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RESEARCH ARTICLE

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Tree phylogenetic diversity structures multitrophic communities

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Abstract

1. Plant diversity begets diversity at other trophic levels. While species richness is the most commonly used measure for plant diversity, the number of evolutionary lineages (i.e. phylogenetic diversity) could theoretically have a stronger influence on the community structure of co-occurring organisms. However, this prediction has only rarely been tested in complex real-world ecosystems.
2. Using a comprehensive multitrophic dataset of arthropods and fungi from a species-rich subtropical forest, we tested whether tree species richness or tree phylogenetic diversity relates to the diversity and composition of organisms.
3. We show that tree phylogenetic diversity but not tree species richness determines arthropod and fungi community composition across trophic levels and increases the diversity of predatory arthropods but decreases herbivorous arthropod diversity. The effect of tree phylogenetic diversity was not mediated by changed abundances of associated organisms, indicating that evolutionarily more diverse plant communities increase niche opportunities (resource diversity) but not necessarily niche amplitudes (resource amount).
4. Our findings suggest that plant evolutionary relatedness structures multitrophic communities in the studied species-rich forests and possibly other ecosystems at large. As global change non-randomly threatens phylogenetically distinct plant species, far-reaching consequences on associated communities are expected.

[Correction added on 21 January 2021, after first online publication: Projekt DEAL funding statement has been added.]

KEYWORDS
arthropods, BEF-China, biodiversity–ecosystem functioning, cross-taxon congruence, forest, fungi, niche, trophic interactions

1 | INTRODUCTION

Green plants constitute by far the largest amount of biomass to terrestrial ecosystems (Bar-On et al., 2018) and are the backbone of species communities and trophic interactions, as they supply matter and energy to all other trophic levels (Hairston et al., 1960). Plant diversity is central for ecosystem functioning and stability, and declining plant species richness (SR) alters manifold ecosystem functions and influences biodiversity of all trophic levels (Cardinale et al., 2011; Hautier et al., 2015; Schuldt et al., 2015). Biodiversity–ecosystem functioning (BEF) theory (Tilman et al., 2014) predicts that diversity at lower trophic levels begets diversity at higher levels, and thus, plant SR has since long been used as proxy for estimating overall biodiversity (Margules & Pressey, 2000) and for investigating ecosystem functions that usually scale with biodiversity (Balvanera et al., 2006; Duffy et al., 2017; Schuldt et al., 2018). An overall positive relationship between plant and animal species richness has often (e.g. Castagneyrol & Jactel, 2012; Scherber et al., 2010; Zhang et al., 2016) but not always (e.g. Schuldt et al., 2011; Staab et al., 2016; Zou et al., 2013) been empirically supported, questioning the general suitability of plant SR as proxy for multitrophic diversity. This indicates that our general understanding of how plant diversity influences diversity and ecosystem functions across trophic levels is still limited.

The diversity of organisms can be quantified at various levels, from counting species (i.e. species richness) to measuring traits (i.e. functional diversity) or using genetic sequences estimating the evolutionary divergence of lineages within a community (i.e. phylogenetic diversity: PD; Cadotte et al., 2009; Tucker et al., 2017). Thus, knowledge about which level of plant diversity most strongly affects multitrophic diversity and ecosystem functions is important to understand, predict and mitigate the consequences of plant species loss (Manning et al., 2019). While (plant) SR is the most intuitive biodiversity measure commonly used in ecological research (Gotelli & Colwell, 2001), it might not be the best diversity measure for investigating BEF relationships and for unravelling how biodiversity begets biodiversity across trophic levels. It may not be the number of plant species per se that affects ecosystem functioning and stability but rather the phylogenetic relatedness affecting the functional properties of those species (Srivastava et al., 2012; Webb et al., 2002). While functional diversity is conceptually promising, the number of measurable traits is often relatively small. Whether or not specific traits are functionally important, e.g. for species interactions, is often unclear (Cadotte & Tucker, 2017; Ma et al., 2018).

Assuming that many traits are phylogenetically conserved (Burns & Strauss, 2011; Cavender-Bares et al., 2009; Purschke et al., 2017; Tucker et al., 2018; but see Mazel et al., 2018), PD may comprehensively incorporate the multitude of functional differences between plant species and thus represent a parsimonious and powerful proxy of biodiversity in practice. Theory predicts that evolutionary divergence and the number of different lineages within a community are suitable surrogates for biotic niche differences (Srivastava et al., 2012; Webb et al., 2002). Two hypothetical plant communities with identical species numbers can differ in PD by consisting of closely or distantly related species (Figure 1). In the low PD community, common descent from a recent ancestor should result in closely related species being, on average, more similar to one another than the more distantly related species in the high PD community. It is expected that plants in the low PD community correspond to largely overlapping niches (often termed niche conservatism) whereas plants in the high PD community correspond to more complementary niches (sensu Hutchinson, 1978). Consequently, these niche differences among plants should provide more niche opportunities for organisms co-occurring with the plants, allowing for the co-occurrence of more associated species via increased resource diversity ('resource heterogeneity hypothesis', MacArthur, 1965), and ultimately for higher levels of ecosystem functionality.

Thus, only relying on SR as a measure of plant diversity can blur cross-taxon diversity relationships (e.g. Dinnage et al., 2012; Schuldt et al., 2019) and mask the magnitude of BEF effects (e.g. Cadotte et al., 2009). For example, it was recently shown that tree PD but not SR explained the ecosystem function parasitism (Staab et al., 2016) and the response of caterpillar communities to changes in host tree diversity (Wang et al., 2019). Additionally, if niche differences among plants enlarge overall biotic niche amplitudes (Figure 1), PD may also increase associated species abundances by allowing higher densities of individuals via higher resource amount ('more individuals hypothesis', Srivastava & Lawton, 1998). This mechanism may potentially explain the contrasting relationships between plant and animal species richness observed across species-rich ecosystems (e.g. Zhang et al., 2016 vs. Schuldt et al., 2011). However, even though phylogenetic data for plants are increasingly available, it remains to be tested whether plant PD is systematically related to organisms in other trophic levels and whether plant PD outperforms plant SR as a predictor of organismic diversity and composition across multiple trophic levels.

To the best of our knowledge, very few studies haves tested this prediction with a comprehensive dataset including multiple trophic guilds (Dinnage et al., 2012; Peralta et al., 2015). Of those, only Dinnage et al. (2012) focused on cross-taxon congruence, finding that plant PD parsimoniously explains the composition and diversity of arthropods. However, this study was conducted in experimental grasslands and it is unclear if relationships between plant PD and associated organisms can be extrapolated to more complex real-world ecosystems such as species-rich forests (Manning et al., 2019). In contrast to grasslands, forests are composed of long-lived and structurally complex plant individuals (i.e. trees), which accumulate high biomass over their life span and can shape their biotic and abiotic environment in many ways, making ecological processes in forests very different from grasslands

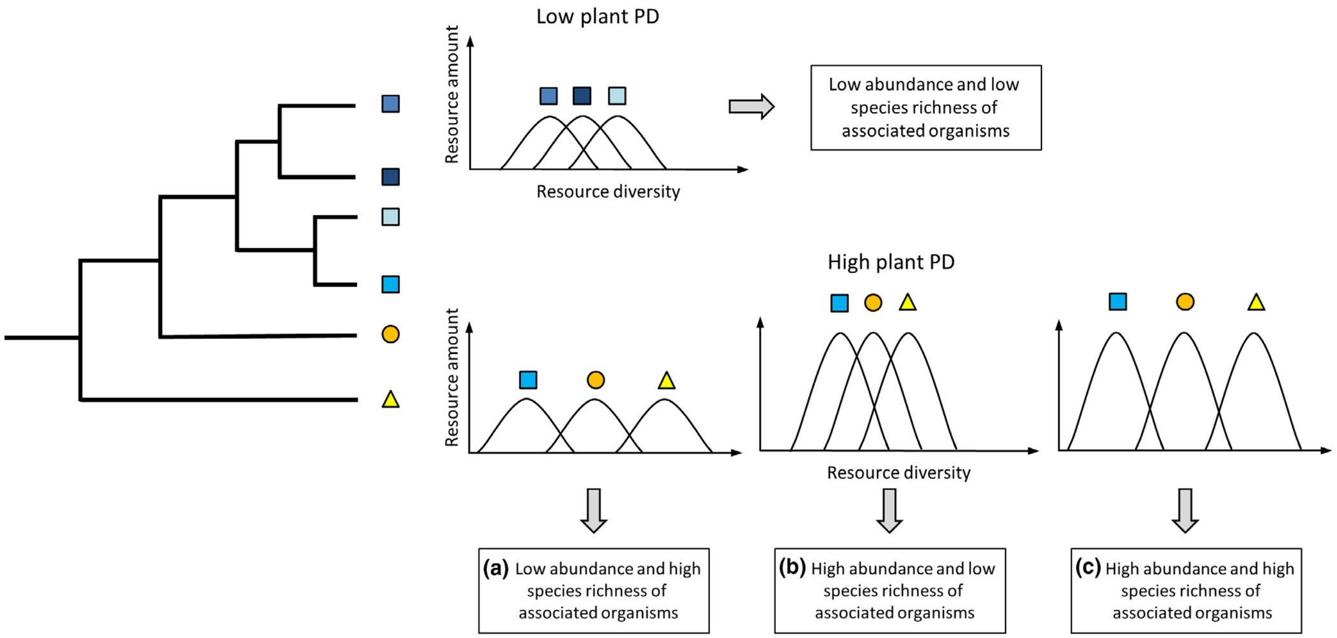

FIGURE 1 Conceptual illustration of the hypothesis. Consider two different plant communities of the same species richness (here three) that differ in phylogenetic diversity (PD) by consisting of closely (low PD; same symbols) or distantly (high PD; different symbols) related plant species. It is expected that the resources provided by the plants in the low-PD community will overlap more, while those in the high-PD community will be (a) less overlapping (i.e. niche opportunities, *x*-axis), which should allow the coexistence of more species of associated organisms, (b) provide higher resource amount (i.e. niche amplitudes, *y*-axis) which should sustain more individuals, or (c) be a combination of (a and b), which should allow for more species and individuals. The outlined association between PD and niches can in practice be shaped by plant species richness. For example, in high PD communities additional species are less likely to expand niche opportunities and amplitudes (except at low plant species richness), while in low PD communities a generally positive correlation between niches and plant species richness is likely (except at very high plant species richness)

(Grossman et al., 2018). This is particularly true for (sub)tropical forests, where tree SR can be exceptionally high and the occurrence of many evolutionarily old lineages theoretically allows for a high variation in PD, potentially making tree PD a promising proxy for comprehensively understanding biodiversity relationships across trophic levels. Using an exhaustive dataset from a species-rich subtropical forest we hypothesize that woody plant PD is more strongly related to the species richness, abundance and community composition of associated guilds of arthropods and fungi from different trophic levels than is woody plant SR. We show for a complex ecosystem that plant PD structures associated diversity and thus that plant PD is a parsimonious proxy of species richness and composition across trophic levels.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in the species-rich subtropics of south-east China (Zhejiang Province). The region has a monsoon climate with mean annual temperature and precipitation of *c*. 15.5°C and 2,000 mm. Within the Gutianshan National Nature Reserve (GNNR, *c*. 8,000 ha, 29°08′–29°17′N, 118°02′–118°11′E, elevation 250–1,260 m), 27 study plots of 30 × 30 m were randomly selected across the accessible parts of the reserve in 2008 (Bruelheide et al., 2011). The GNNR is covered by subtropical evergreen mixed broadleaved forest in varying stages of succession. Over 250 woody species occur in the reserve, of which about 50% are evergreen. Common tree families are Fagaceae (e.g. *Castanopsis eyrei*), Lauraceae (e.g. *Machilus thunbergii*) and Theaceae (e.g. *Schima superba*), among others. Conifers are naturally rare (<2% of woody species), but *Pinus massoniana* and *Cunninghamia lanceolata*, two commercially important species dominating local forestry, were promoted before the GNNR was established and have remained in the forest. The 27 plots cover stratified crossed gradients of woody (tree and shrub) species richness from 25 to 69 species (termed ‘woody plant SR’) and stand age from <20 to >80 years (Liu et al., 2018; Table S1). A map of the GNNR is displayed in Staab et al. (2014).

2.2 | Species sampling and trophic guilds

A broad range of macro-organisms and fungi were sampled with standardized methods in all plots during various sampling campaigns from 2008 to 2012 (see Binkenstein et al., 2018; Schuldt et al., 2015; data: Staab et al., 2019). Sampling for arthropods collected species communities at the forest floor and in the understorey by utilizing pitfall traps, flight interception traps, beating, baiting and trap nests (see Table 1 for a detailed overview). The organisms were grouped according to their ecology into eight trophic guilds (sensu Simberloff & Dayan, 1991; Table S1). Macro-organisms

TABLE 1 Overview on sampling methods and trophic guilds

Sampling method	Sampling effort per plot	Guilds and included taxa
Pitfall traps	Four traps (8.5 cm diameter) at the corners of the central 10 m × 10 m area from March to September 2009; emptied fortnightly	*Herbivores*: Curculionidae (excl. Scolytinae) *Predators*: Araneae, Chilopoda, Formicidae
Flight interception traps	Four traps (collection area 50 cm × 30 cm) in the understorey (~2 m height) at the corners of the central 10 m × 10 m area from May to August 2010; emptied fortnightly	*Saproxylics*: Cerambycidae, Scolytinae *Predators*: Formicidae
Beating	Arthropods from 25 understorey trees and shrubs (average height 1.7 m ± 0.48 *SD*) sampled three times (once in fall 2011, twice in spring 2012) onto a circular beating sheet (diameter 72 cm)	*Herbivores*: Lepidoptera (larvae) *Predators*: Araneae, Formicidae
Trap nests	Two trap nests (filled with reed internodes of 20 cm length and 2 mm to 20 mm diameter) at opposing corners of the central 10 m × 10 m area from September 2011 to October 2012; emptied monthly	*Predators*: Cavity-nesting wasps (including their parasitoids)
Baiting	Nine bait pairs (protein: canned fish; sugar: honey solution) at ground and breast height in May 2012; baits and feeding specimens retrieved after three hours	*Predators*: Formicidae
Vegetation survey	All non-woody plants in the central 10 m × 10 m area recorded from May to July 2008	*Herbaceous plants*
Soil sampling	Eight top soil samples (10 cm) collected in September 2012; combined to four composite samples per plot by merging two spatially proximate samples each; DNA extracted and sequenced from 1 g (dry mass) per composite sample	*Arbuscular mycorrhiza fungi*, *Ectomycorrhiza fungi*, *Pathogenic fungi*, *Saprophytic fungi*

consisted of understorey 'plants', 'herbivores' (Curculionidae excl. Scolytinae, Lepidoptera), 'predators' (Araneae, Chilopoda, Formicidae, predatory wasps and their parasitoids) and 'saproxylics' (Cerambycidae, Scolytinae). Fungi (based on DNA sequences and molecular operational taxonomic units from soil samples) consisted of 'arbuscular mycorrhizae', 'ectomycorrhizae', 'pathogenic' and 'saprophytic' fungi. As the different taxonomic groups have for logistic reasons been collected with various methods in different years (Table 1), and as for most specimens (e.g. from pitfall traps) association to specific plant individuals is not possible, raw data were pooled across sampling methods to guilds at plot level. This approach is necessary for the chosen analytical framework, but precludes an analysis of trophic cascades (sensu stricto) or to distinguish whether some arthropods or fungi are more influenced by herbaceous than woody vegetation. Detailed descriptions of all sampling protocols and fungal DNA barcoding are reported in the Supporting Information.

2.3 | Woody plant phylogenetic diversity

During plot establishment, all woody (tree and shrub) individuals >1 m height were identified to species (in total 147 species) and species-specific abundances (i.e. woody plant density) were recorded (Bruelheide et al., 2011). An ultrametric phylogeny for all woody species was constructed based on the markers *mat*K, *rbc*L and the internal transcribed spacer region including the *5.8s* gene (Baruffol et al., 2013; Purschke et al., 2017). From the many indices available to calculate PD (each with distinct properties, Tucker et al., 2017), we selected abundance-weighted Rao's *Q* that was calculated with the R-package PICANTE (Kembel et al., 2010). Species-specific abundances were used for weighting PD (i.e. Rao's *Q*) because sampling of trophic groups was conducted at the forest floor and in the understorey. Furthermore, individual numbers are the measure of abundance for all other macro-organisms, thus ensuring that analyses across guilds use the same currency (the unweighted presence–absence-based version of the index was also calculated for comparison). Abundance-weighted Rao's *Q* is a commonly used PD index in community ecology (Tucker et al., 2017) and describes the evolutionary mean pairwise distance between all pairs of individuals (see Supporting Information), making it at least in theory mathematically independent of SR, which can be a desirable property when comparing PD with SR. Rao's *Q* will be highest in communities consisting of two equally abundant species that are maximally distinct, making this index less suitable as PD measure for species-poor artificial ecosystems, as adding a species that is not evolutionarily distinct will decrease PD when species richness is low. In contrast, in our species-rich and naturally assembled subtropical forests with a large local pool of species and evolutionary lineages, Rao's *Q* was positively correlated with woody plant SR (Spearman's $\rho = 0.47$, Figure S1), indicating that this PD index is suitable to capture the expected increase in niche opportunities when SR increases. We checked for phylogenetic dispersion with the 'ses.mpd' function in 'picante' (nullmodel 'independentswap', 10,000 iterations).

As even single conifer individuals strongly influence plot-scale PD (due to the deep evolutionary split between angiosperms and gymnosperms), PD was based on angiosperms only (96.4% of individuals, 97.3% of species). Nevertheless, four conifer species are part of the woody communities in the study plots and their presence may influence the diversity of forest organisms (Penone et al., 2019). We accounted for this by using the proportion of basal area of conifers (relative to total basal area, see Baruffol et al., 2013) as covariate next to PD.

Similar to conifers, variation in angiosperm woody plant PD could be driven by few common and evolutionarily distinct species and not by PD per se. To rule out this potential bias, we calculated evolutionary distinctness (following Redding & Mooers, 2006), which was neither related to woody plant occurrence nor to woody plant composition (Figure S2), indicating that evolutionarily distinct species occur randomly among plots and do not cluster in high PD plots.

Traits (i.e. leaf area, leaf nitrogen content, leaf phosphorous content, maximum tree height, specific leaf area, wood density) of woody angiosperms in the study plots were previously analysed by Purschke et al. (2017) and showed strong phylogenetic signals (Table S2).

2.4 | Environmental covariates

The topography in the GNNR is heterogeneous and plots vary in elevation and further abiotic properties (Binkenstein et al., 2018; Table S1), which influences woody species and co-occurring organisms (Schuldt et al., 2015). In addition to plot elevation (in m), we measured slope (in °) and aspect, i.e. the compass orientation of the slope (sine and cosine transformation of the aspect expressed as eastness and northness). Stand age reflecting the successional age of a plot was determined from stem core drillings (details in Bruelheide et al., 2011). Total basal area ($\rho = 0.89$) and woody plant density ($\rho = -0.69$) were highly correlated with stand age (Table S3). Correlation coefficients among the other environmental covariates were relatively lower (maximal $\rho < 0.34$; see Table S3), as were their correlation coefficients with woody plant SR ($\rho < 0.24$) and woody plant PD ($\rho < 0.56$).

2.5 | Data analysis

All statistical analyses were conducted in R 3.4.2 (R Core Team, 2019). We used confirmatory path analyses in the R-package LAVAAN (Rosseel, 2012) to test how woody plant PD and woody plant SR influence the abundance and species richness of trophic guilds. We standardized all variables ($M = 0$, $SD = 1$) prior to analyses to allow direct comparisons of effect sizes. To reduce the dimensionality of environmental variability among plots, we calculated a principal component analysis of aspect eastness, aspect northness, elevation, slope, stand age, total basal area and woody plant density with the R-package VEGAN (Oksanen et al., 2019). The first three PCs (principle components) explained together 74% of variation and were selected for further analysis. PC1 was most strongly positively loaded with stand age and total basal area, and negatively with woody plant density, while PC2 was positively loaded with elevation and aspect northness (negatively with aspect eastness), and PC3 with aspect northness and slope (Table S4).

Path models were calculated on standardized residuals of multiple linear models regressing all included biotic variables (abundance (log-transformed) and richness of trophic guilds, woody plant SR, woody plant PD, conifer basal area) on the first three PC axes of environmental covariates. This approach excludes a common response of trophic guilds and woody plant PD to environmental properties (Proches et al., 2009) and allows for the identification of cross-taxon diversity relations per se. To disentangle effects of woody plant PD, woody plant SR and conifer basal area on abundance and species richness of trophic guilds, we hypothesized an a priori path model (Figure 2) containing direct paths from woody plant PD and conifer basal area to trophic guild species richness. To test whether effects on species richness might also be indirect and mediated by abundance, paths from woody plant PD and conifer basal area to species abundance of associated organisms were included. As PD may increase with SR, we specified a path from woody plant SR to woody plant PD. Likewise, plots with a higher conifer basal area might have lower woody plant SR and lower woody plant PD, and we accounted for these potential relationships by fitting a path from conifer basal area to woody plant PD and by including the covariance between conifer basal area and woody plant SR. This way, we accounted for effects of coniferous trees that are mostly remnants of forestry from the time before the study area became protected. To test the hypothesis that woody plant PD is superior to woody plant SR, path models for all trophic guilds were compared to an alternative model additionally containing paths from woody plant SR to abundance and species richness of associated organisms. Comparisons were based on AICc (Akaike information criterion corrected for small sample sizes), with a lower AICc indicating the model with higher statistical support. No further model selection was applied and model fit was assessed with root mean square error of approximation (*RMSEA*) and Chi-square statistics. As AICc in path models scales with the number of paths, we also calculated and compared models with identical paths in which either only woody plant PD or woody plant SR was included as proxies of woody plant diversity.

To analyse and illustrate variation in species community composition of associated organisms among plots, NMDS (non-metric multidimensional scaling) was used. NMDS ordinations were based on Bray–Curtis dissimilarity and calculated for two and three dimensions, centred and rotated so that the first NMDS axis explained maximum variance. The environmental predictors (woody plant PD, woody plant SR, conifer basal area, environmental PC1, PC2, PC3) were correlated post-hoc with the plot-based axis scores of the first two NMDS axes to test whether community composition was associated to the environment (significance based on 10,000 permutations). All multivariate analyses were calculated in VEGAN.

To check for the role of species-specific abundances of woody plants and to test how woody plant abundances might influence PD results, the path models using standardized residuals for all included variables were repeated with unweighted PD based on presence–absence data. Likewise, the correlations with the plot-based axes

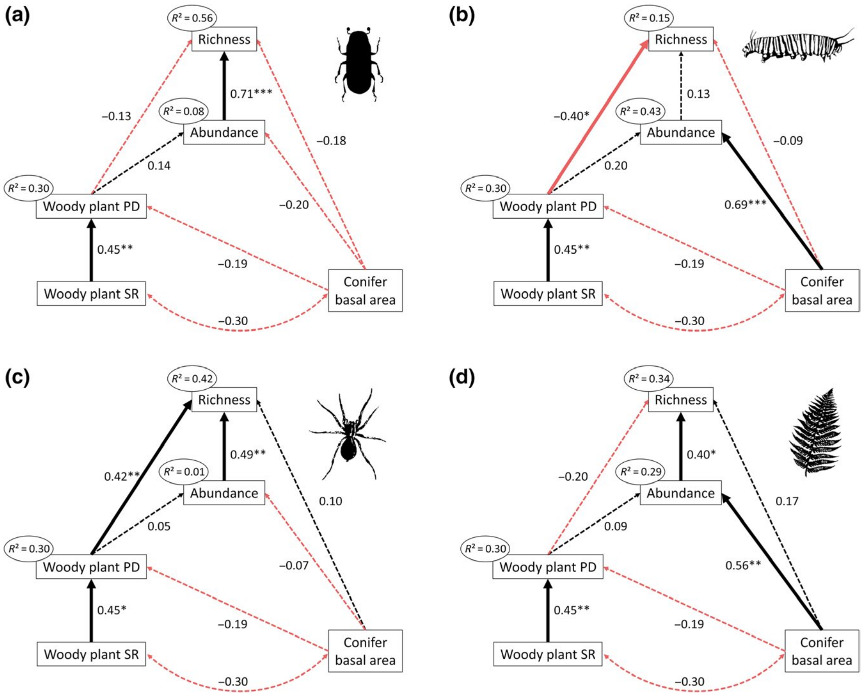

FIGURE 2 Path diagrams for (a) saproxylics ($\chi^2 = 0.394$, $p = 0.821$, ΔAICc = 19.2), (b) herbivores ($\chi^2 = 3.886$, $p = 0.143$, ΔAICc = 15.8), (c) predators ($\chi^2 = 0.329$, $p = 0.857$, ΔAICc = 19.3), and (d) herbaceous plants ($\chi^2 = 1.347$, $p = 0.510$, ΔAICc = 18.3) illustrating direct and indirect relationships between woody plant SR, woody plant PD (expressed as Rao's *Q*), conifer basal area and the abundance and species richness per trophic guild. ΔAICc values refer to comparisons ($\Delta\text{AICc} = \text{AICc}_{(\text{SR + PD model})} - \text{AICc}_{(\text{PD model})}$) with models that include paths from woody plant SR to abundance and species richness of the trophic target guild. All variables are standardized residuals from a priori correlations with the abiotic environment. Numbers next to arrows give standardized path coefficients. Positive and negative relationships are indicated by black and red arrows respectively. Covariance is indicated by a curved double-headed arrow. Significant relationships are ***$p < 0.001$, **$p < 0.01$, and *$p < 0.05$ and indicated with full arrows. See Table S5 for statistical details and Figure S3 for results of fungal guilds

scores of the first two NMDS axes were recalculated for presence–absence PD.

3 | RESULTS

The PD (expressed as Rao's *Q*) of woody plants had a positive influence on the (residual) species richness of predators (path estimate ± *SE* = 0.416 ± 0.156, $p = 0.008$) and a negative influence of similar strength on the species richness of herbivores (−0.400 ± 0.194, $p = 0.039$; Figure 2; Table S5). However, woody plant PD was for all trophic guilds not related to (residual) abundance of associated organisms. Nevertheless, species richness increased with abundance in all guilds except herbivores, ectomycorrhizae and pathogenic fungi (Figure 2; Table S5; Figure S3). Woody plant PD was not related to conifer basal area (−0.193 ± 0.170, $p = 0.256$). Plots with a higher proportion of coniferous trees had higher abundances of herbivores (0.691 ± 0.155, $p < 0.001$) and understorey plants (0.564 ± 0.172, $p = 0.001$). Relationships for fungal guilds were not significant in path models (except some relationships between abundance and richness). Woody plant SR had a positive influence on woody plant PD (0.452 ± 0.170, $p = 0.008$). The covariance between woody plant SR and conifer basal area was negative but not significant (−0.298 ± 0.194, $p = 0.124$). Neither phylogenetic clustering nor phylogenetic overdispersion occurred (Figure S4).

The hypothesized causal relationships specified in the a priori model structure received high statistical support for all guilds ($p_{(\chi^2)} > 0.078$, $p_{(RMSEA)} > 0.091$, Table S5). When compared with the alternative full models that included paths from woody plant SR to abundance and species richness of trophic guilds, the fit of the a priori models was consistently better (ΔAICc > 14.5). Likewise, in models with a constant number of paths containing either only woody plant PD or only woody plant SR, PD models had a better fit than SR models for all macro-organisms (ΔAICc > 2.3, Table S6). Path coefficients for PD models were qualitatively and quantitatively similar to models including both plant diversity variables, with significant paths between woody plant PD (but not woody plant SR) and herbivore (−0.400 ± 0.194, $p = 0.039$) as well as predator species richness (0.416 ± 0.156, $p = 0.008$). In line with the overall weak relationships for fungal guilds, corresponding AICc differences were relatively small (ΔAICc < 1.3) except for ectomycorrhizae fungi. Here the SR model indicated a better fit than the PD model (ΔAICc = 2.5). Taken together, this indicates that woody plant PD was a suitable predictor for the species richness and abundance across macro-organisms. Models using raw instead of residual woody plant diversity variables were

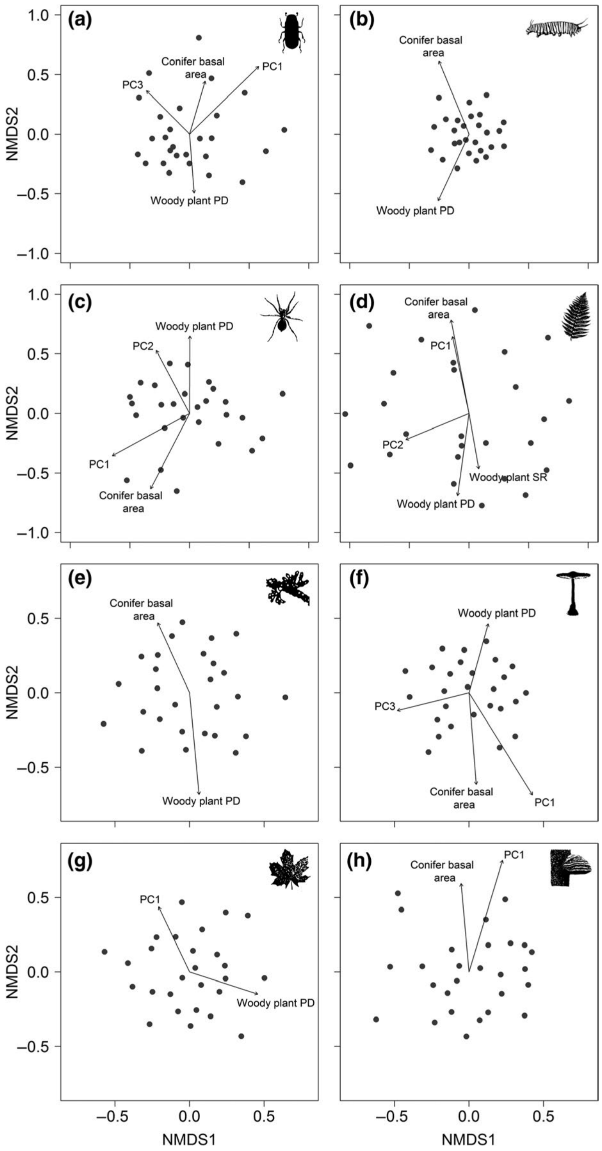

FIGURE 3 NMDS ordinations (2-dimensional) of (a) saproxylics, (b) herbivores, (c) predators, (d) herbaceous plants, (e) arbuscular mycorrhizae, (f) ectomycorrhizae, (g) pathogenic fungi, and (h) saprophytic fungi. Dots refer to the scores of the 27 study plots for each guild. Arrows indicate significant (at $p < 0.05$) correlations of environmental variables with plot-based axes scores. Lengths of arrows are standardized across guilds and proportional to the strength of correlations (details in Table 2; Table S8). PC axes represent the abiotic environment (PC1: positively related to stand age and total basal area, negatively to woody plant density; PC2: positively related to aspect northness and elevation, negatively to aspect eastness; PC3 positively related to aspect northness and slope; details in Table S4)

TABLE 2 Correlation coefficients, explained variance (R^2), and probabilities p (based on 10,000 permutations) for all significant relationships (at $p < 0.05$; full results in Table S8) between the environmental PCs and plant diversity variables and the plot-based axes scores of 2-dimensional NMDS ordinations. PC axes represent the abiotic environment (PC1: positively related to aspect eastness, negatively to elevation and stand age; PC2: positively related to slope and stand age; PC3: positively related to aspect northness and slope; details in Table S4)

Variable	NMDS 1	NMDS 2	R^2	p
Saproxylics (stress = 0.203)				
PC1	0.714	0.701	0.659	<0.001
PC3	−0.704	0.710	0.263	0.025
Conifer basal area	0.283	0.959	0.215	0.048
Woody plant PD	0.080	−0.997	0.246	0.029
Herbivores (stress = 0.245)				
Conifer basal area	−0.380	0.925	0.442	0.001
Woody plant PD	−0.420	−0.908	0.380	0.004
Predators (stress = 0.176)				
PC1	−0.876	−0.482	0.546	<0.001
PC2	−0.467	0.884	0.358	0.005
Conifer basal area	−0.458	−0.889	0.507	<0.001
Woody plant PD	0.005	1.000	0.423	0.002
Herbaceous plants (stress = 0.207)				
PC1	−0.210	0.978	0.435	0.001
PC2	−0.924	−0.383	0.329	0.008
Conifer basal area	−0.188	0.982	0.640	<0.001
Woody plant SR	0.172	−0.985	0.222	0.048
Woody plant PD	−0.137	−0.991	0.487	<0.001
Arbuscular mycorrhiza fungi (stress = 0.265)				
Conifer basal area	−0.414	0.910	0.266	0.025
Woody plant PD	0.093	−0.996	0.473	<0.001
Ectomycorrhiza fungi (stress = 0.216)				
PC1	0.527	−0.850	0.655	<0.001
PC3	−0.970	−0.242	0.246	0.036
Conifer basal area	0.079	−0.997	0.383	0.003
Woody plant PD	0.268	0.963	0.231	0.042
Pathogenic fungi (stress = 0.257)				
PC1	−0.428	0.904	0.235	0.043
Woody plant PD	0.951	−0.309	0.232	0.042
Saprophytic fungi (stress = 0.178)				
PC1	0.287	0.958	0.612	<0.001
Conifer basal area	−0.089	0.996	0.357	0.005

qualitatively and quantitatively similar (Table S7), showing that environmental influences on woody plant diversity were of minor importance.

In the 2-dimensional NMDS ordinations, woody plant PD was significantly related to the species composition of all trophic guilds with the exception of saprophytic fungi. In contrast, woody plant SR was neither related to the composition of arthropod nor of fungal guilds except for understorey plants (Figure 3; Table 2; Table S8). Furthermore, the composition of each trophic guild (except pathogenic fungi) changed with conifer basal area. From the abiotic environment, PC1 (stand age, total basal area, woody plant density) was most prevalent and related to the composition of all guilds except herbivores and arbuscular mycorrhizae. Increasing the number of dimensions in NMDS from two to three reduced stress but did not influence the configuration of the first two axes (Procrustes rotation, 10,000 permutations, $p < 0.001$ each).

Paths between presence–absence PD and the abundance and species richness of trophic guilds had the same sign as paths for abundance-weighted PD (i.e. the metric used in all other analyses) but were weak and not significant (Table S9) except for ectomycorrhizae fungi abundance (0.481 ± 0.209, $p = 0.021$). For community composition, only axes scores of herbaceous understorey plants correlated with presence–absence PD (Table S10), contrasting abundance-weighted PD.

4 | DISCUSSION

Over the last decade, community ecology and BEF research have increasingly adopted a phylogenetic perspective (e.g. Cadotte et al., 2012; Dinnage et al., 2012; Liu et al., 2013; Staab et al., 2016). We found that in a species-rich subtropical forest, PD (as Rao's *Q*) but not SR of woody plants was a parsimonious predictor for the composition of trophic guilds (NMDS ordinations), as hypothesized. This indicates that the diversity of woody plant evolutionary lineages may present a general template for resource diversity and niche opportunities (sensu Hutchinson, 1978; see also Dimitrakopoulos & Schmid, 2004), which can then be utilized by associated organisms in other trophic levels (Srivastava et al., 2012; Webb et al., 2002). Moreover, woody plant PD was related to the species richness of predatory and herbivorous arthropods (paths models), while woody plant SR influenced trophic guilds only indirectly via woody plant PD. Relationships between woody plant PD and trophic guild species richness were direct and not mediated by abundances of associated organisms, suggesting that forests consisting of phylogenetically more diverse tree species provide more diverse resources but not larger resource amounts (i.e. scenario *a* in Figure 1).

4.1 | Potential mechanisms underlying the effect of woody plant phylogenetic diversity

The common assumption for using PD in ecological studies is surrogacy for functional attributes that are phylogenetically conserved (Burns & Strauss, 2011; Tucker et al., 2018) but may be hard or impossible to measure (Srivastava et al., 2012; Webb et al., 2002). At our study site phylogenetic relatedness reflects trait similarity of woody plants and several traits that can mediate relationships between plants and consumers (e.g. specific leaf area, wood density) have a high phylogenetic signal (Purschke et al., 2017). The chosen woody plant PD index describes ecological (dis)similarity between tree species with more closely related species being functionally more similar (note that other PD indices have different properties and might potentially provide specific insights, Tucker et al., 2017). Combined with the particular life history of shrubs and trees as long-lived organisms with high biomass (sensu Jones et al., 1994), this phylogenetic conservatism directly relates to the resource space and thus niche opportunities provided to associated species (Chase & Leibold, 2003; Elton, 1927). In this way plant PD can be considered as a parsimonious predictor of community structure across trophic guilds, consistent with previous research identifying bottom-up effects of plant species composition on associated organisms (Schaffers et al., 2008; Schuldt et al., 2017). We suggest a plausible mechanism, by finding that plant PD determines species composition of organisms by shaping biotic niches. Nevertheless, species composition is not independent of the environment, and PC1 (representing stand age, total basal area and woody plant density; compare Bruelheide et al., 2011) was related to the composition of almost all trophic guilds. However, woody plant PD and PC1 were approximately orthogonal in most ordinations, indicating that the influence of woody plant PD is not confounded by correlated changes in the environment. This also explains that removing environmental variation from the woody plant diversity variables did not influence the results of path models.

For all trophic guilds a model without paths from woody plant SR to abundance and species richness of trophic guilds had a better fit than a model with these paths. Similarly, when comparing models with a constant number of paths in which woody plant SR or woody plant PD were treated as alternatives, PD models for all macro-organismal guilds had better fits than SR models. Taken together this indicates that woody plant PD is related to diversity across trophic guilds, as hypothesized. Nevertheless, the positive path between woody plant SR and woody plant PD further indicates that additional species may indirectly increase niche opportunities. The studied woody plant species communities appeared to be randomly assembled from the regional species pool (Bruelheide et al., 2011; Purschke et al., 2017). In all study plots, observed PD and PD obtained from a null model were similar, indicating that phylogenetic community assembly is likewise random, as no phylogenetic over- or underdispersion occurred. Thus, evolutionarily distinct species occurred randomly among plots without clustering in high PD plots. This indicates that variation in PD was not systematically related to species co-occurrence. Furthermore, the presence–absence PD analyses indicate that rare woody plant species do not disproportionally drive the association between PD and trophic groups, suggesting that species contributed to niche opportunities proportional to their abundance.

It is important to note that our distance-based measure of PD is at least theoretically unrelated to SR and could be highest at low SR when strong similarity constraints allow only few but maximally distinct species to coexist (i.e. phylogenetically overdispersed; see also Allan et al., 2013) or when communities are not assembled naturally, such as in experiments. In these cases, adding additional species can increase SR but decrease PD when added species are closely related to already included lineages (i.e. underdispersed), with at present unknown consequences for associated diversity. However, these constraints do not apply to our data, where woody plant PD was positively correlated with woody plant SR and no plot showed signs of phylogenetic dispersion. This indicates that in species-rich and naturally assembled forests adding woody species increases PD and corresponding niche opportunities for organisms at other trophic levels. Our species-poorest plot counted 25 woody plant species, and even low PD plots contained several common evolutionary lineages. This makes it likely that further added species are from not yet included distinct lineages, thus effectively increasing woody plant PD. In this regard, it is not surprising that the effects of woody plant PD on trophic guilds observed by us were weaker than in a grassland experiment where the species-richest plot had only 16 plant species (Dinnage et al., 2012). Thus, considering the observed positive relationship between woody plant SR and PD, even in sites with relatively low PD niche opportunities related to plant PD were already comparatively diverse, which should result in more moderate relationships between woody plant PD and diversity of trophic guilds. Albeit not explicitly tested, this might reflect the often-observed levelling-off of diversity effects at higher levels of plant diversity (Scherber et al., 2010; Tilman et al., 2014).

Compared with associated macro-organisms, relationships between woody plant PD and fungal trophic guilds were weaker. Path models for fungi were inconclusive and, in case of ectomycorrhizal fungi, slightly favoured woody plant SR over PD. These weak associations may be expected as microscopic fungi likely respond to environmental variability at smaller scales than the studied plots. Nevertheless, species composition of all fungal guilds except saprotrophs changed with woody plant PD. Saprotrophs are often generalists regarding substrate preferences and largely controlled by environmental conditions (Tedersoo et al., 2014). In contrast, arbuscular mycorrhizae, ectomycorrhizae and pathogenic fungi all depend to various degrees on living plants (e.g. van der Linde et al., 2018; Weißbecker et al., 2018), and their ability to interact with a given host may depend on the hosts' phylogenetic relatedness. Previous studies indicated that in species-rich forests the structure of those fungal guilds are strongly related to tree species composition (Gao et al., 2015; Weißbecker et al., 2018; Zinger et al., 2018), which is to some degree captured by woody plant PD. Similar to arthropods, woody plant SR was not directly related to fungal trophic guilds, indicating that also for fungi woody plant PD can be a suitable proxy of woody plant diversity and its effects on niche opportunities for associated organisms (Chen et al., 2017).

In addition to functional consequences via biotic niche opportunities, woody plant PD may at evolutionary time-scales have influenced speciation of associated organisms, at least for herbivores (Ehrlich & Raven, 1964). Past co-speciation between plants and herbivores can result in a phylogenetic signal in herbivore composition and diversity that is independent of niche overlap and resource availability (Becerra, 2015; Pellissier et al., 2013; Wang et al., 2019). Due to their central roles in food webs, herbivores can affect predators, and thus through trophic cascades other trophic levels that are unlikely to have co-speciated with plants. Nevertheless, elucidating the exact mechanisms behind the influence of plant PD on the diversity and community composition of associated organisms requires further study, for example by explicitly testing for signals of co-evolution, by identifying the functional consequences of evolutionarily diverse tree communities or by establishing experiments (Bruelheide et al., 2014) that manipulate plant PD under constant SR (see Figure 1).

4.2 | Influence of woody plant phylogenetic diversity on niche opportunities for multitrophic diversity

The statistical effect of woody plant PD on the species richness of herbivores and predators was always direct and not mediated by changes in their abundances. This suggests that PD of trees in forest operates bottom-up through the diversity of niche opportunities ('resource heterogeneity hypothesis'; MacArthur, 1965), but does not necessarily influence the overall resource amount, which could be expected to increase associated species abundances ('more individuals hypothesis'; Srivastava & Lawton, 1998). As niche differences within a community maintain overall biodiversity (Levine & HilleRisLambers, 2009), evolutionarily more diverse forests may allow for the coexistence of more associated species by increasing resource diversity (Armbrecht et al., 2004; Burns & Strauss, 2011; Cavender-Bares et al., 2009; Warren et al., 2008). Likewise, forest stands consisting of trees from more distant evolutionary lineages may buffer against competitive exclusion and foster the coexistence of similar associated species (Maynard et al., 2017).

The absence of a relationship between woody plant PD and associated organism abundances suggests that overall resource amount for higher trophic levels is in our heterogeneous study sites independent of woody plant PD, possibly as even low diversity sites were already relatively heterogeneous and had high niche availability, as discussed above. Even after accounting for the environment, the species richness of almost every trophic guild was positively related to the abundance of the corresponding guild, suggesting that unmeasured environmental variables or tree community properties not reliably captured by PD influence trophic guild species richness via abundance. In this context, the largely non-significant presence–absence PD results indicate that abundance distributions of woody plant species relate to niche opportunities for associated species. In most ecosystems, plant abundances are not even, and it is likely that species' contributions to niches are, with the exception of 'key-stone' species, approximately proportional to abundances. Nevertheless, our data from a species-rich natural forest are not suitable to disentangle impacts of phylogeny from abundance, which would require experiments manipulating PD while keeping species-specific abundances constant.

The positive effect of woody plant PD on predator species richness supports the prediction that higher trophic levels benefit particularly from diverse and heterogeneous plant communities, following the 'enemies hypothesis' (Root, 1973; Staab & Schuldt, 2020). While predators usually do not directly rely on plant-based resources, they benefit bottom-up from increased habitat heterogeneity, e.g. when a more diverse litter layer allows for the coexistence of more ant colonies (e.g. Kaspari et al., 2000; Skarbek et al., 2020) or when a more heterogeneous vegetation structure facilitates spiders with complementary hunting strategies (e.g. Schmitz, 2009; Schuldt, Bruelheide, et al., 2014). Likewise, woody plant PD may increase prey availability (Dinnage et al., 2012; Schuldt, Baruffol, et al., 2014) and more prey could increase predator diversity, a cascade that has been found in biodiversity experiments (Balvanera et al., 2006). However, we could not test for possible effects of total prey, as the arthropod specimens of the different trophic levels have been collected by different methods over several years. In fact, sites with high woody plant PD in our study had lower herbivore species richness. The statistical effect size for the reduction of herbivore species richness was similar to the increase in predator species richness. This could possibly be due to increased top-down control in high PD sites (Staab et al., 2016) or to reduced resource availability for more specialized herbivores (Castagneyrol et al., 2014). High woody plant PD may lower herbivore species richness as individual feeding niches are relatively smaller and host plant finding may be more difficult when woody plant PD increases (Brezzi et al., 2017; Chen et al., 2019). The most damaging herbivores at our study site are likely dietary generalists and both, herbivore biomass (Schuldt, Baruffol, et al., 2014) and herbivory (Brezzi et al., 2017; Schuldt, Assmann, et al., 2014; see also Egorov et al., 2017) increased with woody plant PD. These positive influences on a lower number of generalist herbivore species might offset negative influences on a larger number of specialized herbivore species, potentially resulting in overall lower herbivore species richness but no net change in herbivore abundances. We acknowledge that our study can only point to potential mechanisms in this case, which further experimental studies need to explore in more detail.

4.3 | Conifer trees attenuate multitrophic diversity in species-rich forests

Conifers separated from angiosperms already in the Carboniferous period and contemporary species are functionally very different to angiosperms (Diaz et al., 2016), with niches provided by each tree clade having little overlap. The deep evolutionary split between conifers and angiosperms makes it methodologically challenging to account for conifers in PD studies, and a different statistical treatment of conifer trees could possibly influence parts of our results. Even though conifers accounted only for 2.7% of woody species and on average for 3.9% of woody individuals, these few conifer trees changed the species composition of almost all trophic guilds and influenced the abundance of herbivores and herbaceous plants. As conifer wood and litter contain resin, many saproxylic (e.g. Bussler et al., 2011) and herbivorous (e.g. Brändle & Brandl, 2006) insects and fungi (Purahong et al., 2018) utilize either conifers or angiosperms. Thus, species composition across trophic guilds can already change when only few conifers are present in a forest. Similarly, conifers influence the light regime (Canham et al., 1994), and higher light availability increases understorey vegetation such as in our study. In managed forests with few tree species and a high overall share of conifers, such as in Central Europe, the proportion of conifer trees is generally a very important feature influencing diversity and community structure of associated organisms (Penone et al., 2019). We suggest that also in unmanaged subtropical forests with high tree SR already few conifer individuals can have a large effect on species diversity and composition of associated organisms. As conifers and other gymnosperms occur in almost all forest types around the world (Slik et al., 2018), it would be interesting to conduct a global analysis about the structuring influence of conifers on associated diversity.

5 | CONCLUSIONS

The observed influence of woody plant PD suggests that evolutionary relatedness can be a powerful tool to understand BEF processes such as cross-taxon relationships across trophic levels in research fields that have traditionally relied on plant SR as the fundamental diversity variable. Furthermore, in a more applied context, the use of distantly related tree species e.g. in reforestation and mixed-species forestry (Messier et al., 2013) can structure associated species communities and potentially increase the inherent resistance and stability of the system (Fornoff et al., 2019; Hautier et al., 2015). As extinction risk due to anthropogenic activities and global change is not random across the plant phylogeny and evolutionarily distinct lineages are disproportionally threatened (Vamosi & Wilson, 2008) and locally going extinct (Uchida et al., 2019), the preservation of phylogenetically diverse plant communities may be a promising strategy to maintain multitrophic diversity and dependent ecosystem functions.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.S. conceived the idea and analysed the data; M.S. wrote the first draft with input by X.L., B.S., and A.S. All authors provided data and revised the manuscript.

DATA AVAILABILITY STATEMENT

Data are deposited in the iDiv Data repository https://doi.org/10.25829/idiv.1809-10-2704 (Staab et al., 2019).

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SUPPORTING INFORMATION

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

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