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Key Points:
- Nutrient-acquisitive species tend to locate on the north of the last glacial limit
- Nutrient-acquisitive species derive limited benefit from local moisture availability
- Heterogeneity in moisture availability may provide drought refuges for moisture-acquisitive species

Supporting Information:
- Supporting Information S1

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Where Resource-Acquisitive Species Are Located: The Role of Habitat Heterogeneity

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Abstract Rising temperatures with increased drought pose two challenges for management of future biodiversity. First, are the most vulnerable species concentrated in specific regions and habitats? Second, where can landscape heterogeneity potentially mitigate impacts? We conducted a comprehensive trait analysis of forest plots spanning the eastern United States to quantify how resource-acquisitive species respond to moisture-soil-climate interactions. We found that resource-acquisitive species, including nutrient-acquisitive and moisture-acquisitive species, respond disproportionately to environmental gradients, and their response is largely explained by soil variation. We showed that the strong boundary of resource-acquisitive species occurs near the last glacial limit, highlighting one of the clearest indicators of soil controls. Although local soil moisture may reduce drought-induced stress for moisture-acquisitive species, nutrient-acquisitive species remain vulnerable on wet soils in dry climates. The results suggest that theories explaining species distributions should devote close attention to the combination of local drainage and soil type.

Plain Summary language Global warming and drought may cause harm to the biodiversity on the planet. But we may be able to protect species if we can identify vulnerable habitats and regions. To address this challenge, we analyzed a large data set of forest plots across the eastern United States. Our study showed that soil type and local soil moisture play important roles in species response to dry and warm conditions. Our results revealed a sharp change in the population of resource-acquisitive species near the boundary of the last glaciation, indicating a strong soil control. While nutrient-acquisitive species did not benefit from local moisture availability, moisture-acquisitive species favored these conditions.

1. Introduction

Warming and drought are implicated in forest diebacks globally (Allen et al., 2010), but the impacts will be mediated by habitat heterogeneity in ways that are poorly understood (Vose et al., 2016). On the one hand, moist and fertile habitats could provide the "drought refuges" needed to preserve the most sensitive species as the climate becomes more arid (Mackey et al., 2012). On the other hand, the sensitive species that occupy these habitats could be the first to respond to drying climate, regardless of local habitat variations (Clark et al., 2014). In other words, tolerance of climate change entails an interaction between the effects of regional climate and local habitat heterogeneity, including soils and drainage. The effects of this interaction could depend on species differences in nutrient and water requirements (Myers-Smith et al., 2019). If foliar traits such as leaf chemistry and leaf thickness provide clues to functional responses (Li et al., 2015; Nardini & Luglio, 2014), then there is a joint trait response to consider (He et al., 2018). In the absence of probabilistic models for joint trait responses, current understanding is limited to analyses of traits as independent responses or as descriptive ordinations (Butler et al., 2017; Lamanna et al., 2014; Uriarte et al., 2016; Westoby et al., 2013; Wright et al., 2005). Generalized joint attribute modeling (GJAM) (Clark et al., 2017) permits probabilistic inference on traits, including full uncertainty. Here, we apply the joint model to anticipate how species with high nutrient and moisture requirements respond to moisture stress at different habitats.

Drought risk could be greatest for resource-acquisitive species (Ficken & Wright, 2019; Lavorel & Garnier, 2002), as reflected in foliar traits. Despite considerable variation within species and even between leaves of the same species (Asner et al., 2014; Field & Mooney, 1986; Hu et al., 2015), there is a positive species-level correlation between foliar concentrations of nitrogen and phosphorus and whole-plant demands for these nutrients (Pastor et al., 1984; Pastor & Post, 1985; Walker et al., 2014). There is also a positive correlation between specific leaf area (SLA) and moisture demand (Rosbakh et al., 2015; Wilson et al., 1999). Species with high SLA are often found where moisture and temperature are both high, while low SLA species are expected where one of the two is lacking (Wright et al., 2017). If species-level differences in drought risk for nitrogen-demanding species (NDS) and phosphorus-demanding species (PDS) are reflected in foliar chemistry, then community-weighted mean (CWM) (Ackerly & Cornwell, 2007; Kunstler et al., 2016; Mouillot et al., 2013) values could identify communities that need more resources and hence potentially vulnerable to drought.

At the continental scale, drought-soil interactions could manifest as divergent responses between young, glaciated soils to the north (Filippelli et al., 2006; Hall & Shroba, 1993, 1995) from highly weathered Ultisols to the south (Figure S2e in the supporting information). On long time scales, weathering can deplete nutrient availability (Chen et al., 2013; Li et al., 2014; Maire et al., 2015; Peltzer et al., 2010; Vitousek et al., 2010; Wu et al., 2014). The net effect of moisture availability further depends on competition with the other species that also benefit from moisture, nutrients, or both. The juxtaposition of contrasting soil age cutting across the continent provides an opportunity to examine climate-soil interactions from moist eastern United States to xeric Midwest. We hypothesized a shift toward NDS and PDS north of the last glacial limit.

At the landscape scale, habitat heterogeneity might cause responses to diverge from those expected for the regional climate. Gradients in moisture availability occur in both wet and dry climates, raising the possibility of interactions. A legacy of studies finding that foliar nitrogen (N) and phosphorus (P) can be correlated with soils (Chadwick et al., 1999; Hedin et al., 2003; Moreno-Martínez et al., 2018; Valencia et al., 2018; Vitousek et al., 1999; Walker & Syers, 1976) and climate (Bjorkman et al., 2018; Bruelheide et al., 2018; Chen et al., 2013; McGroddy et al., 2004; Reich & Oleksyn, 2004; Tjoelker et al., 1999; Wieczynski et al., 2019) suggests an important role for drought-habitat interactions. In dry climates, heterogeneity of soil moisture could provide refuge for drought-intolerant species. On moist sites, both NDS and PDS may benefit from relatively high rates of mineralization (Jin et al., 2013) and microbial activity (Bertiller et al., 2006; Campo et al., 2014; Ramirez et al., 2012) and root uptake (Ordonez et al., 2009). All else being equal, high soil moisture can promote nutrient transport and absorption by roots (He et al., 2014). Alternatively, nutrient-acquisitive species could suffer on anaerobic soils (Walker & Syers, 1976) and nitrate reduction in wet sites (Hobbie et al., 2002; Walker & Syers, 1976). Quantifying foliar nutrient at the community scale can help identify how certain species are distributed in different habitats. In addition to their separate patterns, N:P ratios (Reich & Oleksyn, 2004) can indicate nutrient imbalance that directly influences growth and photosynthesis (Fisher et al., 2012). For example, reproductive investments may suffer in P-limited habitats (Fujita et al., 2014). N limitation reduces photosynthesis (Ghimire et al., 2017; Kolber et al., 1988) and primary productivity (LeBauer & Treseder, 2008). We examine N:P evidence for nutrient imbalance that differs between foliar traits.

CWM foliar traits are largely influenced by leaf habit. Evergreen species have considerably lower leaf N, P, and SLA than deciduous trees. Therefore, to study environmental controls on foliar traits, an analysis should exclude effects raised from evergreenness.

GJAM provides a framework to test whether or not landscape heterogeneity in moisture availability and soils could provide habitat refuges for resource-acquisitive species with increasing moisture stress. First, we ask if there are regions and habitats important for resource-acquisitive species at the community level, as reflected in CWM responses across moisture availability and climate gradients. These are "main effects" of climate and habitat. Second, to what extend do the community-level sensitivities to drought depend on climate, moisture availability, soil type, and the interactions between them? Specifically, do "drought refuges" contribute most to regional survival of resource-acquisitive species in dry climates? Alternatively, are the largest responses expected from moist climates and moist sites due to dominance by species most sensitive to both variables? These are "interaction effects" of climate and habitat. We synthesize regional and local information from a large number of sources on regional climate, local habitat, species abundances, and traits. We show how to quantify the effects of environmental variables where effects are masked by trait correlations. For example, the effect of moisture on foliar nutrient concentrations is overwhelmed by leaf-habit differences anywhere there is a shift in deciduous versus evergreen species. We demonstrate how conditional prediction deconfounds these trait correlations, revealing that foliar responses to environment are general, cutting across leaf-habit differences. We report predictive errors from the joint model compared with alternative methods (e.g., Butler et al., 2017). These joint responses to interacting winter temperature, climatic hydrothermal deficit, local drainage, and soil type are used to evaluate the role of habitat with regional climate variation.

2. Materials and Methods

2.1. Data

Species, traits, and environmental data used in this study include forest inventories, climate, soils, ecoregion boundaries, site topography, and functional traits. Species distribution data were collected from 24,788 plots of the USDA Forest Inventory and Analysis (FIA) data set, including 31 states in the United States, east of the Central Plains. Each plot has an area of 0.0672 ha and randomly located in one of the 6,000-acre FIA hexagons. FIA data include diameters of 65 abundant tree species. Tree allometry analysis was used to estimate species biomass for plots (Jenkins et al., 2003). Climate data, including monthly temperature and precipitation, were used to derive minimum winter temperature and hydrothermal deficit. Winter temperature was derived from PRISM Climate Dataset. Hydrothermal deficit is based on the potential evapotranspiration and precipitation, as the number of degree hours in a season where potential evapotranspiration exceeds precipitation. Hydrothermal deficit summarizes moisture limitation and thermal surpluses at the regional scale. Unlike hydrothermal deficit, which varies at coarse spatial scales, the moisture index is a plot-scale variable that depends on local topography.

Soil data were extracted from the State Soil Geographic database (Soil Survey Staff, 2014). To improve the model convergence, similar or poorly represented soil classes were aggregated and assigned the following acronyms: (1) AlfInc (Alfisols and Inceptisols), (2) EntVert (Entisols and Vertisols), and (3) SpodHist (Spodosols with Histosols). Other acronyms are Mol (Mollisols), UltKan (Ultisols-Kanhapludults), and Ult (Ultisols). AlfInc was selected as the reference soil class, as it is a common soil type across North America. Brief descriptions of soil orders used in this study are listed in Supporting Information S1.

Foliar traits data were compiled from Aber and Martin (1999), Alonso et al. (2010), Beaudet, and Messier (2008), Chapin and Kedrowski (1983), Finzi et al. (2001), Gilmore et al. (1995), Grotkopp and Rejmanek (2007), LeBauer et al. (2010), Ricklefs and Matthew (1982), Reich et al. (1998), Rieske (2002), Van Sambeek et al. (2008), Vergutz et al. (2012), and Walker et al. (2014). References are also listed in Supporting Information S1. CWM trait values were obtained from species traits weighted by species biomass on FIA plots. Allometric equations from (Jenkins et al., 2003) were used to translate tree diameters into biomass and then aggregated for each plot. These species weights were used to obtain CWM values for foliar N, P, and SLA.

2.2. Model

We used the predictive trait model approach, as it is implemented in GJAM, to quantify environmental controls on the distribution of resource-acquisitive species. In this approach, species abundances are fitted, and traits are predicted, incorporating species responses, species covariance, trait responses, and trait covariance. Details about the model structure are explained in Clark (2016), and it is summarized as follows:

$$w_i \sim MVN\left(\beta' x_i, \Sigma\right), \quad (1)$$

where w_i is the relative species biomass at location i, β is the species matrix of coefficients, x is the matrix of predictors, and Σ is the species covariance matrix. The fitted model is then transformed from the species-space into the traits-space:

$$\alpha' = T\beta', \quad (2)$$

$$\Omega = T\Sigma T', \quad (3)$$

where T is the traits-species matrix, α is the traits matrix of coefficients, and Ω is the traits covariance matrix. The interpretation focuses on leaf traits, but to allow for covariance with additional traits, the full analysis includes leaf N concentration, leaf P concentration, SLA, wood density, maximum height, seed mass, and leaf habit including deciduous or evergreen. Community weighted trait values are calculated for each FIA plot based on the species composition and their biomass within the same plot.

Extensive variable selection based on the Deviance Information Criterion included main effects and interactions involving winter temperature, moisture index, hydrothermal deficit, topographic slope and aspect, and soil.

Sensitivity maps were generated as predictive distributions, with full uncertainty, obtained by marginalizing over the posterior distributions of coefficients. Prediction map was generated from climate and habitat variables q on locations j based on the original inventory plots. The predictive mean sensitivity of trait m to predictor q at location j is given by

$$\hat{s}_{mqj} = \frac{\sigma_q}{\sigma_m}\frac{\partial y_{mj}}{\partial x_{qj}} = \frac{\sigma_q}{\sigma_m}\hat{\beta}_{mq} + \frac{\sigma_q}{\sigma_m}\sum_{q' \in Q}\hat{\beta}_{mqq'}x_{q'j},$$

where $\hat{\beta}_{mq}$ is the main effect of q, $\hat{\beta}_{mqq'}$ is the interaction with q', x_{qj} is the value of predictor q at j, Q is the set of predictors that interact with q, and σ_q and σ_m are the standard deviations of predictor q and trait m, respectively. We generated predictive distributions for traits by numerical integration of the posterior distribution. Our analysis of climate-habitat interactions examines how local moisture availability affects resource-acquisitive species across regional hydrothermal deficits and vice versa.

To quantify climate and habitat effects on foliar traits that are correlated with leaf habit, we used conditional prediction. Specifically, the predictive distribution of foliar N and P given leaf habit and environmental predictors is directly available from the posterior distribution, in the form of a conditional distribution (Clark, 2016). To determine if these effects apply to both deciduous and evergreen species, we conditionally predicted foliar chemistry across climate and habitat variables from the fitted model.

Model interpretation combines evidence for main effects of climate and moisture status with their interactive effects. A stronger model coefficient indicates stronger control from its corresponding variable. Support for the hypothesis that locally moist habitats act as refuges from moisture stress comes from positive interaction between local and regional moisture. In other words, a positive interaction between local and regional moisture means that local moisture availability is most important in dry climates, and climatic moisture stresses are most severe on xeric sites.

3. Results

Results confirmed the importance of climate-habitat interactions for the distribution of foliar traits. The selected model included winter temperature, moisture index, hydrothermal deficit, slope and aspect, and soils as main effects and interactions between soil type and hydrothermal deficit, between soil type and winter temperature, between soil type and moisture index, and between moisture index and hydrothermal deficit.

CWM values of foliar N, P, and SLA showed how nutrient- and moisture-acquisitive species are distributed across the eastern United States (Figure 1). Distributions of NDS and PDS showed similarities and differences. Foliar N was low in the Southeast, the Laurentian forests, and the Adirondack forests, reflecting combined effects of climate, habitat, and evergreenness. Low foliar P extended north through the Appalachian Plateau and Cumberland Plateau, with a distinct transition near the last glacial limit (gray line in Figure 1). High foliar P occurred on Mollisols, Alfisols, and Inceptisols in the north central region, in forests that are not dominated by conifers, and in riverine forests of the lower Mississippi. Species with high SLA were relatively abundant in the Appalachian mountains, the Eastern Broadleaf forests, the Adirondack mountains, and the Prairie Parklands. Potential impacts of nutrient limitation are signaled by high N:P in mid-latitude mountains, including Appalachian, Ozark, and Ouachita Forests, and on the Interior Plateau and Piedmont (Figure 1d). N:P values decline abruptly north of the last glacial limit, and they are low again in southern soils, across much of the coastal plain to the lower Mississippi.

The overall patterns of the distributions of resource-acquisitive species depend on all contributing factors including winter temperature, hydrothermal deficit and moisture availability, and soil types. CWM values for foliar N, P, and SLA decline with winter temperature (Figure 2a). NDS tend to marginally decline with hydrothermal deficit, but there was no evidence for a hydrothermal deficit effect on PDS. Results indicated that SLA declines in dry climates, as expected for moisture conservation (Lopez-Iglesias et al., 2014). The moisture-hydrothermal deficit interaction term suggests different trends for NDS, PDS and SLA. While

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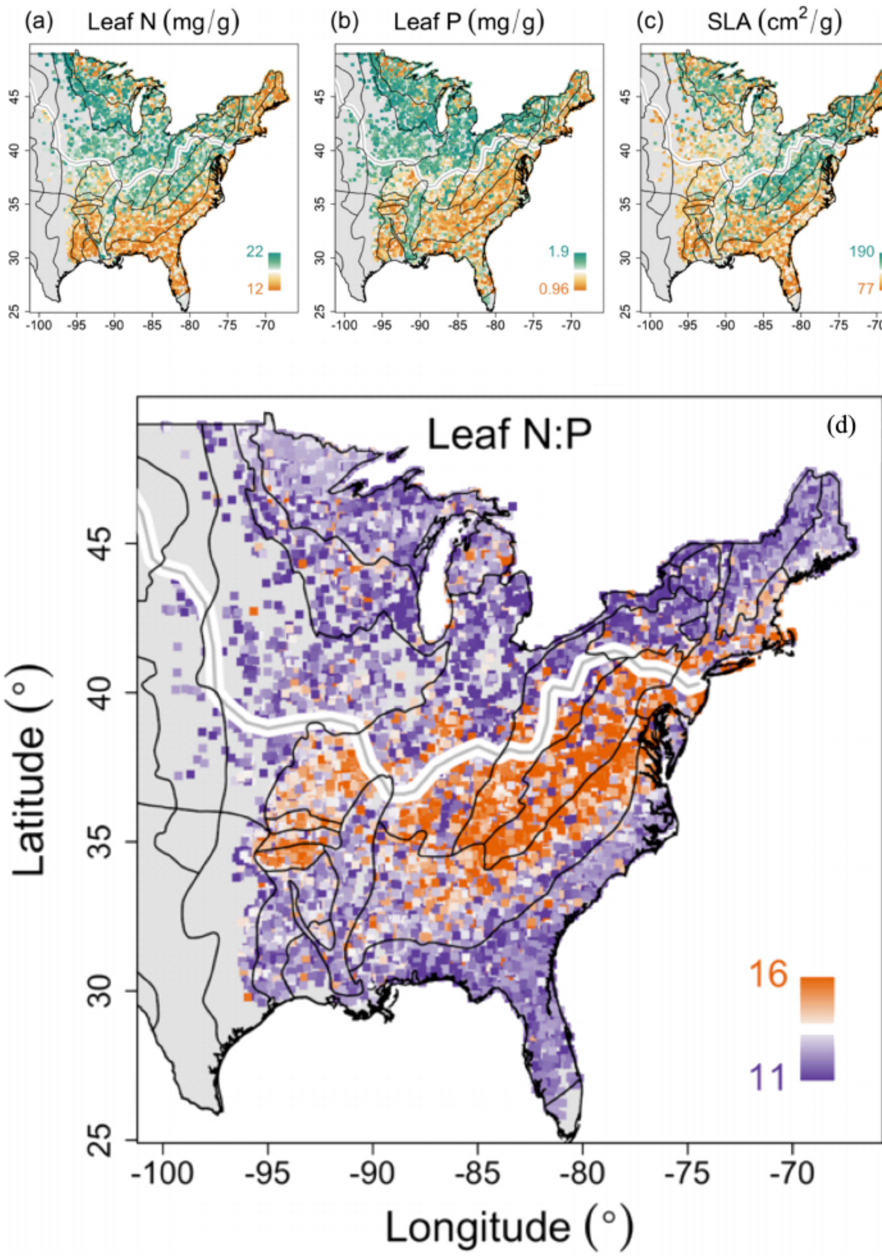

Figure 1. Community weighted mean (CWM) leaf traits across the eastern United States: (a) leaf nitrogen content per unit mass, (b) leaf phosphorus content per unit mass, (c) leaf area per unit mass, and (d) N:P ratio. The distribution of CWM N:P suggests areas of phosphorous limitation in orange and nitrogen limitation in purple. The gray line indicates the last glacial limit.

the interaction term was not significant for NDS, it was negative for PDS and positive for SLA. The negative interaction for PDS means that the moisture control on PDS is weak in dry climates. The positive term for SLA means that moisture control on SLA is amplified by dry climates. NDS declined to a greater degree than PDS with hydrothermal deficit, suggesting NDS may suffer most in dry climates and thus with increased aridity. Soil mediates the responses of species, depending on nutrient demand (Figure 2b). Nutrient-acquisitive species were most abundant on Alfisols-Inceptisols (the reference soil class), which dominate north of the last glacial limits. Spodosols-Histosols showed the strongest negative effects on

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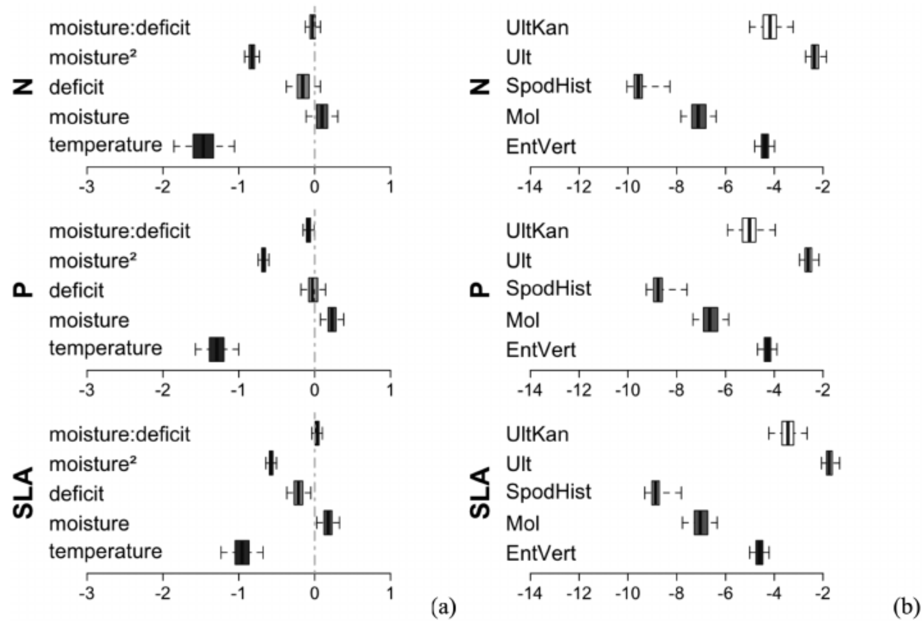

Figure 2. Posterior distributions of model coefficients for response variables (N, P, and SLA) by (a) climate variables and (b) soil types. Coverage is 50% (boxes) and 95% (whiskers). Coefficients for soils in (b) are relative to the reference soil class Alfisols-Inceptisols. Predictor variables are described in Supporting Information S1.

nutrient- and moisture-acquisitive species, following by Molisols, Entisols-Vertisols, and Ultisols. The findings show strong biogeographic evidence for the connections between plant traits and soil chemistry that can include its effects on nutrient uptake (Chen et al., 2013; He et al., 2014; Hobbie et al., 2002; Maire et al., 2015; Mason et al., 2012; McGroddy et al., 2004).

Conditional prediction allowed us to dissect the direct effects of predictors from their indirect effects through leaf habit. The raw data confound strong effects of evergreenness with those of climate and soils. For the full community, foliar N and P values declined in evergreen dominated forests of the Southeast, Northeast, and Upper Midwest (Figures 3a–3c). However, any geographic coherence to climate and soil responses could be masked by the varying ratios of leaf habit. To evaluate the climate-habitat interactions, we supplemented these predictions for the full community with those that are conditional on leaf habit. In simplified form, the fitted model can be written as [evergreenness, N, P |X]. Conditional predictions move leaf habit (evergreenness) to the right side of the bar, [N, P|evergreen, X] and [N, P|deciduous, X] (Figures 3d–3i). The geographic trends that are masked by evergreenness in Figures 3a–3c emerge in conditional predictions as large coherent increases across the last glacial limit moving from south to north. Within both leaf habit types, SLAs were highest in the Appalachians, New England, and Laurentian forests (Figures 4f and 4i).

The importance of interactions in the fitted model resulted in a detailed view of sensitivity to winter temperature, moisture, and hydrothermal deficit that vary with soils and local drainage (Figure 4). Foliar N and SLA increased with winter temperature (positive values in Figures 4a and 4c) in deciduous forest of the central and midwestern forests and decreased (negative values in Figures 4a and 4c) in the southern Piedmont and coastal plains. Foliar P decreased with winter temperature, with the strongest control occurring in mid-latitude forests (Figure 4b). Responses to hydrothermal deficits depend on moisture and soils. Foliar N showed a positive hydrothermal deficit response in the Spodosols-Histosols soils in coniferous forest of the North and Florida, but negative responses elsewhere (Figure 4d). Foliar P and SLA declined with hydrothermal deficit in all regions (Figures 4e and 4f). Regional hydrothermal deficit decreases N, P, and SLA in the Midwest, the Eastern Broadleaf Continental forests, and the northern Appalachians. Unlike the regional hydrothermal deficit, sensitivity to local moisture reverses from positive to negative for foliar traits. Strong positive local moisture effects dominated the interior and Ozark Plateau, whereas evergreen-dominated forests in the North and Florida showed negative local moisture responses (Figures 4g–4i).

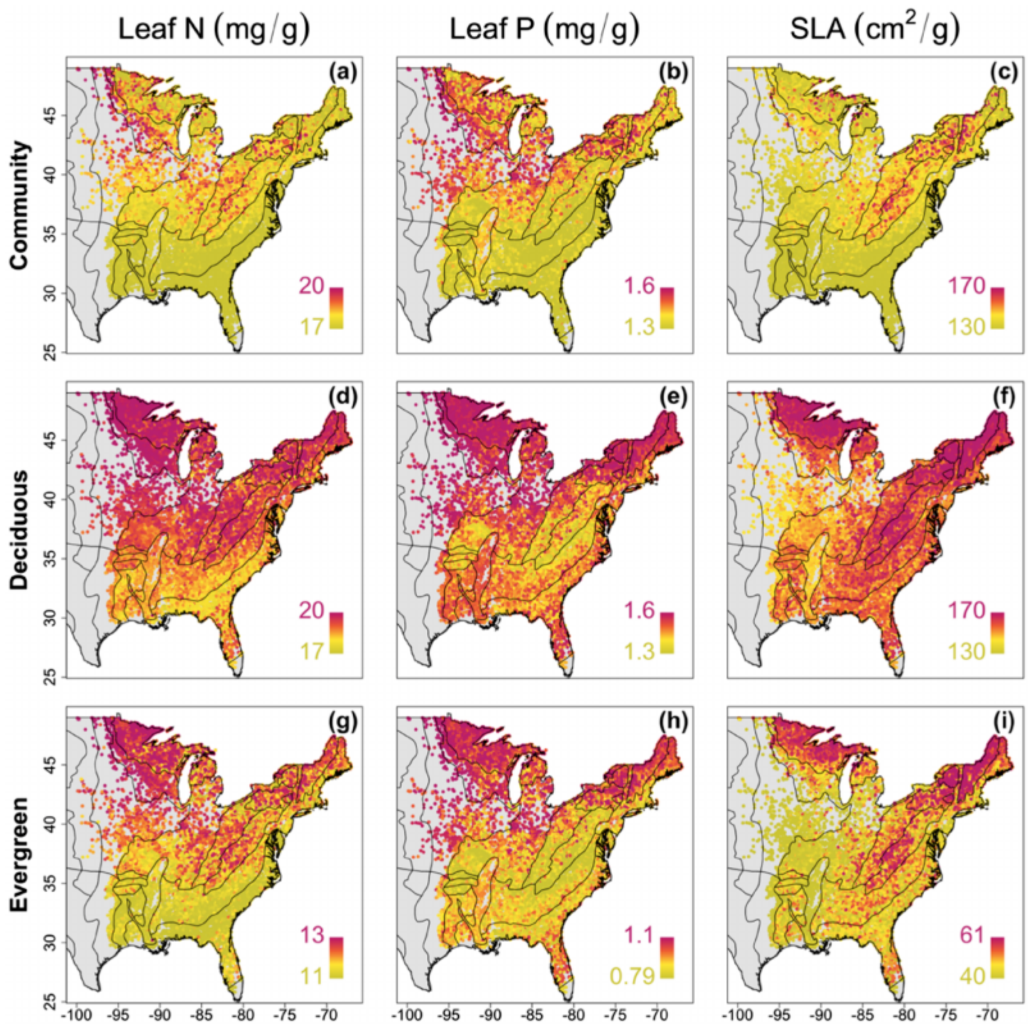

Figure 3. (a–c) Predicted leaf traits and (d–f) conditional predictions for deciduous forests and (g–i) evergreen forests. Variable color range was used for the figures to highlight the main spatial trends for evergreens.

4. Discussion

Habitat heterogeneity, including interactions with soil and moisture availability, will determine how resource-acquisitive species respond to climate change. Results showed that heterogeneity in moisture availability can provide habitat refuges for SLA in dry climates, but PDS and NDS derive limited benefit from local moisture availability where climate is dry. Strong interactions that are geographically coherent support the hypothesis that resource-acquisitive species can respond differently across moisture and soil gradients with increasing drought. Results are consistent with the interpretation that PDS—e.g., *Prunus serotine*, *Tilia americana*, and *Fraxinus americanus*—adapted to dry climates can tolerate water-limiting conditions to a greater extent than NDS such as *Platanus occidentalis* or *Acer negundo*. Negative effects of low soil moisture and increasing hydrothermal deficit can be alleviated on local soil gradients.

4.1. Communities of Resource-Acquisitive Species

Results of this study are apparently the first to establish that NDS and PDS dominate north of the last glacial limit and in the lower Mississippi Riverine forests, both characterized by relatively fertile Molisols, Alfisols, and Inceptisols (Hatten et al., 2014; Yang et al., 2014; Zinke et al., 1998). The strong boundary in resource-acquisitive species and N:P ratio at the last glacial limit is one of the clearest indicators of soil

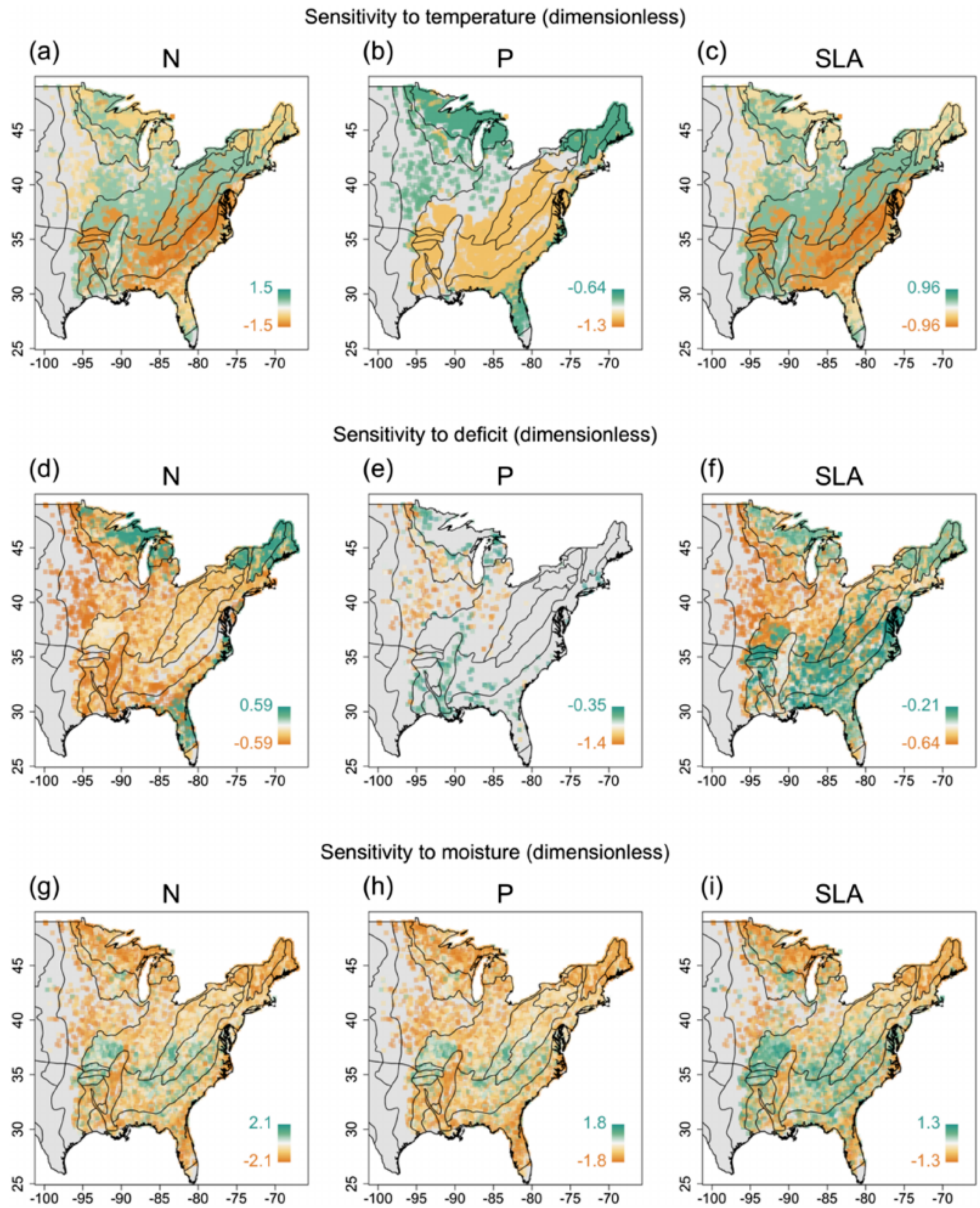

Figure 4. Sensitivity of leaf N, leaf P, and SLA to (a–c) winter temperature, (d–f) hydrothermal deficit, and (g–i) soil moisture.

controls, particularly for P limitation. N-limited communities north of the last glacial limit and P-limited communities to the south span a range of habitats. Conditional predictions showed that they apply both to evergreen and deciduous leaf habits (Figure 3). High PDS north of the last glacial limit in both evergreen and deciduous species is consistent with continental-scale soil impacts on trait distributions. The stronger hydrothermal deficit effect on SLA above this latitude indicates drought is less likely to favor high SLA species such as *Ostrya virginiana*, *Fagus grandifolia*, and *Carpinus caroliniana* in northern, fertile sites than in the older soils in the south. Although previous studies recognized soil effects on foliar N and P limitations (Butler et al., 2017; Reich et al., 2010; Reich & Oleksyn, 2004; Townsend et al., 2007), we found that there are several environmental variables involved. The low predictive errors from our approach (Figure S1) lend confidence to the results. Nutrient-acquisitive species are most vulnerable to drought on older soils south of the last glacial limit. Our results suggest that the high relative abundances of N-fixing legumes in xeric climates (Eskew & Ting, 1978) can be extended to climates where aridity is less extreme. NDS disfavor high hydrothermal deficit and winter temperature to a great degree than PDS, resulting in high N:P ratio in Appalachians, Ozark, Ouachita, and the Eastern Broadleaf forests where winter temperature is moderate and hydrothermal deficit is low. Conditional predictions demonstrated that the overall responses of nutrient- and moisture-acquisitive species transcended the leaf habit, affecting both evergreen and deciduous forests.

4.2. Climate and Soil Controls on Nutrient-Acquisitive Species

Declines in foliar N and P with winter temperature (Kang et al., 2011) could be explained by a temperature-induced imbalance in photosynthetic processes (Reich & Oleksyn, 2004). This is consistent with low photosynthetic rates in cold habitats. If foliar N and P increase to compensate for slowed biochemical processes at low winter temperatures (Weih, 2000; Weih & Karlsson, 2001), then NDS and PDS could benefit in cold regions.

Our results extend several studies suggesting that nutrient-acquisitive species prefer mesic habitats over both xeric and hydric sites (Chen et al., 2013; Wright et al., 2004; Wright et al., 2004). This is evident from the positive linear and negative quadratic moisture coefficients on foliar N and P (Figure 1), as visualized in Supporting Information S1. Responses to local moisture availability and, thus, the interpretation of "drought tolerance" cannot be lifted directly from abundances across regional climate gradients. Just as NDS benefit from increasing soil moisture, they may decline with increasing hydrothermal deficit (dry climate) but not in the same ways. Low nitrogen uptake in areas with dry climate (Kirschbaum, 1995) could explain low foliar N. Despite expectations, we found no evidence that the hydrothermal deficit controls PDS.

4.3. Hydrological Refuge at Wet Sites and Dry Climate

Local moisture and soil gradients could mediate drought impacts on high SLA species, while having less impact on resource-acquisitive species. Despite the general geographical coincidences of CWM foliar traits, NDS, PDS, and SLA follow different strategies. The amplified moisture effect on species with high SLA in dry sites—e.g., *Oxydendrum arboretum* and *Acer negundo*—is consistent with a drought-refuge effect. However, negative impacts of drought on PDS in wet sites can occur due to the drought-intolerant species that dominate there. We found no evidence to support a drought-refuge effect for NDS.

4.4. Implications for Conservation Management

The results from this study identify sites where resource-acquisitive species are especially vulnerable and guide size selection and species selection in forest practice. Results highlight the role of landscape heterogeneity in species vulnerability to drought and warming that can differ for resource-acquisitive species. This may be particularly important for natural resource managers who can allocate resources toward achieving conservation goals.

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