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ARTICLE

Vegetation Ecology

Metabolomic and morphological trait diversity display contrasting patterns in temperate forest tree communities

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Abstract

Studies of community assembly often explore the role of niche selection in limiting the diversity of functional traits (underdispersion) or increasing the diversity of functional traits (overdispersion) within local communities. While these patterns have primarily been explored with morphological functional traits related to environmental tolerances and resource acquisition, plant metabolomics may provide an additional functional dimension of community assembly to expand our understanding of how niche selection changes along environmental gradients. Here, we examine how the functional diversity of leaf secondary metabolites and traditional morphological plant traits changes along local environmental gradients in three temperate forest ecosystems across North America. Specifically, we asked whether co-occurring tree species exhibit local-scale over- or underdispersion of metabolomic and morphological traits, and whether differences in trait dispersion among local communities are associated with environmental gradients of soil resources and topography. Across tree species, we find that most metabolomic traits are not correlated with morphological traits, adding a unique dimension to functional trait space. Within forest plots, metabolomic traits tended to be overdispersed while morphological traits tended to be underdispersed. Additionally, local environmental gradients had site-specific effects on metabolomic and morphological trait dispersion patterns. Taken together, these results show that different suites of traits can result in contrasting patterns of functional diversity along environmental gradients and suggest that multiple community assembly mechanisms operate simultaneously to structure functional diversity in temperate forest ecosystems.

KEYWORDS
biotic interactions, chemical ecology, environmental gradients, ForestGEO, functional traits, metabolomics, plant–enemy interactions, species sorting, temperate forest

INTRODUCTION

A long-standing goal in ecology is to determine the relative roles of different community assembly processes in structuring ecological communities (Chase, 2003; Pavoine & Bonsall, 2011; Weiher et al., 2011). Over the last few decades, there has been a surge of interest in exploring assembly processes using patterns of functional trait diversity (Mason et al., 2013; Purschke et al., 2013; Spasojevic & Suding, 2012). Although limited by observational inference, functional trait approaches have proven effective for helping to identify multiple processes structuring communities, especially in ecosystems where ecological processes operate over longer timescales and organisms have long lifespans (i.e., forests, tundra) (Coyle et al., 2014; Lasky et al., 2015; Muscarella et al., 2016; Schrader et al., 2021). In plant ecology, classic approaches viewed trait-community assembly as a balance between niche selection arising from environmental filtering and competition (Weiher & Keddy, 1995), where environmental filtering results in communities of ecologically similar species with a narrow range of functional strategies adapted to the environmental conditions or limitations (underdispersion; Kraft et al., 2015), while competition via limiting similarity results in communities with a wider range of functional strategies, thus minimizing overlap in strategies (overdispersion; Macarthur & Levins, 1967; Weiher & Keddy, 1995). While initially promising, advances to trait-based community assembly highlighted that multiple processes of niche selection can result in similar patterns of functional diversity within communities (D'Andrea & Ostling, 2016; Mayfield & Levine, 2010; Spasojevic & Suding, 2012). For example, stabilizing niche differences and equalizing fitness processes can both result in a narrow range of functional strategies or evenly spaced clumps of species along trait axes because interactions can result in nearly random outcomes for very similar species that do not favor a single species (D'Andrea et al., 2019; Holt, 2006; Scheffer & Van Nes, 2006). In addition, competition and facilitation can both result in divergent functional strategies in local communities by allowing the coexistence of species with very different functional strategies (Danet et al., 2018). Despite these limitations, many trait-based studies have still sought to infer pattern from process, but few studies have successfully developed robust trait-based predictions for the myriad of biotic interactions that structure plant communities (Albrecht et al., 2018; Larios et al., 2017).

While biotic drivers of niche selection including species interactions within and across trophic levels have been demonstrated to influence plant community assembly (Espelta et al., 2020; Kokkoris et al., 1999; Loiola et al., 2012; Weiher et al., 1998), the inferences drawn about community assembly processes from patterns of functional trait diversity have primarily focused on morphological traits (Bhaskar et al., 2014; Spasojevic & Suding, 2012). These include traits related to carbon economy and resource acquisition (specific leaf area, leaf dry matter content, leaf nitrogen), plant stature (height, wood density), and dispersal (seed mass) (Chaturvedi et al., 2024; Díaz et al., 2016; Westoby, 1998). For example, the global analysis of plant form and function (Díaz et al., 2016) drawn from the TRY plant trait database (Kattge et al., 2020) includes no traits strongly involved in multitrophic interactions, like herbivory and plant–pathogen interactions, likely due to fewer data on these traits or because current databases are not structured for complex and diverse data like metabolomics. Because of this under-representation of traits directly related to multitrophic interactions, most trait-based assembly frameworks have largely remained focused on niche selection associated with resource competition and environmental tolerances. However, herbivores and pathogens are important forces in structuring plant communities (Becerra, 2007; Bever et al., 2015; Janzen, 1970; Terborgh, 2012).

Interactions between plants and specialist insect herbivores are thought to have generated high diversity in plant chemical defenses (Ehrlich & Raven, 1964; Wetzel & Whitehead, 2020) and multitrait defense syndromes (Agrawal & Fishbein, 2006). Consequently, biotic selection from specialist insect herbivores or plant pathogens should increase interspecific variation in plant chemical defenses within communities (Sedio & Ostling, 2013) because higher variation in chemical defense strategies will limit host suitability and thus natural enemy populations (Wetzel & Whitehead, 2020). This expectation depends on the extent to which natural enemies are specialized on certain hosts, as generalist enemies will likely select for similar defense strategies across plant communities (lower community variation) and a mix of specialist and generalist herbivores should generate random variation. These patterns may also depend on resource availability, where high resource availability should increase pressure from natural enemies, while lower resource availability tends to result in greater defense investment (chemical or otherwise) (Coley et al., 1985; Wetzel & Whitehead, 2020).

Plants produce a huge variety of metabolites with diverse functions, including primary metabolites that mediate core metabolic pathways such as photosynthesis, respiration, and other vital processes, as well as secondary metabolites that function in signaling, abiotic stress-response, and defense against natural enemies (Endara et al., 2023; Wetzel & Whitehead, 2020). Importantly, plant metabolite function can be challenging to classify, as individual compounds can serve multiple functions. For example, flavonoids can absorb ultraviolet radiation, mediate abiotic stress, and serve as anti-herbivore and antimicrobial defenses (Volf et al., 2022). In addition, some core amino acids function in defense when expressed in toxic concentrations (Coley et al., 2005). Nevertheless, metabolites may be classified according to structural motifs (Djoumbou Feunang et al., 2016), biosynthetic pathway of origin (Kim et al., 2021), or chemical and physical properties (Walker et al., 2023). While many plant characteristics function as defenses against herbivores and pathogens, including morphological traits such as leaf toughness and trichome density, secondary metabolites are especially evolutionary labile (Carmona et al., 2011; Wang et al., 2022) and likely to differ qualitatively among plant species (Sedio et al., 2017) in a manner that shapes herbivore host use (Becerra, 1997; Endara et al., 2018, 2022; Salazar et al., 2018; Volf et al., 2015).

Whereas both morphological and metabolomic traits may vary quantitatively with environmental gradients, metabolites may exhibit a greater capacity for qualitative variation, or variation in chemical composition. There is evidence that variation in the primary drivers of selection on metabolites may select for greater quantitative investment and convergence in composition of stress-response metabolites in abiotically stressful environments while selecting for divergence in composition of defense-related metabolites in abiotically benign or resource-rich environments with greater biotic pressure (Volf et al., 2022, 2023). Furthermore, despite observations of covariation among morphological and metabolomic traits among congeneric species in a phenomenon described as plant defense syndromes (Agrawal & Fishbein, 2006; Kursar & Coley, 2003), comparative studies at larger phylogenetic scales have found that secondary metabolites may describe a distinct axis in plant functional trait space, varying orthogonally to many commonly measured morphological traits (Sedio et al., 2021; Walker et al., 2023) and indicating their potential value in assessing community assembly mechanisms (Walker et al., 2022). For example, at local scales, secondary metabolites explained more variation in tree species composition than phylogenetic relationships in Amazon tree communities and co-occurring species showed greater than expected dispersion in chemical composition in tropical forests in Amazonia and China (Endara et al., 2022; Wang et al., 2023). These results support the idea that natural enemies with chemically mediated host ranges play a critical role in local community assembly (Endara et al., 2022; Forrister et al., 2019; Vleminckx et al., 2018), a pattern hypothesized to exist more often in tropical than temperate ecosystems (Adams et al., 2009; LaManna et al., 2016; Sedio et al., 2018; Terborgh, 2012). In general, overdispersion in metabolomic traits that function in defense is thought to result from density-dependent interactions with natural enemies of intermediate to high host specificity (Forrister et al., 2019; Sedio & Ostling, 2013; Wetzel & Whitehead, 2020) and has been attributed to the effects of enemy-mediated competition in forest plots in Panama (Forrister et al., 2019) and China (Wang et al., 2023). Alternatively, underdispersion in metabolomic traits may result from the action of generalist enemies that preferentially feed in chemically diverse neighborhoods (Chambers et al., 1996; Wang et al., 2023).

Here, we explore functional diversity patterns of leaf secondary metabolites (metabolomic traits hereafter) as well as "classic" morphological traits among co-occurring tree species in three temperate forest ecosystems across North America. We focus on temperate forests that range in species composition and diversity to examine a range of settings that could influence functional diversity patterns and facilitate comparisons with other community-level studies of metabolomic traits, many of which have focused on tropical forests (Endara et al., 2022). We focus on three sites as case studies for which we have sufficient environmental, spatial tree community, and trait data. These three sites differ in tree species richness, prevalence of coniferous species, climate, and soil resource gradients. Specifically, we ask how do patterns of metabolomic and morphological trait functional diversity differ at the local community scale? We expect that tree communities will tend to be overdispersed for leaf secondary metabolites related to defense against enemies, signaling the potential importance of specialized natural enemies in structuring tree communities (Endara et al., 2022), but underdispersed for morphological traits, potentially indicative of species sorting among habitats that differ in environmental conditions (Ding et al., 2019; Menezes et al., 2020; Muscarella et al., 2016). We also ask how do these functional diversity patterns change along local-scale environmental gradients of soil resources and topography? We expect that differences in trait dispersion among local communities will be associated with changes in resource availability along local topographic and edaphic (topo-edaphic) gradients where more resource-rich conditions will be associated with more overdispersion or less underdispersion in both morphological and metabolomic traits potentially due to reduced resource limitation and stronger species interactions (Chapman & McEwan, 2018; de la Riva et al., 2018; Ding et al., 2019; Muscarella et al., 2016).

MATERIALS AND METHODS

Study sites

Our three study sites (Table 1) are part of a global network of forest-ecology plots coordinated through the Smithsonian Forest Global Earth Observatory (ForestGEO; Anderson-Teixeira et al., 2015). These sites are a subset of those in Sedio et al. (2021) and were chosen (1) based on the availability of fine-scale environmental (soils) data and morphological trait data collected within each plot using standardized methods, and (2) to span a wide range of tree species richness and climate conditions in North American temperate forests (22–85 woody species per plot). The Wind River Forest Dynamics Plot (WFDP) is a 25.6 ha (800 × 320 m) forest-dynamics plot containing 22 woody species >1 cm dbh and located in a Douglas fir-western hemlock dominated coniferous forest in southwestern Washington (USA; 45.8197 N, −121.9558 W; mean annual temperature 16.8°C; mean annual precipitation 2493 mm). Additional information about the WFDP plot is available in Lutz et al. (2013). The Tyson Research Center Plot (TRCP) is a 20-ha (480 × 420 m) forest-dynamics plot containing 42 woody species >1 cm dbh and located in an oak-hickory-dominated deciduous forest on the northeastern edge of the Missouri Ozarks (USA; 38.5178 N, −90.5575 W; mean annual temperature 13.5°C; mean annual precipitation 957 mm). Additional information about the TRCP is available in Spasojevic, Yablon, et al. (2014) and LaManna et al. (2016). The Smithsonian Environmental Research Center (SERC) plot is a 16-ha (400 × 400 m) forest-dynamics plot containing 85 woody species >1 cm dbh (42 used in this study) and located in a tulip poplar–beech–oak–sycamore deciduous forest in Maryland (USA; 38.8891 N, −121.9958 W; mean annual temperature 14.1°C; mean annual precipitation 1128 mm). Additional information about SERC is available in Mcmahon and Parker (2015). For this study, we used WFDP tree-census data from 2015, TRCP tree-census data from 2013, and SERC tree-census data from 2013 (Mcmahon & Parker, 2015). At all three sites, all free-standing stems of woody species greater than 1 cm dbh have been identified, tagged, measured, and mapped following CTFS-ForestGEO protocols (Condit, 1998). Each forest plot is subdivided into 20 × 20 m quadrats (WFDP: N = 640; TRCP: N = 504; SERC: N = 399).

Environmental heterogeneity

To quantify local environmental gradients within each forest plot, we measured 14 soil variables and 5 topographic

TABLE 1 Characteristics of the three forest-dynamics plots.

Plot name	Lat	Lon	Forest type (dominant genera)	Plot size (ha)	No. species (no. with complete trait measures)	No. trees (percentage with complete trait measures)	Mean no. species/quadrat (SD)
Wind River (WFDP)	45.81	−121.95	Needle-leaf evergreen (fir-hemlock)	25.6	22 (13)	31,162 (99.6)	5.5 (1.3)
Tyson Research Center (TRCP)	38.51	−90.55	Broadleaf deciduous (oak-hickory)	20	42 (26)	31,800 (98.0)	8.3 (2.4)
Smithsonian Environmental Research Center (SERC)	38.88	−76.55	Broadleaf deciduous (tulip poplar, oak, beech, ash, sycamore, elm)	16	85 (42)	33,500 (97.7)	7.7 (2.0)

variables. Following the sampling design described in John et al. (2007), we measured available nitrogen (total N and NH_4), base saturation, effective cation exchange capacity (ECEC), exchangeable cations (Al, Ca, Fe, K, Mg, Mn, Na), pH, plant-available phosphorous (P), and total exchangeable bases (TEB) at each site. Details on soil sampling methods can be found in Spasojevic, Yablon, et al. (2014). Quadrat-level estimates of each soil variable were derived from kriged values using the geoR package (Ribeiro & Diggle, 2001) in R (R Core Team, 2022). All soil analyses were performed at the Soils Laboratory at the Smithsonian Tropical Research Institute, Panama.

For each 20 × 20 m quadrat, we calculated aspect, convexity, mean elevation, and slope. Mean elevation above sea level was quantified as the mean elevation of the four corners of each quadrat. Slope and aspect were quantified using the slope and aspect tools in ArcGIS 10.1. Aspect was measured as the direction of the steepest slope within each quadrat. Because aspect is a circular variable (measured as an angle), we used both sine(aspect) and cosine(aspect) in our analyses to relate to North–South or East–West orientations (Legendre et al., 2009). Convexity was measured as the elevation of a given quadrat minus the mean elevation of the eight surrounding quadrats (Legendre et al., 2009). For the edge cells, convexity was measured as the elevation of the center point minus the mean of the four corners (Legendre et al., 2009).

Trait sampling

To describe variation in functional diversity, we measured two suites of traits on as many species as possible within the three sites. For the purposes of our questions, we focus on interspecific variation in traits and thus pooled all observations of each species at a given site to calculate a species average from the many individuals sampled for traits at each site. First, we measured six key morphological plant functional traits at each site: leaf area (in square centimeters), specific leaf area (SLA, in square centimeters per gram), leaf water content (LWC, calculated as the difference between wet and dry mass divided by dry mass, the inverse of leaf dry matter content, in grams per gram), wood density (in grams per cubic centimeter), bark thickness (in millimeters), and seed mass (in grams). Leaf area is associated with leaf energy and water balance, where small leaf size represents a strategy to cope with heat stress, drought stress, cold stress, and photo-oxidative stress (Pérez-Harguindeguy et al., 2013). Specific leaf area is associated with resource uptake strategy and tissue N, where high SLA represents a strategy to maximize carbon gain and relative growth rate (Reich et al., 1997). Specific leaf area might also be related to herbivory as high SLA leaves are more palatable and nutrient rich (Schädler et al., 2003). LWC is associated with relative growth rate (Garnier & Laurent, 1994) and tolerance to low water availability (Farooq et al., 2009). Wood density is associated with mortality rate under abiotic and biotic stress, hydraulic lift, and the relative mechanical strength of the plant (Chave et al., 2009). Bark thickness is associated with protection against biotic and abiotic damage and respiration (Paine et al., 2010). Seed mass is related to dispersal ability and a reproductive strategy where species that produce few large seeds are thought to be better competitors and those that produce many small seeds are thought to be better dispersers (Cadotte, 2007; Muller-Landau, 2010). Trait collection followed protocols outlined in Pérez-Harguindeguy et al. (2013). Specifically, we collected sun-exposed leaves with minimal damage or senescence from each of 5–10 representative individuals of each species and fully hydrated the leaves in 7.6-cm floral water tubes. For all species except conifers, we collected three leaves per individual. Due to the small size of conifer leaves (needles), we collected approximately 0.5 g of leaves (between 40 and 70 needles) per individual per species. In the laboratory, we weighed each leaf (or group of needles) to obtain fresh mass and scanned them using a digital scanner. We calculated leaf area (in square centimeters) from scanned leaves and petioles using Image-J (Schneider et al. 2012). For compound-leaved species, we calculated leaf area as the mean leaflet area per leaf including petioles. For needle leaves, we calculated the total area of all leaves and divided that area by the number of leaves collected. We calculated SLA (in square centimeters per gram) as leaf area per unit dry mass after leaves were dried in an oven at 60C for 4 days. Using the branches from which leaves were collected, we cut out a section that was 2.5 cm long and at least 1 cm in diameter. We calculated bark thickness as the difference in diameter of the branch section (measured using digital calipers) with the bark intact and with the bark removed. We calculated wood density (in grams per cubic centimeter) as the volume of the branch section per unit of dry mass after branch section was dried in an oven at 60 C for 4 days. Seed mass data were compiled from the Kew Royal Botanical Gardens Seed Information Database (http://data.kew.org/sid/). Species with missing seed mass data were assigned a value based on the average of all other members of their genus, as seed mass is generally phylogenetically conserved (Moles et al., 2005). The number of individuals measured per species varied across species and sites based on abundance, ranging from 1 individual measured when there was only 1 individual stem of that species to 10 or more individuals for more abundant species. The TRCP was sampled more intensely for morphological traits as part of a different project (Spasojevic et al., 2016; Spasojevic, Yablon, et al., 2014).

In addition to morphological functional traits, we also measured a suite of leaf metabolomic traits using untargeted metabolomics (Sedio et al., 2021). Untargeted metabolomics data include small organic molecules between ca. 50 and 2000 Daltons in molecular mass, including primary metabolites involved in the plant's core metabolism (e.g., carbohydrates, nucleotides) as well as secondary metabolites that include chemical defenses against herbivores and pathogens. We sampled three to five leaves from five individuals of each species at each site. These leaves were flash frozen, freeze-dried, pulverized, and extracted in a methanol solution overnight. We used liquid chromatography–mass spectrometry to generate tandem mass spectra for each sample. We aligned chromatograms using MZmine 2 (Pluskal et al., 2010) and generated a "feature-based molecular network" (Nothias et al., 2020) using the Global Natural Products Social (GNPS) Molecular Networking platform (Wang et al., 2016) and used Qemistree (Tripathi et al., 2020) to represent structural similarities among compounds as a hierarchical dendrogram. We inferred molecular formulae using Sirius (Dührkop et al., 2019), predicted molecular structures using CSI:FingerID (Dührkop et al., 2015), and classified metabolites using ClassyFire (Djoumbou Feunang et al., 2016). For complete methodological details, see Sedio et al. (2021). For our analyses, we used only compounds belonging to seven chemical classes, corresponding to the "superclass" level of classification used by ClassyFire, that include known anti-herbivore and antimicrobial defenses: benzenoids, glycosides, organic acids and derivatives, organoheterocyclic compounds, phenylpropanoids and polyketides, prenol lipids and terpenoids, and steroids and steroid derivatives. Focusing on compounds in these classes allowed us to evaluate patterns exhibited by specialized metabolites, rather than those involved in core metabolic pathways, although these specialized or secondary metabolites include diverse functions in addition to chemical defense, including abiotic stress tolerance.

Analysis

We included as many species from each site as possible in all analyses, but this was limited by incomplete trait coverage of rare species. For WFDP, we included 13 of the 22 species, for TRCP, we included 26 of the 42 species, and for SERC, we included 42 of the 85 species. For all sites, the species that we included make up over 97.5% of the surveyed individual trees. Within each quadrat, however, it is possible that there was lower representation of the tree community if the rare species for which we do not have traits are abundant in any quadrats. Depending on whether rare species have unique functional traits, this could affect the functional diversity metric that we calculated. In addition, some species are present at multiple sites, but as they have locally measured trait values, we use these local trait values for all analyses. For all analyses, species trait values were scaled and centered prior to analysis. We used principal components analyses (PCAs) to describe covariation in species trait values and in environmental values. For the species trait PCA, each point denotes a species, and we used all 13 traits (seven metabolomic and six morphological) for all species. We also used separate PCAs for each site to describe the primary topographic and edaphic (topo-edaphic) gradients at each site because we expected that each site would have different environmental variables that characterize the main environmental gradients. For these PCAs, each point represents a 20 × 20 m quadrat, and we used all 14 soil variables and 5 topographical variables—each variable was scaled and centered prior to analysis. We subsequently extracted the values for each quadrat along the first two principal component (PC) axes to describe where each quadrat lies along the primary axes of environmental variability. All PCAs were conducted using the "prcomp" function in R 4.2.2 (R Core Team, 2022).

We calculated the functional dispersion (FDis), for each 20 × 20 m quadrat using the "FD" function (Laliberte & Legendre, 2010) as a multivariate measure of functional diversity. Functional dispersion is a measure of distance of each species from the centroid of all species included in our analysis in functional trait space weighted by abundance and provides an estimate of trait variability in a community. We calculated FDis for quadrats in each forest plot separately to account for the fact that each forest plot has a different species pool. To assess the extent to which FDis values differ from random expectations, we constructed null models to simulate random communities in each quadrat. To construct our null model, we first defined the species pool as the total number of species and the total abundance of each species observed in each forest plot. We then simulated functional composition 999 times in each quadrat by randomly sampling individuals from the regional species pool while preserving the relative abundance of each species in the regional pool and the total number of individuals in each quadrat and recalculating FDis trait values for each quadrat (Spasojevic, Copeland, et al., 2014) using the "permatfull" function (Oksanen et al., 2010). We then calculated standardized effect sizes for the FDis deviation from null expectations in each quadrat by taking the difference between the observed FDis value and the mean expected FDis value, and then dividing this by the standard deviation of the expected values. These FDis deviations indicate whether observed FDis values are overdispersed (positive values) or underdispersed (negative values) based on null expectations. Because standardized effect sizes assume that the distribution of null model results is not skewed, we tested the skewness or our null model results and found that some skewness exists (mean skewness = 0.63, range = −0.35 to 1.59). Due to this skewness, we also calculated effect sizes using methods from Botta-Dukat (2018) and found a correlation of 0.98 between standard effect sizes and these modified effect sizes, so we used standardized effect sizes for our analyses. Finally, to assess to what extent FDis deviations for each quadrat are related to topo-edaphic characteristics, we ran generalized least squares models with an exponential spatial correlation structure to account for spatial autocorrelation in model residuals where the FDis deviation is the dependent variable and the first two PC values for each quadrat as the independent variables.

Because these multivariate trait diversity assessments may mask dynamics occurring with single traits, in addition to the multivariate trait analyses, we also calculated FDis, FDis deviations, and community-weighted mean (CWM) for each trait individually. We calculated CWM for each trait as the trait value for each species weighted by the relative abundance of that species in each plot and then summed these values for all species in a plot to calculate the CWM. We use the same methods as above for the FDis calculations and use simple linear models to examine the relationship between the environmental gradients and the functional diversity metrics. We report these results in Appendix S1, because interpreting patterns for each trait individually is outside the scope of our analyses but may be of interest to others.

RESULTS

Trait covariation

Morphological and metabolomic traits tended to load on separate axes of trait space (Figure 1). The functional trait space of these traits involves many dimensions, as the first two axes represent 43.5% of the total variation and five axes represent over 75% of the total variation. All metabolomic traits loaded positively on PC1, although steroids and prenol lipids were more strongly related to trait PC2 (Appendix S1: Figure S1). On the other hand, morphological traits tended to load more strongly on PC2, although they are still somewhat related to trait PC1. Bark thickness and seed mass negatively loaded on trait PC2 while leaf size, LWC, SLA, and wood density loaded positively on trait PC2 (Appendix S1: Table S1). While species from SERC and TRCP tend to occupy similar trait space, the coniferous species at WFDP (e.g., *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Abies amabilis*) were found in the lower left quadrant with high concentrations of steroids and prenol lipids and *Prunus serotina* and *Cornus florida* (both present at SERC and TRCP) had high PC1 values, indicative of high values for most metabolomic traits (Figure 1).

Local environmental gradients

Across all sites, there were some topographical and edaphic variables that consistently characterized the primary environmental gradient (topo-edaphic PC1, Figure 2). At all sites, variables related to cation concentrations in the soil (e.g., TEB, Ca, Mg, and BS) loaded strongly on topo-edaphic PC1. Soil N was strongly related to topo-edaphic PC2 at SERC and TRCP, but less so at WFDP. At WFDP, Fe, Al, and P are most closely aligned with topo-edaphic PC2 (Appendix S1: Table S2).

Functional dispersion patterns

On average, metabolomic traits were overdispersed, especially at SERC and TRCP, while morphological traits were, on average, underdispersed at all sites to varying degrees (Figure 3). Metabolomic trait dispersion deviations changed along the environmental gradients where tree communities at SERC became more overdispersed along topo-edaphic PC1 while WFDP and TRCP had no relationship. Morphological traits became less underdispersed at SERC and TRCP along topo-edaphic PC1 while WFDP shifted from under- to overdispersed along PC1 (Figure 3, Table 2). Relationships between PC2 and the trait dispersion deviations were weaker with morphological trait dispersion deviation shifting from over- to underdispersion at WFDP showing the only trend (Table 2; Appendix S1: Figure S1). We provide individual trait relationships with topo-edaphic PC1 and PC2 at each site in Appendix S1: Figures S2–S13.

DISCUSSION

Our results show that morphological and metabolomic trait functional diversity patterns tend to differ in temperate forest tree communities: local communities of co-occurring tree species tend to be overdispersed with respect to metabolomic traits but underdispersed with respect to morphological traits compared with plot-wide species pools representing each community. Examining both

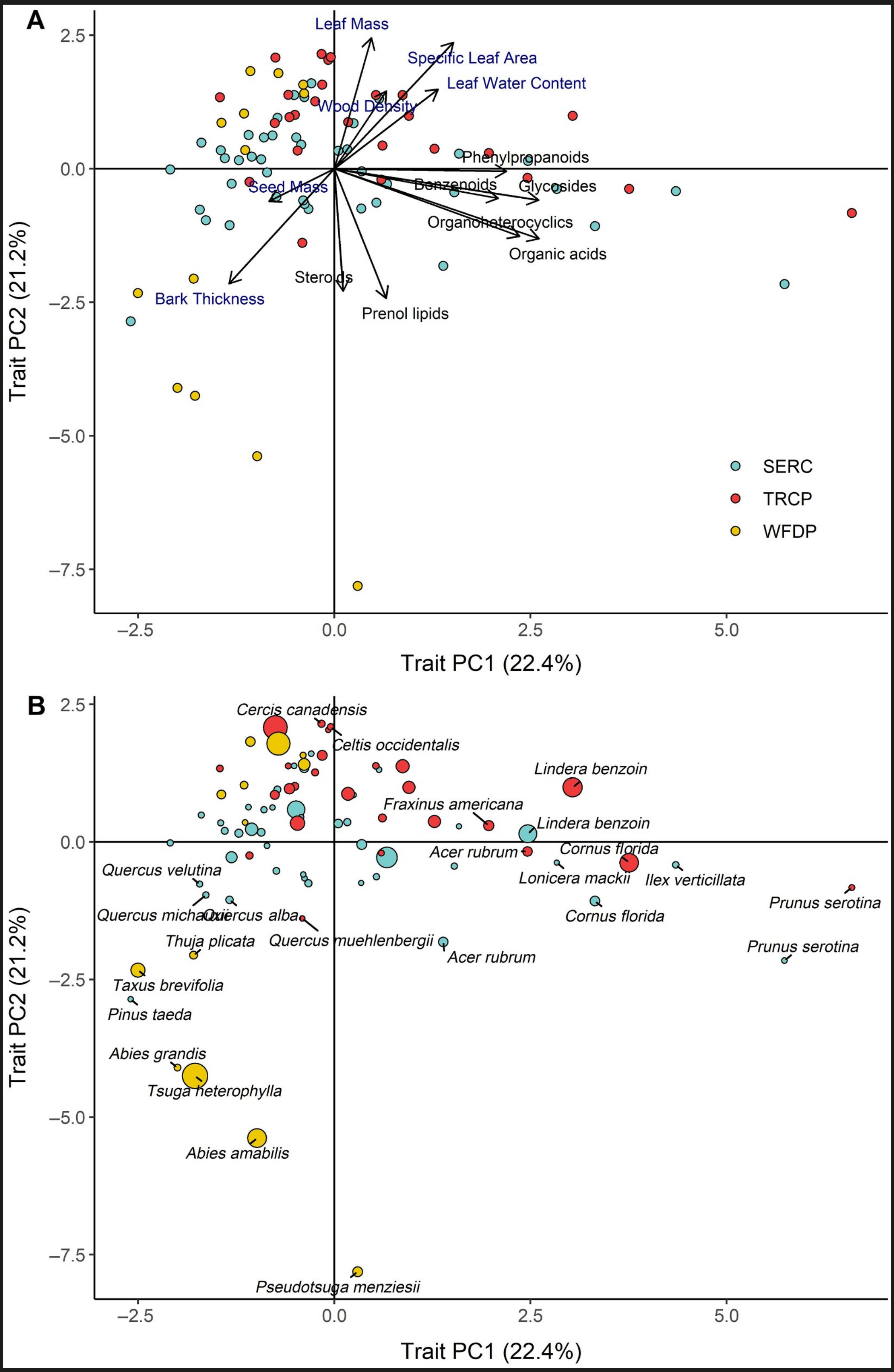

FIGURE 1 Species morphological and metabolomic traits separate them in multivariate functional space. Each point represents a species and the site where it is found is indicated by point color. Point positions are the first two axis scores from a principal components analysis (PCA) including all traits. In (A), the text color of trait labels indicates whether traits are metabolomic (dark blue) or morphological (black). In (B), the size of the point is proportional to the relative abundance of that species in the forest plot and labels indicate species names for some species. Percentage numbers on each axis represent the proportion of the total variation related to each axis. All trait values were scaled and centered prior to analysis. See Table 1 for identification of site abbreviations.

morphological and metabolomic traits revealed patterns that would have been overlooked by a focus on only traditional morphological functional traits. Specifically, we found that metabolomic traits are largely orthogonal to other commonly measured morphological traits. Greater than expected variability in community-weighted metabolomic trait values point towards a potential scenario where biotic pressure from species-specific natural enemies drives the diversification of chemical defense production among co-occurring tree species, while lower than expected variability in community-weighted morphological trait values suggests the importance of environmental filtering in physiological structures. There are, however, challenges to these interpretations, especially as chemical compounds associated with defense can also be produced for other functions, making it important for future research to explicitly measure natural enemy interactions and communities to confirm their role in forest tree community assembly.

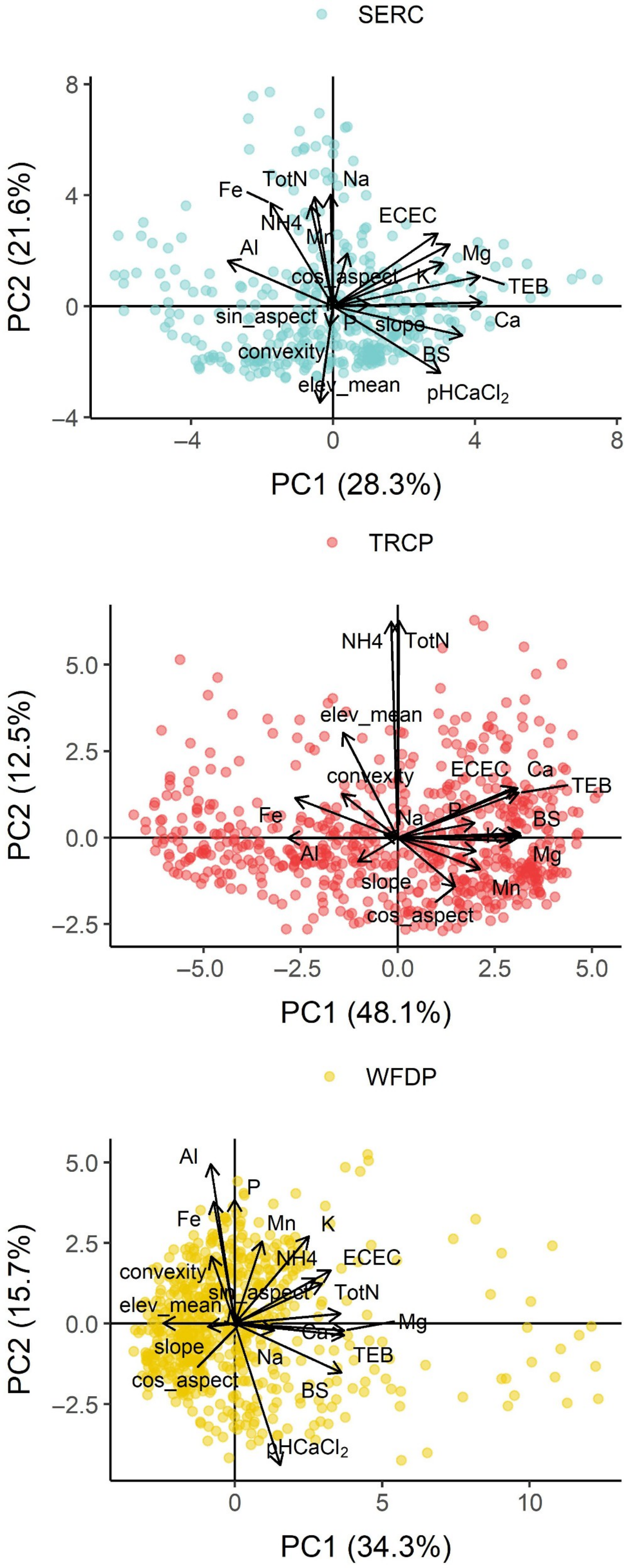

FIGURE 2 Topographical and edaphic characteristics covary differently between sites. Each site has a different principal components analysis (PCA) to capture differences in the most important drivers of environmental gradients between sites. Each point represents a quadrat at a given site (number of quadrats = 399 at SERC, 506 at TRCP, and 640 at WFDP) and colors represent sites. The numbers on each axis represent the percentage of the total variation related to each axis. Al, aluminum; BS, base saturation; Ca, calcium; cos_aspect, cos(aspect); ECEC, effective cation exchange capacity; elev_mean, mean elevation; Fe, iron; Mg, magnesium; MN, manganese; Na, sodium; NH4, ammonium; P, phosphorus; pHCaCl$_2$, pH of calcium chloride; sin_aspect, sin(aspect); TEB, total exchangeable bases; TotN, total nitrogen. See Table 1 for identification of site abbreviations.

In multivariate trait space, the morphological and metabolomic traits largely occupied different axes of variation, suggesting that they provide different information about functional trait strategies and their drivers (Walker et al., 2023). This is consistent with the results from Sedio et al. (2021), who found similar patterns for the same species but for a different subset of sites and chemical compounds, as well as Kergunteuil et al. (2018) who found that morphological traits varied orthogonally with secondary metabolites in alpine plants. Importantly, in our study and others, not all metabolomic traits are completely orthogonal. For example, in studies of intraspecific variation or variation across a few closely related species, Izhaki et al. (2002) and Labarrere et al. (2019) found that metabolomic and morphological traits were correlated, which could reflect plant defense syndromes that involve both morphological and metabolomic traits (Agrawal & Fishbein, 2006). In our study, a few metabolomic classes such as steroids and prenol lipids/terpenoids aligned more closely with the morphological traits. Orthogonal variation between metabolomic and morphological traits could be due to the relatively weak

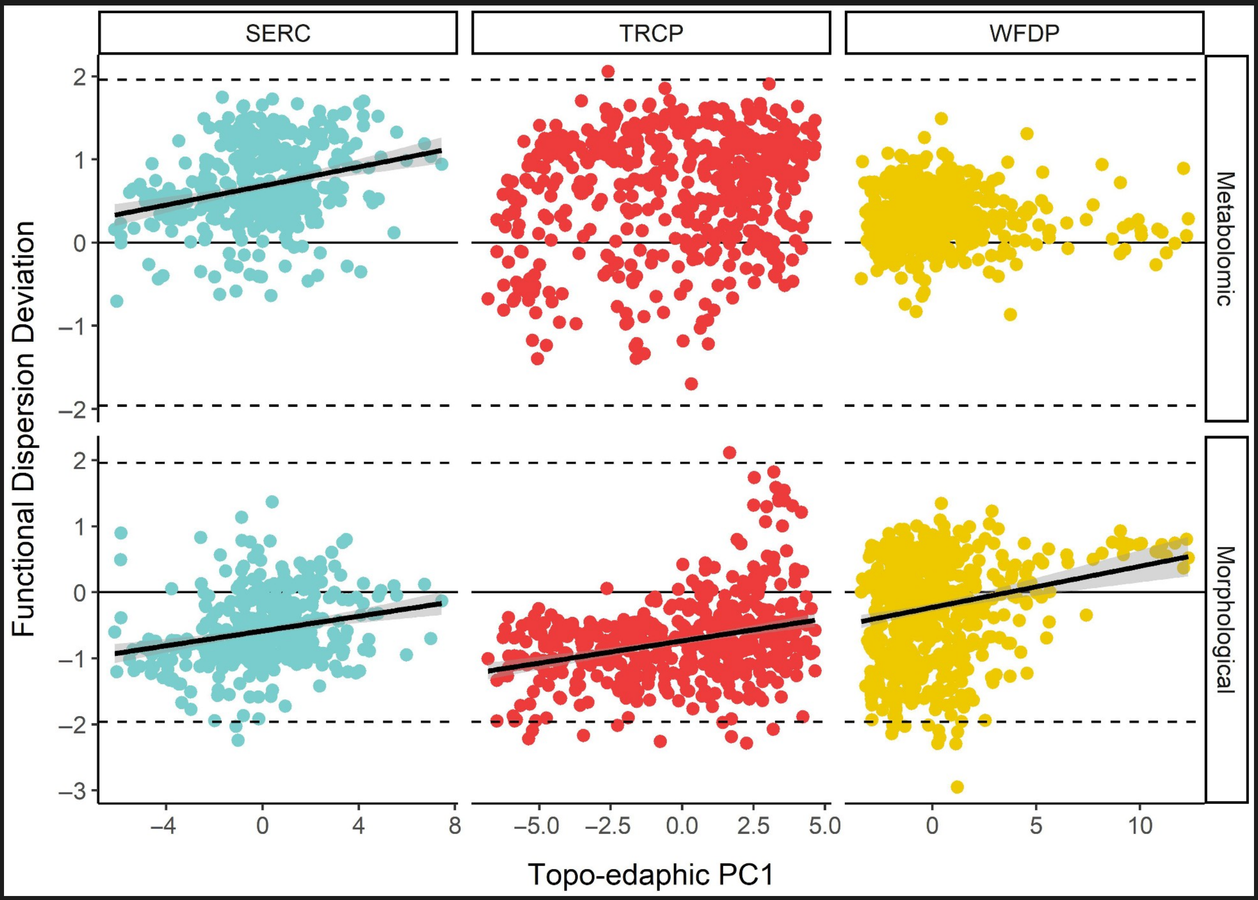

FIGURE 3 Standardized effect size of functional dispersion (FDis) deviations from null expectations at three forest sites for metabolomic and morphological suites of traits that vary along the main topographical and edaphic (topo-edaphic) gradient at each site (PC1, for more information on the principal components, see Figure 2; Appendix S1: Table S2). Each point represents a quadrat (number of quadrats = 399 at SERC, 506 at TRCP, and 640 at WFDP) and each color represents a site. Black lines indicate linear model fits for the generalized least squares relationship between the SES FDis deviation and PC1. Dashed lines indicate significance thresholds where any points falling beyond the dashed line were significantly different from null expectations, with $p < 0.05$. Each panel includes text that indicates the proportion of quadrats that were overdispersed or underdispersed and the average value of all the quadrat deviation values. See Table 1 for identification of site abbreviations.

TABLE 2 Slope estimates for change in functional dispersion deviations along the first two topo-edaphic principal component (PC) axes.

	Metabolomic traits						Morphological traits					
	PC1			PC2			PC1			PC2		
Site	Est.	SE	p	Est.	SE	p	Est.	SE	p	Est.	SE	p
SERC	0.03	0.02	0.05	−0.02	0.02	0.44	0.05	0.02	0.008	−0.01	0.02	0.56
TRCP	0.02	0.02	0.44	−0.05	0.04	0.18	0.06	0.02	<0.001	−0.04	0.03	0.2
WFDP	−0.007	0.008	0.41	0.007	0.01	0.50	0.07	0.02	0.006	−0.08	0.03	0.003

Note: Values reported are the slope estimates (Est.) with SEs and p values testing whether the slope is different from zero. See Table 1 for identification of site abbreviations.

phylogenetic signal that is often detected in metabolomes while some morphological traits are more phylogenetically conserved (Sedio et al., 2021; Westbrook et al., 2011). The fact that many metabolomic traits vary orthogonally to morphological traits suggests that these two classes of traits can generate independent patterns of community-level functional diversity. Further, the morphological traits collected here are not generally strongly associated with defense, and therefore might indicate a distinction between defense versus physiological function. This distinction would support the idea that chemical classes used in this study align more with nonphysiological function, and therefore, perhaps, defense. Indeed, we chose chemical classes thought to include many defenses against herbivores or other natural enemies; however, individual metabolites can serve multiple functions, including defense, abiotic stress tolerance, and core metabolic functions (Coley et al., 2005; Volf et al., 2023).

Functional dispersion patterns generally confirmed our predictions that metabolomic traits would show overdispersion while morphological traits would show underdispersion. These patterns suggest that community assembly mechanisms like enemy-mediated competition and environmental filtering might both play important roles in temperate forest community assembly. Pressure from specialist herbivores or other natural enemies is often cited as a mechanism behind conspecific negative density dependence, which is a stronger force structuring communities in tropical ecosystems (LaManna et al., 2017). Although conspecific negative density dependence is relatively low at our sites (LaManna et al., 2017), our results suggest that natural enemies with chemically mediated host ranges may play an important role in three temperate forests by limiting the success of chemically similar heterospecific individuals, and thereby promoting chemically diverse neighborhoods within the plant community. Such defense-trait overdispersion is thought to result from enemy-mediated competition over a wide range of variation in natural enemy host specificity, whereas species diversity maintenance is likely much more sensitive to natural enemy host range (Sedio & Ostling, 2013). However, we do not have high-quality data of pest abundance or host use for these sites, so we cannot confirm the inferences from functional diversity patterns with other data. Moreover, secondary metabolites in the chemical classes we considered serve functions in addition to defense. As with other trait-based studies of community assembly, these functional diversity patterns provide an avenue for identifying potential mechanisms to be explored with more detailed experiments/studies and measuring enemy host interactions to evaluate the contribution of chemically mediated interactions to diversity maintenance in our focal forests is a key next step.

On the other hand, the pattern of underdispersion in morphological traits may suggest that species are sorted into local communities based on their morphological functional strategies. This pattern has been observed at the TRCP site before in both the tree community (Spasojevic, Yablon, et al., 2014) and the understory community (Lemoine et al., 2015). This sorting is likely based on environmental tolerances, as there is substantial variation in topo-edaphic conditions at each site and the morphological traits that we selected are all related to environmental tolerances or resource acquisition. The underdispersion in morphological traits likely occurs due to strong constraints on seedling and sapling survival where leaf and stem traits have strong survival consequences (Lebrija-Trejos et al., 2010; Lusk & Laughlin, 2017; Spasojevic, Yablon, et al., 2014). However, we cannot rule out the role of competition for resources, which could also manifest as underdispersion if trait hierarchies are most important for species success in these forests (Kunstler et al., 2012) or if emergent neutrality results in clusters of similar species (Scheffer & Van Nes, 2006). In addition, the spatial scale of analysis affects which traits tend to be important for community assembly (Spasojevic et al., 2016; Yuan et al., 2016) and interactions between tree species at earlier life stages, when competition is likely to be most important, involve interactions at finer spatial scales than the quadrats included in this study.

WFDP is a notable exception to the functional dispersion patterns discussed so far. As the only site with abundant evergreen gymnosperm species mixed with deciduous broad-leafed angiosperms, more overdispersion in morphological traits may suggest that resource partitioning within and between these groups may play a larger role in community assembly. This suggests that deciduous and coniferous species tend to co-occur more frequently than expected by chance. Interestingly, Wind River had the least overdispersion in the metabolomic traits, with almost all plots showing no difference from random expectations. This may be a result of the high variation in metabolomic traits within the WFDP plot-scale species pool (Sedio et al., 2021). Also, coniferous plants are known to invest more heavily in primary defenses like thick waxy cuticles and tough leaves (Lirette & Despland, 2021), which are morphological traits, and thus some of the variation in their defenses were not captured in our chosen traits.

Results at SERC support hypotheses of how dispersion is likely to change along resource gradients. The first PC axis for each site tended to relate to soil cation availability, which is consistent with the soil nutrients that exhibited the greatest influence on tropical tree distributions in Panama (John et al., 2007). Soil cations might be influential at SERC and TRCP because cations such as calcium and aluminum may be variable across the landscape and limiting to tree growth due to a history of acid rain in Eastern US forests (Bal et al., 2015; Halman et al., 2014). At SERC, we saw increasing metabolomic trait functional overdispersion along topo-edaphic PC1, a result that supports the hypothesis that when more resources are available, there is likely to be stronger enemy pressure and greater divergence with respect to secondary metabolites. On the other hand, morphological trait underdispersion became less extreme along topo-edaphic PC1 at all sites, suggesting that resource constraints are minimized at higher values of PC1, allowing a greater variety of morphological strategies. The second topo-edaphic PC had few relationships with functional dispersion deviations, suggesting that environmental variables related to topo-edaphic PC1 are more important. SERC was also the site with highest species richness, which may allow for stronger dispersion patterns and trends along the topo-edaphic gradient because there are more species to be assembled into communities. In the future, data linking topo-edaphic gradients to insect herbivory or abundance would be important for understanding how soil resources translate to biotic interactions and leaf metabolomic traits.

Recent theoretical work suggests that the expectation that communities structured by competition should result in assemblages of coexisting species that are maximally different from one another is often not met (Barabás et al., 2013; D'Andrea et al., 2019). Rather than resulting in overdispersion along a trait axis, competition may alternatively result in clusters of species with similar trait values within which species would compete via nearly neutral dynamics governed by fitness differences within a strongly overlapping niche space (Chase & Leibold, 2003; D'Andrea et al., 2019; Scheffer & Van Nes, 2006). These findings have two implications for interpreting our results. First, the morphological underdispersion we observed cannot be unequivocally attributed to abiotic filtering, as classical competition may generate similar patterns (D'Andrea et al., 2020; Mayfield & Levine, 2010; Spasojevic & Suding, 2012). On the other hand, the relationship we observed between morphological trait underdispersion and soil resource gradients suggests that the mechanism responsible for structuring local assemblages varies with underlying environmental gradients, and this may be driven by variation in abiotic stress. Second, our observation of metabolomic overdispersion is all the more striking when compared with the range of theoretical outcomes of competition, which include trait underdispersion and the formation of nearly neutral clusters of species in trait space (D'Andrea et al., 2019). Our results therefore suggest that the classical expectation that competition limits trait similarity may be most relevant to defensive metabolites with a high capacity for qualitative variation among species driven by selection for divergence in chemical composition driven by reciprocal coevolution of plants and their enemies, even while other metabolomic and morphological traits vary quantitatively along underlying environmental gradients.

Finally, better understanding of the role of the environment and species pools on functional diversity patterns of morphological and metabolomic traits would help inform where and when different community assembly mechanisms might be important. For example, negative biotic interactions are thought to be strongest in warmer and wetter climates (Schemske et al., 2009) and we see somewhat stronger overdispersion at the two warmer sites (SERC and TRCP). However, WFDP is much wetter on average, potentially counteracting the cooler average temperatures. In addition, WFDP has not seen large-scale disturbance for the longest period (over 500 years since the last fire and never logged) compared with the other sites, allowing more time for community assembly dynamics to play out. The abundance of conifers at WFDP and not at other sites also likely plays a role in generating the functional diversity patterns we observed, especially for morphological traits. However, as our three sites differ in a range of factors, we are unable to determine which factors ultimately generate the differences in functional diversity patterns that we observed. Future research, combined with the accumulation of more data on metabolomes and natural enemy abundances across more sites, will lead to greater general understanding of the drivers of metabolomic functional diversity patterns.

In all, our results suggest that the assembly of temperate tree communities may be influenced by a combination of species sorting across environmental gradients and enemy-mediated competition at fine spatial scales (Sedio & Ostling, 2013). Selection for local divergence in plant defense strategies has often been observed in tropical tree communities, and our results suggest that natural enemies with chemically mediated host ranges may play a role in shaping community assembly in temperate forests as well. Overall, these results are based on indirect inferences, and we believe that the patterns found in this study merit further investigation into the role of natural enemies in structuring tree assemblages in temperate forests. Understanding the interaction between enemy host use, plant metabolites, and plant performance on a mechanistic level will require community-wide insect and pathogen bioassays to test the hypothesis that interspecific variation in the foliar metabolome partitions niche space with respect to natural enemies (Coley et al., 2005).

AUTHOR CONTRIBUTIONS

Jonathan J. Henn, Marko J. Spasojevic, Jonathan A. Myers, and Brian E. Sedio conceived the idea. Marko J. Spasojevic, Jonathan A. Myers, Emily Dewald-Wang, Brian E. Sedio, and James A. Lutz acquired funding. Geoffrey Parker, James A. Lutz, Jonathan A. Myers, and Sean M. McMahon oversaw forest plot data collection.

Brian E. Sedio led metabolomic trait data collection and Marko J. Spasojevic led soils and morphological trait data collection with the help of Christopher P. Catano, Emily Dewald-Wang, Dilys Vela Díaz, and Jonathan A. Myers. Jonathan J. Henn led data analysis and writing. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code (Henn, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.14277911.

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