RESEARCH ARTICLE

Niche differentiation along multiple functional-trait dimensions contributes to high local diversity of Euphorbiaceae in a tropical tree assemblage

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Abstract

1. Understanding the mechanisms that drive community assembly in species-rich tropical forest remains a fundamental challenge in ecology. Here, we integrated multivariate functional trait dimensions, phylogeny and metabolomics to test fundamental predictions concerning the role of differentiation with respect to abiotic and biotic niche axes in the maintenance of high local diversity of woody plants in the Euphorbiaceae.

2. We measured 40 functional traits related to resource acquisition, photosynthetic capacity, hydraulic efficiency and secondary-metabolite profiles generated using untargeted metabolomics in all 26 Euphorbiaceae species in a 20-ha forest dynamics plot in tropical southwestern China. We examined the correlation structure of 40 traits using a trait networking approach. We coupled these traits with variation in soil nutrients, light environment, soil water content and leaf herbivory, respectively. Most resource utilization traits showed significant phylogenetic signal, whereas almost all defensive traits lacked phylogenetic signal, including species similarity with respect to plant secondary metabolites.
4. Synthesis. Our results suggest that resource-utilization traits and the habitat associations play a significant role in the niche segregation of co-occurring woody plants in the Euphorbiaceae. Secondary metabolites, however, may enhance diversity at a finer spatial scale by allowing closely related species with similar functional traits to partition biotic niche space within shared habitats in tropical rainforest.

**KEYWORDS**
closely related species, convergent evolution, divergent evolution, Euphorbiaceae, functional trait dimensions, herbivores, plant secondary metabolites

1 | INTRODUCTION

Co-occurrence of numerous closely related species at a local scale is a hallmark of diverse tropical forests (Gentry, 1989). Understanding the mechanisms that maintain such diversity in the face of intense competition for resources remains a long-standing challenge in ecology. Closely related species are often phenotypically and ecologically similar due to phylogenetic conservatism and are likely to occupy similar niches (Harvey & Pagel, 1991; Wiens et al., 2010). Classical niche theory predicts that ecologically similar species should not stably coexist due to habitat overlap, resource competition, and shared natural enemies (Chesson, 2000; Gause, 1934; Holt, 1977). The idea that natural enemies with highly specialized host ranges may maintain plant diversity through conspecific negative density dependence (Connell, 1971; Janzen, 1970) has been proposed to an attractive potential solution to the paradox. Yet many insect herbivores and microbial pathogens are not single-host specialists (Gilbert & Webb, 2007; Novotny et al., 2002; Ødegaard et al., 2005) and hence are likely to mediate competitive exclusion among plants within their host ranges (Chesson & Kuang, 2008; Sedio & Ostling, 2013). Fortunately, while plant lineages with high local species richness challenge our understanding of coexistence, the very tendency toward phylogenetic niche conservatism that makes the high local diversity of these lineages such an apparent paradox also makes them excellent study systems in which to tease apart the niche axes that underpin their diversity.

Identifying the niche differences that distinguish co-occurring, closely related plants requires the measurement of traits as well as species interactions with the abiotic and biotic environment. Recent research on ‘functional’ traits of plants suggests that variation in life-history strategy and environmental distribution may be highly multivariate in the space of measurable morphological and physiological traits (Condit et al., 2013; Laughlin & Messier, 2015; Rüger et al., 2018; Trisos et al., 2014), even among closely related species (Sedio et al., 2012). Focusing on a single dimension may overlook niche differentiation in other dimensions of trait or niche space and limit explanatory power, yet the integrated study of multivariate trait space and the interaction of multivariate dimensions with multiple axes of variation in the abiotic and biotic environment has the potential to reveal niche segregation that would not be reflected in a single dimension (Burton et al., 2020; Futuyma & Moreno, 1988; Yang et al., 2018). Furthermore, it is increasingly recognized that physiological tradeoffs that characterize interspecific variation in stress tolerance, resource use, and life-history strategy are best described by multivariate trait dimensions rather than individual traits (Díaz et al., 2016; Messier et al., 2018; Mouillot et al., 2021). However, many previous studies have been limited to consider trait relationships within a leading dimension, but have not considered whether the trait dimensions represent independent axes of variation in plant physiology and resource use (Chave et al., 2009; Wright et al., 2004). To overcome this problem, correlations among multiple traits or trait dimensions can be expressed as a trait network, in which the network nodes represent traits and edges reflect highly correlated traits in the network (Kleyer et al., 2019; Messier et al., 2017). Such trait networking approaches can enhance our understanding of trait correlations and interactions between trait dimensions and further revealing a small number of high-centrality traits that represent interspecific variation in physiology and life-history strategy.

Understanding the coexistence of closely related species within ecological communities may require the consideration of variation with respect to multiple fundamental eco-physiological strategies (Silvertown, 2004), such as photosynthetic traits, hydraulic traits, resource acquisition traits, and physical defensive traits. In addition to morphological variation, much of the functional trait variation of plants is a result of small organic molecules that comprise the metabolome. The plant metabolome includes primary metabolites involved in core metabolic pathways and the molecular building blocks of large organic polymers, such as nucleotides, amino acids and mono- and disaccharides. However, much of the interspecific variation in plants is a result of the astonishing diversity of secondary metabolites (SMs) with specialized functions (Sedio et al., 2021; Walker et al., 2022). SMs can mediate plant responses to abiotic stressors, such as ultraviolet radiation and freezing temperatures (Rasmann et al., 2014), and can serve as antinutritive agents or acute toxins against herbivores and pathogens (Coley, 1983) and play an important role in shaping natural enemy host ranges (Pagare et al., 2015; Salazar et al., 2018). Much like the shared resources, shared natural enemies such as insect herbivores and pathogens can mediate competitive exclusion of host plants (Chesson & Kuang, 2008; Sedio & Ostling, 2013). But unlike abiotic stressors,
natural enemies are capable of reciprocal coevolution in response to the evolution of chemical defenses on the part of their plant hosts, which may make them strong agents of selection for divergence in chemical composition and the evolution of novel chemical defenses (Ehrlich & Raven, 1964; Schemske et al., 2009; Volf et al., 2020). The vast diversity of plant SMs has long precluded the study of metabolomics at the community scale. However, the recent rapid rise of ecological metabolomics (Sedio et al., 2021; Sedio, Boya, & Rojas Echeverri, 2018; Walker et al., 2022) promises to illuminate the role of plant SMs even in species-rich and understudied communities such as tropical forests.

Closely related species are derived from a recent common ancestor and hence expected to exploit a limited range of trait space. Furthermore, closely related species are expected to be more ecologically similar than distantly related species (Ackerly, 2004; Burns & Strauss, 2011). For these reasons, divergence along trait or niche axes among closely related species should be observable against a phylogenetically conserved background and help to reveal the niche dimensions along which interspecific differentiation has contributed to the diversification of, and maintenance of diversity within, the lineage (Ackerly, 2004; Ackerly et al., 2006; McKown et al., 2016; Sedio et al., 2012; Swenson, 2011). Traits are likely to evolve as correlated suites or syndromes that reflect ecological tradeoffs in function (Arnold, 1983). Hence, consideration of phylogenetic patterns with respect to multivariate trait space may reveal conservation or divergence in multivariate ecological strategies (Rüger et al., 2020). Finally, a comparison of phylogenetic patterns among multiple axes of trait variation can reveal which niche dimensions have played a role in ecological differentiation within a plant lineage and at what phylogenetic scale, for example at the crown or at the tips of the phylogeny. For example, Sedio et al. (2012) found that hydraulic traits were phylogenetically conserved among the Psychotria of Barro Colorado Island (BCI), Panama, resulting in fine-scale co-occurrence of close relatives in shared hydraulic niches, whereas photosynthetic traits were more variable. Similarly, Vleminckx et al. (2018) observed phylogenetically conserved resource-use strategies, but phylogenetic divergence in defenses. There is growing evidence of widespread phylogenetic divergence in SMs within tropical tree lineages (Becerra, 1997; Kursar et al., 2009; Sedio, 2017). However, few studies have integrated the comprehensive study of morphological and physiological traits related to resource-utilization strategy with a metabolomics-based study of variation in SMs in a community and phylogenetic context.

Here, we assessed interspecific, ecological, spatial and phylogenetic variation in morphological, physiological and chemical traits to identify the key axes of variation that contribute to the high local diversity of trees in a single plant family in a local community. We measured 40 functional traits related to resource acquisition, photosynthetic capacity, hydraulic conductivity and efficiency and secondary-metabolite profiles for all 26 free-standing woody species of Euphorbiaceae in tropical seasonal rain forest in Xishuangbanna, southwestern China. We examined the correlation structure of interspecific variation among these 40 traits using a trait networking approach (Messier et al., 2017) and interspecific variation in leaf SMs through the use of untargeted metabolomics (Sedio et al., 2021; Sedio, Boya, & Rojas Echeverri, 2018). We coupled these traits with detailed measurements of variation in soil nutrients, light environment, soil water content and herbivore pressure to identify the axes of trait variation that may define niche differences among co-occurring woody Euphorbiaceae with the potential to facilitate ecological coexistence through segregation along key abiotic and biotic gradients. Specifically, we asked the following questions: (i) Could a few traits with central correlational relationships reflect interspecific variation in ecological strategy among co-occurring Euphorbiaceae? (ii) Do interspecific variation of multivariate trait dimensions contribute to niche partitioning by segregating Euphorbiaceae in time and space? and (iii) Whether major axes of trait variation differ in phylogenetic signal, and hence the phylogenetic scale at which they contribute to niche differentiation among the Euphorbiaceae in a tropical tree community? We expected a few traits with central correlational relationships to represent interspecific variation in ecological strategy among co-occurring Euphorbiaceae species. In addition, we expected the local Euphorbiaceae to exhibit evidence of niche partitioning along multiple trait and environmental axes. We also expected that morphological and physiological trait axes and the abiotic niches to show greater phylogenetic signal than SMs, showing evidence of trait divergence among closely related species.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in a seasonal tropical rainforest dynamics plot (FDP) in Xishuangbanna, southwestern China (101°34'E, 21°36'N; Figure 1a). The most dominant family in the plot is Icacinaceae, followed by Lauraceae and Euphorbiaceae, based on the importance index (Lan et al., 2008). The mean annual temperature is 21.8°C and the mean annual precipitation is 1492.9 mm in the plot. The forest is influenced by a tropical monsoonal climate, with 84% of mean annual precipitation (1246 mm) occurring during the rainy season from May to October, and a long dry season that lasts from November to next April. Soil type in the plot is mainly laterite with deep soil layers and thin humus (Cao et al., 2006). Habitat heterogeneity was caused by the three perennial streams which traverse the plot and merge together at the southeastern corner. The 2012 census recorded a total of 392 tree species belonging to 196 genera and 69 families represented by individuals with ≥1 cm diameter at breast height.

2.2 | Focal species

All 26 species of Euphorbiaceae (Appendix S2: Table S1) in the plot were selected as focal species for the following reasons: (1) Euphorbiaceae is one of the largest families of all flowering plants

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(Ernst et al., 2015) and nearly global in distribution with the exception of boreal areas, although it is more abundant in tropical regions (Rahman & Akter, 2013). (2) Euphorbiaceae ranked third with respect to the importance value among families in our plot, including 9827 individuals with DBH > 1 cm and 25.51% of the total basal area (Lan et al., 2008, Figure 1b). (3) Euphorbiaceae includes both pioneer and late successional species, components of both the canopy layer and understory, and is distributed from valley to ridge, reflecting variations in resource acquisition ability, photosynthesis capacity, shade tolerance and water requirements (Davies et al., 1998). (4) Most species of the Euphorbiaceae have extraordinary chemical diversity and these chemical compounds are thought to play an important ecological role through herbivore feeding deterrence and antimicrobial activity (Vasas & Hohmann, 2014). Thus, Euphorbiaceae provides an excellent system to examine niche segregation and assembly among closely related species.

2.3 | Functional traits measurements

To explore the species coexistence with respect to multiple niche axes, we classified functional traits into five multivariate dimensions based on specific ecological functions (Appendix S2: Table S2). We collected 13 traits for resource acquisition, 8 traits for photosynthetic ability, 11 hydraulic traits, 8 physical defensive traits and secondary-metabolite profiles that likely include interspecific variation in chemical defenses against herbivores and pathogens (Figure 1c; Appendix S2: Table S3). See Appendix S1 for detailed functional trait measurements. Descriptive statistics of 40 functional traits are reported in Appendix S2: Table S4.

2.4 | Environmental variables

Numerous environmental parameters have been proposed to be major drivers of species distributions. We measured soil nutrient properties, soil water content, light environment and insect herbivory to provide environmental context for species variation in traits that mediate resource acquisition, hydraulic ability, photosynthetic capacity and defensive ability (Both et al., 2019; Rosas et al., 2019; Sun et al., 2016). Soil available nitrogen (N), extractable phosphorus (P), extractable potassium (K), total carbon (C) and soil water content were published in Yang et al., 2014. Light environment was measured using a digital camera (Nikon Coolpix 4500; Nikon Corporation) with a fisheye lens (Nikon FC-E8 Fisheye Converter; Nikon Corporation, Japan) to take hemispherical photographs at low light conditions, with no strong direct light in the sky before sunrise or after sunset (Hale & Edwards, 2002) in each quadrat. We used the software Gap Light Analyzer Version 2.0 to analyze all images and calculated the canopy gap fraction for each photograph, in which light environment was quantified as the fraction of the image not occupied by vegetation cover (Frazer et al., 2000).

To quantify herbivore pressure, we measured herbivory on all species of Euphorbiaceae encountered (Halpern et al., 2010). We...
randomly selected five mature individuals with height ranging from 5 to 6m for each species (Caldwell et al., 2016), and for each individual, three branches were taken from each direction and 10 leaves per branch were selected beginning from the tip. All collected leaves were scanned (Epson Co.), and leaf area was calculated using ImageJ (Abramoff et al., 2004). We measured the percent loss in area for each leaf by comparing the damaged leaf area to the area of the inferred intact leaf shape using the scanned images (Kurokawa & Nakashizuka, 2008). For each leaf, we calculated the herbivory ratio as the ratio of the damaged area to the estimated undamaged area of the leaf (i.e. leaves that suffered greater herbivore damage have a higher herbivory ratio). We classified herbivore damage as hole feeding and marginal feeding based on a guide of >140 distinctive patterns of damage caused by chewing and mining herbivores, excluding fungal and mechanical leaf damage (Labandeira et al., 2007). In addition to classifying herbivore damage, we used the Bug-Net protocol ‘Detailed Protocol: Estimating Leaf Damage’ (https://bug-net.org/detailed-protocol-estimating-leaf-damage/) to quantify herbivore damage. Following Labandeira et al. (2007), we divided insect herbivore types into three diet breadth categories: generalized, intermediate or specialized.

Principal component analysis (PCA) was conducted on each type of environmental factor to reduce the trait data into major orthogonal axes. We used the first three principal components for further analysis of environment distance (Appendix S2: Tables S5 and S6).

2.5 | Network analysis: Exploring trait and trait-dimension correlations

We evaluated relationships between measured traits and broad, multivariate trait dimensions representing resource-acquisition, photosynthetic, hydraulic and physical defense traits using network analysis in which we calculated the connectivity and distance properties of interconnected traits. We used the igraph package to construct the functional-trait network (Csardi & Nepusz, 2006). In this form of network analysis, nodes represent distinct traits, which are linked by edges that represent correlations among traits (Messier et al., 2017). We used Pearson’s correlation to calculate the observed trait correlations. Pairwise trait correlations with \( r > 0.2 \) were significant at \( p < 0.05 \) and were shown in the network. All correlations below this threshold were set to zero. Because some trait correlations were negative, network connection strength between pairs of traits were weighted by the absolute correlation strength (Kleyer et al., 2019). Moreover, based on network analysis, we calculated network centrality and then found traits representing strong effects on the plant phenotype in each trait dimension. We calculated the indicator of ‘degree’ to denote the centrality of each trait following Messier et al. (2017), which is the number of connections leading to a trait. Through this network analysis, we screened traits with large degree values one by one and selected the top four traits with large degree values in each trait dimension. In subsequent analyses, we explored the environmental and spatial turnover with respect to these top four traits with the greatest ‘centrality’ in each dimension (centrality) and with respect to all traits in each trait dimension (all).

To explore the degree of trait integration that characterizes interspecific variation with respect to major dimensions representing resource-acquisition, photosynthetic, hydraulic, and physical-defense traits among the Euphorbiaceae, we used a network-based expectation-testing framework following Messier et al. (2017). For each of the four major trait dimensions, we compared two alternative expectations: the expectation that four traits with high network centrality describe interspecific variation (\( E^{CENTRALITY}_{CENTRALITY} \)) and the expectation that interspecific variation is better described using all measured traits (\( E^{CENTRALITY}_{ALL} \)). For each expectation test, we used standardized Mantel’s tests, which calculate the Pearson’s correlation coefficient for two correlation matrices (Zuur et al., 2007): the expected correlation matrix (\( E^{CENTRALITY}_{CENTRALITY} \) or \( E^{CENTRALITY}_{ALL} \)) and the observed trait correlation matrix (\( D \)) calculated from our empirical data (Cheverud et al., 1989). We repeated these expectation tests for \( E^{CENTRALITY}_{CENTRALITY} \) and \( E^{CENTRALITY}_{ALL} \) for each of four major trait dimensions (Appendix S2: Tables S8–S11). These comparisons thus allowed us to test the expectation that each trait dimension is defined by its most central traits as opposed to a wider range of measurable traits. We did not have a specific expectation regarding the relative strengths of trait correlations, so we only included values of -1, 0 and 1 in the expectation matrices. For all traits, if the relationship between traits was expected to be positive, it was set to 1, if it was expected to be negatively correlated, it was set to -1, and if no relationship between traits was expected, it was set to 0, with expectations based on Messier et al. (2017). For \( E^{CENTRALITY}_{CENTRALITY} \) the correlation value was set to 0 if one of the traits was not a high-centrality trait and -1 or 1 for pairs of high-centrality traits (Yang et al., 2019; Yao et al., 2021). Note that these values do not test whether the correlations are perfect, but simply specify the signs of the correlation.

2.6 | Functional-trait turnover along environmental gradients

To test functional-trait turnover along environmental dimensions, we first calculated functional beta diversity between subplots at local scale on 20m x 20m. For each of the five trait dimensions, we calculated the functional dissimilarity between each pair of subplots using the trait distance (\( D_{pw} \)) of the four traits with the greatest centrality values and all functional traits (Ricotta & Borrascano, 2008). \( D_{pw} \) was calculated as follows:

\[
D_{pw} = \frac{\sum_{i=1}^{n_1} \bar{y}_{i2} \sum_{j=1}^{n_2} \bar{y}_{j1} - \sum_{i=1}^{n_1} \bar{y}_{i1} \sum_{j=1}^{n_2} \bar{y}_{j2}}{n_1 + n_2},
\]

where \( n_{k1} \) represents the number of species in community \( k1 \); \( n_{k2} \) represents the number of species in community \( k2 \); \( \bar{y}_{i2} \) is the mean pairwise trait distance between species \( i \) in community \( k1 \) to all species in
community k2 and $\delta_{jk}$ is the mean pairwise trait distance between j species in community k2 to all species in community k1.

We used generalized additive models (GAMs; Wood, 2006) to test for significant nonlinear pattern of our hypothesized relationships between environmental drivers and turnover in functional traits in each dimension. We treated soil nutrients, light environment, soil water content, and leaf herbivory ratio as environmental factors. For the GAMs, we restricted the number of knots to three to avoid locally overfitting the data but still allowing unimodal or slightly more complex model fits. To identify the most relevant and best fitting environmental driver for each functional trait dimension, we calculated GAMs for the turnover of each functional trait with environmental distance. We also estimated functional-trait turnover with respect to spatial distance. Thus, we considered distance with respect to environmental factors and space as the independent variable and similarity with respect to trait dimensions as the dependent variables. Cubic splines were used to fit non-linear relationships in regression models.

2.7 | Phenylogenetic signal of traits and trait dimensions

We measured the phylogenetic signal of all 40 functional traits and chemical defense profiles defined by SMs and 16 traits with the greatest ‘degree’ values in each trait dimension to test whether functional traits and trait dimensions plus SMs varied in phylogenetic signal within the community. A phylogenetic tree of Euphorbiaceae was reconstructed based on previously reported DNA barcode sequences (Yang et al., 2014). A DNA supermatrix was generated from three chloroplast regions—rbcL, matK, trnH-psbA—and the nuclear ribosomal internal transcribed spacer. See Yang et al. (2014) for detailed methods of phylogenetic tree reconstruction. We then used phylogenetically independent contrasts to test for phylogenetic signal of functional traits and trait dimensions. We calculated the $K_{\text{mult}}$ from Adams (2014), which provides a useful means of evaluating phylogenetic signal in high-dimensional multivariate traits. The $K_{\text{mult}}$ is found from the equivalency between statistical methods based on covariance matrices and those based on distance matrices that is not possible with alternative procedures based on likelihood (Freckleton et al., 2002). We used this approach because it does not rely on the inversion of covariance matrices, thus it is not restricted to cases where the number of trait dimensions is less than the number of species in the phylogeny (Adams, 2014). This is particularly important for our traits, where the number of trait dimensions frequently exceeds the number of species in a phylogeny. Using computer simulations based on Brownian motion, values of $K_{\text{mult}} < 1$ imply that taxa resemble each other phenotypically less than expected under Brownian motion whereas values of $K_{\text{mult}} > 1$ imply that close relatives are more similar to one another phenotypically than expected under Brownian motion.

All analyses were performed using the R packages ‘igraph’ (Csardi & Nepusz, 2006), ‘ade4’ (Chessel et al., 2004), ‘vegan’ (Oksanen et al., 2015) and ‘picante’ (Kembel et al., 2010).

3 | RESULTS

3.1 | The relationship between traits and trait dimensions

Different traits were connected between and within trait dimensions except max tree height, showing that different trait dimensions do not form distinct modules (Figure 2). Mantel’s test provided support for the expectation that four traits with large ‘degree’ values ($E_{\text{CENTRALITY}}$: resource-acquisition traits: C, N, LDMC and N:P; hydraulic traits: Cft*, SWC, πtlp and RWC; physical defense traits: hemi-cellulose, thickness, toughness and ADL; photosynthetic traits: ST, CO, PT and R; Appendix S2: Table S7) were significantly correlated with our empirical data (Table 1; p ≤ 0.05) and further implied that interspecific variation with respect to these high-centrality traits represents species-level variation in all the traits in each dimension. For photosynthetic and physical-defense traits, four traits with large ‘degree’ values better reflected our empirical data than did all traits in each trait category, with $r_M = 0.64$ and $r_M = 0.34$ for photosynthetic and physical-defense traits, respectively. For resource acquisition and hydraulic traits, all traits ($E_{\text{ALL}}$) better reflected our empirical data ($r_M = 0.44$ and 0.36, respectively) than did four traits with large ‘degree’ values in the trait network ($r_M = 0.29$ and 0.30, respectively).

![Figure 2](image-url) Network analysis of the relationship between traits and trait dimensions. Orange: resource acquisition traits; Blue: hydraulic traits; Green: physical defensive traits; Red: photosynthetic traits. Yellow dashed and solid green edges show negative and positive correlations, respectively. Only significant correlations ($r > 0.2$) are shown; line thickness reflects strength of correlation; the circle size indicates the degree value. See Table 1 for trait abbreviations.
TABLE 1  Standardized Mantel’s statistic ($r_M$) and associated $p$-value comparing empirical support for two expectations regarding the structure of phenotypic integration

| Trait dimensions               | $r_M$ | $p$-value |
|-------------------------------|-------|-----------|
| Resource capture traits       |       |           |
| $E_{CENTRALITY}$              | 0.29  | 0.045     |
| Correlated traits: C, N, LDMC, N:P |       |           |
| $E_{ALL}$                     | 0.44  | 0.002     |
| Correlated traits: C, N, LDMC, N:P, C:N, Ca, Mg, dry mass, leaf area, SLA, fresh mass, P, K |       |           |
| Photosynthetic traits         |       |           |
| $E_{CENTRALITY}$              | 0.64  | 0.002     |
| Correlated traits: ST, CO, PT, R |       |           |
| $E_{ALL}$                     | 0.27  | 0.089     |
| Correlated traits: ST, CO, PT, R, $A_{max}$, Ls, chlorophyll content, max height |       |           |
| Hydraulic traits              |       |           |
| $E_{CENTRALITY}$              | 0.30  | 0.014     |
| Correlated traits: $C_t^*$, SWC, $\pi_{tip}$, RWC |       |           |
| $E_{ALL}$                     | 0.36  | 0.015     |
| Correlated traits: $C_t^*$, SWC, $\pi_{tip}$, RWC, $\pi_o$, $C_{tlp}$, $C_{tip}$, r, wood density, conductance, WUE |       |           |
| Physical defensive traits     |       |           |
| $E_{CENTRALITY}$              | 0.34  | 0.040     |
| Correlated traits: hemicellulose, thickness, toughness, ADL |       |           |
| $E_{ALL}$                     | 0.29  | 0.066     |
| Correlated traits: hemicellulose, thickness, toughness, ADL, Si, cellulose, upper epidermal thickness, lower epidermal thickness |       |           |

Notes: $E_{CENTRALITY}$—Centrality defined trait dimensions: only four traits with large degree value. $E_{ALL}$—All defined trait dimension: all traits in each dimension. For each trait dimension, the best supported expectation is highlighted in grey.

Abbreviations: ADL, acid detergent lignin; $A_{max}$, maximum photosynthetic rate; $C_{t*}$, absolute capacitance per leaf area at full turgor; $C_{tlp}$, relative capacitance at full turgor; CO, canopy openness; $C_{tip}$, relative capacitance at turgor loss; LDMC, leaf dry matter content; Ls, stomatal limitation; PT, palisade tissue; R, dark respiration; RWC, relative water content; SLA, specific leaf area; ST, spongy tissue; SWC, saturated water content; WUE, water use efficiency; $c$, elasticity modulus; $\pi_o$, saturated osmotic potential; $\pi_{tip}$, turgor loss point.

3.2 | Turnover in functional-trait dimensions along environmental gradients

Similarity with respect to trait dimensions that reflect photosynthetic traits, hydraulic traits, resource-acquisition traits and physical defenses significantly decreased with increasing environmental and spatial distance (Figure 3a–d, $p < 0.001$), indicating that these functional traits turned over along environmental gradients and spatial distance to a greater extent than expected by chance. In contrast, similarity of SMs increased with average herbivory distance in the local scale and then stabilized (Figure 3e, $p < 0.001$). In addition, the turnover with respect to axes representing functional traits was significantly greater with environmental distance than spatial distance, especially for physical defensive traits and SMs at large spatial scales.

3.3 | Phylogenetic signal in functional trait dimensions

Most resource-acquisition, photosynthetic and hydraulic traits and trait dimensions showed significant phylogenetic signal (Table 2; Figure 4; Appendix S2: Table S12; $p < 0.005$). Specifically, photosynthetic traits, such as stomatal limitation (Ls) and canopy openness (CO) and hydraulic traits, like water-use efficiency (WUE) and relative capacitance at turgor loss ($C_{tlp}$) exhibited strong phylogenetic signal ($K > 1$; Appendix S2: Table S12). However, almost all defensive traits, especially SMs ($K_{mult} = 0.213, p = 0.930$) exhibited no significant phylogenetic signal (Table 2; Appendix S2: Table S12).

4 | DISCUSSION

The co-occurrence of numerous closely related species challenges expectations of species coexistence, but also presents an opportunity to better understand the mechanisms that generate and maintain diversity in tropical forests. Here, we have explored multiple dimensions of variation in morphological, physiological, and chemical functional traits to identify key axes that may contribute to niche segregation among co-occurring confamilial species. Our results revealed substantial differentiation in trait dimensions related to photosynthetic, hydraulic, resource-acquisition and defensive strategies with the potential to contribute to species coexistence by allowing species to segregate with respect to variation in resource availability and herbivore pressure over time and space. Whereas, resource-acquisition traits exhibited phylogenetic signal, the diversity of closely-related Euphorbiaceae within the Xishuangbanna forest is likely further enhanced by phylogenetic divergence among the closest relatives with respect to SMs. We conclude that differentiation in chemical anti-herbivore defenses among closely related species may define another key trait axis that elevates species community richness beyond what would be supported by resource and habitat-defined niche partitioning alone.

4.1 | Resource-utilization and defense traits exhibit contrasting community patterns

Interspecific competition for resources is expected to result in the competitive exclusion of inferior competitors from a community (Palmer, 1994). Competitive exclusion can be avoided, and species coexistence maintained, if species differ in their niche, such as their abiotic requirements and biotic interactions, such that intraspecific competition is stronger than interspecific competition and hence intraspecific negative feedback prevents complete exclusion of
Species differ in intrinsic fitness; the greater the differences in fitness, the greater niche differences must be to stabilize coexistence among competitors (Adler et al., 2007).

In a forest, the most obvious opportunities for niche segregation among tree species are habitats defined by spatial heterogeneity in edaphic resources, soil moisture, and light. Variation in species abundances over environmental gradients are mediated by morphological and physiological traits. Turnover with respect to traits can reflect filtering that habitat variation exerts on local assemblages, which provides a window on niche segregation among co-occurring species (Condit et al., 2000; Le Bagousse-Pinguet et al., 2017; Ravenscroft et al., 2014). A previous study demonstrated trait turnover with respect to both geographic and environmental distance within the Xishuangbanna plot (Yang et al., 2015). Here, we observed greater turnover in mean trait values of subplots with respect to environmental distance than simple geographic distance among subplots (Figure 3). Differences between mean photosynthetic, hydraulic, resource-acquisition and physical-defense traits all increased with increasing distance in light, soil moisture, soil resources and herbivory, respectively (Figure 3a–c). This turnover likely reflects species differences in abiotic niches that vary over fine-scale gradients in soil, moisture and light.

Our results for the Euphorbiaceae at Xishuangbanna are largely concordant with other recent studies of trait turnover. For example, Fine et al. (2006) and Vleminckx et al. (2018) found significant turnover in functional traits related to resource acquisition in Protium with increasing dissimilarity of soil texture and nutrient availability, but little turnover with respect to SMs along these same environmental axes. Fortunel et al. (2014) demonstrated that functional turnover for 15 traits related to leaf and wood strategies and resource acquisition was strongly related to an edaphic gradient in lowland Amazonian forests in Peru and French Guiana. Our results further support the hypothesis that niche partitioning with respect to habitat heterogeneity contributes to the maintenance of species diversity in locally species-rich tree lineages at intermediate to large spatial scales.

FIGURE 3 Differentiation of traits with large centrality values and secondary metabolites with respect to environmental and spatial distance. Panels (a)–(f) illustrate distance decay of (a) photosynthetic traits with light environment and spatial distance, (b) hydraulic traits with soil water content and spatial distance, (c) resource acquisition traits with soil resource content and spatial distance, (d) physical defensive traits with average herbivory ratio and spatial distance, (e) secondary metabolites with average herbivory and spatial distance, (f) all traits with all environmental and spatial distance. To calculate environmental distance with respect to soil variables and all variables, we used the first PC of variation in soil variables and in all traits, respectively. The contour lines represent the density of the traits and distance values.
In addition to abiotic resource requirements, trees exhibit a fundamental trade-off between growth rate and survival (Rüger et al., 2018, 2020), which manifests at the extremes as species that grow fast in high-resource (especially high-light) environments but invest comparatively little in defense and those that grow slowly in resource-poor environments but invest heavily in defense (Coley, 1983). We observed significant heterogeneity in herbivore pressure within the forest plot (Figure S1), likely driven by variation in light availability and hence productivity. Likewise, the turnover we observed in physical defenses was greater with respect to variation in herbivory than with spatial distance (Figure 3d), most likely because physical defenses were low and herbivory was high in high-resource environments, particularly canopy gaps (Coley, 1983).

Competition mediated by shared natural enemies is equivalent to resource competition in its capacity to mediate competitive exclusion (Chesson & Kuang, 2008), hence species differences with respect to SMs that shape insect and pathogen host ranges can define niche differences that stabilize coexistence (Connell, 1971; Janzen, 1970; Sedio & Ostling, 2013). The turnover we observed in SMs either spatial distance or distance defined in terms of similarity of herbivory rates was much less than that observed for other traits (Figure 3). This is likely because natural enemies that respond to the density of host plants promote local neighborhoods of chemically dissimilar individuals, which tends to reduce turnover in chemistry at larger spatial scales (Sedio & Ostling, 2013).

**TABLE 2** Phyllogenetic signal of four large centrality traits examined using $K_{\text{mult}}$ value of the Brownian motion evolutionary model test

| Functional traits dimensions | PCA axis | $K_{\text{mult}}$ | p-value |
|-----------------------------|---------|-----------------|---------|
| Photosynthetic traits       | PCA1    | 1.423           | 0.001   |
|                             | PCA2    | 0.389           | 0.358   |
|                             | PCA3    | 0.754           | 0.002   |
| Hydraulic traits            | PCA1    | 1.080           | 0.001   |
|                             | PCA2    | 0.922           | 0.001   |
|                             | PCA3    | 0.848           | 0.001   |
| Resource acquisition traits  | PCA1    | 0.951           | 0.004   |
|                             | PCA2    | 0.526           | 0.065   |
|                             | PCA3    | 0.293           | 0.680   |
| Physical defensive traits   | PCA1    | 0.469           | 0.04    |
|                             | PCA2    | 0.480           | 0.079   |
|                             | PCA3    | 0.496           | 0.070   |
| Secondary metabolites       |         | 0.213           | 0.930   |

*Note:* Values significantly are indicated in bold ($p<0.05$).

**FIGURE 4** Relationships between phylogenetic distance and species disparity with functional traits. (a) photosynthetic traits, (b) hydraulic traits, (c) resource acquisition traits and (d) physical defensive traits. Phylogenetic disparity with respect to the first component of variation in high-centrality traits is illustrated here.
4.2 Resource-utilization and defense traits exhibit contrasting phylogenetic signal

Evaluating the phylogenetic signal in functional traits can provide an opportunity to assess the interaction between trait evolution and community assembly (Kembel & Hubbell, 2006). Our results indicate that most resource-acquisition, photosynthetic and hydraulic traits exhibit significant phylogenetic signal (Table 2; Figure 4; Appendix S2: Table S12). The phylogenetic signal in hydraulic traits that we observed among the Euphorbiaceae of Xishuangbanna is reminiscent of that observed among the Psychotria (Rubiaceae) of Barro Colorado Island (BCI), Panama (Sedio et al., 2012). More broadly, our results are consistent with a previous evaluation of phylogenetic signal in a wide range of functional traits in the Xishuangbanna plot as a whole (Yang et al., 2014) as well as studies in other tropical forest plots such as those at Yasuni, Ecuador (Kraft & Ackerly, 2010) and BCI, Panama (Westbrook et al., 2011). Our observations of trait turnover with environmental distance suggest that species of Euphorbiaceae exploit distinct habitats within the forest plot based on their morphological and physiological adaptations, and habitat filtering selects a subset of species with traits appropriate for the local environment. The phylogenetic signal we observed for functional traits implies that these habitat differences facilitate niche segregation primarily among distantly related species, while potentially exacerbating competitive interactions among physiologically similar, closely related species of Euphorbiaceae.

In contrast to physiological traits related to resource acquisition, species similarity with respect to SMs did not exhibit phylogenetic signal (Table 2; Figure 4). This result is consistent with a growing number of studies of SMs in tropical tree lineages, including Bursera (Burseraceae) in Mexico (Becerra, 2007), Eugenia (Myrtaceae), Inga (Fabaceae), Ocotea (Lauraceae), Piper (Piperaceae), Psychotria and Protium (Burseraceae) in Panama (Kursar et al., 2009; Sedio, Parker, et al., 2018), Ficus (Moraceae) in Papua New Guinea (Volf et al., 2018), Piper in Costa Rica (Salazar et al., 2016) and Inga and Protium in Peru (Endara et al., 2017; Salazar et al., 2018; Vleminckx et al., 2018). Such commonplace divergence in SMs among closely related species is likely driven by selection by insect herbivores and microbial pathogens that suppress local assemblages of chemically similar hosts (Erb & Kläbenstein, 2020; Forristler et al., 2019; Sedio & Ostling, 2013; Wink, 2018), thereby favoring the evolution of novel chemical defenses. Hence, our results contribute to an emerging consensus that species composition with respect to SMs may be more evolutionarily labile than morphological and physiological traits that mediate plant interactions with the abiotic environment. This has important implications for our understanding of the relative contribution of niche segregation with respect to traits that mediate plant interactions with the abiotic and biotic environment, as divergence in SMs that permits closely related species to avoid sharing herbivores and pathogens may significantly enhance diversity beyond that maintained by segregation according to relatively phylogenetically conserved physiological niches.

Overall, the study found substantial differentiation in trait dimensions related to photosynthetic, hydraulic, resource-acquisition and defensive strategies with the potential to contribute to species coexistence by allowing species to segregate with respect to variation in resource availability and herbivore pressure over time and space. However, it remains unclear how these traits and SMs impact the demographic processes underlying the mechanisms discussed. Therefore, future studies should focus on how these traits, including SMs that shape the host use patterns of herbivores and pathogens, directly impact species coexistence through their effects on growth, survival and reproduction.

5 CONCLUSIONS

Identifying the factors that permit closely related species to co-exist in species-rich tropical forests continues to be a major challenge in ecology. Traditional functional trait-based approaches have explored species differences with respect to a small number of traits that may not reflect the range of abiotic and biotic niche dimensions along which co-occurring species may segregate. Our results indicate that a small number of traits with high network centrality within the Euphorbiaceae reflect interspecific variation in ecological strategy with respect to global trait dimensions, representing resource acquisition, photosynthetic capacity, drought resistance and hydraulic efficiency and physical defense. Furthermore, analyses of turnover with respect to environmental gradients suggest that species differences among multiple axes of trait variation may contribute to species coexistence in the Xishuangbanna forest by allowing Euphorbiaceae to exploit distinct microhabitats defined in terms of light, moisture and soil nutrients. These physiological niche differences exhibit phylogenetic signal, whereas SMs do not, possibly as a result of diversifying selection by insect herbivores and pathogens. Our results suggest that phylogenetic divergence among closely related species with respect to SMs may enhance the local diversity of Euphorbiaceae beyond that supported by resource-based niche segregation by promoting coexistence among close relatives with similar habitat preferences in tropical rainforest.

AUTHOR CONTRIBUTIONS

Jie Yang, Xue-Zhao Wang and Jiao-Lin Zhang designed the study; Xue-Zhao Wang performed the analysis; Shan-Wen Sun, Xue-Zhao Wang, Suphanee Glomglieng, Kun-Fang Cao, Jian-Hong Yang and Jiao-Lin Zhang collected and measured the data; Xue-Zhao Wang, Jie Yang and Brian E. Sedio wrote the manuscript, and all authors provided comments.

ACKNOWLEDGEMENTS

This research was supported by the NSFC China-US Dimensions of Biodiversity Grant (DEB: 32061123003), National Natural Science Foundation of China (31870410, 32171507), the Chinese Academy of Sciences Youth Innovation Promotion Association (Y202080), the Distinguished Youth Scholar of Yunnan (202001AV070016)
and the West Light Foundation of the Chinese Academy of Sciences and the Ten Thousand Talent Plans for Young Top-notch Talents of Yunnan (YNWR-QNBJ-2018-309). We are grateful for support from Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies. Leaf chemical contents were performed at the Institutional Center for Shared Technologies and Facilities of Xishuangbanna Tropical Botanical Garden, CAS. Plant secondary metabolites were analyzed at State Key Laboratory of Phytochemistry and Plant Resources in West China, Chinese Academy of Science. We thank Yazhou Zhang and Lu Sun for assistance with data analysis.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://publon.com/publon/10.1111/1365-2745.13984.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.jwstjqcw (Wang et al., 2022).

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How to cite this article: Wang, X.-Z., Sun, S.-W., Sedio, B. E., Glomglieng, S., Cao, M., Cao, K.-F., Yang, J.-H., Zhang, J.-L., & Yang, J. (2022). Niche differentiation along multiple functional-trait dimensions contributes to high local diversity of Euphorbiaceae in a tropical tree assemblage. *Journal of Ecology*, 110, 2731–2744. https://doi.org/10.1111/1365-745.13984