



# Host functional and phylogenetic composition rather than host diversity structure plant–herbivore networks

Ming-Qiang Wang<sup>1,2,3</sup> | Yi Li<sup>1,2</sup> | Douglas Chesters<sup>1</sup> | Helge Bruehlheide<sup>4,5</sup> | Keping Ma<sup>6</sup> | Peng-Fei Guo<sup>7,1</sup> | Qing-Song Zhou<sup>1</sup> | Michael Staab<sup>8</sup> | Chao-Dong Zhu<sup>1,2,9</sup> | Andreas Schuldt<sup>3</sup>

<sup>1</sup>Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

<sup>2</sup>University of Chinese Academy of Sciences, Beijing, China

<sup>3</sup>Forest Nature Conservation, Georg-August-University Goettingen, Goettingen, Germany

<sup>4</sup>Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

<sup>5</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

<sup>6</sup>Institute of Botany, Chinese Academy of Sciences, Beijing, China

<sup>7</sup>College of Plant Protection, Yunnan Agricultural University, Kunming, China

<sup>8</sup>Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany

<sup>9</sup>State Key Laboratory of Integrated Pest Management, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

## Correspondence

Chao-Dong Zhu, Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China.  
Email: zhucd@ioz.ac.cn

Andreas Schuldt, Forest Nature Conservation, Georg-August-University Goettingen, Buesgenweg 3, 37077 Goettingen, Germany.  
Email: andreas.schuldt@forst.uni-goettingen.de

## Funding information

Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDB310304; National Science Fund for Distinguished Young Scholars, Grant/Award Number: 31625024; External Cooperation Program of BIC, Chinese Academy of Sciences, Grant/Award Number: 15211 1KY5B20160001; German Research Foundation, Grant/Award Number: DFG FOR 891-3 and 319936945/GRK2324; National Science Foundation of China, Grant/Award Number: 31772495

## Abstract

Declining plant diversity alters ecological networks, such as plant–herbivore interactions. However, our knowledge of the potential mechanisms underlying effects of plant species loss on plant–herbivore network structure is still limited. We used DNA barcoding to identify herbivore–host plant associations along declining levels of tree diversity in a large-scale, subtropical biodiversity experiment. We tested for effects of tree species richness, host functional and phylogenetic diversity, and host functional (leaf trait) and phylogenetic composition on species, phylogenetic and network composition of herbivore communities. We found that phylogenetic host composition and related palatability/defence traits but not tree species richness significantly affected herbivore communities and interaction network complexity at both the species and community levels. Our study indicates that evolutionary dependencies and functional traits of host plants determine the composition of higher trophic levels and corresponding interaction networks in species-rich ecosystems. Our findings highlight that characteristics of the species lost have effects on ecosystem structure and functioning across trophic levels that cannot be predicted from mere reductions in species richness.

## KEYWORDS

BEF-China, DNA barcoding, functional traits, insect decline, phylogenetic composition, plant–insect interactions

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## 1 | INTRODUCTION

Human-induced environmental change is altering ecosystems worldwide, with consequences for biodiversity and ecosystem functioning (Cardinale et al., 2012; Díaz et al., 2019). However, for many ecosystems we lack a general understanding of how changes in biodiversity will affect trophic interaction networks (Grossman et al., 2018; Tylianakis, Didham, Bascompte, & Wardle, 2008). Such an understanding is not only critical when it comes to developing strategies to protect and promote species in times of globally declining biodiversity (Díaz et al., 2019; Tittensor et al., 2014). It is also highly relevant to predict how ecological networks that determine the strength and stability of important trophic interactions might change in the future—such as herbivory and the regulation of pest outbreaks and invasive species (Jactel et al., 2017; Scherber et al., 2010; Thebault & Fontaine, 2010). For many forest ecosystems in particular, herbivores and outbreaks of herbivorous pests are one of the key challenges likely to be faced in the near future (Seidl et al., 2017; Semizer-Cuming, Krutovsky, Baranchikov, Kjær, & Williams, 2019). Therefore, understanding how plant-herbivore networks respond to changing plant diversity and composition is necessary to better understand how environmental change and adaptive management decisions affect the functioning and stability of forest ecosystems (Hines et al., 2015).

The role of plant diversity in modifying plant-herbivore networks has been studied extensively in grasslands (Eisenhauer et al., 2019; Giling et al., 2019; Petermann, Müller, Weigelt, Weisser, & Schmid, 2010). These studies have shown that plant-herbivore networks can become more generalized with increasing plant species richness and that the resulting increase in the number of linkages between consumers and plants can increase network stability (Haddad, Crutsinger, Gross, Haarstad, & Tilman, 2011; Welti, Helzer, & Joern, 2017). This is because higher plant diversity might, for example, promote diet mixing and spillover effects of herbivores among alternative host species, and increase the spatial and temporal stability of resource availability (Fornoff, Klein, Blüthgen, & Staab, 2019; Haddad et al., 2011; Manning et al., 2019). For forests, large-scale studies have shown that herbivore specialization increases towards regions with high plant diversity and for plant families with high species richness (e.g. Dyer et al., 2007; Forister et al., 2015). Within the highly biodiverse subtropical and tropical forests, where herbivores are particularly important in influencing tree growth and performance (Bagchi et al., 2014; Terborgh, 2012), there is increasing evidence that the loss of tree species richness may influence host-herbivore network specialization (Abdala-Roberts et al., 2015; Fornoff et al., 2019; López-Carretero, del-Val, & Boege, 2018; Redmond et al., 2019; Staab, Blüthgen, & Klein, 2015). A comprehensive understanding of these effects requires more information on how host functional traits modify diversity effects on network interactions. This is not only because changes in the species composition, but also because changes in the functional and phylogenetic composition caused by nonrandom changes in tree species composition and diversity will affect ecological networks and

trophic interactions (Becerra, 2015; López-Carretero et al., 2018; Muiruri et al., 2019). Previous studies have shown that traits related to the palatability, defence and climatic niche of host trees, as well as their functional diversity and phylogenetic structure, can predict herbivory and herbivore diversity in species-rich forests (e.g. Novotny et al., 2010; Richards et al., 2015; Salazar, Jaramillo, & Marquis, 2016; Salazar et al., 2018; Schuldt, Baruffol, et al., 2014; Schuldt et al., 2012; Whitfeld et al., 2012). Understanding how such trait relationships contribute to the effects of tree diversity loss on the structure and interaction strength of plant-herbivore networks, however, requires further research (Fornoff et al., 2019; López-Carretero et al., 2018).

Here, we focus on species-rich assemblages of key herbivores, lepidopteran caterpillars, and network associations with their host plants in a large-scale biodiversity experiment in subtropical forests. We aimed to quantify the strength of associations between herbivore and tree communities and to identify key components of the functional and phylogenetic composition of the host trees that explain the degree of network specialization. Specifically, we tested whether network metrics at both the species level (all analysed tree individuals per species across all plots) and the community level (all analysed tree individuals per plot across all species) are related to functional and phylogenetic properties (diversity and composition) of the tree community. Our data set is based on more than 6,000 sequences of 447 molecular operational taxonomic units (MOTUs) of caterpillars, sampled from a set of 32 broadleaved tree species planted experimentally along a gradient in tree species richness in southeast China (Bruehlheide et al., 2014). We hypothesized that (a) plant-herbivore networks will become more generalized (and therefore potentially more stable; Haddad et al., 2011) with increasing tree species richness. Moreover, we expected that (b) plant functional and phylogenetic diversity—as well as host phylogenetic composition and leaf traits related to palatability and defence—contribute to explaining these relationships, by modifying interaction strength and specialization among individual host and herbivore species and across entire communities.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The sites of the “BEF-China” tree diversity experiment are located in subtropical southeast China near Xingangshan, Jiangxi province (29°08′–29°11′N, 117°90′–117°93′E). The mean annual temperature is 16.7°C, and the mean annual precipitation is 1,821 mm (Yang et al., 2013). Currently, it is the largest tree diversity experiment in the world (Bruehlheide et al., 2014). Two study sites (Site A and Site B), 4 km apart from each other, were established in 2009 (Site A) and 2010 (Site B). A total of 566 plots (25.8 × 25.8 m) were established, each planted with 400 tree seedlings in a regularly arranged 20 × 20 grid system with 1.29 m distance among trees. Tree seedlings were completely randomly planted to the planting positions

within each plot, and the total number of individuals per plot was divided equally among the planted species (Bruelheide et al., 2014). For our study, we selected 62 intensively studied plots that were randomly distributed on the two sites (31 plots per site; average distance among plots per site = 298.3 m for Site A and 289.5 m for Site B) and represented a tree species richness gradient from monocultures to 16-species mixtures (1, 2, 4, 8 and 16 species; S1). The species pool included 32 locally common broadleaved tree species, with 16 species specific to each site. The selected plots included sixteen monocultures, and eight, four, two and one mixtures of 2, 4, 8 and 16 species, respectively, on each study site. Tree species composition of the mixtures represented nonoverlapping subsets of the 16-species mixtures of each site (see Bruelheide et al., 2014). In total, the data from 53 plots were used for further analysis, because nine plots had to be excluded due to high mortality of trees.

## 2.2 | Sampling design

We sampled externally feeding lepidopteran larvae, a species-rich component of the herbivore community of many subtropical and tropical forests (Forister et al., 2015; Zhang et al., 2017), six times in 2017 and 2018 (April, June and September in each year). We used a beating method, knocking the lepidopteran larvae down onto a white sheet (1.5 × 1.5 m) to collect fallen caterpillars (Campos, Vasconcelos, Ribeiro, Neves, & Soares, 2006; Schuldt, Baruffol, et al., 2014). This method allows lepidopteran larvae to be assessed at the tree individual level (see also Peralta, Frost, Didham, Varsani, & Tylianakis, 2015). We note that this sampling method is restricted to externally feeding caterpillars (leaf chewers, skeletonizers and those using resources associated with the leaf surface, such as those feeding on algal biofilms). Other specific groups such as leaf miners and gallers cannot be assessed reliably and were therefore excluded from our study. Nevertheless, our method provides data on a large share of Lepidoptera (21 Lepidoptera families; see Wang et al., 2019). We sampled 80 living trees per sampling date from the first rows of trees in each plot. Because of the random planting design, the sampled trees adequately covered the tree species composition and species richness at the plot level. All caterpillars were placed individually in tubes filled with 99.5% ethanol and stored at -20°C until further processing. We note that our sampling method cannot fully exclude vagrant species (although the low mobility of most caterpillars and the spacing between trees in our experiment make them likely to be sampled from their host trees in most cases), but see “statistical analysis” below on how we accounted for this in our analyses.

## 2.3 | DNA sequencing and phylogenetic analysis

Details on DNA extraction, amplification and sequencing are provided in Appendix S1. In brief, we extracted DNA following standard methods to amplify and sequence a region of the mitochondrial

cytochrome oxidase subunit I (COI) gene of the samples (Hebert, Ratnasingham, & de Waard Jeremy, 2003), used three methods for inferring molecular operational taxonomic units (MOTUs) and selected the most consistent results by comparing the Hubert and Arabie's (HA) adjusted Rand index for each pair of methods (see Appendix S1). We generated a high-quality reference phylogeny for placement of plot MOTUs, by integrating DNA of identified moths collected at the BEF-China sites, and mined DNA barcode data, and information on topology and monophyly from published phylogenies of Lepidoptera. In preliminary analysis, we noted poor placement of some caterpillar sequences occurred due to lack of similarity between them and the existing reference data (which comprised adult moth species collected from the light traps at the site; Wang et al., 2019). To address this, we supplemented the site-based reference data with DNA barcodes mined from BOLD (Ratnasingham & Hebert, 2007). All DNA barcodes for Lepidoptera families for which species are known to occur at the BEF-China site were downloaded from the BOLD API ([www.boldsystems.org/index.php/API\\_Public/](http://www.boldsystems.org/index.php/API_Public/)) and processed using the “barcodePD” pipeline, with some modifications (available at [github.com/dchesters/barcodePD](https://github.com/dchesters/barcodePD)). From this database, we extracted all barcodes with broad similarity to plot MOTUs, achieved by a search with locally installed Blast+ (v 2.2.28; Camacho et al., 2009). The Blast output file was parsed with a Perl script, giving a DNA barcode for each of an additional 3,234 Lepidoptera species. Barcodes were then aligned with a high-throughput aligner (Chesters, 2019). A phylogeny was constructed for the DNA barcodes, integrating information from backbone trees, according to the approach described in Chesters (2020). Three backbone phylogenies were selected; we used Kawahara et al. (2019) for the general topology, being the most robustly supported phylogeny currently available. Additional information on monophyletic groups was inferred from the phylogeny of Heikkilä, Mutanen, Wahlberg, Sihvonen, and Kaila (2015), which had additional genus-level coverage, and Regier et al. (2017), a Noctuoidea-specific phylogeny, which are a group of Lepidoptera well-represented at the BEF-China plots. Relational constraints inferred from the topology of Kawahara et al. (2019) are given in Figure S2, and taxon constraints inferred from all three backbone trees are given in Table S1. Note, taxa particularly relevant to the plot species which were not inferred as monophyletic on these phylogenies and thus were unconstrained herein included Noctuidae, Erebidae (Kawahara et al., 2019) and subfamilies of the Notodontidae (Regier et al., 2017). The phylogeny was constructed with Raxml version 8.2.4 (Stamatakis, 2014) with a single outgroup sequence (*Druceiella* sp), with only reference members constrained, and plot MOTU phylogenetically placed. The ultrametric phylogenetic tree of Lepidoptera was transformed using TreePL (Smith & O'Meara, 2012).

## 2.4 | Plant traits and environmental covariates

To characterize the nutritional quality and potential defence traits of the tree species, we used morphological and chemical leaf traits

commonly found to affect herbivores (Muiruri et al., 2019; Pérez-Harguindeguy et al., 2003; Schuldt, Assmann, et al., 2014; Zhang et al., 2017). Leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf toughness (LT) were included as morphological traits. Leaf carbon (C), the ratio of leaf carbon to nitrogen (C:N) content, leaf potassium (K) content, leaf sodium (Na) content, leaf calcium (Ca) content and leaf phosphorus (P) content were included as chemical leaf traits. For analyses at the level of individual tree species, we also considered leaf tannin concentrations (which we were not able to use for comparisons of tree communities across study plots because tannin data were missing for some tree species). All of the traits were measured on a minimum of five randomly sampled, sun-exposed, mature and undamaged leaves of at least five individuals per tree species (Kröber, Zhang, Ehlig, & Bruelheide, 2014) according to standardized protocols (Pérez-Harguindeguy et al., 2013). Total tannin content was measured with the radial diffusion method and standardized against tannic acid (as mg per g dry weight tannic acid equivalents; see Eichenberg, Purschke, Ristok, Wessjohann, & Bruelheide, 2015 for details). Traits were only weakly or moderately correlated with each other ( $r < .7$  in all cases; Figure S3).

We calculated the community-weighted mean values (CWMs) of all leaf traits per study plot, that is the mean value of each trait in each study plot weighted by tree wood volume. Tree wood volume, as a proxy of tree size and leaf biomass (Brezzi, Schmid, Niklaus, & Schuldt, 2017), was estimated from data of basal area and tree

height (Fichtner et al., 2017) measured on trees in the centre of each plot in October 2016. We upscaled the values to represent plot-level wood volume of each tree species.

In the analyses comparing community patterns among study plots, we further accounted for potential effects of environmental variation by using plot means of slope, elevation, “northness” (cosine-transformed radian values of aspect) and “eastness” (sine-transformed radian values of aspect) as environmental covariates that characterize the heterogeneous topography of the study plots. All environmental data were obtained from a 5-m resolution digital elevation model based on differential GPS measurements (Scholten et al., 2017).

## 2.5 | Statistical analysis

All analyses were conducted in R 3.4.3 with the packages *ape*, *vegan*, *picante*, *bipartite*, *caper* and *MuMIn* (<http://www.R-project.org>). All analysis approaches used in this study are summarized in Table 1. To exclude the effects of rare herbivore species for a conservative estimate of plant–herbivore associations in our study, we only considered MOTUs that were sampled with at least 5 individuals per tree species and had at least of 5% of their total number of recorded interactions with this tree species. This resulted in a data set with 31 tree species with 2,834 individual trees and 157 lepidopteran MOTUs with 6,361 individuals.

**TABLE 1** Overview of the analyses conducted in the study

Spatial scale	Sample	Response	Level of response	Predictors	Statistics
Species	All individuals per tree species	Interaction specialization ( $d'$ )	Host plants	Leaf morphological and chemical traits	PGLS regression
Species	All individuals per tree species	Effective partners per tree species	Host plants	Leaf morphological and chemical traits	PGLS regression
Community	Set of communities (all tree individuals) of the same richness level	Generality (degree of herbivore specialization)	Herbivore species	Tree species richness, study site	Linear model
Community	Set of communities (all tree individuals) of the same richness level	Vulnerability (degree of host plant specialization)	Host plants	Tree species richness, study site	Linear model
Community	Set of communities (all tree individuals) of the same richness level	Linkage density (degree of network specialization)	Hosts and herbivores	Tree species richness, study site	Linear model
Community	Set of communities (all tree individuals) of the study plot	Vulnerability (degree of host plant specialization)	Host plants	Tree species richness, tree functional diversity, tree phylogenetic diversity, CWMs of leaf traits, environment	Linear model

Note: Analyses were either conducted at the level of tree species, or for the overall communities of trees per study plot or species richness level. See Methods for details.

## 2.5.1 | Functional composition and phylogenetic diversity of host plants

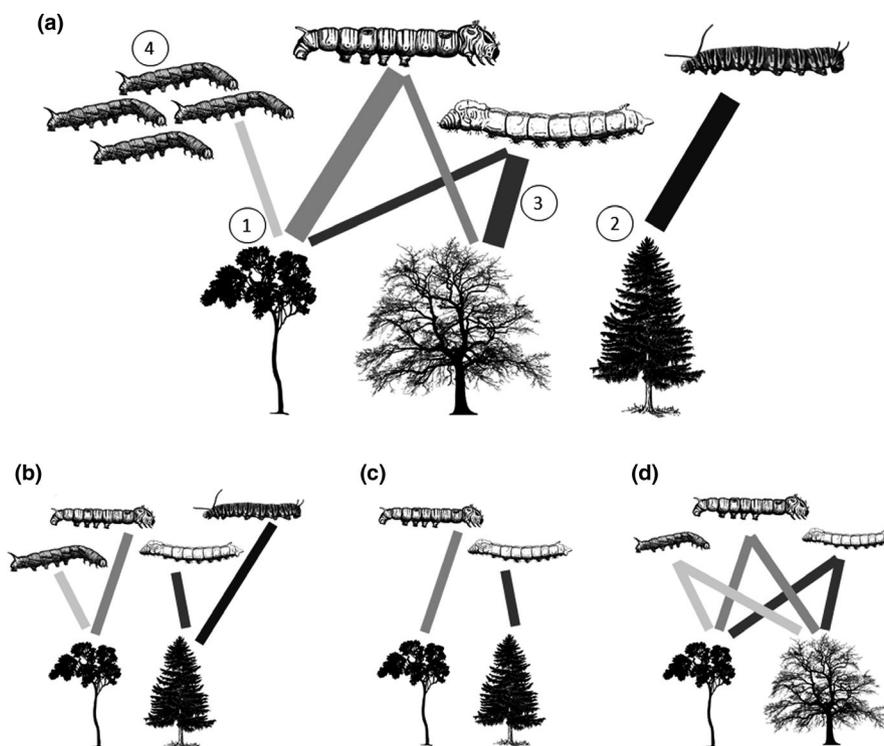
We quantified tree species and phylogenetic community composition for each study plot with nonmetric multidimensional scaling (NMDS) analysis based on Morisita–Horn distances. For phylogenetic composition, we calculated the mean pairwise distance among the tree communities per plot using the R package “picante.” The minimum number of required dimensions in the NMDS based on the reduction in stress value was determined in the analysis ( $k = 2$  in our case). To acquire maximum variance on the first dimension, results were centred, and principal components rotation was used in the analysis.

We calculated tree functional diversity of the study plots as the mean pairwise distance in trait values among tree species (weighted by tree wood volume) and expressed as Rao’s Q (Ricotta & Moretti, 2011). Likewise, the phylogenetic diversity of the tree

communities per study plot was quantified by calculating wood volume-weighted phylogenetic mean pairwise distance (MPD), which is equivalent to Rao’s Q for trait distances (Tucker et al., 2017). We also calculated the phylogenetic mean nearest taxon distance (MNTD) for trees per study plot, which quantifies the average phylogenetic distance of each individual tree species to the closest relative on the phylogenetic tree (Webb, 2000). Phylogenetic metrics for trees were calculated using an ultrametric phylogenetic tree available for the host tree species of our study region (Purschke, Michalski, Bruelheide, & Durka, 2017).

## 2.5.2 | Lepidopteran larvae species and phylogenetic composition across study plots

We analysed changes in species and phylogenetic composition of lepidopteran larvae across study plots and across seasons with



**FIGURE 1** Relationships between host trees and lepidopteran caterpillars can be defined with various network metrics. *Species-level metrics* summarize interactions for individual host or herbivore species (a), such as the *interaction specialization* ( $d'$ ) of host trees or the *effective partners* they interact with. These metrics depend on whether plants interact with many different (1 = low specialization, high number of effective partners) or very few (2 = high specialization, low number of effective partners) herbivore species. For both indices, not only the number of linkages between host species and herbivore species plays a role, but also the relative abundance of (4) and host use by (5 = line thickness increasing with number of interactions) individual herbivores; *effective partners* is based on the Shannon diversity of interactions (and calculated for a scenario that assumes that all herbivores are equally abundant), while *index  $d'$*  takes into account the frequency with which herbivores interact with other host species in the system. *Community-level metrics* summarize the average interaction strength across all species in a community. Our analyses focus on *weighted generality*, which is the mean effective number (based on Shannon diversity) of hosts per herbivore species (i.e. focused on the consumer level), and *weighted vulnerability* as the mean effective number of herbivores per host species (focused on the producer level). The community in panel (b) has low generality (one host interaction per herbivore), but higher vulnerability (two herbivore species per host plant = more generalized), whereas community (c) also has low vulnerability (one herbivore species per host = specialized), and community (d) has high generality (multiple hosts per herbivore species) and high vulnerability (multiple herbivores per host). Finally, *weighted linkage density* provides an assessment of the generalization of the overall network, as the arithmetic mean of generality and vulnerability (highest in panel d, lowest in panel c)

nonmetric multidimensional scaling (NMDS) analysis, using the same approach as described above for the tree communities. We obtained relationships with study plot characteristics by fitting their standardized values to the ordination on the basis of a regression with the NMDS axis scores (Quinn & Keough, 2002). As plot characteristics, we included tree species richness, tree functional and phylogenetic diversity, CWM trait values and environmental covariates as described above. The significance of the correlations was assessed with permutation tests (permutation:  $n = 999$ ). In addition, to confirm the relationship between trees and caterpillars at the plot level, we also used Mantel tests on caterpillar community composition and tree composition (species dissimilarity and MPD of both trees and caterpillars).

Moreover, we tested whether the associations in the phylogenetic structure of the communities of lepidopteran herbivores and their individual host trees are independent of each other, based on a subset of the most abundant MOTUs ( $\geq 20$  individuals, including 64 lepidopteran MOTUs with 5,457 individuals on 28 tree species with 2,285 individuals) of caterpillars, by using the parafit test (9,999 permutations) in the *ape* R package (Paradis, Claude, & Strimmer, 2004). For species composition and abundance of this data subset, see Tables S2 and S3.

### 2.5.3 | Plant–herbivore associations

We constructed quantitative plant–herbivore interaction networks using the *bipartite* package in R (Dormann, Fründ, Blüthgen, & Gruber, 2009). We analysed plant–herbivore associations at both the level of individual tree species (based on networks for individual tree species across all study plots of the two study sites; Figure 1) and the level of tree communities (based on networks either across all tree species per study plot, or across all trees in a specific tree species richness level (monoculture, 2-, 4-, 8-, 16-species mixture) per study site; see Table 1 for an overview).

For the tree species level (Figure 1), we used standardized Kullback–Leibler distance (the index  $d'$ ) to calculate the degree of interaction specialization per tree species, which is defined as

$$d_i = \sum_{j=1}^c \left( p'_{ij} \ln \frac{p'_{ij}}{q_j} \right),$$

where  $i$  and  $j$  represent host species  $i$  and herbivore species  $j$ , and  $p'_{ij}$  and  $q_j$  represent each partner and overall partner availability, respectively (see Blüthgen, Menzel, & Blüthgen, 2006, for details). This index takes into account the proportional utilization and availability of interaction partners and therefore provides a robust estimate of specialization at the species level. We also calculated the number of “effective partners” per tree species, which is the Shannon diversity of the interactions of each tree species with herbivores, raised to the power of  $e$  (see Bersier, Banašek-Richter, & Cattin, 2002; Dormann, 2011).

For tree communities (Figure 1), we focused on three of the most commonly used quantitative indices to characterize interaction networks: weighted “generality” (degree of herbivore specialization),

weighted “vulnerability” (degree of host plant specialization) and “linkage density” (degree of network specialization). Generality is the weighted mean number of host species per herbivore species,

$G_{qw} = \sum_{j=1}^J \frac{A_j}{m} 2^{H_j}$ , with  $A_j$  being the number of interactions of herbivore species  $j$ ,  $m$  the total number of interactions of all species, and  $H_j$  the Shannon diversity of interactions of species  $j$ . Vulnerability is the weighted mean number of herbivore species per host species,

vulnerability =  $\sum_{i=1}^I \frac{A_i}{m} 2^{H_i}$  (Bersier et al., 2002). Both indices provide an estimate of the effective number of interaction partners per herbivore or host species and therefore indicate the extent to which interaction networks are generalized and potentially redundant (high index values) or specialized and complementary (low index values). Linkage density estimates the realized proportion of possible links between the two trophic levels as the mean number of interactions per species across the entire network  $L_q = 0.5$

$\left( \sum_{j=1}^J \frac{A_j}{m} 2^{H_j} + \sum_{i=1}^I \frac{A_i}{m} 2^{H_i} \right)$  (as the average of generality and vulnera-

bility; Tylianakis, Tschirntke, & Lewis, 2007). We calculated all network indices based on pooled data for all trees per tree species richness level at each of the two study sites. To account for a decreasing sampling intensity per species with increasing levels of species richness, we randomly drew eight tree individuals per tree species in each of the different tree species richness levels and then calculated the network indices based on the data from resampling (repeated 1,000 times; see Appendix S1 for details). Because we were interested in the effects of leaf traits on vulnerability (which varies freely among plots), we additionally calculated vulnerability at the plot level (i.e. for all trees per study plot) for a further analysis of network patterns. We used Patefield null models (Dormann et al., 2009) to test whether the network indices across study plots are significantly different from chance. To achieve this, all corresponding indices were simulated 10,000 times each and null model-based indices compared with observed values.

### 2.5.4 | Linear and phylogenetic regression models

To test whether herbivore–host associations were significantly different among the three sampling seasons per year, analysis of variance (ANOVA) was performed for herbivore generality and plant vulnerability across tree species richness levels in the three sampling seasons per year.

At the level of individual tree species, we tested for effects of tree species-specific mean trait values on the network metrics  $d'$  and effective partners, using phylogenetic generalized least-squares (PGLS) regression to account for potential phylogenetic signals in our comparative data set. This method enables simultaneous estimation of phylogenetic signal together with the regression parameters (Revell, 2010). PGLS models were fitted using the *caper* package (Orme et al., 2012) with maximum-likelihood estimation of Pagel's  $\lambda$

(Revell, 2010). As predictors, we used the eleven species-specific leaf traits assembled for each tree species. We simplified the linear models based on values of the Akaike information criterion corrected for small sample sizes (AICc) using a stepwise procedure and selected the subset models with the lowest AICc. We log-transformed  $d'$ , effective partners, leaf area and specific leaf area to improve normality and variance homogeneity of the model residuals.

To test for potential predictors of network indices at the level of tree communities (comparing different levels of tree species richness), the mean values of generality, vulnerability and linkage density (calculated by random sampling) were analysed as response variables, with tree species richness level and study site as predictors. For vulnerability, we additionally used the plot-level data to test for effects of tree species richness, tree functional and phylogenetic diversity, the leaf traits including the CWMs of LA, SLA, LDMC, leaf toughness, leaf carbon content, leaf C:N content, potassium content, leaf sodium content, leaf phosphorus content and leaf calcium content and tree wood volume. Tree phylogenetic MPD was excluded in the models where tree species richness was a predictor, due to the strong correlation with tree species richness (Pearson's  $r = .74$ ,  $p < .001$ ). However, we replaced tree species richness with tree MPD in an alternative set of models and compared the AICc of both model variants to evaluate whether network associations were more strongly influenced by tree species richness or tree MPD. As abiotic predictors, we used elevation, slope, eastness, northness and study site. In addition, the interactions between study site and tree species richness and between study site and tree functional diversity were included, because tree species composition differed between study sites. We further included latitude and longitude of the study plots as predictors to test whether the spatial location of the study plots affected the results of our analyses. Models were again simplified in a stepwise procedure to obtain the most parsimonious model with the lowest AICc. We also checked the correlations among latitude, longitude, lepidopteran species and abundance, and used a Mantel test to check whether the communities were influenced by spatial location (using dissimilarity in spatial location and in caterpillar species composition as matrices).

### 3 | RESULTS

Altogether, 8,036 lepidopteran larvae were collected from almost 25,440 tree individuals across the six sampling periods in 2017 and 2018, for which 447 molecular operational taxonomic units (MOTUs) were clustered based on 6,821 successfully generated COI sequences. Out of these, 157 lepidopteran MOTUs with 6,361 individuals were sampled with at least five individuals (and which had at least 5% of their total number of recorded interactions with a given tree species). The phylogeny of the Lepidoptera is shown in Figure S4. Average numbers of MOTUs increased from monocultures (31.4 MOTUs) to mixtures (35.5 in 2-species mixtures, 44.3 in 4-species mixtures, 48.5 in 8-species mixtures, 58.0 in 16-species mixtures). Lepidopteran species richness and abundance were not strongly

correlated with longitude or latitude ( $|r| < .2$ ), and a Mantel test indicated that there was no significant relationship between lepidopteran species composition and spatial location (Site A:  $r = .07$ ,  $p = .14$ ; and Site B:  $r = .10$ ,  $p = .15$ ).

#### 3.1 | Lepidopteran community composition

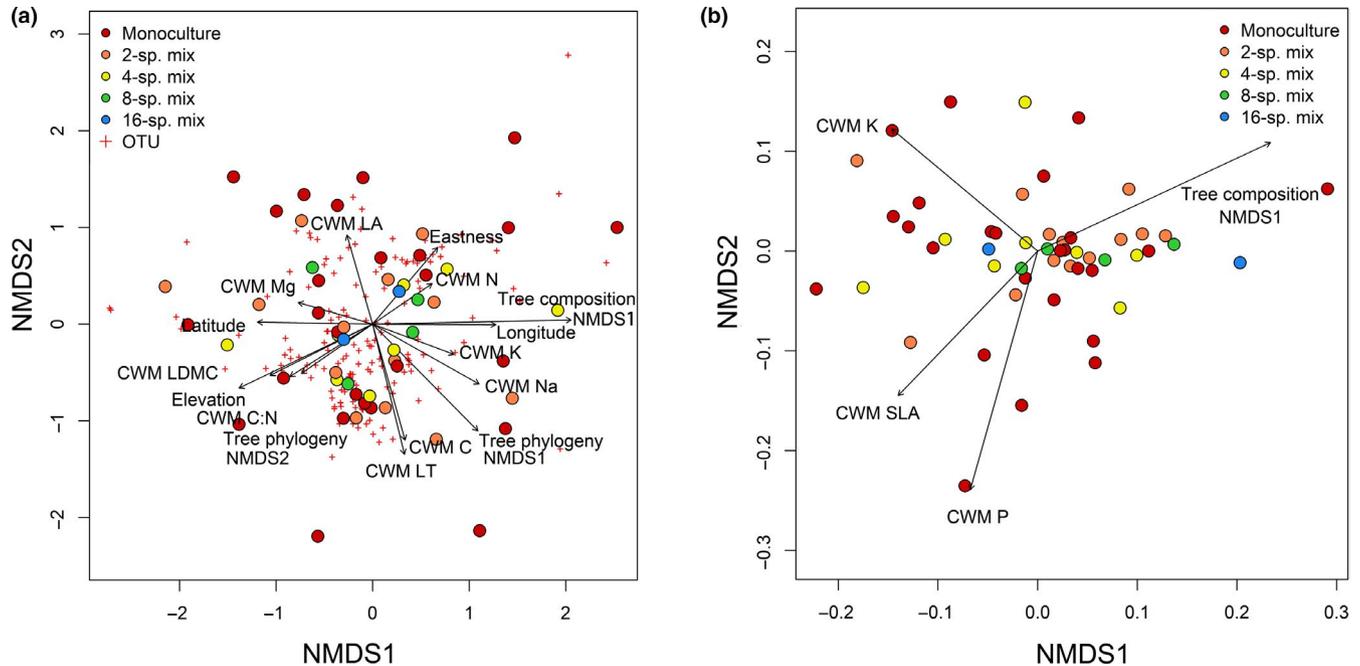
Both the species and the phylogenetic community composition of lepidopteran larvae differed across the study plots (Figure 2). However, neither species nor phylogenetic composition was significantly affected by changes in tree species richness. Instead, lepidopteran species composition was strongly related to the species and phylogenetic composition of the tree communities (NMDS scores), as well as to the community-weighted mean values of leaf dry matter content (LDMC), leaf toughness (LT) and carbon content (Figure 2a, Table S4). The phylogenetic composition of the lepidopteran communities was particularly affected by tree species composition, and CWM values of specific leaf area (SLA) (Figure 2b, Table S5). Tree species richness and tree functional diversity (Rao's Q) were not significantly related to the species or phylogenetic composition (Figure 2). Moreover, the effects of tree species composition on lepidopteran community composition were also confirmed by results of Mantel tests, which showed that species and phylogenetic composition of caterpillars was significantly related to tree species and phylogenetic composition (Table S6). Moreover, additional Mantel tests showed that changes in lepidopteran community composition were unrelated to differences in tree species richness of the study plots ( $r = -.12$ ,  $p = .908$  for species composition;  $r = -.06$ ,  $p = .700$  for phylogenetic composition).

An effect of tree species composition on the composition of the lepidopteran caterpillar communities was further indicated by a significant parafit test ( $p = .039$ ; based on a subset of the 64 most abundant MOTUs with >20 sampled individuals), which indicated nonrandom associations in the phylogenetic structure of the communities of lepidopteran herbivores and their host trees (Figure 3, Figure S5).

#### 3.2 | Plant-herbivore network associations

At the level of individual tree species, the phylogenetic regression model results showed that host-plant specialization with respect to associated caterpillars ( $d'$ ) was significantly positively related to the tree species' specific leaf area (SLA), leaf toughness and leaf area, whereas other functional traits had no effect (Table 2b, Figure 5c,d). The number of effective partners was positively related to LDMC (Table 2b). Leaf tannin concentration and other leaf chemical traits were unrelated to these network metrics and not retained in the final models (Table 2).

Null model analyses showed that the observed network indices were significantly different from a random distribution (47 out of 53 values for vulnerability analysed at the plot level; all



**FIGURE 2** Ordination plot of the nonmetric multidimensional scaling (NMDS) analysis of (a) lepidopteran species (MOTU) composition and (b) phylogenetic composition across the study plots (filled circles) in the BEF-China experiment. Stress = 0.182 and 0.201, respectively. Arrows indicate significant (at  $p < .05$ ) correlations of environmental variables with NMDS axes scores. Lengths of arrows are proportional to the strength of correlations. Red crosses refer to the lepidopteran species in each community. See Tables S4–S5 in Supplementary Material for abbreviations and statistical values [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

values for generality, vulnerability and linkage density analysed at the tree species richness level per study site), which strongly suggests that interactions between species are not driven by random processes.

Network analyses showed that the generality of plant–herbivore associations was significantly different among the three sampling seasons (April, June, September;  $F_{1,5} = 3.96$ ,  $p = .009$ ; Figure 4a). Network generality was significantly higher in April and June of each sampling year, compared with September (Figure 4a, Table S7). This was accompanied by notable changes in herbivore community composition (e.g. Geometridae and Erebidae) across seasons (Figure 4b). In contrast, host tree vulnerability did not change significantly across seasons ( $F_{1,5} = 1.97$ ,  $p = .120$ ).

However, neither generality nor vulnerability or linkage density of lepidopteran host use was significantly related to tree species richness (Table S8). Instead, vulnerability—that is the effective number of herbivore interaction partners per tree species—was positively related to the CWM of leaf toughness, LDMC and leaf Ca content (Figure 5a,b, Table 2).

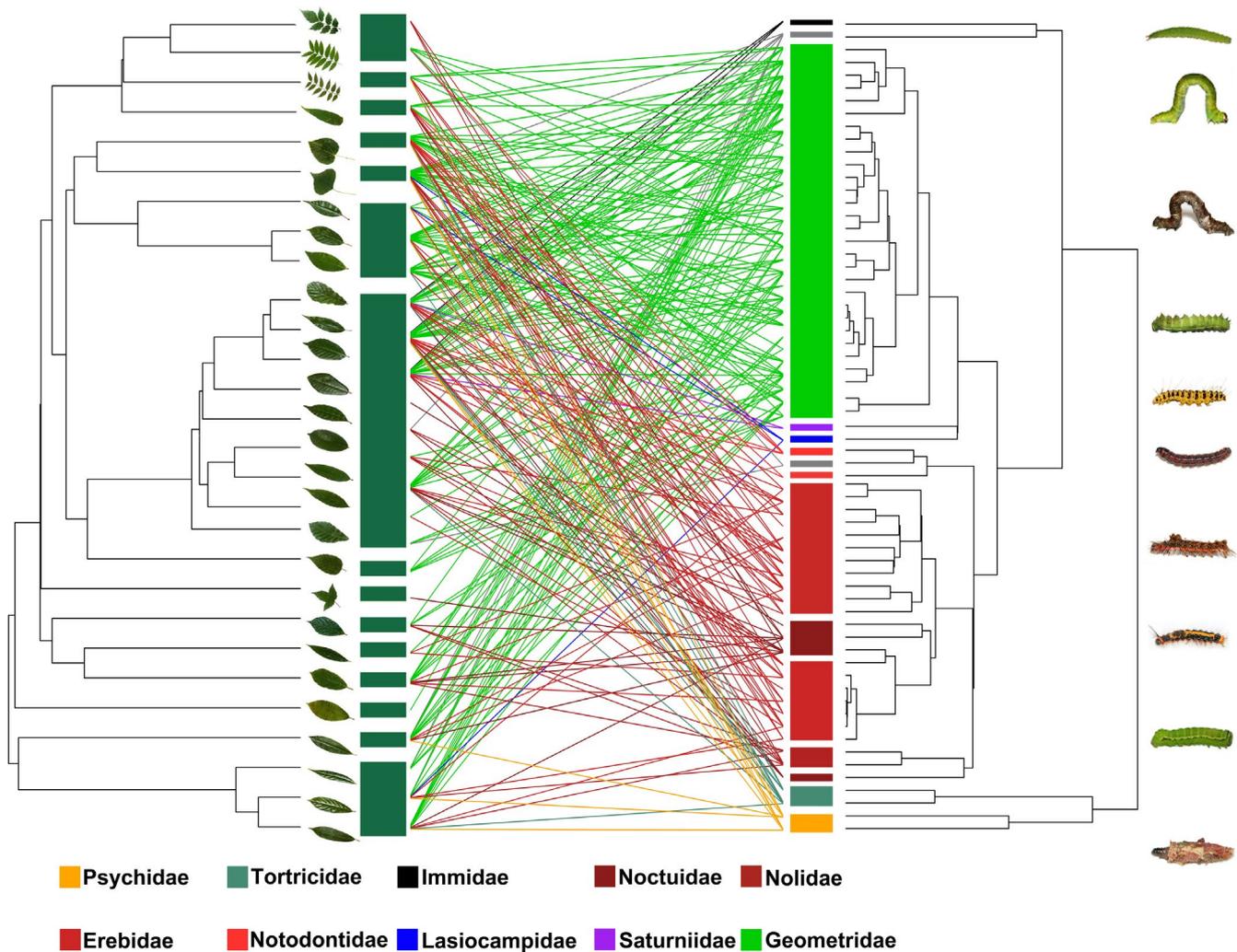
The sequencing failures were not related to tree species richness (Pearson's  $r = -.10$ ,  $p = .47$  for a correlation of per cent of failed sequences and tree species richness per plot) or tree species identity (Pearson's  $r = -.03$ ,  $p = .876$  for a correlation of per cent of failed sequences and  $d'$ , Pearson's  $r = .10$ ,  $p = .587$  for a correlation of per cent of failed sequences and effective partners). In addition, there was no significant relationship between sequencing failures and  $d'$  ( $F = .03$ ,  $p = .876$ ) or effective partners ( $F = .30$ ,  $p = .587$ ).

## 4 | DISCUSSION

Our study highlights that phylogenetic associations among herbivores and their hosts, but not necessarily host species richness, play a key role in structuring herbivore communities and their interaction network with trees. These interactions may be further modified by the functional traits of the host plants. We could trace effects of phylogenetically structured (see below and Wang et al., 2019) plant traits from the interaction network of individual species to the level of entire communities. These patterns were independent of changes in tree species richness, indicating that nonrandom (i.e. trait- and phylogeny-mediated) processes are key to understanding the consequences of biodiversity loss.

### 4.1 | Species-level dependencies

The dependence of herbivore community structure on the phylogenetic and functional identity of their host species in our study highlights the close phylogenetic linkages between herbivores and their hosts that have developed during the diversification of plant and herbivore lineages (Ehrlich & Raven, 1964; Pellissier et al., 2013). Adaptations to nutritive and defence characteristics of the host plants can be phylogenetically conserved in many cases (Nakadai, Murakami, & Hirao, 2014; Volf et al., 2018). In our study, this probably resulted in the structuring of herbivore communities based on similarities and differences in the relatedness and the functional traits of their host trees (Becerra, 2015; Cavender-Bares, Kozak, Fine, &



**FIGURE 3** Dendrogram of phylogenetic congruence for the most abundant (>20 individuals,  $N = 64$ ) lepidopteran species (right) and associated plant species (left) recorded in the study. Each rectangle represents a family for tree species; colours indicate different lepidopteran superfamilies (grey lines represent interactions between plants and unidentified Lepidoptera). The trophic network of lepidopterans and angiosperms was nonrandomly structured (parafit test:  $p = .039$ ). Tree species names are given in Figure S4. See Table S3 for family associations and abundances of the 64 lepidopteran species [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Kembel, 2009). For SLA, LDMC and leaf toughness—three traits with a strong effect on the herbivore communities in our study—we previously found strong phylogenetic signal in the distribution of trait values among the tree species at our study sites (Wang et al., 2019). This structuring based on phylogenetic covariation was further shown in our study by the significant *parafit* correlation between the phylogenetic trees of the host plants and their most abundant associated herbivores (see also Pellissier et al., 2013). Interestingly, this result differed from NMDS results of analyses at the plot level. This discrepancy might result from strong phylogenetic associations between individual hosts and their herbivores that are detectable at the species level, but which might be blurred at community level because not all interactions are specialized (e.g. when herbivore species can interact with more than one host).

Our finding of a positive relationship between SLA and the degree to which host trees were specialized in their associations with herbivores ( $d'$ ) was unanticipated, as high SLA often goes along with

high palatability to herbivores (Pérez-Harguindeguy et al., 2003; Salgado-Luarte & Gianoli, 2017) and should make such plant species a target for a wider range of herbivore species. However, the tree species with high SLA leaves at our study site are better protected by chemical defences (Eichenberg et al., 2015), which could make them less accessible to many generalist herbivores. In this context, it will be important to analyse the role of secondary metabolites in modifying plant–herbivore network structure. We were only able to test for the influence of leaf tannin concentrations on network metrics, which did not have any effect in our analyses. Previous studies have indicated that a high diversity of herbivores, in particular specialized herbivores which have often overcome specific defence mechanisms of their host plants (Salazar et al., 2018), can make it difficult to detect strong signals of individual secondary compound classes on plant–herbivore interactions (Carmona, Lajeunesse, & Johnson, 2011; Schuldt et al., 2012). Nevertheless, secondary metabolite composition has been observed as a driver of herbivore

**TABLE 2** Summary results of final linear models for (a) vulnerability at network level across all study plots, and (b) specialization index  $d'$  and effective partners at species level across host tree species

(a) Community level				
	Vulnerability			
	Estimate	SE	t	p
(Intercept)	9.371	0.724	12.95	<.001
Northness	-1.811	0.877	-2.07	.045
Slope	1.607	0.854	1.88	.066
CWM LDMC	1.878	0.837	2.25	.030
CWM LT	2.708	0.959	2.83	.007
CWM Na	-1.633	0.907	-1.80	.078
CWM Ca	-2.003	0.890	-2.25	.029
$\Delta$ AICc	66.27			
(b) Species level				
	$d'$			
	Estimate	SE	t	p
(Intercept)	-0.583	0.042	-13.93	<.001
LA (log)	0.158	0.059	2.66	.016
SLA (log)	0.137	0.054	2.51	.022
LDMC	-0.069	0.046	-1.51	.149
LT	0.165	0.070	2.36	.030
$\Delta$ AICc	37.37			
Effective partners				
	Estimate	SE	t	p
(Intercept)	2.352	0.146	16.10	<.001
LDMC	0.356	0.149	2.38	.027
$\Delta$ AICc	53.74			

Note: Standardized parameter estimates (with standard errors,  $t$  and  $p$  values) are shown for the variables retained in the minimal models.  $\Delta$ AICc values show difference between initial and final model  $\Delta$ AICc values.

ML estimation of  $\lambda = 0$  in the phylogenetic models in (b).

Abbreviations: Ca, leaf calcium; CWM, community-weighted mean value; LA, leaf area; LDMC, leaf dry matter content; LT, leaf toughness; Na, leaf sodium; SLA, specific leaf area.

community composition (Richards et al., 2015; Salazar et al., 2016, 2018), and quantifying effects of leaf chemical diversity might further advance our understanding of how multiple types of plant traits (related to morphology, nutrients and defences) jointly affect trophic interaction networks. Moreover, we cannot exclude that effects of individual compounds or ratios between compounds (e.g. ellagitannins or condensed tannins; Barbehenn, Jones, Hagerman, Karonen, & Salminen, 2006) were masked by our total content quantification for tannins and other compound classes (see also Volf, Salminen, & Segar, 2019).

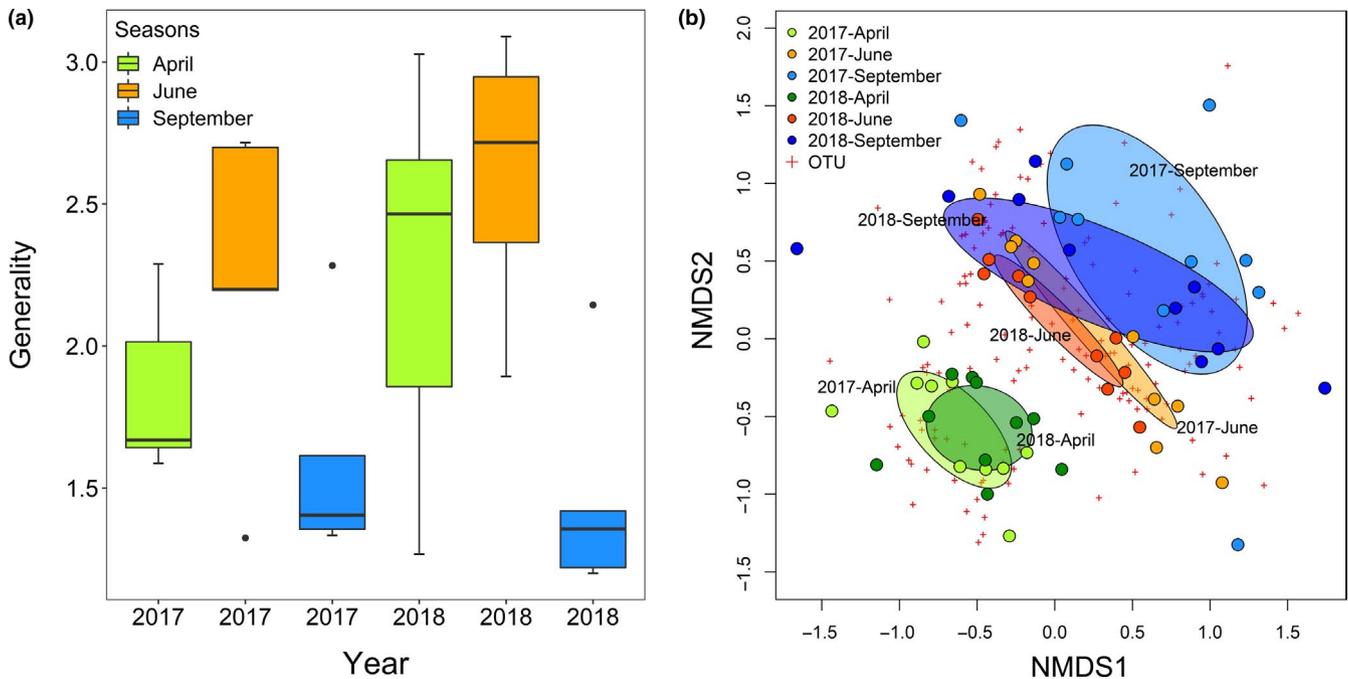
At the same time, our study showed that tree species with higher leaf toughness have more specialized herbivores, which is in line with the finding of López-Carretero, Boege, Díaz-Castelazo, Domínguez, and Rico-Gray (2016) that high levels of leaf toughness restrict host use to rather specialized herbivores. Taken together, these findings

indicate that leaf traits related to palatability and physical defence might drive a higher specialization of species-level interactions (see also López-Carretero et al., 2016), which in turn might cascade up to the community level. In our case, higher interaction specialization for trees with high SLA at the species level might be reflected by lower generalization (i.e. higher specialization) of plant–herbivore networks in plant communities with low LDMC (as LDMC is often negatively correlated with SLA, which tended to be the case also in our study: Pearson's  $r = -.37$ ,  $p = .058$ ).

## 4.2 | Herbivore–host network interactions at the community level

Importantly, the dependence of herbivore–host tree associations on functional traits and the composition of the host plant communities affected network structure. The positive effects of traits such as LDMC and leaf toughness on vulnerability were rather unexpected, as high values of both traits are usually considered to render plants less palatable (Pérez-Harguindeguy et al., 2003). As mentioned above, these traits showed a strong phylogenetic signal in our study sites (Wang et al., 2019). The observed relationships could therefore reflect co-evolved adaptations of groups of herbivores to their host trees in an environment that is generally characterized by trees with rather tough, evergreen leaves (see also Pérez-Harguindeguy et al., 2003; Schuldt et al., 2012).

The species richness of the tree communities did not significantly influence the generality of host plant use by herbivores, and the same was true for the number of herbivores per host species (vulnerability) and the connectance between both trophic levels (linkage density). Our findings contrast with results of a previous study (López-Carretero, Díaz-Castelazo, Boege, & Rico-Gray, 2014), where higher resource diversity was assumed to increase niche differentiation in lepidopteran herbivores and therefore network specialization. However, in that study effects of plant diversity were assessed across contrasting types of ecosystems. Turnover of herbivores within individual ecosystems is less pronounced than across different ecosystems, where environmental filtering may be an overriding confounding factor. Moreover, specialized herbivores are less likely to be affected by changes in plant species richness because of their limited host plant spectrum (Knuff, Staab, Frey, Helbach, & Klein, 2019; Staab et al., 2015) and reduced likelihood of spillover effects by the less mobile lepidopteran larvae to neighbouring trees. This was also indicated in our study, as the spatial proximity of the study plots did not influence network metrics, indicating that immigration from surrounding plots was unlikely to have affected the relationship between tree diversity and network metrics (especially since we excluded rare and potentially vagrant individuals). Although values of network generality around two indicate that the caterpillars we studied were not necessarily all monophagous specialists, they were much more specialized than other dominant groups of herbivores observed at our study sites (such as leaf-feeding beetles; Zhang et al., 2017; see also Novotny et al., 2010). Our findings also contrast with results from



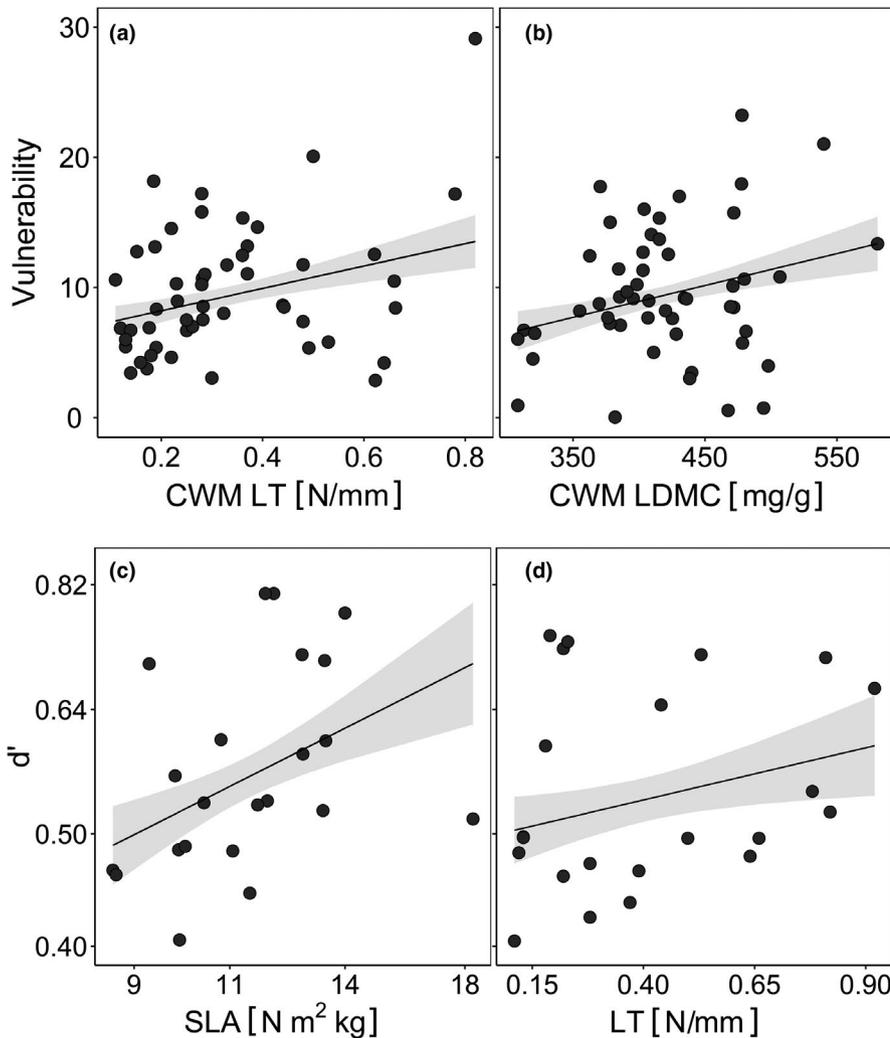
**FIGURE 4** (a) Generality of herbivore–host use calculated by tree species richness level across six sampling seasons. Boxes and whiskers represent the data distribution around the median, and filled circles represent extreme values. Generality in the September samples was significantly lower than in the April and June samples ( $p = .009$ ). (b) Nonmetric multidimensional scaling (NMDS) analysis showing lepidopteran community composition across the three sampling seasons per year (stress = 0.206). Ellipses represent the standard deviation around the centroids of each sampling date, red crosses refer to the lepidopteran MOTUs in each community [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

grasslands, where some studies found strong effects of plant diversity on plant–herbivore network metrics (e.g. Giling et al., 2019; Rzanny & Voigt, 2012). These contrasting results are unlikely caused by our experimental design, as studies finding significant effects were often conducted in biodiversity experiments with a very similar design and even smaller plot sizes (Bommarco & Banks, 2003; Weisser et al., 2017), or even in the same study sites for different groups of organisms (Fornoff et al., 2019). Differences in the strength of diversity effects might therefore rather reflect biological differences that are caused by the groups of interacting taxa considered, their degree of host specialization or their mobility. We note that our findings are based on relatively small-scale variation in tree diversity, and further research should establish the extent to which these findings can be scaled up to larger scales, such as entire forest regions varying in tree diversity (e.g. Skarbek et al., 2020).

It is interesting to note that in both study years, the generality index of herbivores, calculated at the community level, was significantly higher in spring and early summer than in fall. This means that herbivores with more generalized host use dominated in the first half of the year, whereas later in the year more specialized herbivores prevailed. The shift in community composition across the seasons (Figure 4b) shows that this pattern is likely driven by turnover in species composition. These changes were particularly evident within the highly abundant Geometridae and Erebidae in June and September, respectively. Previous studies have indicated that in tropical forests, specialists should be better able to handle young and highly defended leaves, whereas generalists might prefer older and less defended

leaves (Blüthgen & Metzner, 2007; Quintero & Bowers, 2018). However, defence mechanisms might vary across regions and with species composition, and in temperate regions, specific defences (e.g. condensed tannins and leaf toughness) might accumulate with leaf age (Coley & Barone, 1996). Nutrient relocation from senescent leaves might have similar effects (Coley & Barone, 1996) and make it harder for generalists to cope with these leaves. Our subtropical forest site with both deciduous and evergreen tree species might show intermediate patterns, and future research should investigate to what extent leaf phenology and associated changes in leaf trait across the growing season can explain shifts from more generalized to more specialized herbivore communities. Due to limited sample size per sampling period, we were not able to analyse seasonal effects on network relationships at finer scales (at the plot level or for individual tree species), which means our analyses largely represent average conditions over the entire growing season. It will be an interesting avenue for further research to address how such network relationships, especially at the level of individual tree species, are affected by seasonal changes in herbivore communities and plant functional traits (López-Carretero et al., 2014)—and what the consequences for ecosystem functions such as herbivory will be.

Overall, the absence of an effect of tree species richness on herbivore community structure (Figure 2a,b) and the strong effects of tree species composition and trait characteristics highlight that the consequences of changes in plant diversity—as they will be occurring for instance with increasing effects of climate and environmental change—can be challenging to predict for herbivore communities.



**FIGURE 5** Relationships at community level between vulnerability and (a) community-weighted mean values of leaf toughness and (b) community-weighted mean values of leaf dry matter content. Relationships at species level between  $d'$  and (c) specific leaf area and (d) leaf toughness. Values were adjusted for covariates of the final regression model. Regression lines (with 95% confidence bands) show significant ( $p < .05$ ) relationships. Note that axes are on a log scale for  $d'$  and specific leaf area

Not only declines in the number of plant species will determine how herbivore community structure, and potentially their diversity, will be affected by the loss of host plant species. Rather, the nonrandom loss of species from individual evolutionary lineages and with trait combinations particularly sensitive to environmental change (Vamosi & Wilson, 2008) will play an important role.

## 5 | CONCLUSIONS

Our study shows that the influence of host plant palatability and attractiveness to herbivores on host-herbivore networks can be traced from species-level interactions to community-level patterns. Environmental changes that alter the trait composition of host plant communities may therefore result in nonrandom changes in interaction networks that cannot be predicted from plant species richness loss alone. Our study provides insights into how trophic networks are influenced by host traits and phylogeny. Inferring the detailed structure of plant-herbivore interactions was only possible by using molecular data, helping to identify morphologically often indistinguishable larval stages at high throughput and to separate cryptic species (Hebert, Penton, Burns, Janzen, & Hallwachs, 2004; Hrccek &

Godfray, 2015). Future studies should also address the role of herbivore functional traits, as they likely play a critical role in modifying the associations of plants and herbivores and the way in which nonrandom changes in these communities affect network structure and functioning.

## ACKNOWLEDGEMENTS

We thank Bo Yang, Xiaojuan Liu, Shan Li, Yu-Xi Xue and all members of the BEF-China consortium who co-ordinated and helped with the establishment and maintenance of the experiment. We acknowledge Chun-Sheng Wu for his tremendous work of adult moth identification. We are grateful to Stefan Michalski for providing plant phylogenetic data. We thank Ren-Jie Zhang, Jing-Ting Chen and several local assistants for their help in the sampling. We would like to thank Maria Heikkilä (Finnish Museum of Natural History, Zoology Unit, University of Helsinki) and Charles Mitter (Department of Entomology, University of Maryland) for providing computer files of Lepidoptera phylogenies. We are grateful to Wenzel Kröber for the assessment of tree traits. We thank Jitendra Gaikwad (German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig) for his help in uploading data set to the iDiv data portal. This work was supported by the Strategic Priority Research Program

of the Chinese Academy of Sciences (XDB310304), the National Science Fund for Distinguished Young Scholars (31625024) and the External Cooperation Program of BIC, Chinese Academy of Sciences, Grant No. 15211 1KYSB20160001. We acknowledge funding of the BEF-China experiment by the German Research Foundation (DFG FOR 891-3 and 319936945/GRK2324). Douglas Chesters was supported by National Science Foundation of China (No. 31772495). Ming-Qiang Wang was supported by the UCAS Joint Ph.D. Program (UCAS [2017-26]) to study for one year at Andreas Schuldt's Lab, Georg-August-University of Göttingen.

## AUTHOR CONTRIBUTION

A.S. conceived the idea for the manuscript; C.D.Z. and M.Q.W. designed research; M.Q.W., Y.L., D.C., H.B., K.M., P.F.G., Q.S.Z. and M.S. collected and/or contributed data and advice; M.Q.W. and D.C. conducted the Lepidoptera phylogenetic analyses; and M.Q.W. and A.S. conducted the statistical analyses, with input by M.S., and wrote the manuscript, with input from all co-authors.

## DATA AVAILABILITY STATEMENT

Data on community- and species-level network data are available on the iDiv data repository (<https://doi.org/10.25829/ivdiv.1857-15-3061>), as well as on the BEF-China project database (community data: <https://china.befdata.biow.uni-leipzig.de/datasets/627>, species data: <https://china.befdata.biow.uni-leipzig.de/datasets/626>, phylogenetic tree: <https://china.befdata.biow.uni-leipzig.de/datasets/628>). DNA sequence data can be accessed on GenBank (accession numbers: MN131188–MN132787) and on BOLD (BEFCN001-19–BEFCN1600-19).

## ORCID

Douglas Chesters  <https://orcid.org/0000-0001-7352-5770>

Keping Ma  <https://orcid.org/0000-0001-9112-5340>

Andreas Schuldt  <https://orcid.org/0000-0002-8761-0025>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Wang M-Q, Li Y, Chesters D, et al. Host functional and phylogenetic composition rather than host diversity structure plant–herbivore networks. *Mol Ecol*. 2020;29:2747–2762. <https://doi.org/10.1111/mec.15518>