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Quantifying foliar trait variation and covariation in sun and shade leaves using leaf spectroscopy in eastern North America

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ABSTRACT

Characterizing foliar trait variation in sun and shade leaves can provide insights into inter- and intra-species resource use strategies and plant response to environmental change. However, datasets with records of multiple foliar traits from the same individual and including shade leaves are sparse, which limits our ability to investigate trait-trait, trait-environment relationships and trait coordination in both sun and shade leaves. We presented a comprehensive dataset of 15 foliar traits from sun and shade leaves sampled with leaf spectroscopy, including 424 individuals of 110 plant species from 19 sites across eastern North America. We investigated trait variation, covariation, scaling relationships with leaf mass, and the effects of environment, canopy position, and taxonomy on trait expression. Generally, sun leaves had higher leaf mass per area, nonstructural carbohydrates and total phenolics, lower mass-based chlorophyll a + b, carotenoids, phosphorus, and potassium, but exhibited species-specific characteristics. Covariation between sun and shade leaf traits, and trait-environment relationships were overall consistent across species. The main dimensions of foliar trait variation in seed plants were revealed including leaf economics traits, photosynthetic pigments, defense, and structural traits. Taxonomy and canopy position collectively explained most of the foliar trait variation. This study highlights the importance of including intra-individual and intra-specific trait variation to improve our understanding of ecosystem functions. Our findings have implications for efficient field sampling, and trait mapping with remote sensing.

1. Introduction

Plant traits reflect the ways plants influence and are being influenced by their environment (Lavorel and Garnier, 2002; McGill et al., 2006; Pérez-Harguindeguy et al., 2013). Trait variation can result from many factors including evolutionary and environmental drivers across scales (Oliveras et al., 2020; Maynard et al., 2022; Thomas, 2022), differences in community composition (Messier et al., 2010; Vilà-Cabrera et al., 2015), genetic variation within species (Anderegg et al., 2018; Fajardo and Siefert, 2018), stress responses (Skelton et al., 2015; Niinemets, 2016), and a combination of these factors (Ustin et al., 2004; Messier et al., 2017). Trait based ecology provides a framework to generalize patterns of species distribution (Wright et al., 2004; Moles et al., 2014; Vilà-Cabrera et al., 2015; Díaz et al., 2016), community assembly (Lavorel and Garnier, 2002; McGill et al., 2006; Laughlin, 2014), and ecosystem-level gross primary productivity (Ollinger et al., 2008; He et al., 2023; Huxley et al., 2023), which are key components for modeling global biogeochemical cycles (van Bodegom et al., 2014; Rogers et al., 2017). As plants with dissimilar traits tend to use resources, including water, nutrients, and light, differently and together more completely (Tilman et al., 1997), the variation in plant traits within communities provides the basis for calculating functional diversity metrics (Díaz and Cabido, 2001; Liu et al., 2024). Moreover, such trait variation can be used to predict ecosystem functions across spatial scales (Jetz et al., 2016; Miedema Brown and Anand, 2022; Butler et al., 2022).

Important foliar traits for understanding and predicting plant community composition, resource partitioning, ecosystem function, and biogeochemical cycles are leaf nitrogen (N) concentration and leaf mass per area (LMA) (Dong et al., 2017; Kattge et al., 2020). In addition, leaf pigments, macro-nutrients, structural and non-structural carbon (C), and phenolics are important for resource uptake, allocation, and sequestration. Structural carbon components, including cellulose and lignin, play

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critical roles in biomechanics and water transport at the plant level (Barros et al., 2015; Grantham et al., 2017), as well as in litter decomposition and nutrient turnover at the ecosystem level (Melillo et al., 1982; Cornwell et al., 2008; Fortunel et al., 2009). Non-structural carbon components, including sugars and starches, which are direct products of photosynthesis, provide energy for plant growth (Chapin, 1991) and a reserve of carbon for plants under conditions of environmental stress (Signori-Müller et al., 2022), while phenolic compounds, which comprise a broad range of secondary metabolites, help plants defend against herbivores and pathogens (Taiz and Zeiger, 2010; Xiao et al., 2024). Chlorophyll and carotenoid pigments are critical for light harvesting during photosynthesis. Xanthophylls – the group of carotenoids containing oxygen atoms – can dissipate excess light to provide photoprotection under high illumination (Demmig-Adams and Adams, 2006; Croft and Chen, 2018). Macro-nutrients, including phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca) and sulfur (S), have important regulatory function in photosynthesis, respiration, and plant growth (Taiz and Zeiger, 2010), while leaf water content is critical for many physiological processes, including photosynthesis, nutrient transport, transpiration, and respiration (Teulat et al., 1997; Galmés et al., 2007).

Plants adjust resource use and growth along light gradients within the canopy through variation in foliar traits (Niinemets, 2007; Poorter et al., 2019). A key acclimatization to canopy gradients is increasing leaf photosynthetic capacity (A_{max}, the maximum net C assimilation rate per unit area, $\mu mol \cdot m^{-1} \cdot s^{-1}$) with long-term light availability, although this is limited by architectural constraints, herbivory, CO_2, and water availability (Niinemets et al., 2015). Within these limits, A_{max} scales with N per unit area (N_{area}) because proteins for carbon fixation (ribulose-1, 5-bisphosphate carboxylase/oxygenase; Rubisco) and electron transport (cytochrome f) are costly to produce and require N which is often limited in supply (Field, 1983). Generally, plants can increase N_{area} through investments in LMA and N per unit mass (N_{mass}). Sun and shade leaves mark the endpoints of a continuum in leaf adaptions from full sun to full shade (Niinemets, 2007; Valladares and Niinemets, 2008). Sun leaves are generally smaller and have higher LMA than shade leaves (Givnish, 1988; Niinemets, 2007; Durand et al., 2022). Their long palisade cells increase the space per unit area available for chloroplasts (Lichtenthaler et al., 1981; Niinemets, 2007). At high light, sun leaves photosynthesize more and reach light saturation more gradually and at higher irradiance than shade leaves (Lichtenthaler et al., 1981). Higher photosynthetic rate under high light also allows sun leaves to dissipate heat more efficiently than shade leaves (Givnish, 1988; Niinemets, 2007), while a more robust and waxy cuticle reduces water loss and increases specular reflectance at high light. Although, A_{max} and N_{mass} decrease with decreasing light availability (Chen et al., 1993; Niinemets et al., 2015), shade leaves show a series of adaptations to offset this decline, allowing them to exceed the A_{max} of sun leaves when both leaf types experience low light (Lichtenthaler et al., 1981). Shade leaves are often larger and thinner (lower LMA) than sun leaves, and they have a higher proportion of spongy mesophyll cells, which increases path length through light scattering within leaves and thus the probability of photon absorption by chlorophyll (Lichtenthaler et al., 1981; Poorter et al., 2019). In addition, shade leaves can increase A_{max} by investing relatively more N into chlorophyll per chloroplast compared to sun leaves (Lichtenthaler et al., 1981; Niinemets, 2007).

In addition to these general patterns, plant functional and economic types differ in their responses to canopy light gradients (Niinemets et al., 2015). While fast growing species with high leaf turnover tend to actively increase A_{max} at high light by increasing C-fixation and electron transport through N re-allocation to rate-limiting proteins (Chen et al., 1993), slow growing species with long-lived leaves tend to increase A_{max} passively by investing more resources in leaf thickness, which increases LMA and the space per unit area for chloroplasts (Niinemets et al., 2015). Plant functional types broadly map onto this gradient with forbs located at the fast-growing end of the leaf economic spectrum (Wright et al., 2004; Maynard et al., 2022), with low LMA but high N_{mass} and A_{max}, followed by grasses, winter-deciduous and evergreen broadleaved trees, and conifers located on the slow-growing end of the spectrum, with high LMA but low N_{mass} and A_{max} (Niinemets et al., 2015; Díaz et al., 2016).

These distinctions are important for calibrating land surface models (LSMs). For example, it has been shown that LSMs based on a "two-leaf" or "multilayer" model, which take differences in A_{max} between sun and shade leaves into account, provide more accurate estimations of gross primary production (GPP) than LSMs based on a "big-leaf" model, which only considers A_{max} of sun leaves (Wang and Leuning, 1998; Thornton and Zimmermann, 2007; Coble et al., 2016; Bonan and Doney, 2018). In addition, it has been shown that accounting for horizontal as well as vertical variation in foliar traits by using site-specific trait distributions instead of single mean values per functional type further increases the accuracy of GPP estimates (Butler et al., 2022).

Due to the fundamental importance of photosynthesis in plant physiology, there is a large body of literature dealing with differences in photosynthesis traits, including structural (LMA) and chemical (N_{mass}, N_{area}) controls, between sun and shade leaves (reviewed e.g., in Niinemets et al., 2015). However, studies have also found considerable increases in foliar contents of macro-nutrients, carbon compounds, defense and stress avoidance traits with increasing sun exposure (Martin et al., 2020; Paź-Dyderska et al., 2020; Schweiger et al., 2020). Understanding the variation in these traits across many species would allow characterizing ecosystem processes, including nutrient and water cycling, more completely. In addition, there is limited data to test trait covariation, as datasets with records of multiple foliar traits from the same plant (and including shade leaves) are sparse (Jetz et al., 2016; Chauvin et al., 2018; Kattge et al., 2020; Martin et al., 2020). This limits our ability to investigate trait-trait and trait-environment relationships, and thus to predict trait responses to environmental change.

Characterization of foliar trait variations across the sun to shade continuum is also important for remote sensing. Imaging spectroscopy, also called hyperspectral remote sensing, allows mapping foliar traits across large areas (Asner et al., 2015; Singh et al., 2015; Martin et al., 2018; Wang et al., 2020), but it likely generates biased estimates at the canopy scale when intra-individual trait variation is unaccounted for. For example, Gara et al. (2019) found that including area-based foliar traits from different canopy layers improved their prediction because canopy reflectance integrates signals from different canopy layers. In addition, Li and Wang (2013) and Wang and Li (2013) showed that including the vertical distribution of foliar traits, such as LMA and equivalent water thickness (EWT), improves the accuracies in modeling radiative transfer processes.

Traditional measurements of foliar traits rely on destructive sampling and laboratory chemical analysis. Leaf spectroscopy can provide narrowband reflectance by measuring the absorbing and scattering of radiation within leaves, which includes valuable information to infer foliar traits (Jacquemoud et al., 2009; Serbin et al., 2019; Féret et al., 2021). Leaf spectroscopy offers a novel and efficient approach of obtaining multiple leaf morphological and biochemical traits across species, growing seasons and geographic areas, including leaf mass per area, water, pigments, cellulose, lignin, nonstructural carbohydrates, phenolics, nitrogen and phosphorus (Yang et al., 2016; Chen et al., 2022; Wang et al., 2023). The use of leaf spectroscopy can obtain concurrent measurements of an extensive set of foliar traits and facilitate studies of trait variation within species and individuals (Serbin et al., 2014; Schweiger et al., 2018; Wang et al., 2022). The goal of this study is a comprehensive assessment of foliar trait variation and covariation for sun and shade leaves of common trees and shrubs across eastern North America. We use contact spectroscopy to measure a total of 15 foliar traits of fresh and dried sun and shade leaves across 110 plant species with the specific objectives to: (1) evaluate trait variation for sun and shade leaves; (2) assess trait correlations and trade-offs for sun and shade leaves; (3) analyze trait-environment relationships, including the effects of canopy position and taxonomy on trait expression, for sun and shade leaves. Characterizing foliar trait variation in sun and shade leaves will provide insights

into differences in inter- and intra-species resource use strategies and contribute to describing global biochemical cycles and radiative transfer within canopies more accurately.

2. Materials and methods

2.1. Study area

The long-term National Ecological Observatory Network (NEON) operates field sites across the United States covering 20 ecoregions (domains) characterized by different climate and environmental conditions (Kampe et al., 2011; Kao et al., 2012). For terrestrial ecosystems, three or four 10 km × 10 km sites can be found in each domain. Each site is equipped with an eddy covariance flux tower and NEON routinely collects a series of measurements, including inventories of vegetation, soil, and animal communities. In addition, NEON collects hyperspectral imagery at each site in most years, which motivated our collection of foliar traits (Wang et al., 2020). We conducted our field campaigns at peak greenness across 19 sites situated in seven domains in the summer of 2017 (Fig. 1). Peak greenness periods were determined by identifying end-of-spring (>90%) and start-of-fall (>90% or 80%) phenophase transition dates in the enhanced vegetation indices (EVI) time series from the MODIS sensor onboard NASA's Terra and Aqua satellites. In total, we sampled 424 individuals covering 110 woody plant species, including deciduous broadleaf trees (n = 340), evergreen conifer trees (n = 64), and shrubs (n = 20). The sampled trees or shrubs were densely leaved with a canopy cover of over 75%. Shrubs were all from open areas without trees growing above them. We collected branches and leaves from both the sunlit top of canopy and the lowest shaded inside canopy layer from each individual tree or shrub, defined as "sun" and "shade" leaves, respectively. We used a shotgun, line-launcher or pole pruner to collect the top canopy sunlit branches of trees. Although the intercepted sun radiation was not measured for the sampled shade leaves with PAR (photosynthetically active radiation) sensors due to logistic reasons, we obtained the gap fraction at the lowest canopy to characterize the light environment using airborne LiDAR data. We also extracted the fPAR (fraction of photosynthetically active radiation) from the airborne directional surface reflectance. The low gap fraction and high fPAR (with a mean of 0.116 and 0.633, respectively) indicated that the leaves from the lowest inside canopy can be approximated as fully shaded leaves. For both sun and shade needles of conifer species (except for deciduous species tamarack (*Larix laricina*) and bald cypress (*Taxodium distichum*)), we split them to growth of the current year and earlier years. The old needles were mostly collected from growth of the previous year except for a few species (eastern hemlock, *Tsuga canadensis*; western hemlock, *Tsuga heterophylla*; black spruce, *Picea mariana*) that required needles from multiple ages to obtain enough tissues for chemistry analysis. For each species, we sampled 1–25 individuals (3.8 ± 3.6; Table S1).

2.2. Leaf spectroscopy and trait measurements

We measured leaf spectra of fresh and dried foliar samples using an ASD FieldSpec 3 spectrometer and a leaf contact probe (Malvern Panalytical Ltd, Malvern, UK). Fresh leaf spectra of broadleaf trees and

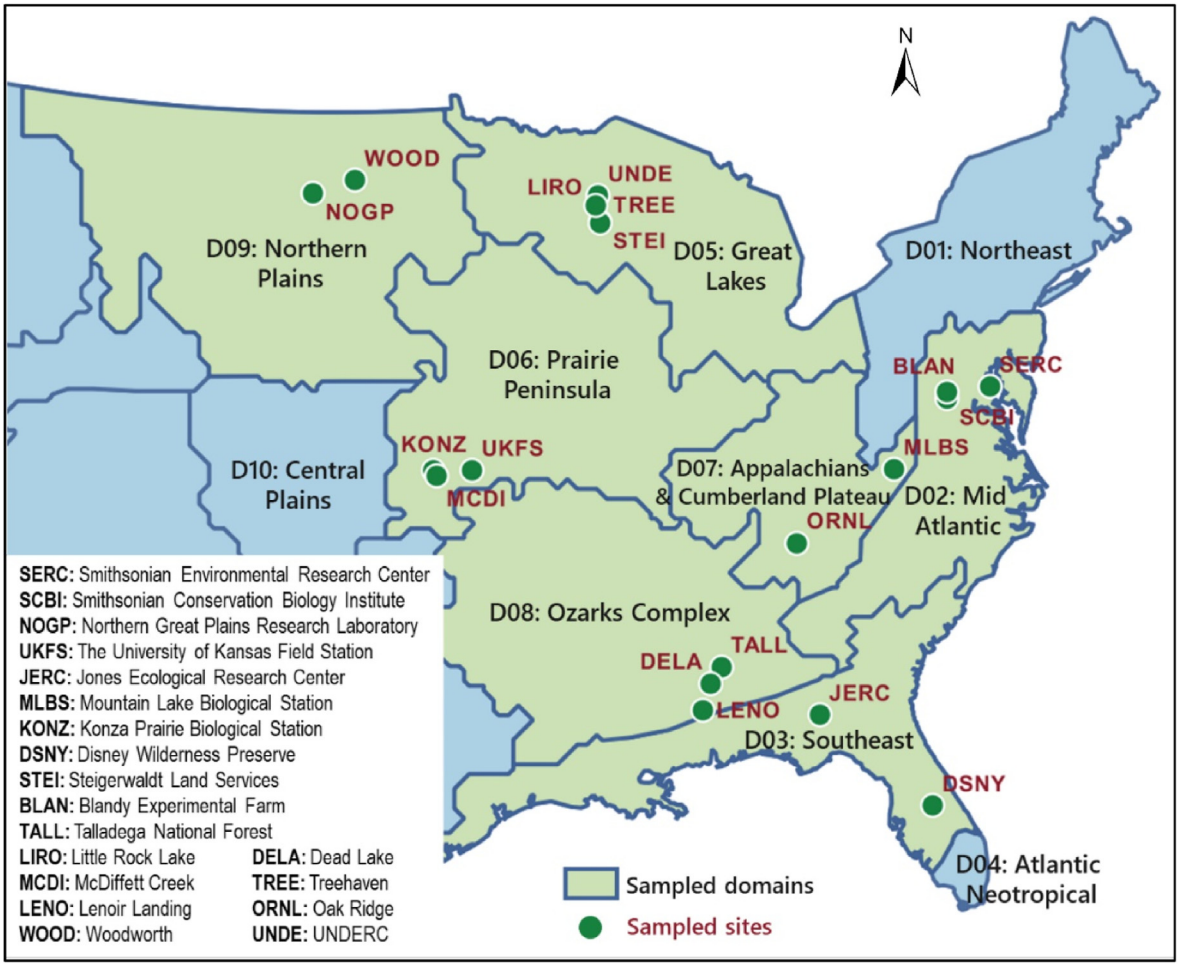

Fig. 1. Locations of the 19 field sites across seven domains of the National Ecological Observatory Network (NEON) domains in eastern North America sampled in 2017.

shrubs were collected using the ASD FieldSpec 3 spectrometer (Malvern Panalytical Ltd, Malvern, UK) and its leaf contact probe with an external light source. For conifer species, we clipped needles to ~1 cm length, and stacked them to 2 cm deep in a black cup, and measured the infinite reflectance. Dry leaf spectra were measured on the dried and ground material using the ASD FieldSpec 3. Details of the spectral measurements can be found in Wang et al. (2020). We recorded the total leaf area of fresh leaves immediately after collection using a flatbed scanner (Epson, Nagano, Japan). A subset of the samples was flash-frozen in liquid N in the field and used to determine the concentrations of pigments, sugars, starches, and total phenolics in the lab. Pigments were determined by high-performance liquid chromatography (HPLC) with details in Schweiger et al. (2018). Sugars and starches were analyzed following the protocols in Prado (1998) and Lindroth et al. (2002), while total phenolics following Ainsworth and Gillespie (2007) and Makkar et al. (2007). After measuring the spectra of fresh leaves, we recorded their fresh weight (precision 0.001 g). Leaves were then oven-dried at 65 °C for 48 h and reweighed for dry mass. Next, we measured the spectra of the dried and ground leaf samples. Leaf mass per area (LMA, $g{\cdot}m^{-2}$) was calculated as dry mass/leaf area. Equivalent water thickness (EWT, $g{\cdot}m^{-2}$) was calculated as (fresh mass – dry mass)/leaf area. Leaf dry matter (LDMC, %) was calculated as dry mass/fresh mass. Cellulose ($mg{\cdot}g^{-1}$), lignin ($mg{\cdot}g^{-1}$), C ($mg{\cdot}g^{-1}$), N ($mg{\cdot}g^{-1}$), P ($mg{\cdot}g^{-1}$), and K ($mg{\cdot}g^{-1}$) were analyzed using sequential digestion and elemental analysis, respectively (for details see Wang et al., 2020). To assess scaling effects with LMA and differences in the responses of species to within-canopy light gradients, we expressed all chemical traits also on an area basis ($mg{\cdot}m^{-2}$) by multiplying their mass-basis traits ($mg{\cdot}g^{-1}$) with LMA.

On average, 187 leaf samples (around 23% of all samples) were chemically analyzed and used to build leaf trait models from spectra. Leaf samples were chosen to capture the range and variation of foliar traits by covering the sampled species and field sites. The foliar traits of the remaining samples were predicted from fresh and dry leaf spectra (Section 2.3), and the spectrally predicted foliar traits were used for later analysis.

2.3. Prediction of leaf traits from spectra

All values of LMA, LDMC and EWT reported here were obtained using field measurements. For the remaining foliar traits, we developed partial least squares regression (PLSR) models to predict traits from fresh or dry spectra. We used different protocols for measuring fresh leaf spectra of broadleaf and conifer species (Wang et al., 2020), thus separate PLSR models were developed for the two leaf types. PLSR transposes the original data into a new coordinate system using latent factors based on the covariance between the response and the predictor variables (Wold et al., 1983) and has been widely used to estimate foliar traits from leaf spectra (Asner et al., 2011; Schweiger et al., 2018; Serbin et al., 2019; Wang et al., 2022).

PLSR models were developed using fresh leaf spectra from 400 to 2,400 nm for pigments and total phenolics. For C, N, P, K, cellulose, lignin, and non-structural carbohydrates (NSCs = sugars + starches), we developed PLSR models from dry leaf spectra, due to the negative effect of water absorption on model performance (Wang et al., 2020). Dry spectra models were built using wavelengths from 1,400 to 2,400 nm since the absorption features of those foliar traits were mainly located in the shortwave infrared region (Curran, 1989; Fourty et al., 1996). For each trait, the original dataset was first split into calibration (70%) and external validation (30%) subsets. Then, we permuted the calibration data 200 times by randomly selecting 70% of the calibration data to build 200 PLSR models, the remaining 30% of the calibration data were used for model testing (or internal validation). To avoid overfitting, we determined the number of latent factors by minimizing the Prediction Residual Error Sum of Squares (PRESS; Chen et al., 2004).

Model performance was evaluated based on the external validation dataset using the coefficient of determination (R^2) and the normalized root mean squared error (NRMSE = normalized root mean squared error/range) between measured and estimated foliar traits (Table S2). The 200 PLSR models developed on the calibration subset were applied to fresh and dry leaf spectra to predict foliar traits. We calculated the mean and standard deviation (a measure of relative uncertainty) of the predictions and removed predictions which exceeded the range of field measurements by 25% [$\text{trait}_{min} - |\text{trait}_{min}| \times 25\%$, $\text{trait}_{max} + |\text{trait}_{max}| \times 25\%$], or which had relative uncertainties of over 30%. In general, a high proportion of records (ranging from 72% to 97% with a mean of 92.9%) were kept for the following analysis.

2.4. Environmental data

We determined the latitude, longitude and elevation of each sampling location using a differential GPS (Trimble Geo 7X, Trimble Inc., Sunnyvale, USA). Then, for each location, we derived mean annual temperature (MAT) and mean annual precipitation (MAP) averaged for the years 1970–2000 using the data from WorldClim (version 2.1; Fick and Hijmans, 2017) with a spatial resolution of 1 km.

2.5. Statistical analysis

We compared the spectrally predicted foliar traits of sun and shade leaves for all species combined as well as for each species separately using Student's *t*-test and the Wilcoxon rank-sum test. We assessed the scaling effect of LMA and mass-based traits to area-based traits by partitioning the trait variation using a response coefficient analysis (Poorter and Nagel, 2000; Niinemets et al., 2015). We used ordinary least squares regression to explore trait co-variation between sun and shade leaves for all species combined and for each functional group, broadleaved trees, conifers, and shrubs, separately. All foliar trait values were log-10 transformed and *z*-scaled (mean = 0, SD = 1) to ensure normal distributions. We also evaluate bi-trait relationships for sun and shade leaves, separately, and the pooled dataset, using Pearson's correlation coefficient (*r*), and the slope and intercept of standardized major axis (SMA) regression for each pair of traits. We used a likelihood ratio and Wald statistic to test for differences in SMA slopes and intercepts between sun and shade leaves. To assess multi-trait co-variation, we performed principal component analysis (PCA) of the foliar traits for sun leaves, shade leaves and for the pooled dataset.

We assessed trait-environment relationships first, by calculating the correlation between foliar traits and environmental variables (MAT, MAP, and elevation) for sun leaves, shade leaves and for the pooled dataset. Then, we implemented a generalized linear mixed model (GLMM) using the environmental variables as fixed effects, and canopy position nested within species, nested within family as random effects to investigate the sources of variations in foliar traits. We used the marginal and conditional R^2 values to differentiate between the variance explained by fixed effects and random effects, respectively.

All analysis was performed in R v.3.6.1 (R Core Team, 2019). For SMA, PCA, and GLMM, we used the LMODEL2 package (Legendre, 2018), the *prcomp* function from the stats package (R Core Team and contributors worldwide, 2019), and the LME4 (Bates et al., 2015) and *MuMIn* packages (Nakagawa and Schielzeth, 2013), respectively.

3. Results

3.1. Prediction of multiple foliar traits using leaf spectroscopy

Fresh and dry leaf spectra showed considerable variation between sun and shade leaves (Fig. 2). For sun leaves, the fresh leaf spectra were higher in the near infrared region (NIR) because of multiple scattering in thicker leaves. In contrast, the fresh leaf spectra of sun leaves were lower in the short-wave infrared region (SWIR) due to absorption of higher dry matter and water content. Similarly, the dry leaf spectra in the SWIR

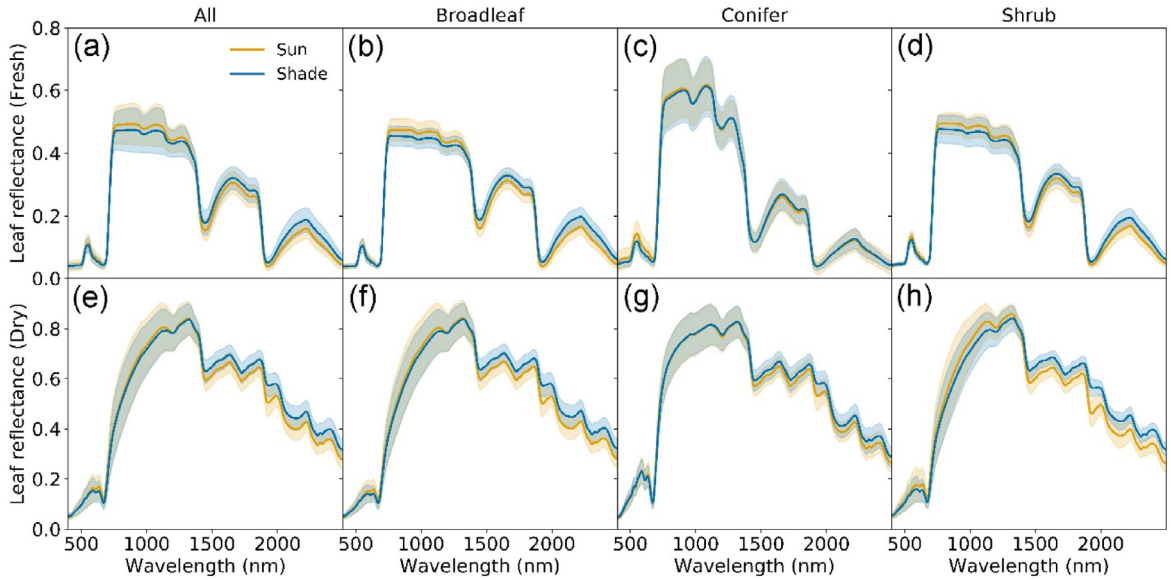

Fig. 2. Fresh and dry leaf reflectance (mean ± standard deviation) of sun and shade leaves for pooled dataset, broadleaf trees, conifers and shrubs. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

were lower in sun leaves. Leaf spectra accurately predicted the 15 foliar traits with NRMSE ranging from 5.70% to 23.53% (Table S2). Carbon, cellulose, lignin, nonstructural carbohydrates, N, P and K were most accurately estimated from dry leaf spectra with R^2 varying from 0.70 to 0.92. Pigments and phenolics were accurately predicted for broadleaf trees and shrubs from fresh leaf spectra (R^2 = 0.61–0.83), and moderately predicted for conifer species (R^2 = 0.33–0.69). The following results were obtained from the spectrally predicted foliar traits.

3.2. Trait variation in sun and shade leaves

Overall, we found that sun leaves had higher LMA ($g{\cdot}m^{-2}$) and EWT ($g{\cdot}m^{-2}$) than shade leaves (Fig. 3, Table S3), while mass-based N ($mg{\cdot}g^{-1}$) concentration and area-based chlorophyll ($\mu g{\cdot}cm^{-2}$) showed little variation between the two leaf types. Mass-based chlorophyll and carotenoids ($mg{\cdot}g^{-1}$) were lower in sun than shade in leaves. Also, the concentrations of P, K, and lignin ($mg{\cdot}g^{-1}$) were lower in sun than shade leaves, while C and cellulose concentrations ($mg{\cdot}g^{-1}$) were similar in both leaf types, and the concentrations of phenolics ($mg{\cdot}g^{-1}$) and NSC ($mg{\cdot}g^{-1}$) were higher in sun than in shade leaves. We also assessed species-specific trait differences between sun and shade leaves for species with at least 4 measured individuals (Table S4). Most area-based traits were higher in sun than shade leaves (Fig. S1), although the number of species with significantly higher trait values in sun leaves varied (Fig. 4, Table S4). The scaling effect of LMA was generally lower for chemical compounds with low concentrations in leaf tissue compared to those with high concentrations (Fig. S2).

3.3. Trait covariation and coordination in sun and shade leaves

Looking at all functional types combined, traits of sun and shade leaves were highly correlated with R^2 values ranging from 0.54 to 0.92 (Fig. 5 and Table S5), except for area-based chlorophyll a + b (R^2 = 0.41) and area-based carotenoids (R^2 = 0.36) which correlated less. Most strongly correlated among sun and shade leaves was EWT (R^2 = 0.92). This means that plants with high water content in sun leaves tended to also have high water content in shade leaves. In most cases, foliar traits of sun and shade leaves showed higher correlations ($R^2 = 0.58 \pm 0.10$) for broadleaf trees compared to conifers ($R^2 = 0.46 \pm 0.22$), and shrubs (R^2 < 0.30 for mass-based carotenoids, mass-based chlorophyll a + b, LMA, Table S5, Fig. 5), but this could be an effect of the small number of observations in shrubs and the smaller range of trait values in conifers (Fig. 3).

Combining sun and shade leaves, we found a very strong positive correlation between mass- (r = 0.97) as well as area-based carotenoids and chlorophyll a + b (r = 0.92; Table S6, Fig. 6). Likewise, LMA and EWT, P and K, and P and N were strongly positively correlated (r ranging from 0.78 to 0.67), while LMA and mass-based chlorophyll ($r = -0.79$) as well as mass-based carotenoid content ($r = -0.78$) were strongly negatively correlated (Table S6, Fig. 6). Comparing bi-trait correlations between sun and shade leaves, we found that the SMA slope of the area-based carotenoids and chlorophyll a + b was significantly lower in sun than shade leaves ($P < 0.001$). The slope of the area-based chlorophyll a + b and N relationship was higher for shade leaves than sun leaves ($P < 0.01$). The slopes of the N-LMA regression were also different for sun and shade leaves (−0.71 vs. −0.62; $P < 0.05$). This can be attributed to LMA being higher in sun leaves than shade leaves while N concentration was similar. In contrast, the slopes of P-N, K-N, and phenolics-N were not significantly different, although P and K were higher in shade leaves and N was similar in both leaves. Phenolics and LMA were significantly correlated for shade leaves, but not for sun leaves.

The first 6 principal components (PCs) explained over 85% of the total trait variation (Table S7). PC1 was mainly influenced by LMA, N, P, and K concentration, and PC2 by EWT, chlorophyll a + b, and carotenoid content (Fig. 7). These two axes explained close to 50% of the total trait variation. PC3 was mainly influenced by chlorophyll a + b, EWT and N. PC4 was mainly influenced by cellulose and lignin. In the PC plots, the trait differences between sun and shade leaves can be still noticed, for example, higher concentrations of NSCs, phenolics, LMA and EWT, but lower concentrations of P and K in sun leaves compared to shade leaves (Fig. 5).

Environmental factors (MAT, MAP, and elevation) included in GLMMs explained 8% of the total variation in LDMC, 12% for area-based carotenoids, and 6% for area-based chlorophylls, while the fraction of total variance explained for all other traits was small (1%–4%, Table S8). In contrast, canopy position and taxonomy combined explained 86% and 87% of the total variance in EWT and LMA, respectively, and between 28% and 72% of the total variance of all other traits (Fig. 8, Table S8). Plant taxonomy (family and species identity) explained between 40% and 72% of the total variance for most traits, with family contributing more, except for pigments with only 26%–32% of the total variance explained. Canopy position explained 36% and 38% of the total variance

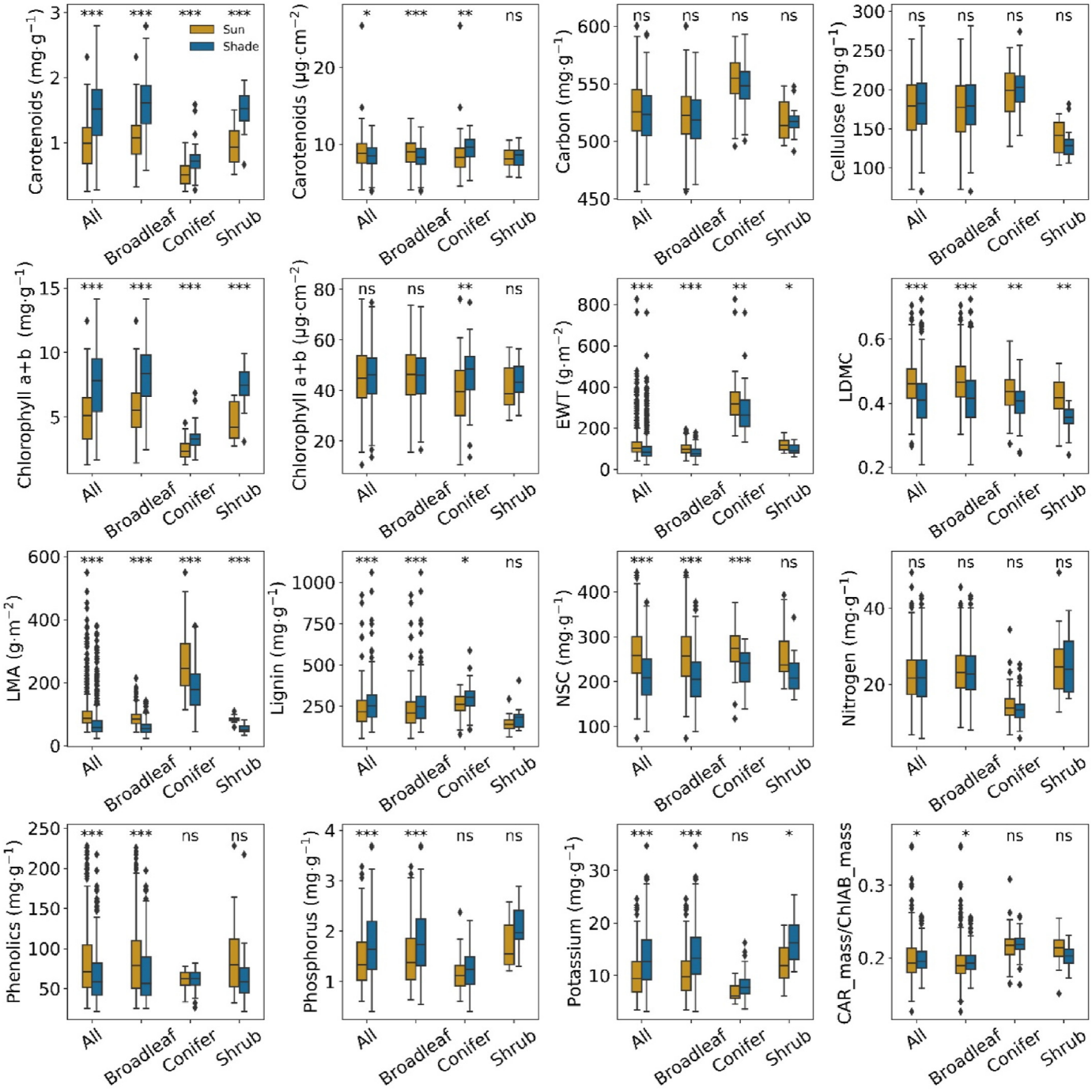

Fig. 3. Differences between foliar traits for sun and shade leaves. Significance levels are indicated by ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P \geq 0.05$. The abbreviations are EWT = equivalent water thickness, LDMC = leaf dry matter content, LMA = leaf mass per area, NSC = nonstructural carbohydrates, CAR_mass = mass-based carotenoids, ChlAB_mass = mass-based chlorophyll a + b. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in mass-based chlorophyll a + b and carotenoid content, respectively, as well as 32%, 25%, 20%, and 28% for LMA, NSC, LDMC, and K concentration, respectively. For all other traits, canopy position explained around 10% of the total variation, except for N, cellulose, and C concentrations, and area-based chlorophyll a + b and carotenoids, as those traits were similar in sun and shade leaves (Fig. 3).

3.4. Trait-environment relationships for sun and shade leaves

In summary, trait-environment relationships were consistent for sun and shade leaves, with few exceptions: mass-based carotenoids and area-based chlorophyll increased with MAT only in sun leaves, while K concentration decreased with MAT, and LMA decreased with MAP only in shade leaves (Fig. 9, Table S9). Regarding the potential effects of elevation on overall trait distribution, we found that chlorophyll contents on a mass and area basis, as well as EWT, and the concentrations of N and P increased with terrain elevation, while LDMC, and the concentrations of lignin and phenolics decreased with elevation. In line with this, we found that EWT, N, P, and K concentration decreased with MAT, while LDMC, and the foliar concentrations of C, cellulose, lignin, and phenolics increased with MAT. For MAP, we found an overall increase for foliar concentrations of C, cellulose, lignin, NSCs, and phenolics, while LMA

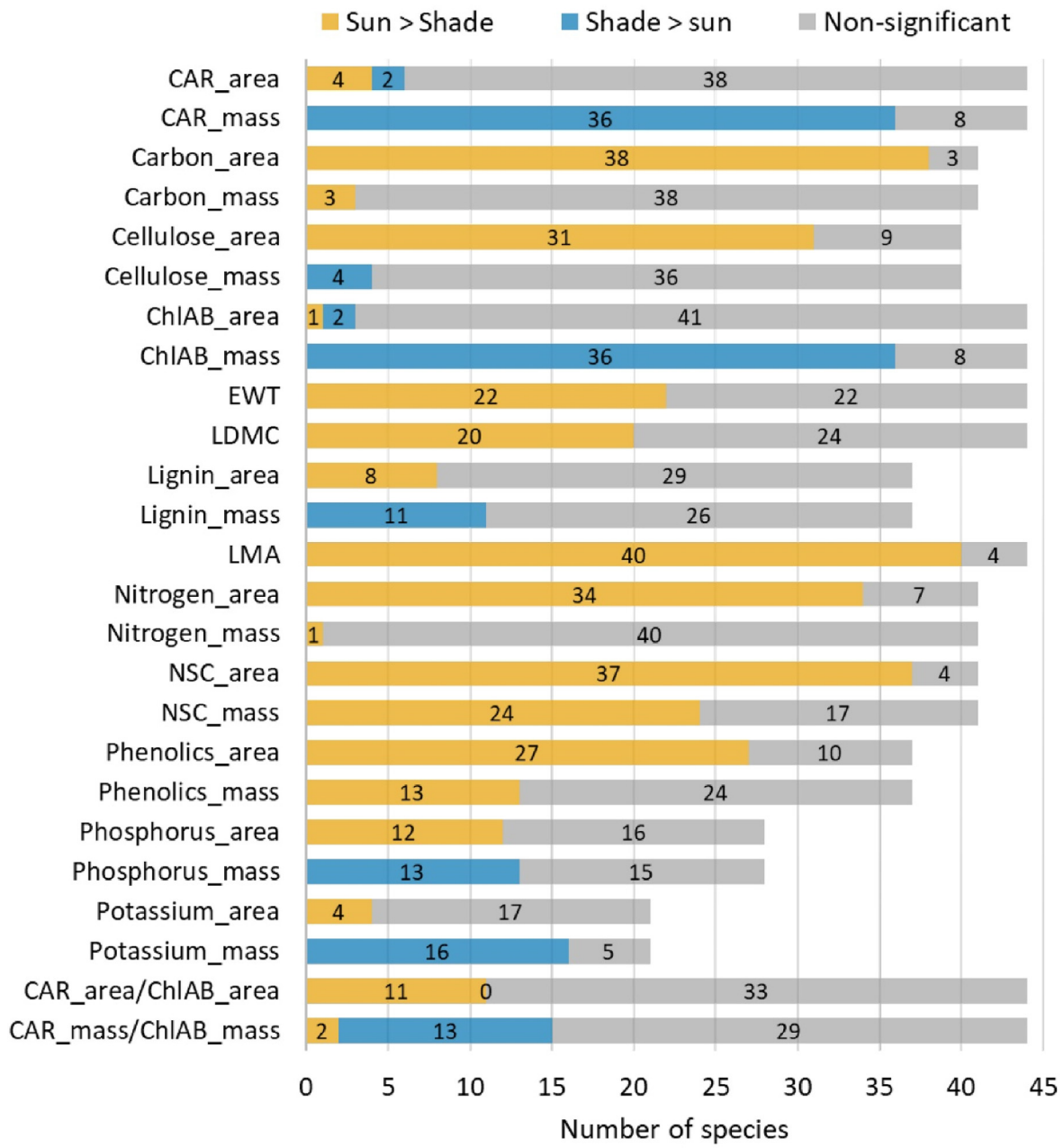

Fig. 4. Species-specific foliar trait variation in sun and shade leaves. Orange or blue colors denote the number of species with significantly higher trait values in sun leaves or shade leaves, respectively ($P < 0.05$, Table S4). Grey color denotes the number of species with non-significant differences. The abbreviations are ChlAB = chlorophyll a + b, CAR = carotenoids, EWT = equivalent water thickness, LDMC = leaf dry matter content, LMA = leaf mass per area, NSC = nonstructural carbohydrates. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and EWT, as well as N, P, and K concentrations decreased with MAP (Fig. 7, Table S9). The regression slopes between sun and shade leaf traits and environmental factors were only different for MAP and P ($P < 0.05$). The intercepts for most trait-environment relationships differed for the two leaf types (Table S9).

4. Discussion

We used a novel spectroscopy approach to obtain 15 foliar traits, analyzed differences between sun and shade leaves for 110 species across eastern North America, and assessed the variation, co-variation, and coordinated expression of the spectrally predicted foliar traits, including leaf economic traits (LMA, N), structural traits (LMA, LDMC, cellulose, C), defense traits (lignin, phenolics), stress response traits (NSCs, carotenoids), photosynthesis traits (chlorophylls, water), and macronutrients (N, P, K).

4.1. Variation of foliar traits in sun and shade leaves

Both the variation in area-based and mass-based foliar traits are important for understanding ecological variation and resource use in plants and plant communities (Lloyd et al., 2013; Westoby et al., 2013; Niinemets et al., 2015). Studies of plant growth and leaf economics generally use mass-based traits, since investment and return are typically expressed in units of mass (Hikosaka et al., 2004; Westoby et al., 2013). In contrast, studies of photosynthetic physiology focus on area-based traits, because light interception, CO_2 diffusion, and transpiration are generally measured as fluxes per unit leaf area (Lloyd et al., 2013;

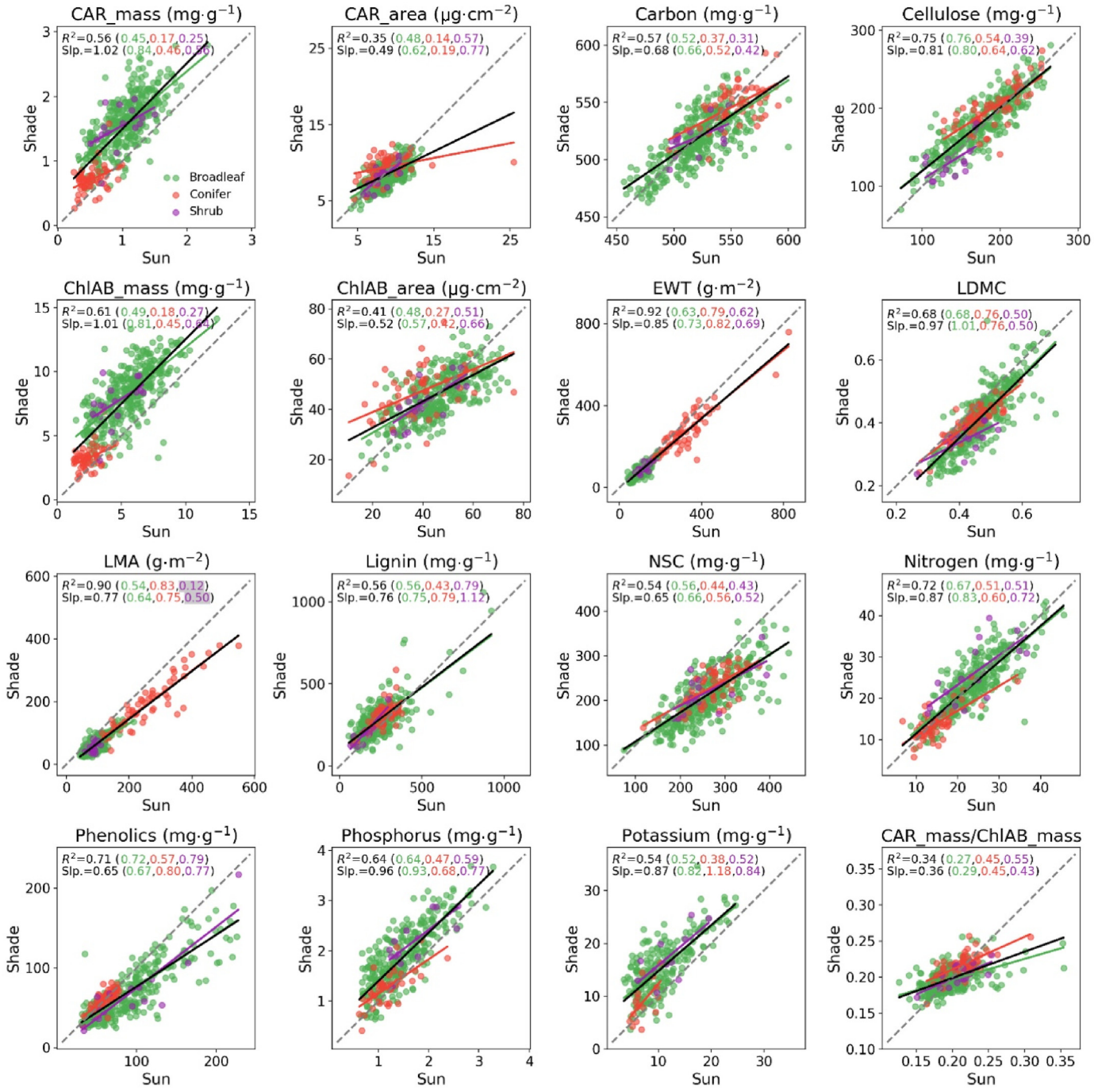

Fig. 5. Relationships between foliar traits of sun and shade leaves. Green, red, and purple lines are the regression lines for broadleaf trees, conifers, and shrubs, respectively. The grey dashed line is the 1:1 line. The black solid line is the regression line for pooled dataset. Slp. is the abbreviation for slope. The R^2 values in the brackets are the coefficients of determination for broadleaf trees, conifers, and shrubs, respectively. All correlations were significant at $P < 0.05$ (Table S5) except for LMA between sun and shade leaves in shrubs (highlighted in grey). The abbreviations are CAR_mass = mass-based carotenoids, ChlAB_mass = mass-based chlorophyll a + b, CAR_area = area-based carotenoids, ChlAB_area = area-based chlorophyll a + b, EWT = equivalent water thickness, LDMC = leaf dry matter content, LMA = leaf mass per area, NSC = nonstructural carbohydrates. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Westoby et al., 2013). From photosynthetic physiology we know that $A_{max} = E_N \times N_{area}$ (or $E_N \times N_{mass} \times$ LMA), where E_N represents photosynthetic N-use efficiency which varies widely at any given photosynthetic rate (Niinemets et al., 2015). A_{max} can be achieved by adjusting N_{mass} or LMA, but their relative controls on A_{max} varied by plant functional types. Species with high leaf turnover such as herbaceous species and grasses, adjust A_{max} mostly through within-canopy variation of N_{mass} by nitrogen reallocation. Species with low leaf turnover such as most trees, adjust A_{max} mainly through within-canopy variation of LMA by the acclimation of leaf structure to growth light (Niinemets et al., 2015). In contrast to N-allocation, which is a dynamic process, LMA can only be modified while leaves are developing. Therefore, structural optimization of leaves through variation of LMA is beneficial mostly for trees, as their leaves experience a relatively stable light environment during their lifetime. Corroborating this idea, 40 out of 44 woody species in our study showed higher LMA in sun compared to shade leaves and the remaining 4

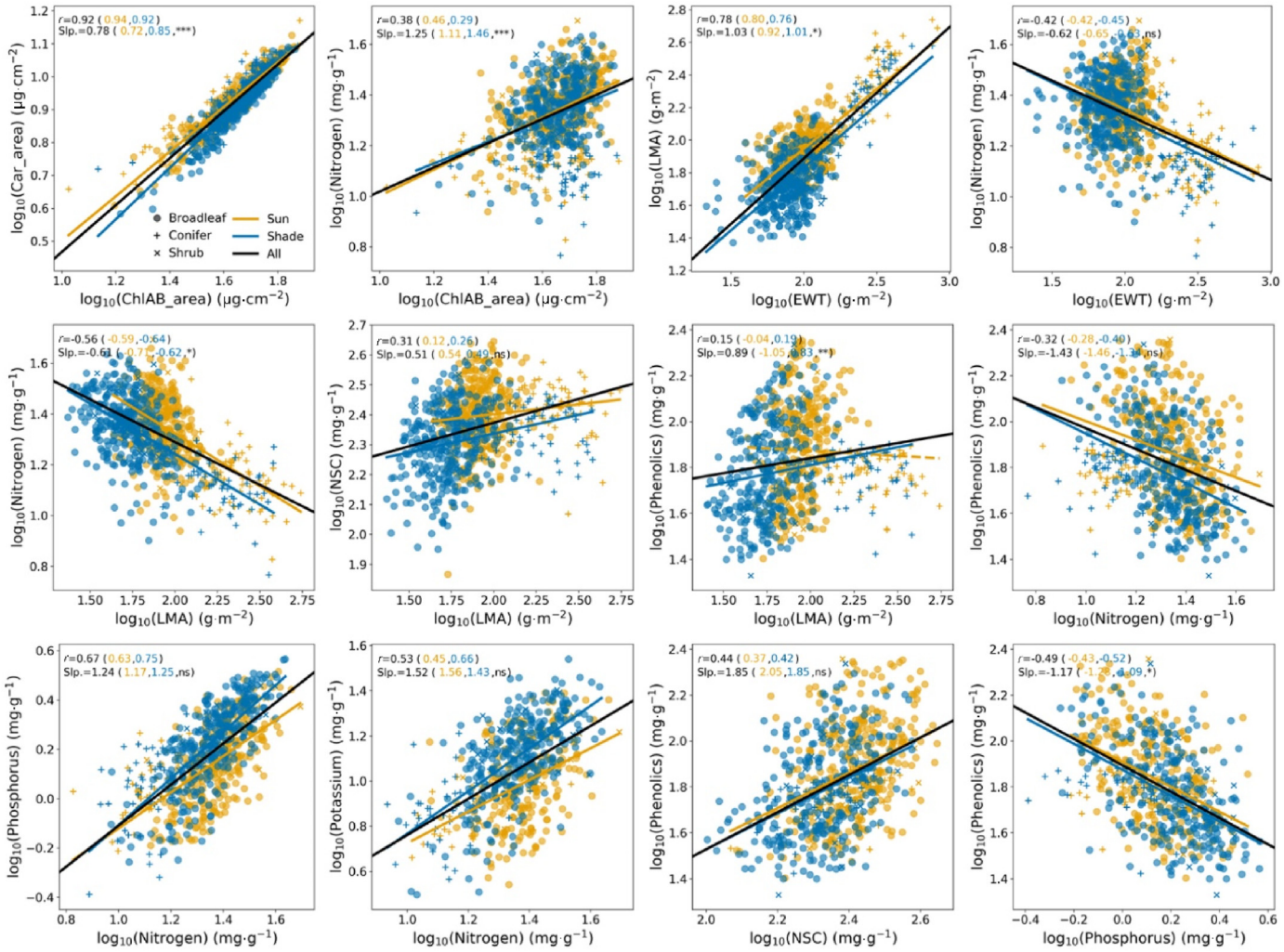

Fig. 6. Bi-trait relationships for sun (orange) and shade leaves (blue), and both leaf types combined (black). All relationships are significant at $P < 0.05$. Significance levels for differences among slopes for sun and shade leaves are indicated by ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P \geq 0.05$. The abbreviations are CAR_area = area-based carotenoids, ChlAB_area = area-based chlorophyll a + b, EWT = equivalent water thickness, LMA = leaf mass per area, NSC = nonstructural carbohydrates. For all pairs of trait relationships see Table S6. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

species showed no significant differences, while only one species, *Magnolia acuminata* (a fast-growing tree species), showed higher N_{mass} in sun leaves (Fig. 4).

We also quantified the contributions of mass-based traits and LMA to the variation in area-based traits and confirmed that the variation in area-based measurements of leaf chemistry arise largely through scaling with LMA (Ellsworth and Reich, 1993; Fig. S2). Plants in high light environments tend to have longer palisade cells and denser cell tissues to decrease evapotranspiration and increase photosynthesis leading to thicker leaves with higher LMA in full sun (Niinemets, 2007; Poorter et al., 2009). In terms of pigment content there exists a trade-off between the number of chloroplasts per unit area and the chlorophyll content per chloroplast. Across all 110 species used in our study, we found that area-based chlorophyll a + b was relatively stable along the light gradient, although area-based chlorophyll can be higher in sun leaves than shade leaves because more chloroplasts per unit area fit into thicker leaves (Lichtenthaler et al., 1981). In our study, the mass-based contents of chlorophyll a + b and carotenoids were higher in shade leaves for most species (Table S4), probably because thinner leaves with fewer chloroplasts tend to contain more chlorophyll per chloroplast to increase light capture (Niinemets, 2007). In contrast, area-based carotenoid content, as well as the ratio of area-based carotenoids and chlorophyll a + b, tended to be higher in sun leaves, pointing towards increased constitutive photoprotection with high light (Gamon and Berry, 2012; Gamon et al., 2023).

Our species-specific analysis showed that mass-based P and K were both higher in shade leaves possibly to better support the construction of light harvesting system and increase photosynthesis through nutrient allocation (Balaguer et al., 2001; Richardson, 2004). We found that 13 and 16 species followed this pattern, while the remaining species did not show significantly different P and K in sun and shade leaves. Mass-based NSCs, including sugars and starches, were higher in sun leaves for 24 out of 41 species with the remaining species showing a non-significant relationship, indicating increased photosynthesis rates with high light availability (Lichtenthaler et al., 1981; Poorter et al., 2006). In addition, mass-based content of phenolics, which provide antioxidant function and photoprotection (Poorter et al., 2006; Scartazza et al., 2016), was higher in sun leaves than shade leaves for 13 out of 37 species with the remaining species showing a non-significant relationship. In contrast, Martin et al. (2020) did not find significant differences in NSCs or phenolics in sun and shade leaves in tropical forests in Peru indicating that species might adopt diverse strategies in acclimation to the light environment (Valladares et al., 2000; Richardson, 2004).

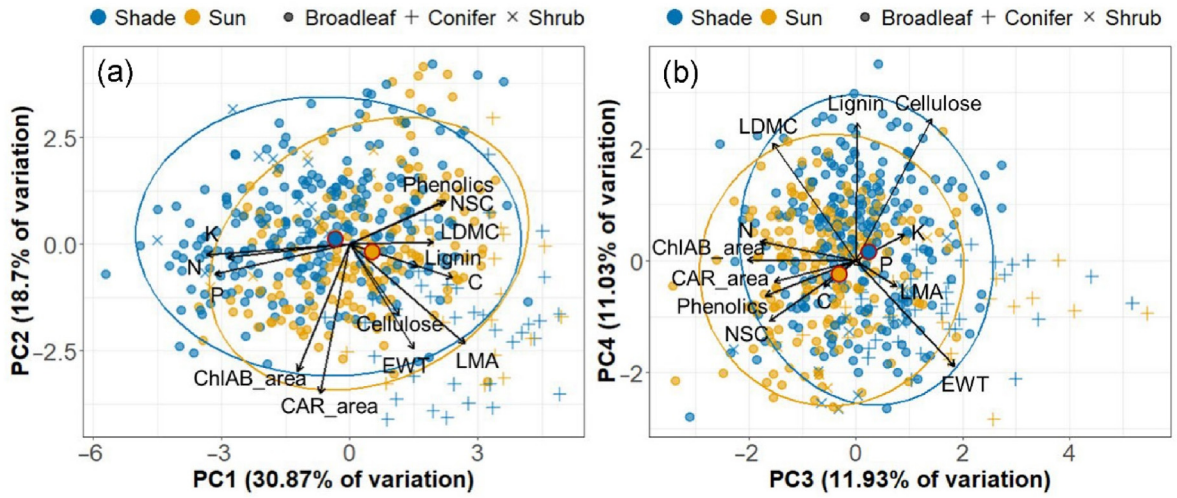

Fig. 7. Ordination plots showing the first four principal component (PC) axes. The large orange and blue points with red outline in each subplot are the centroids of PCs for sun and shade leaves, respectively. The abbreviations are CAR_area = area-based carotenoids, ChlAB_area = area-based chlorophyll a + b, EWT = equivalent water thickness, LMA = leaf mass per area, NSC = nonstructural carbohydrates. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

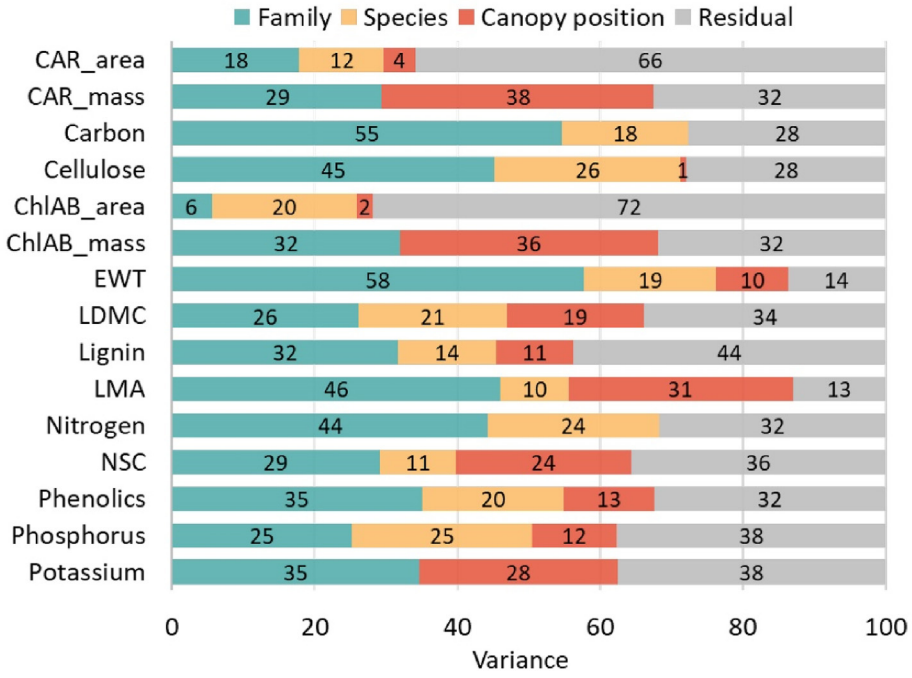

Fig. 8. ANOVA results showing the total variance in 15 foliar traits explained by family, species, and canopy position, respectively, and the residual variance. The abbreviations are CAR_mass = mass-based carotenoids, ChlAB_mass = mass-based chlorophyll a + b, CAR_area = area-based carotenoids, ChlAB_area = area-based chlorophyll a + b, EWT = equivalent water thickness, LDMC = leaf dry matter content, LMA = leaf mass per area, NSC = nonstructural carbohydrates.

4.2. Trait covariation and coordination in sun and shade leaves

Covariations between sun and shade leaves were found across all traits, although the strength of the relationships, slopes and intercepts varied. Individuals and species with high trait values in sun leaves tended to have high trait values in shade leaves as well (Fig. 5). This indicates that traits expression and plasticity is closely linked to taxonomy (Keenan and Niinemets, 2017; Paź-Dyderska et al., 2020) which is confirmed by our trait-environment analysis and GLMMs. This finding can help field sampling to be more cost-effective by focusing on sampling a broad spectrum of species across the tree of life (Albert et al., 2010). Our PCA analysis showed that foliar traits varied with LMA and N, representing the main axis of the leaf economic spectrum (Wright et al., 2004). Other major axes of foliar trait variation revealed by our analysis were related to macro-nutrients (N, P, K; PC1), photosynthetic pigments (chlorophyll a + b and carotenoids; PC2, PC3), defense (phenolics, LDMC; PC3), and stress response traits (NSCs, EWT; PC2 and PC3; Fig. 7 and Table S7).

4.3. Trait-environment relationships in sun and shade leaves

Trait-environment relationships were relatively weak, but the direction and slope for sun and shade leaves were consistent across all foliar traits. Cellulose and lignin contents decreased with higher elevation ($r = -0.12$; $r = -0.18$) and lower temperature ($r = 0.18$; $r = 0.17$), one

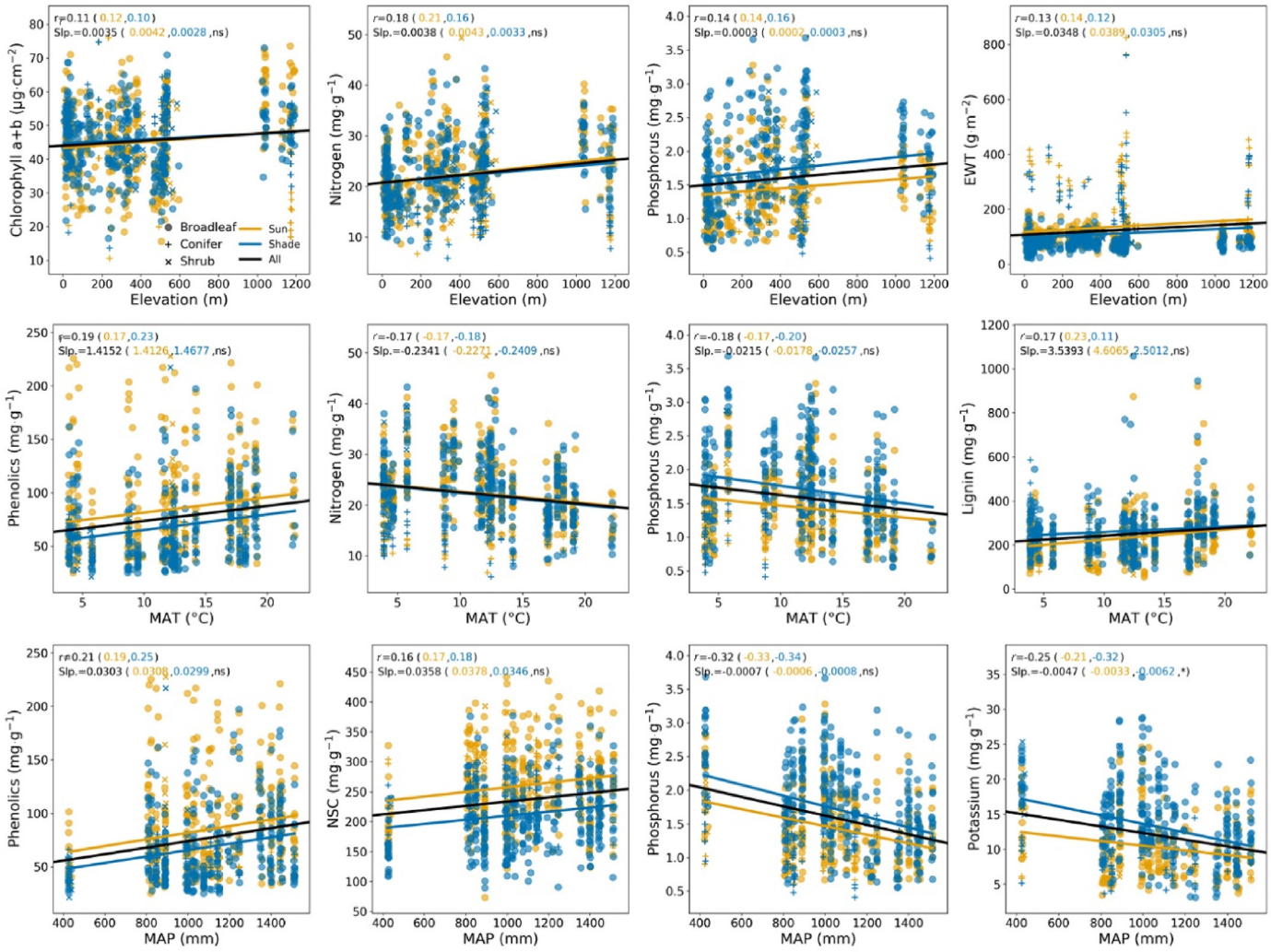

Fig. 9. Trait-environment relationships for sun (orange) and shade leaves (blue), and both leaf types combined (black). All the relationships are significant at $P < 0.05$. Significance levels for differences among slopes for sun and shade leaves are indicated by ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P \geq 0.05$. The abbreviations are EWT = equivalent water thickness, NSC = nonstructural carbohydrates. For all pairs of trait-environment relationships see Table S9. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

possible explanation being that C limitation at higher elevation reduces the synthesis of lignin (Richardson, 2004; Martin et al., 2020). Foliar contents of macro-nutrients can exhibit opposite trends to C along the elevation gradient. Indeed, we found that foliar N and P tended to be higher at higher elevations ($r = 0.18$; $r = 0.14$) and colder environments ($r = -0.17$; $r = -0.18$), which could improve metabolic capacity in energy limited areas and, together with lower cellulose and lignin contents, speed up decomposition rates. However, opposite findings have been reported for conifers in the northeastern US and tropical trees (Richardson, 2004; Martin et al., 2020). The foliar contents N, P, and K were lower in wetter regions compared to drier regions ($r = -0.24$; $r = -0.31$; $r = -0.25$), a trend also reported by Wright et al. (2001), while NSCs and phenolics tended to be higher ($r = 0.16$; $r = 0.21$) proving increased defense against herbivory in wetter regions. As the concentration of nutrients, lignin, NSCs, and phenolics affects nutrient cycling and litter decomposition rates (Melillo et al., 1982; Fortunel et al., 2009), their variations along geographic gradients are important factors to consider in studies on ecosystem functions and processes.

4.4. *Implications for trait-based ecology and remote sensing modeling*

This study provides at least three implications as follows. First, our results highlight the feasibility of leaf spectroscopy in predicting foliar traits in a rapid and efficient way (Serbin et al., 2019; Wang et al., 2023). Previous studies on foliar traits in sun and shade leaves were often limited to a small set of foliar traits, a small number of species or small geographic areas due to trade-offs in field sampling and chemical analysis (Paź-Dyderska et al., 2020). The novel leaf spectroscopy approach enabled us to evaluate an extensive list of foliar traits, which facilitated analysis of trait variation within individuals and across species (Wang et al., 2022). The capability of obtaining multiple foliar traits can help fill the gap in the global plant trait database – TRY, which only had 2.4 traits measured per entity on average (Kattge et al., 2020). With the novel framework of plant trait network, the datasets generated by this study provide the potential to better understand the multidimensional trait covariation and uncover the responses of plants to global change (He et al., 2020; Li and He, 2024).

Second, this study emphasizes the consideration of trait variation of shade leaves in ecological studies. Many trait-based studies used species' means to illustrate trait variation among species, often neglecting intra-specific variation (Wright et al., 2004; McGill et al., 2006; Díaz et al., 2016). Our findings demonstrate that canopy position is an important source of intra-specific trait variation and deserves more attention (Messier et al., 2010; Fajardo and Siefert, 2018; Paź-Dyderska et al., 2020). Detailed characterization of foliar traits across the canopy is required to better understand how plants respond to differences in light

availability and environmental change (Pérez-Harguindeguy et al., 2013; Messier et al., 2017; Anderegg et al., 2018). Such information is also valuable for improving process-based models with more accurate parameterization of litter decomposition, nutrient cycling, and light interception, and reducing uncertainties in ecosystem models, e.g., for estimating gross primary productivity (Wang and Leuning, 1998; Coble et al., 2016).

Third, this work has important implications for radiative transfer modeling and model inversion. Previous studies linked canopy reflectance and foliar traits measured from sunlit top-of-the-canopy branches by assuming that canopy reflectance is mainly driven by the upper canopy (Ustin et al., 2004; Asner et al., 2015; Singh et al., 2015; Wang et al., 2020). However, estimating traits values for sun leaves only, may lead to over-estimating trait values for the whole stand (Martin et al., 2018; Wang et al., 2020). Our results presented distinct differences of foliar traits in sun and shade leaves, and highlighted the importance of incorporating vertical distribution of foliar traits in radiative transfer models and trait retrieval (Wang and Li, 2013; Li and Wang, 2013; Gara et al., 2019). Recent studies have demonstrated great potential for mapping the three-dimensional variation of leaf mass per area and nitrogen with imaging spectroscopy and LiDAR (Chlus et al., 2020; Kamoske et al., 2021). The state-art-of three-dimensional radiative transfer models (3D RTMs) such as LESS and DART, can accurately simulate the radiation with detailed description of leaf properties and canopy structure (Gastellu-Etchegorry et al., 2015; Qi et al., 2019). The integration of 3D RTMs and multiple sources of remote sensing data, offers the opportunity to quantify the vertical profiles of foliar traits in forest ecosystems at large scales, which can further improve our understanding of intra-individual trait variation and its effect on ecosystem functions and processes.

5. Conclusions

This study evaluated trait variation, covariation, and correlation with environmental factors for 15 foliar traits of sun and shade leaves from 424 individuals of 110 woody species along a broad environmental gradient in eastern North America. Foliar traits, including LMA, and the contents of mass-based chlorophyll a + b, carotenoids, NSCs, phenolics, P, and K showed marked differences between sun and shade leaves, illustrating adaptations of leaves along the light gradient. We also found that increased photosynthetic capacity with increased light availability was mainly driven by high LMA and not by N-reallocation to sun leaves, confirming differences in light acclimatization strategies along the slow- (woody species) to fast-return (herbaceous species) on investment gradient. Principal component analysis revealed that the main axes of foliar trait variation were related to leaf economics, protection against herbivory, and environmental stress. Although we found consistent correlations between environmental factors and foliar traits of sun and shade leaves, environmental factors explained little of the total variation in foliar traits, compared to canopy position and taxonomy. These findings not only allow the design of more efficient field sampling strategies focusing on species' differences, but also highlight the importance of considering intra-specific foliar trait variation for trait mapping with remote sensing and in process-based models for light interception, radiative transfer, carbon, and nutrient cycling.

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Data availability

Data are available on request from the authors.

CRediT authorship contribution statement

Zhihui Wang: Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Philip A. Townsend:** Writing – review & editing, Resources, Project administration, Funding acquisition, Data curation, Conceptualization. **Eric L. Kruger:** Writing – review & editing, Resources, Project administration, Funding acquisition, Data curation, Conceptualization. **Anna K. Schweiger:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100230.

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