





More diverse tree communities promote foliar fungal pathogen diversity, but decrease infestation rates per tree species, in a subtropical biodiversity experiment

Gemma Rutten^{1,2}  | Lydia Hönig¹ | Rowena Schwaß¹ | Uwe Braun¹ |
Mariem Saadani^{1,2} | Andreas Schuldt³  | Stefan G. Michalski⁴  | Helge Bruelheide^{1,2} 

¹Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

³Forest Nature Conservation, Georg-August-University Göttingen, Göttingen, Germany

⁴Department of Community Ecology, Helmholtz Centre for Environmental Research –UFZ, Halle (Saale), Germany

Correspondence

Gemma Rutten
Email: ggpmrutten@gmail.com

Funding information

German Centre for Integrative Biodiversity Research, Grant/Award Number: DFG FZT 118; Deutsche Forschungsgemeinschaft, Grant/Award Number: FOR 891/3

Handling Editor: Liesje Mommer

Abstract

1. Fungal pathogens have the potential to affect plant biogeography and ecosystem processes through their influence on the fitness and functioning of their plant hosts. Simultaneously, changes in plant communities can influence fungal pathogen communities. Exactly which host plant attributes determine the composition of fungal pathogen communities on the leaves remains poorly understood.
2. Here, we characterized foliar fungal pathogen communities in subtropical tree communities along an experimental diversity gradient in Jiangxi, South-East China. On 32 tree species, we identified all visible fungal structures and symptoms microscopically and studied fungi-specific traits such as conidia or spores in detail. We asked how different facets of biodiversity, including taxonomic, phylogenetic and functional tree diversity, shape fungal diversity and fungal infestation at different scales.
3. We found a positive relationship between tree richness and fungal richness at the plot level. At the level of individual trees of the same species, the relationship between tree species richness and fungal species richness was marginally significantly negative. Importantly, the fungal infestation rates decreased as tree species richness increased, suggesting that colonization of hosts by specialist fungi was impeded by dilution of the pool of available hosts. Moreover, we found evidence for similar topologies between phylogenetic topologies of trees and fungal genera which is a precondition for coevolution and we identified leaf traits, including leaf habit (deciduous/evergreen), leaf magnesium content and stomata size that predicted fungal richness and infestation.
4. *Synthesis.* Our study indicates that host tree species harbour different foliar fungal pathogens, which sums up to the highest fungal pathogen richness in more diverse forest stands. At the same time, the foliar fungal pathogen infestation rate for each tree species decreased with increasing tree richness in forests. We identified leaf traits that can help to better predict fungal pathogen richness and

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infestation, and we show that phylogenetically closely related tree species harbour phylogenetically closely related foliar fungal pathogens. These new insights might be helpful to improve the pest resilience of future forests and plantations.

KEYWORDS

BEF-China, co-occurrence, dilution effects, diversity–disease relationship, host specific, leaf traits, phylogenetic signal, plant–microbe interactions

1 | INTRODUCTION

The positive relationship between plant diversity and productivity has been found in natural and experimental communities and is now widely accepted (Huang et al., 2018; Liang et al., 2019; Zak et al., 2003). Several studies have shown that diversity of primary producers also can enhance the diversity of associated trophic levels (Fornoff et al., 2019; Lefcheck et al., 2015; Scherber et al., 2010; Schuldt et al., 2019). As such, an increased plant diversity can provide a larger number of niche opportunities, allowing for a higher diversity at additional trophic levels (Cardinale et al., 2012; Eisenhauer et al., 2019). In turn, recent studies have shown that these higher trophic levels, specifically pests and pathogens, play a major role in regulating the diversity of plant communities (Bever et al., 2015; Van der Putten et al., 2013). This has led to a shifted focus in biodiversity ecosystem functioning (BEF) studies: Where former explanations have been focussing on plant–plant interactions, the current focus is moving to plant–pathogen interactions (van Ruijven et al., 2020; Whitaker et al., 2017).

Most evidence for the importance of plant pathogens in affecting plant diversity comes from plant–soil feedback studies, which suggest that below-ground pathogens regulate some plant species more than others, resulting in competitive advances within the plant community (Bever et al., 2015; Rutten et al., 2015; Schnitzer et al., 2011; Van Der Heijden et al., 2008). However, also generalist pathogens, like *Phytophthora ramorum*, can promote plant diversity, by exerting stronger effects on common than on rare species in a community (Haas et al., 2011). Far fewer studies have assessed the relationship between foliar fungal pathogens and plant diversity (Whitaker et al., 2017), and many of them have been carried out in grasslands (Cappelli et al., 2020; Liu et al., 2016; Rottstock et al., 2014) and temperate forests (Hantsch, Bien, et al., 2014; Hantsch, Braun, et al., 2014; Hantsch et al., 2013; Nguyen et al., 2017; Nguyen, Castagnyrol, et al., 2016). Most of these studies have reported a higher diversity of above-ground pest and disease species at higher host plant diversity.

At the same time, more diverse plant communities often experience less damage from fungal pathogens. According to the disease–diversity hypothesis, a high species diversity confers disease resistance through dilution of host density (Burdon, 2001; Mitchell et al., 2003), which is also referred to as *dilution effects* (Keesing et al., 2006). This might be explained by a reduced average susceptibility of individuals in a more diverse plant community

(Liang et al., 2019; Shurtleff & Averre III, 1997). Moreover, a reduced host abundance and an increased host spatial distance might reduce the pathogen transmission, reducing the pathogen impact in more diverse plant communities as predicted by the encounter reduction mechanism (Johnson et al., 2015; Keesing et al., 2010). Such dilution effects have been shown in temperate grasslands (Rottstock et al., 2014) and forests (Hantsch, Bien, et al., 2014; Hantsch et al., 2013), where plant communities with a low host diversity showed higher fungal pathogen damage than communities with a higher host diversity.

Recent studies have questioned the generality of dilution effects (Huang et al., 2016; Rohr et al., 2019) and evidence for context- or scale-dependent dilution effects has been reported (Liu et al., 2016; Nguyen, Castagnyrol, et al., 2016). Moreover, pathogen spillover and a certain degree of host-generality might result in a positive relationship between tree richness and fungal pathogen load, coined *amplification effect* (Keesing et al., 2006). We need to understand the underlying mechanisms to better predict when dilution effects are to be expected and when amplification effects are more probable.

Therefore, tree species richness can be complemented with measures of phylogenetic or functional diversity of the plant community. Phylogenetically related hosts are more likely to share attributes and functional traits that might determine the severity of pathogen infections (Flynn et al., 2011) and phylogenetic diversity might capture unmeasured traits important for disease impact (Gilbert & Webb, 2007; Parker et al., 2015). Thus, a plant community consisting of taxonomically more distinct hosts is likely to show stronger dilution effects in pathogen damage, whereas more similar host species in a plant community might amplify disease.

In addition, fast-growing plant species are thought to invest less in pathogen defence than slow-growing plant species, often referred to as the growth-persistence trade-off (Cappelli et al., 2020). Moreover, other traits of the host plants can affect the host's susceptibility to fungal pathogens. For example, foliar fungal richness in a tree diversity experiment was found to be unaffected by host functional diversity but influenced by the phenolic content of the host species (Hantsch, Braun, et al., 2014). Thus, functional identity, that is, the presence of certain trait values might explain compositional variation in foliar fungal communities among host species. Previous experiments assessing the relationships between tree diversity and foliar fungal richness and diversity have used smaller host species pools making it difficult to generalize the results by accounting for plant traits and phylogeny. Moreover, under-representing

high-diversity communities, both in temperate and tropical forests, might result in an under-representation of dilution effects (Halliday & Rohr, 2019). In this study, we used the world-largest biodiversity ecosystem functioning experiment (BEF-China) and included 32 tree species of a wide range of genera and families, growing in tree communities along an experimental tree diversity gradient ranging from monocultures to 16 species mixed stands. We characterized foliar fungal communities by identifying all visible fungal structures and symptoms microscopically and estimated the proportion of leaf area which was infested by fungal structures of 574 individual trees.

We studied disease–diversity relationships at the plot level and the level of the individual tree species, and specifically assessed the functional and phylogenetic aspects at both levels. We hypothesized that (a) the richness of foliar fungal pathogens increases while fungal pathogen damage decreases along an experimental tree species richness gradient, for both tree communities and individual tree species. Furthermore, we expected (b) phylogenetically closely related, functionally more similar tree communities to have more similar fungal pathogen communities (e.g. lower fungal species richness) and higher fungal pathogen infection rates than distantly related, functionally more dissimilar tree communities, thus testing for phylogenetic and leaf trait-based functional diversity effects. Finally, we expected (c) that phylogenetically related tree species harbour more phylogenetically related fungal genera and have more similar traits, some of which might help explain foliar fungal pathogen richness and infestation. By testing these hypotheses, we aim at a better understanding of how different aspects of tree diversity, host leaf traits and evolutionary relatedness of host species can affect foliar fungal pathogen species richness and infestation.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Our study was embedded in the BEF-China experiment (Bruehlheide et al., 2014), located near the village of Xingangshan, Jiangxi Province in Southeast China. The subtropical climate is characterized by a mean annual temperature of 15.1°C and a total annual precipitation of 1,964 mm (Yang et al., 2013). To assess the effects of tree species extinction on ecosystem functioning, two experimental study sites were established in 2009 (site A, 29°07'N 117°54'E) and 2010 (site B, 29°05'N 117°55'E; Bruehlheide et al., 2014). At each site, 16 tree species were planted in monocultures and mixtures according to a broken-stick design, by which the tree species composition at a lower diversity level is a random nested subset of the higher diversity level. This design makes sure that every tree species occurs in all diversity levels but is only represented in a single mixture per diversity level. At each site, there were eight 2-species mixtures, four 4-species mixtures, two 8-species mixtures and one 16-species mixture per site, resulting in a total of 62 plots and 32 tree species (Table S1). All species in the species pool naturally occur in the study region (Bruehlheide et al., 2014).

2.2 | Leaf collection and foliar fungal screening

After 5 years, in September 2014, we randomly selected four individuals per tree species in the central area of each plot (25.8 m by 25.8 m with 400 individual trees in total). Concentrating the sampling on the central plot area guaranteed that the target trees were surrounded by the plot's tree composition and excluded edge effects. To assess fungal pathogen richness and infestation, we randomly collected 10 leaves from each individual tree, using scissors. We made sure the collected leaves were of the current year. We used telescopic scissors for tall trees. We sampled a total of 5,584 leaves, from 574 tree individuals across 60 plots, excluding some tree individuals that were not established in the plots or had no leaves (Table S1). The leaves were individually packed in paper bags and dried for 3 days at 60°C and stored under dry and dark conditions until fungal screening.

In the laboratory, the upper and lower leaf surfaces were screened for fungal structures such as hyphae, stomata, fruiting bodies, as well as for pathogenic necrosis by using a stereomicroscope (ZEISS Stemi DV4). Visible fungal structures and symptoms were studied in more detail by examining species-specific traits such as conidia or spores with light microscopy (Schwass, 2015). If possible, fungi were identified to the species or genus level (Bai et al., 2000; Uwe Braun & Cook, 2012; Kieffer & Morelet, 2000; Nag Raj, 1993; Seifert & Gams, 2011; Sutton, 1980; Tai, 1979). In total, visual identification was achieved for 20 species and 25 genera (Schwass, 2015), which were assigned to a guild using the FunGuild-database (Nguyen, Song, et al., 2016) and U. Braun's expert knowledge (Table S2). Most commonly found fungi are closely related to pathogenic strains (Delaye et al., 2013), and some are able to switch guilds and can also found as saprotrophs (Kembel & Mueller, 2014). As the fungal species were identified based on disease symptoms on the leaf, we considered all identified fungi as, to some degree, harmful to the plants. If a fungal necrosis was populated by different fungal species, these fungi were treated as a fungal complex, where each species was equally represented within the necrosis. Fungal species richness was the sum of all fungal species per individual tree. For the fungal infestation, one and the same observer (RS) assessed the proportion of visually affected leaf area for all samples, which was then averaged over the 10 leaves per individual tree (Schwass, 2015). The average proportion of leaf area per species infected by disease, sometimes referred to as severity index (V_i) or infection incidence, is a common measure in disease ecology (Cappelli et al., 2020; Liu et al., 2016; Rottstock et al., 2014).

2.3 | Tree and fungal phylogenetic diversity

Tree phylogenetic diversity was based on an ultrametric phylogenetic tree of all angiosperm tree species recorded in the nearby Gutianshan National Reserve (Michalski & Durka, 2013), and pruned to the 32 tree species covering 16 different families occurring in our experimental sites. For the fungal phylogenetic

diversity, a dated phylogenetic super tree was assembled from existing literature sources (Supplementary Methods). The phylogenetic tree of the fungi was based on both species and genus-level information, to reduce limitations due to incomplete species identification.

2.4 | Tree functional diversity and trait measures

To calculate tree functional diversity (Dray & Dufour, 2007), we made use of 47 leaf traits measured in the BEF-China experiment (Kröber et al., 2015). These included contents of macro-elements such as Ca, Mg, K, Fe, N, Al and leaf traits that had been demonstrated to be relevant for fungal infestation or herbivory (Schuldt et al., 2012, 2017). Typically, fast-growing leaves have a high specific leaf area (SLA), and are softer and susceptible to damage. On the other side of the spectrum, slow-growing leaves have a higher C:N ratio, leaf dry matter content (LDMC) and leaf toughness (LT). Additional morphological leaf traits that are important for fungal defence include trichomes, leaf hydrophobicity, leaf density thickness, parenchyma layer thickness and density and size of stomata (for a recent review see Van Bael et al., 2017).

2.5 | Statistical analysis

At the plot level, we used linear mixed-effects models to assess foliar fungal pathogen diversity and infestation in tree communities as a function of tree richness. To achieve a normal distribution of errors, fungal pathogen richness was square-root transformed while fungal pathogen infestation (in %) was $\log_{10}(x + 0.1)$ transformed. We included 60 plots and five tree richness levels (mono, 2 species, 4 species 8 species and 16 species). Log-transformed tree richness was included as fixed and site as random factor. We analysed the relationship of several commonly used tree diversity metrics with foliar fungal pathogen species richness (number of fungal species per plot) and fungal pathogen infestation (mean infestation over all trees per plot): Shannon tree diversity (SD), functional tree diversity (FD) as Rao's Q, phylogenetic tree diversity (PD) as Rao's Q, and functional and phylogenetic redundancy (Debastiani & Pillar, 2012), as well as mean pairwise distance (MPD), and mean nearest taxon distance (MNTD) for the phylogenetic data of the trees (Kembel et al., 2010). In order to be able to compare the coefficients of the predictors measured on different scales, we standardized the tree diversity metrics by subtracting the mean and dividing by the standard deviation. Phylogenetic tree diversity was calculated as total branch length defined by the subset of species occurring in a plot (Kembel et al., 2010; Webb et al., 2002). While abundance-weighted MPD corresponds to Rao's Q (Vellend et al., 2011) and more reflects phylogeny-wide patterns of phylogenetic clustering, MNTD is more sensitive to clustering closer to the tips of the phylogeny (Kembel et al., 2010), hereby quantifying the degree of phylogenetic relatedness between the taxa within a

community of trees. Finally, the metrics of functional and phylogenetic redundancy assess the difference between tree species diversity and Rao's Q in each community (de Bello et al., 2007). The separate models for fungal pathogen species richness or fungal pathogen infestation that differed in single predictors were compared by the Akaike's Information Criterion (AIC), using maximum likelihood estimation (ML), while final parameter estimates were based on restricted maximum likelihood (REML). As the single predictors were strongly correlated (Figure S1), we preferred this approach over a multi-predictor approach.

At the level of individual trees, we performed a similar analysis to assess host-specific differences in foliar fungal pathogen diversity and pathogen load as a function of tree richness ($n = 574$). In addition to the log-transformed tree richness as fixed factor, we included site and tree species as random intercept. To allow for testing species-specific responses to the richness gradient, we also included the interaction of tree richness and tree species as random slope in the linear mixed-effect models. Then we added the species-specific leaf trait values, to test which traits can help predict foliar fungal pathogens. All predictors were scaled to mean = 0 and $SD = 2$ (Gelman, 2008), thus allowing to compare parameter estimates. To reduce multicollinearity between the leaf traits used, we selected traits that significantly improved the predictions of fungal pathogen richness and infestation to tree richness in the two-factor models. We performed a principal component analysis on these traits (Figure S2) and determined whether adding the resulting components to our models improved fit, while accounting for additional model complexity, using AIC.

We used the phylogenetic trees of the tree species (hosts) and fungal pathogens (parasites) and a set of host-parasite linkages in the ParaFit function in the R-package APE version 5.3 (Paradis & Schliep, 2019), with 999 permutations, to test if these agree with a model of coevolution of hosts and parasites (Legendre et al., 2002). The null hypothesis is that the evolution of the two groups has been independent, in other words the host phylogenetic tree is random in respect to the phylogenetic tree of the parasites (Legendre et al., 2002). We included all tree species and all morphospecies of foliar fungal pathogens which could be identified up to the genus level. Furthermore, we tested for a phylogenetic signal of fungal pathogen species richness and fungal infestation, as well as of all leaf traits across the 32 tree species, using Blomberg's K as implemented in the R-package PICANTE, version 1.8 (Kembel et al., 2010). Values >1 indicate higher levels of phylogenetic conservation than what would be expected based on a Brownian motion model of trait evolution. The significance of the phylogenetic signal was tested by randomizing the species identities (999 times) across the tips of the phylogenetic tree and comparing the observed values of K to those expected by chance.

All analyses were done in R 3.6.1 (R Core Team, 2019) using the packages LME4, version 1.1-21 (Bates et al., 2014), LMERT-EST, version 3.1-0 (Kuznetsova et al., 2017), GGLOT2, version 3.2.1 (Wickham, 2011), PICANTE, version 1.8 (Kembel et al., 2010), PHYLOBASE (Hackathon et al., 2019) and APE, version 5.3 (Paradis & Schliep, 2019).

3 | RESULTS

3.1 | Characterization of the foliar fungal pathogen communities

In total, 154 fungal taxa were found on the leaves across our 32 tree species (Table S2). On average, 4.1% of the leaf area was infested by fungal pathogens, with a maximum of 96.5% leaf area infested. Almost 20% of the leaves showed no signs of fungal pathogens (1,050 of 5,584 leaves). Of the 20 fungal taxa that were identified at the species level, all were found to be pathogenic (Table S2), with

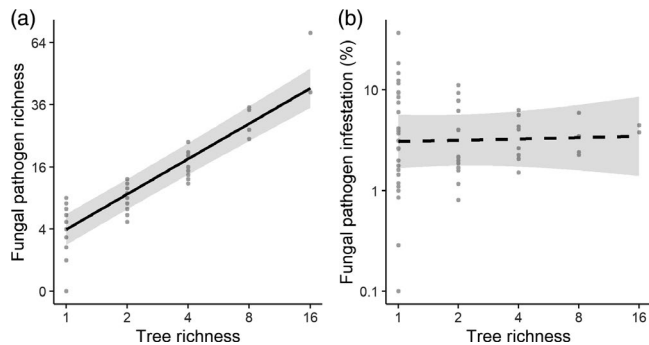


FIGURE 1 Community-level patterns of (a) fungal pathogen richness (number of fungal taxa) and (b) fungal pathogen infestation (percent leaf area infested) along the log-transformed tree species richness gradient. Trend lines indicate significant ($p < 0.05$ full line) and non-significant ($p > 0.05$ dashed) relationships between variables with 95% estimated confidence intervals (shaded area)

TABLE 1 Statistical summary for fungal richness (number of fungal taxa) and infestation (% of leaf area infected) as a function of taxonomic, functional and phylogenetic tree diversity metrics at the tree community level ($n = 60$). Linear models fit is indicated by Akaike's Information Criterion (AIC). Functional and phylogenetic tree diversity metrics were calculated as Rao's Q, whereas redundancy measures compare the latter with the community species richness. Mean nearest taxon distance assess the average distance between each tree species and its nearest functional or phylogenetic neighbour in the tree community. R_m^2 are marginal R^2 values, which indicate the amount of variance exclusively explained by the fixed factors in the model R_c^2 indicates the total variance explained. The models included a single fixed predictor and site as a random factor. Parameter estimates and p values are based on REML while AIC values are based on ML. Significant effects ($p < 0.5$) are shown in bold

	Estimate	SE	t-value	p value	R_m^2	R_c^2	AIC
Fungal richness (sqrt)							
Tree richness (\log_2)	1.24	0.07	17.25	<0.001	0.79	0.84	114.8
Tree functional diversity	1.12	0.10	11.02	<0.001	0.64	0.69	153.8
Functional redundancy	1.12	0.10	10.96	<0.001	0.63	0.69	154.4
Tree phylogenetic diversity	1.07	0.11	9.58	<0.001	0.55	0.65	164.7
Phylogenetic redundancy	0.92	0.14	6.76	<0.001	0.44	0.44	185.6
Mean nearest taxon distance	0.60	0.16	3.70	<0.001	0.18	0.24	206.8
Fungal infestation (\log_{10})							
Tree richness (\log_2)	0.01	0.05	0.26	0.795	<0.01	0.14	80.9
Tree functional diversity	0.03	0.05	0.47	0.642	<0.01	0.14	80.8
Functional redundancy	0.01	0.05	0.26	0.799	<0.01	0.14	80.9
Tree phylogenetic diversity	0.02	0.05	0.39	0.697	<0.01	0.14	80.8
Phylogenetic redundancy	0.01	0.06	0.15	0.880	<0.01	0.13	80.9
Mean nearest taxon distance	0.02	0.05	0.37	0.710	<0.01	0.14	80.9

the exception of the foliicolous sooty mould *Triposporiopsis spinigera* (Table S2). Sooty moulds usually subsist on diffusates or guttation fluids, honey dew secretions from insects, such as aphids and whiteflies, etc., organic and inorganic dust particles, pollens and remnants of other phylloplane fungi (Kwee, 1988). In total, 28 genera could be identified, together accounting for 110 morphotypes (Table S2). Together the taxa that were identified at the genus level accounted on average for 64% of all fungal morphotypes and 26% of the fungal infestation per plot. Additionally, 21 morphotypes were assigned to ascomycetes, five to hyphomycetes (asexual morphs of ascomycetes), two to black mildews and three were sooty moulds, and could not be further identified.

3.2 | Foliar fungal communities at the plot level

In line with our expectations, mixed forest stands harboured more foliar fungal pathogens than monocultures and the richness of foliar fungal pathogens increased with increasing tree species richness (Figure 1a). While 131 fungal taxa were confined to monocultures, 23 foliar fungal pathogens were unique to mixed forest stands. Additionally, fungal richness increased with phylogenetic diversity (PD), mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), suggesting that an increased phylogenetic distance between tree species within a forest stands resulted in higher foliar fungal pathogen richness (Table 1).

In contrast to our expectations, we found no significant relationship between the fungal pathogen infestation rates and tree

species richness (Figure 1b). Particularly, the fungal pathogen infestation rates in the monocultures were very variable and contributed to the lowest infestation rates (0% in *Meliosma flexuosa*) as well as the highest infestation rates (36.6% in *Rhus chinensis*) in this study. In fact, all tree communities with infestation rates higher than 10% were monocultures (12.2% *Lithocarpus glaber*, 18.4% *Castanea henryi*, 14.6% *Koelreuteria bipinnata* and 11.5% *Idesia polycarpa*), except for a two-species mixture (11% in the mixture of *Castanea henryi* and *Nyssa sinensis*). Repeating analyses using data from only those fungal pathogens that were identified to the genus level generated similar results (Figure S3). Moreover, including phylogenetic information did not result in a negative relationship between the fungal pathogen infestation rates and phylogenetic diversity, MNTD or MPD (Table 1).

3.3 | Foliar fungal pathogen richness and infestation at the tree level

The responses of foliar fungal pathogens to the tree species richness gradient varied among tree species, resulting in an overall negative marginally significant relationship between fungal pathogen richness and tree richness ($t_{1,27} = -1.82$; $p = 0.080$; Table 2; Figure 2a). Likewise, fungal pathogen infestation decreased with increasing tree richness, showing an overall significant negative relationship ($t_{1,25} = -2.52$; $p = 0.018$; Table 2; Figure 2b). However, individual tree species varied in their response to tree richness (Figure 2). To assure these patterns resulted from our treatments and not from the spatial structure of our experimental setup, we plotted the residuals

TABLE 2 Two-predictor models including fungal richness per tree and mean infestation per tree as a function of tree species richness and host traits at the individual tree level ($n = 574$). The models show the effects for tree richness as single-predictor and two-predictor models including a significant or non-significant additional leaf trait. Model fits are indicated by Akaike's Information Criterion (AIC). Variance inflation factor (VIF) shows the amount of multicollinearity in a set of multiple regression variables. R_m^2 are marginal R^2 values, which indicate the amount of variance exclusively explained by the fixed factors in the model. All models included tree species and experimental site in the random structure and parameter estimates and p values are based on REML while AIC values are based on ML. Significant effects ($p < 0.5$) are shown in bold. All predictors were scaled by subtracting the mean and then dividing by 2 SDs. Note that VPD describes difference between the vapour pressures of leaf and atmosphere

	Estimate	SE	t-value	p value	R_m^2	AIC	VIF
Fungal richness (number of taxa)							
Leaf magnesium content	-0.67	0.13	-5.32	<0.001	0.24	551	1.00012
Deciduous/Evergreen	0.58	0.14	4.07	<0.001	0.18	557	1.00000
Density of spongy parenchyma	-0.43	0.16	-2.78	0.010	0.12	563	1.00004
Specific leaf area	-0.42	0.16	-2.69	0.012	0.12	563	1.00020
Leaf toughness	0.43	0.15	2.84	0.009	0.12	563	1.00025
Stomata size (ellipse)	-0.40	0.15	-2.62	0.015	0.11	563	1.00000
Palisade parenchyma layers	0.42	0.15	2.76	0.010	0.11	563	1.00011
Leaf carbon content	0.36	0.15	2.37	0.024	0.08	564	1.00039
Leaf calcium content	-0.32	0.16	-2.05	0.050	0.06	566	1.00069
Stomata density	0.26	0.17	1.52	0.139	0.05	567	1.00024
Tree richness (\log_2) $R_c^2 = 0.68$	-0.08	0.05	-1.56	0.132	0.00	568	
Fungal infestation (percent leaf area)							
Stomata size (ellipse)	-0.49	0.17	-2.86	0.009	0.12	870	1.00000
Density of spongy aparenchyma	-0.44	0.19	-2.35	0.027	0.09	873	1.00001
Leaf magnesium content	-0.43	0.18	-2.31	0.028	0.08	873	1.00005
Leaf carbon content	0.37	0.18	2.00	0.054	0.07	874	1.00006
Leaf calcium content	-0.35	0.18	-1.92	0.064	0.06	874	1.00019
VPD at relative fitted maximal stomatal conductance	0.35	0.20	1.75	0.093	0.06	875	1.00001
VPD at point of inflection of fitted Stomatal conductance	0.34	0.20	1.73	0.096	0.06	875	1.00000
Palisade parenchyma layers	0.34	0.19	1.76	0.090	0.06	875	1.00004
Leaf carbon nitrogen ratio	0.32	0.19	1.62	0.116	0.05	875	1.00003
Leaf nitrogen content	-0.30	0.19	-1.54	0.135	0.05	875	1.00003
Relative fitted maximal stomatal conductance	0.31	0.20	1.52	0.140	0.05	875	1.00000
Specific leaf area	-0.26	0.20	-1.35	0.189	0.04	876	1.00006
Tree richness (\log_2) $R_c^2 = 0.62$	-0.17	0.08	-2.06	0.054	0.01	876	

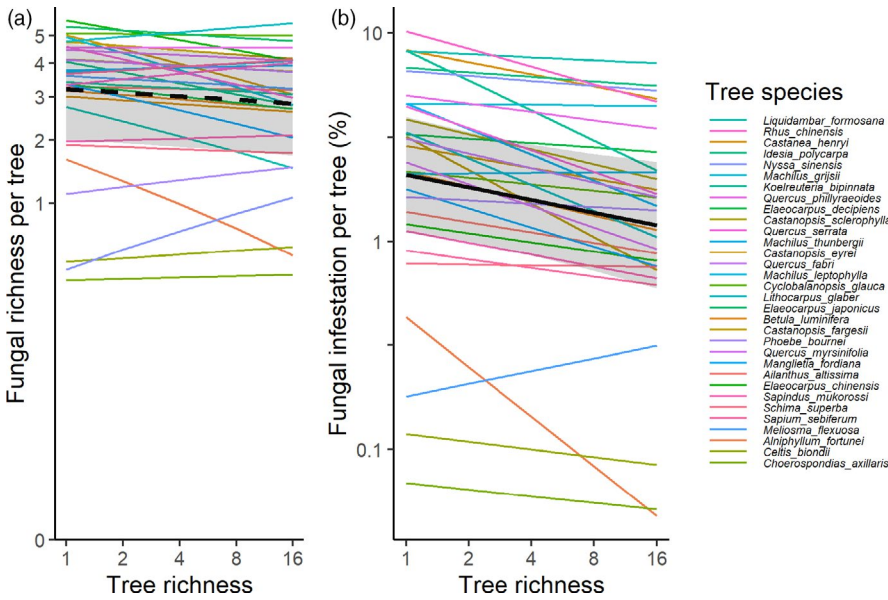


FIGURE 2 Individual tree species-level patterns of (a) fungal pathogen richness and (b) fungal pathogen infestation along the tree species richness gradient. Coloured lines show the predicted relationships for the different tree species. Black trend lines indicate overall negative relationships for fungal richness ($p < 0.1$ dashed) and fungal infestation ($p < 0.05$ full line), with 95% estimated confidence intervals (shaded area)

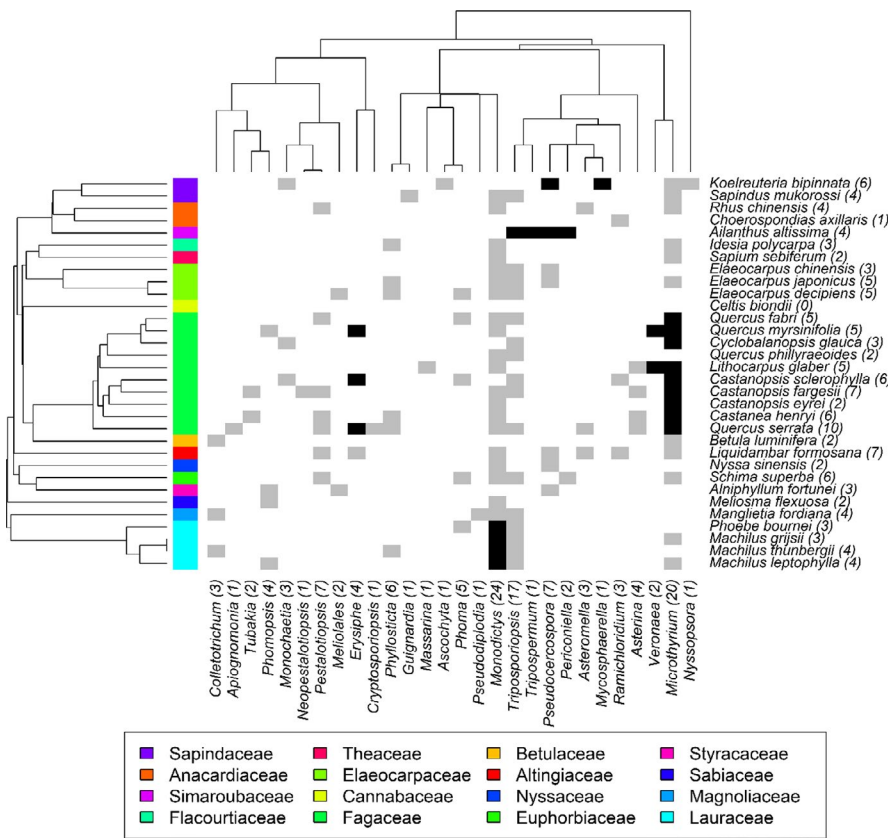


FIGURE 3 Heatmap showing the associations between tree species (rows) and the genera of foliar fungi (columns) across all plots and tree richness levels. More closely related tree species harbour more closely related foliar fungi (ParafitGlobal; $p = 0.038$, permutations $n = 999$). In all, 24 host-pathogen associations had non-random distribution over the phylogenetic trees (black), the remaining 104 of 128 host-pathogen associations showed non-significant associations (grey). Tree species belong to 16 families (as indicated by the coloured bar and the legend in same order) from upper to lower Sapindaceae, Anacardiaceae, Simaroubaceae, Flacourtiaceae, Theaceae, Simaroubaceae, Flacourtiaceae, Theaceae, Elaeocarpaceae, Cannabaceae, Fagaceae, Euphorbiaceae, Nyssaceae, Magnoliaceae, Lauraceae). Number of associations of the fungal genera per tree species and numbers of host tree species per fungal genus are indicated in brackets in rows and columns, respectively

in space (Figure S4) and confirmed the spatial independence of the residuals, using Moran's I (Paradis & Schliep, 2019). Ninety-eight percent (151 of 154) of all fungal taxa and 85% (18 of 20) of the taxa identified at the species level occurred on only one single host species. The biotrophic *Phyllosticta anacardiacearum* was found on two congeneric hosts, whereas the plurivorous sooty mould *Tripsoportiopsis spinigera* was found on the phylloplane of 17 plant species as substrates (Table S2).

The analyses of co-occurrence patterns between tree host species and fungal genera revealed that more closely related tree species harboured more closely related foliar fungal pathogens (ParafitGlobal test p value = 0.038, permutations $n = 999$). In detail, 24 of 128 host-pathogen associations were shown to have a non-random distribution over the phylogenetic trees (Figure 3). Specifically, foliar fungal pathogens of the genera *Microthyrium* (including *Veroneae* species) and *Erysiphe* were significantly

associated with species of the *Fagaceae* family while the fungal genus *Monodictys* was significantly associated with species of the *Lauraceae* family.

Finally, we asked which leaf traits might help explain these patterns and if these leaf traits were phylogenetically conserved. Including leaf traits such as leaf carbon content, leaf magnesium content, density of the spongy parenchyma or stomata size, SLA, leaf toughness, number of parenchyma layers and leaf calcium content significantly improved our models (Table 2). However, leaf habit was negatively correlated with SLA and positively with leaf toughness. Moreover, negative correlations were found between stomata size and leaf calcium content and between magnesium content and number of parenchyma layers

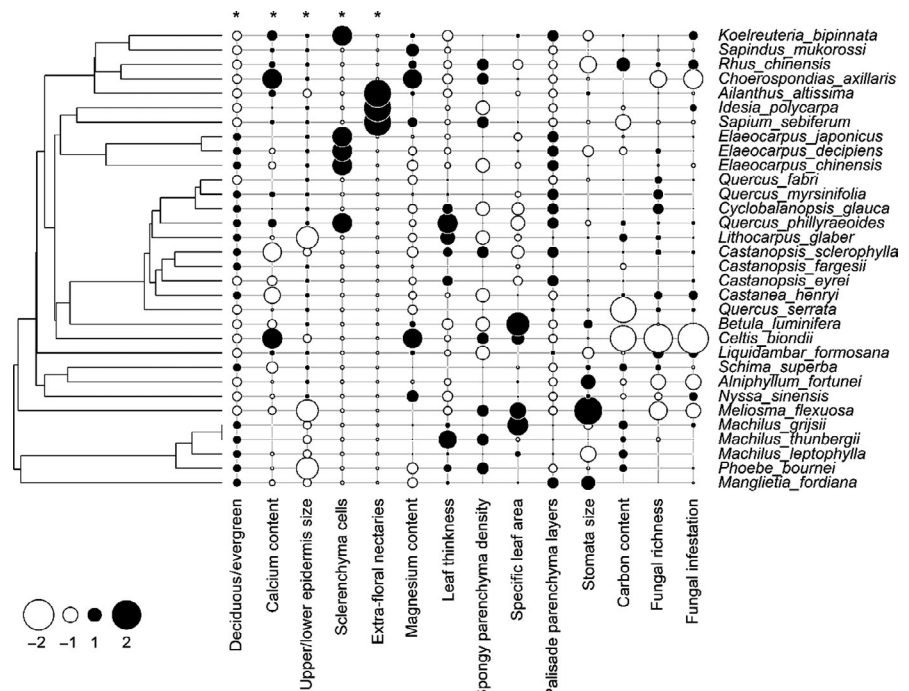
(Figure S2). In a full model excluding multicollinear traits, we found that the fungal pathogen richness was higher in deciduous than evergreen tree species and negatively related to stomata size, leaf magnesium content and density of spongy parenchyma. In addition, fungal pathogen infestation was negatively related to stomata size, leaf magnesium content and density of spongy parenchyma, but did not seem to be affected by leaf habit (Table 3).

Two of the above-mentioned leaf traits were phylogenetically conserved within tree species, namely leaf habit and leaf calcium content. However, we found no evidence for phylogenetic signals in fungal pathogen richness or fungal pathogen infestation (Figure 4; Table S3).

TABLE 3 Multiple factor models for fungal richness and infestation as a function of tree species richness and host leaf traits at the individual tree level ($n = 574$). Model selection was based on Akaike's Information Criterion (AIC). Variance inflation factor (VIF) shows the amount of multicollinearity in a set of multiple regression variables. R_m^2 are marginal R^2 values, which indicate the amount of variance exclusively explained by the fixed factors in the model. Both models included species and experimental site in the random structure and parameter estimates and p values are based on REML while AIC values are based on ML. Significant effects ($p < 0.5$) are shown in bold. All predictors were scaled by subtracting the mean and then dividing by 2 SDs

	Estimate	SE	df	t-value	p value	AIC	VIF
Fungal richness $R_m^2 = 0.43$; $R_c^2 = 0.68$							
Tree richness (\log_2)	-0.10	0.05	27	-2.02	0.053	566	1.00
Leaf magnesium content	-0.49	0.12	26	-4.06	<0.001	550	1.78
Deciduous/evergreen	0.17	0.12	24	1.43	0.166	549	1.71
Density of spongy parenchyma	-0.28	0.09	24	-2.93	0.007	545	1.09
Stomata size (ellipse)	-0.37	0.09	24	-4.06	<0.001	532	1.07
Fungal infestation $R_m^2 = 0.23$; $R_c^2 = 0.63$							
Tree richness (\log_2)	-0.16	0.06	26	-2.58	0.016	880	1.00
Stomata size (ellipse)	-0.50	0.16	24	-3.22	0.004	874	1.00
Density of spongy parenchyma	-0.36	0.17	24	-2.17	0.041	869	1.09
Leaf magnesium content	-0.32	0.17	26	-1.92	0.066	867	1.09

FIGURE 4 Phylogenetic signals for plant traits, fungal richness and infestation over the phylogenetic tree of the 32 tree species. The significance of the phylogenetic signal was tested by randomizing the species identities (999 times) across the tips of the phylogenetic tree and comparing the observed values of K to those expected by chance and indicated above the columns (*). All tested trait variables and Blomberg's K values are shown in Table S3. Circles indicate scaled trait values that served for testing the phylogenetic signal



4 | DISCUSSION

Understanding of the relation between plant diversity and fungal pathogen infection and infestation can help to develop more effective measures to regulate disease in forest conservation. By characterizing foliar fungal pathogen communities of 32 tree species in a BEF experiment in South-East China, we determined tree community characteristics and host-species attributes that shape foliar fungal pathogen diversity and infestation. On a plot level, the richness of foliar fungal pathogens increased with tree species richness, whereas the average fungal pathogen infestation on the plot level was not affected by tree species richness. On an individual tree, species-level fungal pathogen richness was independent of tree richness, but the trees in more diverse communities showed lower fungal pathogen infestation, indicating dilution effects. We identified leaf traits, including magnesium content, density of spongy parenchyma and the size of the stomata that help predicting the linkages between foliar fungal pathogens and their host trees. Overall, our study suggests that a combination of tree community and tree species characteristics could be used to better predict foliar fungal pathogen infection and infestation which might prove to be useful, for example, for forest conservation or when planning tree plantations.

4.1 | Tree richness effects on fungal pathogen species richness and infestation at the plot level

Current and ongoing biodiversity loss may alter many ecosystem services including lowering a system's pest resistance (Cardinale et al., 2012; Keesing et al., 2010). Here, we found that fungal pathogen richness increased with tree richness at the plot level. Such positive relationship is likely the result of some degree of host specificity of the fungal pathogens, which mathematically increases the number of pathogen species with increasing number of host species. On average, however, the infestation rate of the fungal pathogens was not significantly affected by tree species richness at the plot level. Thus, our study is in line with former studies in forests where pathogen load was not related to the number of host species within a tree community (Hantsch et al., 2013), and it contradicts studies that found a decrease in fungal richness with increasing tree richness at the plot scale (Griffin et al., 2019). It might well be that the dilution effects were blurred by specific responses of pathogens associated with particular tree species. In this study and contrary to our expectations, neither trait distance (functional diversity) nor evolutionary history (phylogenetic diversity) of the tree species in our communities were better predictors for fungal infestation than tree richness itself.

Previous studies have shown that mean nearest taxon distance (MNTD), which quantifies the degree to which a community is composed of phylogenetically closely related species (Webb et al., 2002), can capture competitive differences between species because related plant species more often share specialized pathogens (Gilbert & Webb, 2007; Parker & Gilbert, 2018). Likewise, phylogenetic plant

diversity was found to be a useful measure particularly because it has the potential to capture unmeasured traits (Le Bagousse-Pinguet et al., 2019; Schuldt et al., 2019; Srivastava et al., 2012). To better separate the different tree community diversity measures and their effects on foliar fungal pathogen diversity and infestation, artificial communities designed to address this question could be used.

As the various tree diversity measures did not capture the variation in the tree richness-pathogen infestation relationship very well, we additionally analysed individual tree species level.

4.2 | Individual tree species effects on foliar fungal pathogen richness and infestation

At the scale of individual trees of the same species, we found evidence of a reduced fungal pathogen infestation in mixed stands as compared to monocultures. In contrast to the analysis at the plot level, both fungal pathogen richness and fungal pathogen infestation decreased with increasing tree richness at the tree species level. Such a negative relationship was shown before for fungal richness at the neighbourhood scale (Griffin et al., 2019). In this study, we found a weak but significant effect of tree species richness on fungal pathogen infestation, indicating that the same tree species suffered less pest damage in heterospecific mixtures than in monocultures. Despite the overall negative trend of fungal pathogen infestation with increasing tree species richness, the different tree species showed a high variation in responses, varying both in the strength of this relationship and the direction of the slope. This is in line with former results from temperate forests, where certain tree species were less infected by foliar fungi when surrounded by a more diverse tree community, whereas other tree species were more susceptible to disease in a more diverse community (Grossman et al., 2019). We found that both phylogenetic and functional characteristics can help predict the effects of these tree species.

First, our results suggest evolutionary links between the tested tree species and their foliar fungal pathogens, as indicated by more closely related tree species harbouring more closely related foliar pathogens. It seems, however, that also closely related fungi are largely occurring on one host, even when grown in mixed stands. This indicates a rapid evolution in both foliar fungal pathogens and host defence mechanisms. However, we cannot exclude that those fungal pathogens that were not identified at the species level (e.g. unknown Ascomycete or Hyphomycete) occurred in multiple hosts, and thus might show some degree of host overlap. One example was the plurivorous sooty mould, *Triposporiopsis spinigera*, that occurred on several unrelated host species. The additional use of high-throughput sequencing (Nguyen et al., 2017) might help to resolve such issues further, but many more taxa may be detected that do not directly reflect their ecological relevance. For example, Nguyen and colleagues (2017) visually observed the dominant fungal taxon (*Discula betulina*) on all inspected trees of *Betula pendula*, but it was not detected by sequencing techniques, possibly due to problems with the DNA extraction from the fruiting bodies.

Importantly, many fungi have never been isolated and many remain unidentified for both techniques. Over the last 40 years, an average of 1,300 new fungal species per year have been described (Hawksworth & Lücking, 2017) including *Periconiella liquidambaricola* and *Pseudocercospora daphniphylicola* from the BEF-China platform (Braun et al., 2014, 2015). Experimental tests on the exact ecology of these newly described, isolated foliar fungi under a range of biological and environmental circumstances were out of the scope of this study, but would surely be interesting and advancing the field.

Second, tree species with similar functional traits harboured a similar fungal pathogen richness and were similarly infected by fungal pathogens. Particularly, leaf magnesium content was an important predictor for fungal pathogen richness, as well as stomata size, the density of the spongy parenchyma and the phylogenetically conserved leaf habit distinction between tree species. Most of these leaf traits, with the exception of leaf habit, also improved the predictions for fungal pathogen infestation. In fact, Mg deficiency in the plant's leaf might affect fungal taxa indirectly as Mg is essential for photosynthesis but also involved in all pathways involving ATP in the plant's metabolism, including those for pathogen defence. This helps explaining why magnesium additions led to reduced disease risk in 22 of 45 tested crops (Huber & Jones, 2013). At our sites, Mg was probably particularly important because of a general Mg deficiency of soils (Scholten et al., 2017). Another possible explanation results from the fact that magnesium content is correlated with other traits that might be possible determinants for fungal hyphae growth. In this study, for example, leaf magnesium content was inversely correlated with the number of palisade parenchyma layers of the leaves, indicating that tree species with more layers harboured a richer foliar fungal pathogen community, possibly simply because the resources and space increase with the number of layers. On the contrary, the density of spongy parenchyma was negatively related to the fungal pathogen richness and infestation, suggesting that fungal hyphae growth might be restricted by denser leaf tissue (Van Bael et al., 2017). It is thought that thinner and less dense leaves can be more easily colonized by fungi that germinate on the leaf surface and penetrate the leaf surface (Arnold & Herre, 2003). As other fungal pathogens colonize the leaf via stomata (Van Bael et al., 2017), a relation between stomata size and fungal richness and infestation was to be expected. However, this relation was negative and not positive. Leaves with smaller stomata showed higher fungal pathogen infestation and had a higher leaf carbon content. As stomata size was inversely related to stomata density, it is possible that the number of potential entry points for fungi infecting the leaves is more important than their size. However, the physiology behind this relationship needs further investigation. Additionally, it would be interesting to further assess the specific characteristics of palisade parenchyma as compared to spongy parenchyma but this was out of the scope of our study.

Third, we found no phylogenetic signals for fungal pathogen species richness and infestation. Therefore, these responses to fungal pathogens were not affected by the phylogenetic relatedness of the

tree species. It seems that tree species were all affected by fungal pathogens to some degree, showing that fungal attack is a common and variable process in these subtropical forests. This conforms to the findings of Schuldt et al. (2017) that mean fungal pathogen damage was 5.4% across all tree species, but reaching maximum levels of more than 75%. Differences among host species have been found, for instance, for susceptibility against fungal pathogens (Gilbert & Webb, 2007) and for foliar fungal community structure (Kembel & Mueller, 2014). It would be interesting to combine the results of our and former studies in a quantitative review covering a wider host phylogeny and more distinct habitats.

5 | CONCLUSIONS

In this study, we show that host tree species harbour different foliar fungal pathogens. This sums up to the highest fungal pathogen richness in more diverse tree communities. At the same time, the fungal pathogen infestation rate per tree species decreased in more diverse forest stands. This supports former evidence suggesting that foliar fungal pathogens have the potential to maintain competitive differences between tree species (Spear & Mordecai, 2018) and can be regulated by the diversity of the surrounding tree community (Grossman et al., 2019).

Second, we show that less conserved leaf traits like leaf magnesium content and stomata size are important in determining foliar fungal pathogen richness and infestation, besides other commonly found phylogenetically conserved traits, that are linked to the growth-persistence trade-off, such as leaf habit and specific leaf area (Cappelli et al., 2020; Kembel & Mueller, 2014). With this our results urge future studies to include a wide range of leaf traits, including phylogenetically conserved and less conserved leaf traits to better predict foliar fungal pathogen richness and infestation.

Third, we made an effort to identify fungal pathogen species to uncover specific host-pathogen associations and reliable measures of active fungal pathogen abundance. Former studies often assess broad fungal groups such as rusts, smuts and leaf spots (Cappelli et al., 2020; Liu et al., 2016; Nguyen, Castagnayrol, et al., 2016; Rottstock et al., 2014), making it hard to assess specific host-pathogen associations. Moreover, studies using sequencing techniques, usually do not allow to assess which of the found taxonomical units were responsible for the disease symptoms or if they were active at all (Griffin et al., 2019; Kembel & Mueller, 2014).

Together, our results suggest a role for foliar pathogens in plant population and community dynamics, including biodiversity experiments and plant-pathogen feedback approaches. We provide a joint approach of measuring effects of leaf traits, phylogeny at the community and individual tree species scale, which helps to better understand and predict the patterns of foliar fungal pathogen richness and infestation along tree richness gradients. Such improved understanding can help to select a combination of tree species with fungal pathogen repelling traits for healthy, future tree plantations and reforestation measures.

ACKNOWLEDGEMENTS

We thank B. Schmid and K.P. Ma for helping to establish and run the BEF-China experiment, X.F. Yang, S. Both, X.J. Liu and Y. Bo for coordinating the platform, and G. Seidler for help on the maps. We thank L. Mommer and two anonymous reviewers for very constructive comments that much improved the manuscript. This study was funded by the German Research Foundation (DFG FOR 891/3). G.R. was supported by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jana-Leipzig/DFG FZT 118).

AUTHORS' CONTRIBUTIONS

H.B., U.B. and L.H. conceived the ideas and designed the methodology; L.H. and R.S. collected the data; S.G.M. provided the fungal phylogeny; L.H., H.B., U.B. and G.R. analysed the data; L.H. and G.R. led the writing of the manuscript. G.R., L.H., R.S., U.B., M.S., A.S., S.G.M. and H.B. contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13620>.

DATA AVAILABILITY STATEMENT

The datasets used to analyse the current study are available from the BEF-China website FoliarFungi2014 <https://data.botanik.uni-halle.de/bef-china/datasets/635> and from the iDiv Biodiversity Data Portal (iBDP) <https://doi.org/10.25829/ividiv.1915-15-3293> (Rutten et al., 2021).

ORCID

Gemma Rutten  <https://orcid.org/0000-0001-9552-4605>

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

Stefan G. Michalski  <https://orcid.org/0000-0002-8969-7355>

Helge Bruelheide  <https://orcid.org/0000-0003-3135-0356>

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SUPPORTING INFORMATION

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

How to cite this article: Rutten G, Höning L, Schwaß R, et al.

More diverse tree communities promote foliar fungal pathogen diversity, but decrease infestation rates per tree species, in a subtropical biodiversity experiment. *J Ecol.* 2021;109: 2068–2080. <https://doi.org/10.1111/1365-2745.13620>