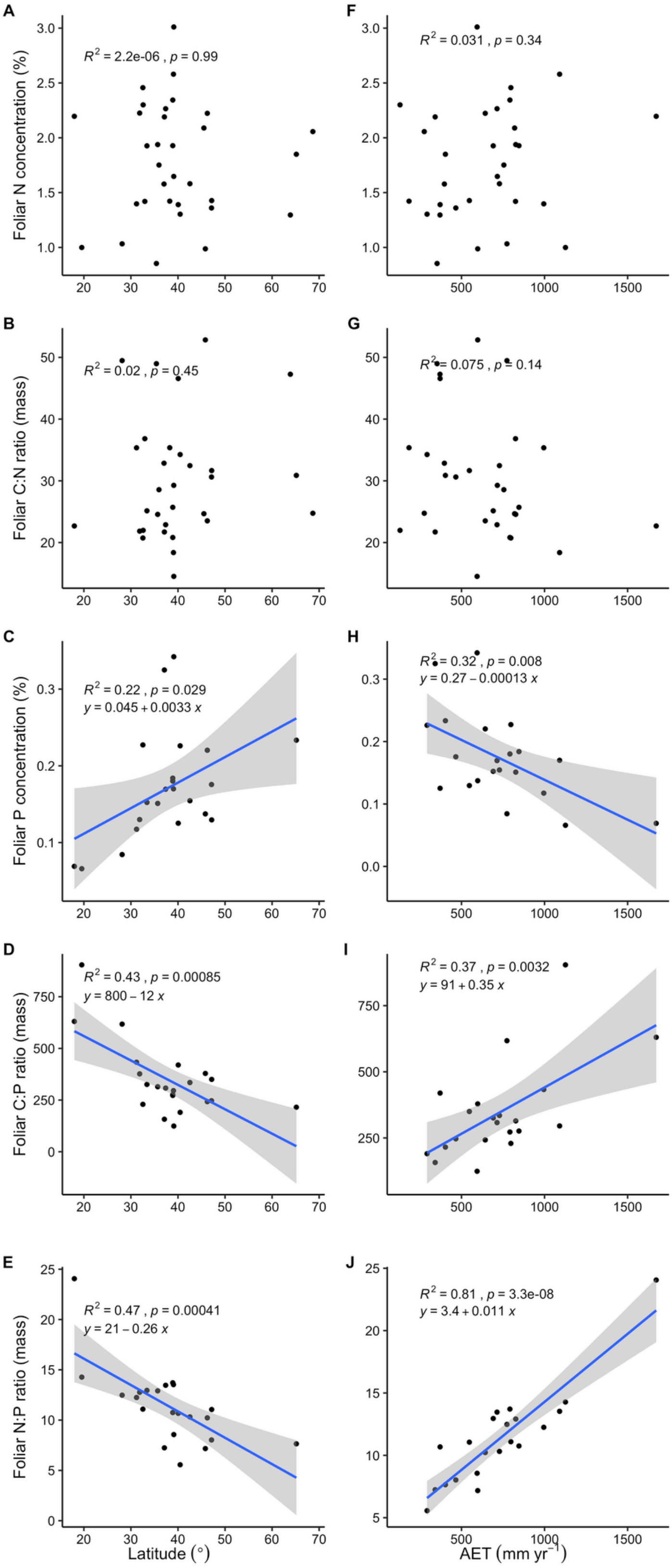
Figure 1. Site-averaged foliar N concentration (panels A, F), C:N ratio (panels B, G), P concentration (panels C, H), C:P ratio (panels D, I, and N:P ratio (panels E, J) plotted against latitude (left column) and AET (right column). Blue lines represent statistically significant simple linear regressions and gray shading represents the 95% confidence intervals. Regression equations, R^2 values, and *P*-values were calculated using simple linear regression.

Figure 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.

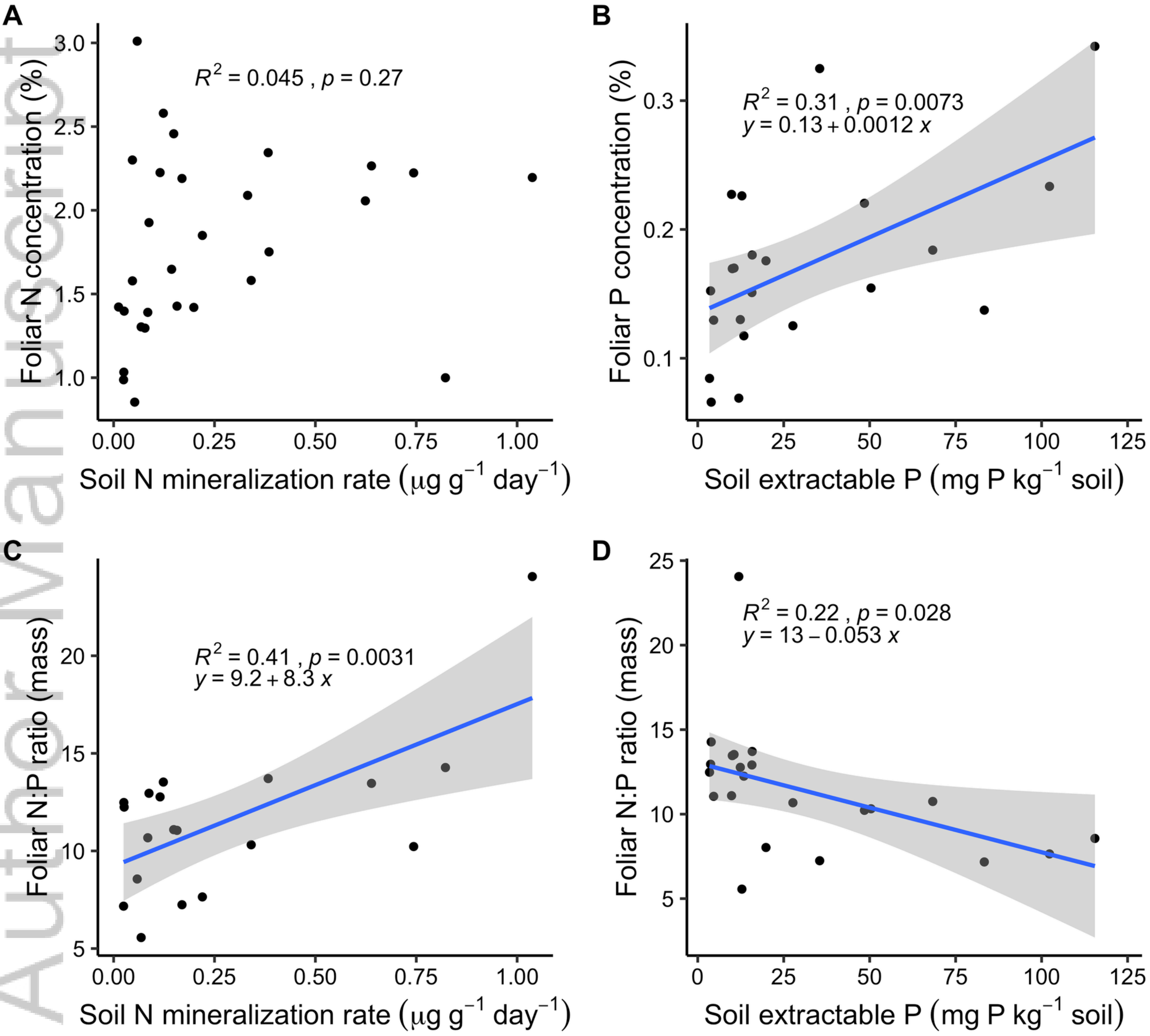
Figure 3. Variance partitioning between site and taxonomic effects for each foliar chemistry variable (foliar N, P, C:N, N:P, and C:P). Variance partitioning was calculated using a nested random effects model with two random effects: 1) site and 2) family, genus, and species as a nested variable.

Figure 4. Relative importance of climate (green bars) and soil (brown bars) variables in explaining: (A) foliar N; (B) C:N (B); (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 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.

Figure 5. Boxplots showing foliar N concentrations in: (A) *A. rubrum*; (B) *L. styraciflua*; (C) *L. tulipifera*; (D) *Q. alba*; and (E) *Q. 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 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.



ECY_3909_Fig1.png



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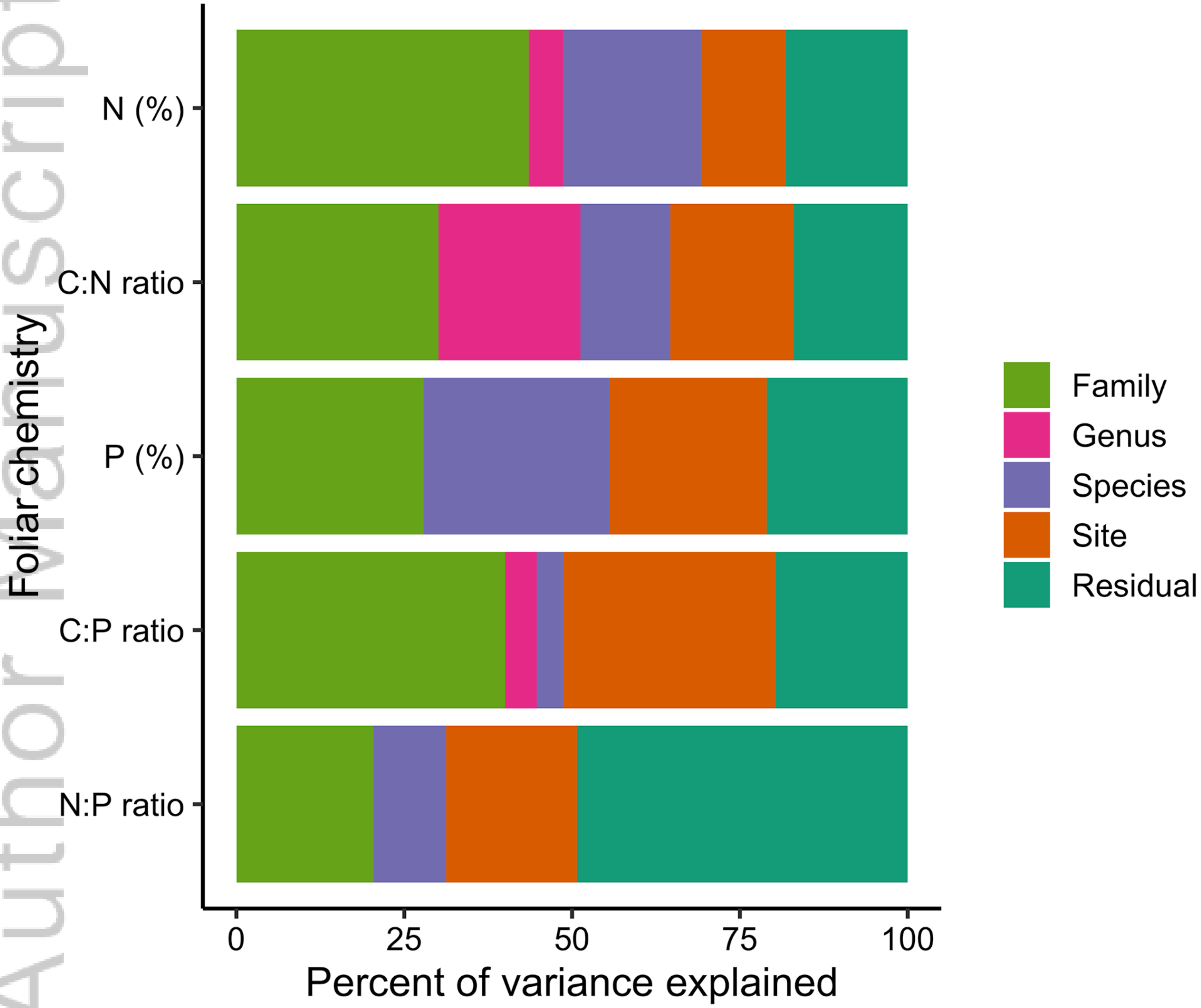

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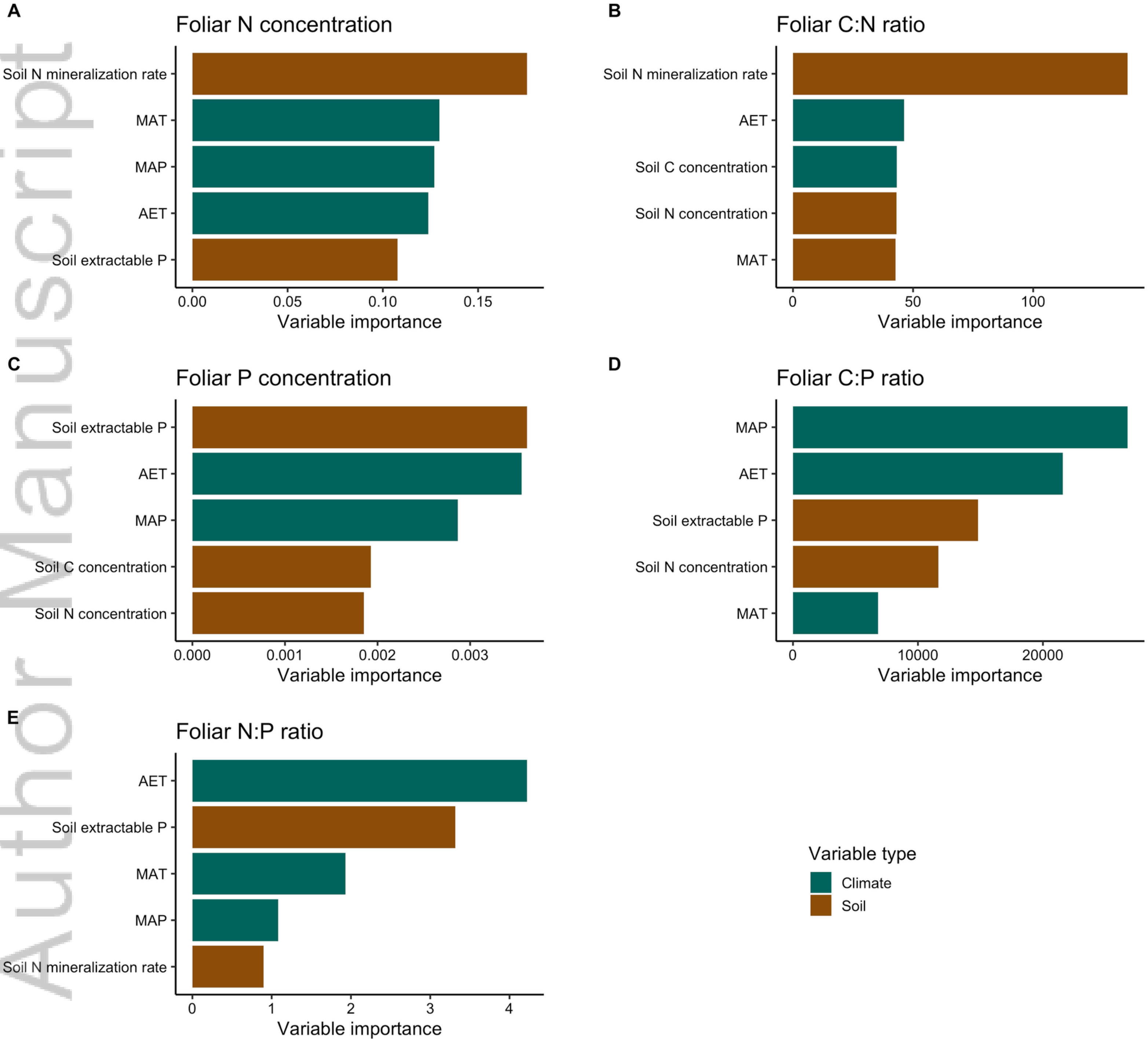

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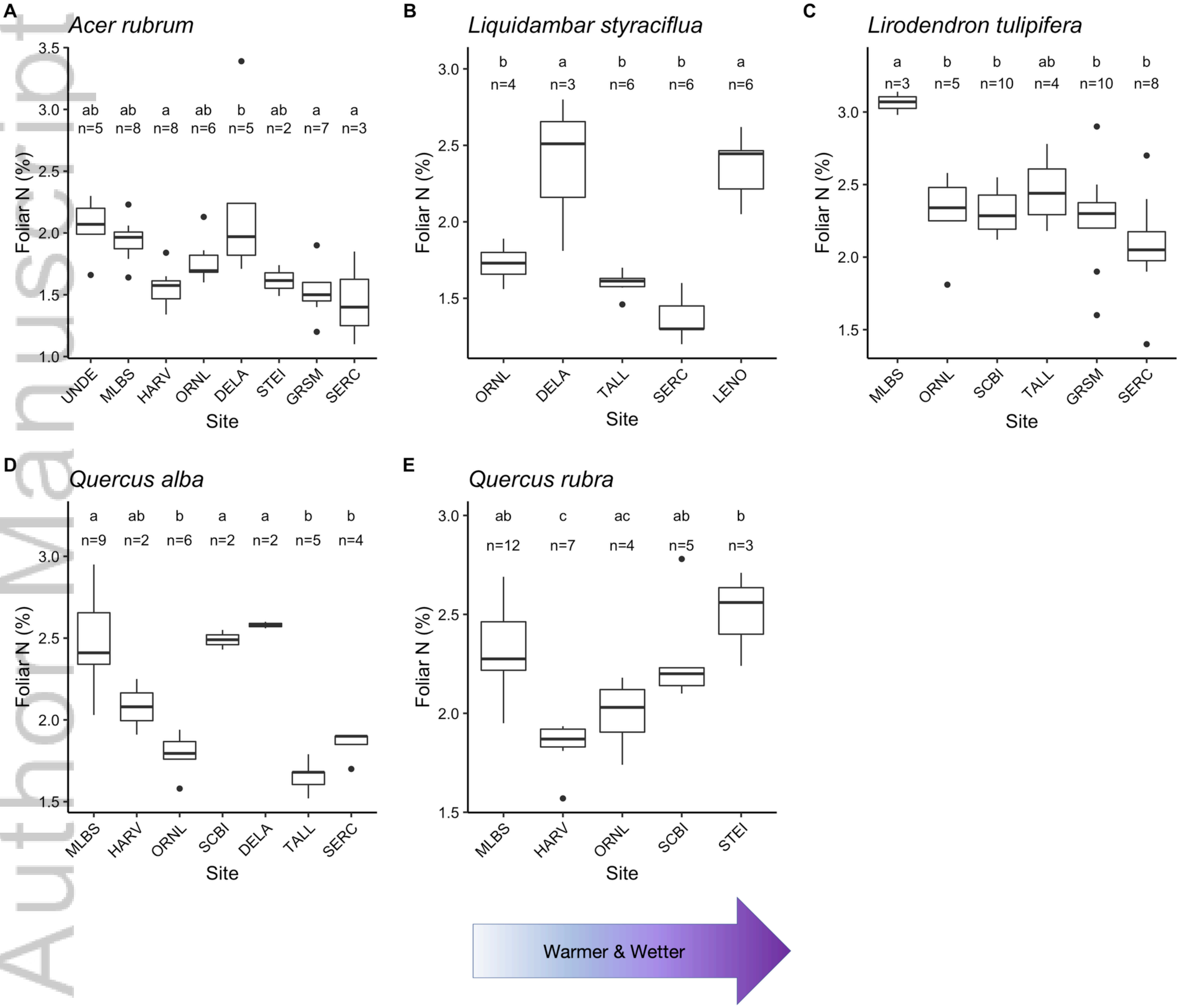

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