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RESEARCH ARTICLE

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Rare and phylogenetically distinct plant species exhibit less diverse root-associated pathogen communities

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Abstract

1. One of the central questions in ecology is why some species are abundant while others are rare. In plant communities, some studies show that rare plant species are rare because they suffer stronger negative density-dependent effects from pathogens compared to abundant plant species. Moreover, such pathogen effects are also suggested to be related to phylogenetic distance among plant species. However, the importance of pathogens has been commonly inferred by treating the entire pathogen community as a "black box" without explicitly characterizing pathogen richness and community composition.
2. Here, we test two predictions. First, if rare plant species are more susceptible to pathogens, we predict that rare plant species are associated with a higher richness of specialists (i.e., pathogens that attack only a single plant species) and/or the total pathogen community. If phylogenetically distinct plant species are less susceptible to pathogens, we predict that plant species with higher phylogenetic distinctiveness (i.e., a measure of how phylogenetically distant a species is from other co-occurring species) are associated with a lower richness of phylogenetic specialists (i.e., pathogens that attack closely related plant species) and/or the total pathogen community.
3. We conducted a survey of the root-associated pathogen communities from 45 plant species in a subtropical forest. We showed that approximately 40% and 25% of the pathogens were specialists and phylogenetic specialists respectively. In contrast to our first prediction, the richness of the total pathogen community but not the richness of the specialists was found to be positively related to plant species abundance, indicating that rare plant species suffer less from pathogens. Consistent with our second prediction, both the richness of the phylogenetic specialists and the total pathogen community were found to be negatively related to plant species phylogenetic distinctiveness. Furthermore, these correlations were stronger at the earlier plant life stages examined.
4. *Synthesis.* We found that the root-associated pathogen communities were less diverse in rare plant species and plant species with few close relatives. These associations varied across multiple plant life stages, suggesting that the strength of the

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above-ground–below-ground interactions change dynamically across plant life span.

KEYWORDS
coexistence, negative density-dependent effects, phylogenetic distinctiveness, plant–pathogen associations, root-associated pathogens, species abundance, subtropical forest

1 | INTRODUCTION

The extraordinarily high plant diversity as well as the commonness and rarity of plant species in tropical and subtropical forests have long intrigued ecologists (Givnish, 1999; Hubbell, 2001; Preston, 1948; Wright, 2002), yet the underlying mechanisms are still poorly understood. Plant fungal pathogens have been increasingly claimed to play critical roles in maintaining plant species abundance and diversity (Bever, Mangan, & Alexander, 2015; Comita, Muller-Landau, Aguilar, & Hubbell, 2010; Johnson, Beaulieu, Bever, & Clay, 2012; Mangan et al., 2010), especially if the relative strengths of the pathogen effects on abundant and rare plant species are different and appropriately scaled (Chisholm & Muller-Landau, 2011; Freckleton & Lewis, 2006; Hubbell, 1980; Mack & Bever, 2014). Moreover, recent emphasis has been placed on how pathogen effects vary with phylogenetic distance among plant species (Kempel, Rindisbacher, Fischer, & Allan, 2018; Liu et al., 2012). Therefore, pathogens are widely suggested to be associated with the community composition and phylogenetic structure of plant communities (Parker et al., 2015).

Pathogens, especially specialists (i.e., pathogens that attack only a single plant species), are commonly suggested as key agents driving density- and/or distance-dependent seedling mortality in plant communities (Bell, Freckleton, & Lewis, 2006; Reinhart & Clay, 2009). Such negative density-dependent effects have been shown to simultaneously maintain plant species abundance and coexistence (Fricke & Wright, 2017). Empirical studies have shown that rare plant species suffer greater negative density-dependent effects compared to abundant plant species (Comita et al., 2010; Johnson et al., 2012; Mack & Bever, 2014; Mangan et al., 2010; but see Reinhart, Johnson, & Clay, 2012; Zhu, Woodall, Monteiro, & Clark, 2015), especially in the tropics (LaManna et al., 2017). Therefore, we predict that rare plant species are more susceptible to pathogens. The negative density-dependent effects also facilitate plant species coexistence by stabilizing plant species abundances to their equilibriums (Chisholm & Muller-Landau, 2011; Yenni, Adler, & Ernest, 2012). A plant species with a higher abundance relative to its equilibrium should suffer stronger negative density-dependent effects from pathogens and obtain a lower growth rate (Chisholm & Muller-Landau, 2011; Yenni et al., 2012). Conversely, a plant species should experience weaker negative density-dependent effects and pathogen infections when its abundance is lower than its equilibrium, which would prevent it from being extinct by increasing its growth rate (Chisholm & Muller-Landau, 2011; Yenni et al., 2012).

Pathogens can also be crucial for regulating the phylogenetic structure of plant communities (Gilbert, Briggs, & Magarey, 2015; Liu, Liang, Etienne, Gilbert, & Yu, 2016) because some pathogens are phylogenetic specialists (i.e., pathogens that attack plant species that are closely related) (Gilbert & Webb, 2007). This suggests that the phylogenetic distance between a plant species and other plant species could be used to predict whether it suffers more or less from pathogens. For example, it has been shown that closely related plant species are less likely to co-occur because they tend to attract similar pathogens and thus suffer greater pathogen infections (Liu et al., 2012). As a consequence, we predict that phylogenetically distinct plant species, which have higher phylogenetic distinctiveness (i.e., a measure of how phylogenetically distant a species is from other co-occurring species in a community), should be less susceptible to pathogens (Parker et al., 2015).

The importance of pathogens in determining plant species abundance and phylogenetic structure has generally been identified by combining fungicide and soil sterilization treatments (Bagchi et al., 2014; Bell et al., 2006; Fricke, Tewksbury, & Rogers, 2014; Liu et al., 2012). However, it remains unclear how pathogen richness and community composition vary along gradients of plant species abundance and phylogenetic distinctiveness. Additionally, these manipulative experiments remove the full spectrum of fungal taxa, including beneficial fungi (e.g., arbuscular mycorrhizal fungi and ectomycorrhizal fungi), which would bias their results because these fungal taxa also play important roles in shaping plant species abundance patterns and phylogenetic structures (Fukami et al., 2017; Peay, Kennedy, & Talbot, 2016). Most importantly, this results in two crucial and similar questions. First, are the effects of pathogens on plant species abundance driven by specialists or the total pathogen community? Second, are the phylogenetic specialists or the total pathogen community associated with plant species phylogenetic distinctiveness? Recent advances in next-generation sequencing offer an unprecedented opportunity to shed light on the pathogen community in vulnerable plant tissues such as leaves, stems, and roots (Peay et al., 2016). If rare plant species are more susceptible to pathogens, we predict that the vulnerable tissues in rare plant species exhibit a higher richness of specialists and/or the total pathogen community. If phylogenetically distinct plant species are less susceptible to pathogens, we predict that the vulnerable tissues in phylogenetically distinct plant species exhibit a lower richness of phylogenetic specialists and/or the total pathogen community.

We conducted a survey of root-associated pathogen communities in 529 plant individuals from 45 species in a 50 ha stem-mapped

subtropical forest plot in southern China. We aimed to test whether rare plant species are more susceptible to pathogens by linking the richness of specialists and the total pathogen community to plant species abundance. Moreover, we examined whether phylogenetically distinct plant species are less susceptible to pathogens by linking the richness of phylogenetic specialists and the total pathogen community to plant species phylogenetic distinctiveness. Furthermore, we explored how these relationships shift across multiple plant life stages including the sapling, juvenile, and adult stages. We considered these plant life stages because it has been shown that the susceptibility to pathogens for rare plant species was most evident at the earlier plant life stages (Green, Harms, & Connell, 2014; LaManna, Walton, Turner, & Myers, 2016; Zhu et al., 2018) and that phylogenetically distinct plant species suffered less from pathogens at the adult stage (Zhu, Comita, Hubbell, & Ma, 2015). This evidence suggests that the relationships we examined between pathogen richness and plant species abundance and phylogenetic distinctiveness might change across multiple plant life stages (Green & Harms, 2018).

2 | MATERIALS AND METHODS

2.1 | Study site

Samples were collected from a 50 ha subtropical forest plot in Heishiding Nature Reserve (111°53′E, 23°27′N), located in Guangdong Province, China. It is characterized by a moist monsoon climate and subtropical evergreen broad-leaved forest. The plot census was completed in 2013. In total, 218,838 free-standing plants with diameters at breast height (DBH) ≥1 cm were tagged and mapped spatially, including 71 families, 160 genera, and 237 species.

2.2 | Root tip sampling

Our aim was to select focal species to represent the wide ranges of both abundance and phylogenetic relatedness of the overall plant community in the plot. Here, we used stem counts to measure the abundance of the selected focal plant species because stem counts are appropriate for measuring the density of the plant species. In addition, this measurement of plant species abundance can make our results comparable to previous studies (Comita et al., 2010; Mangan et al., 2010). According to the plant species abundance distribution in the plot, we divided the plant species into three groups based on their abundances: ≥1%, 0.1%–1%, and ≤0.1%. We selected 15 species from each group; thus, a total of 45 plant species were selected as focal species, with abundances ranging from 0.05% to 10.74% of the plot (Supporting Information Table S1). These species were assigned to 25 families, including *Lauraceae*, *Fagaceae*, *Pinaceae*, etc. Notably, the pathogen effects on seedling survival of *Ardisia quinquegona*, *Litsea elongata*, *Ormosia glaberrima*, and *Schima superba* have been previously examined in this plot (Liang et al., 2016; Liu, Fang, Chesson, & He, 2015).

We randomly selected between 3 and 19 individuals from each of the 45 species, and a total of 529 individuals were sampled in the plot (Supporting Information Figure S1; Supporting Information Table S1). All selected plant individuals were subsequently classified into three plant life stages according to their DBH: 1–4.9 cm for saplings, 5–9.9 cm for juveniles, and ≥10 cm for adults (Peters, 2003). To confirm that the sampled root tips were from each of our target individuals, we first identified the primary root and then partially excavated three root tip samples from each individual. The adhering soil and plant debris on the root tips were carefully removed. The root tip samples were sealed in sterilized plastic bags and then transported on ice for subsequent DNA extraction. They were further cleaned by running distilled water over them (Toju et al., 2013). For each individual, the three root tip samples were frozen using liquid nitrogen, milled into powder and then mixed thoroughly to provide a composite sample.

2.3 | Molecular characterization of fungal pathogens

The entire genomic DNA of the root tip samples was extracted by using an E.Z.N.A.® HP Plant DNA Extraction Kit (Omega BioTek, Doraville, GA, USA) following the product instructions. Given that the second internal transcribed spacer (ITS2) region of the fungal rRNA genes was reported to be appropriate for revealing the fungal communities (Bazzicalupo, Bálint, & Schmitt, 2013), we amplified the ITS2 region following the procedure described by Davey, Heegaard, Halvorsen, Ohlson, and Kauserud (2012). An error-correcting 12-bp barcode was added to the forward primer for multiplexing different samples. Each PCR reaction was performed in triplicate. PCR products were pooled in equimolar concentrations and then purified using an E.Z.N.A.® Gel Extraction Kit (Omega BioTek). The pooled PCR products were subsequently sequenced on a 2 × 250 bp paired-end Illumina MiSeq platform.

Raw sequences were trimmed to remove the short and low-quality sequences and then merged with paired-end reads following the Mothur pipeline (Schloss et al., 2009). Chimeric sequences were removed using UCHIME (Edgar, Haas, Clemente, Quince, & Knight, 2011). The quality sequences were subsequently clustered into operational taxonomic units (OTUs) at 97% sequence similarity using USEARCH (Edgar, 2010). Taxonomic classification of each OTU was determined using the RDP classifier with a confidence interval of 80% trained on the UNITE database (Abarenkov et al., 2010). Sequences that were not assigned to a fungal kingdom and singletons (including 7,795 OTUs) were removed.

Each sample was first rarefied to 3,000 sequences to eliminate the unequal sequencing depth between samples. The pathogenicity of OTUs was determined by searching against the fungal database program FUNGuild (Nguyen et al., 2016). According to the suggestions from Nguyen et al. (2016), OTUs that were assigned to only one single guild called “plant pathogens” with “highly probable” or “probable” confidence ranking were identified as putative fungal pathogenic OTUs. For each plant species, only the pathogenic OTUs that

were found in more than half of its total sample size were treated as effective infections and were retained in subsequent analyses (Liu et al., 2016). Using this procedure, we aimed to remove false positive OTU occurrences and acquire reliable plant–pathogen associations in our dataset. It has been shown that there was high variation in microbial community composition among technical replicates when using high-throughput sequencing technology (Wen et al., 2017; Zhou et al., 2011). This suggests that pathogenic OTUs that are detected in multiple replicates (e.g., found in more than half of the samples for each plant species) are reliable and thus can be treated as effective plant–pathogen associations. To test whether our conclusions are robust to the threshold we used to remove the false-positive OTU occurrences, we repeated our linear mixed-effects modelling (described below) by considering OTUs that occurred in more than 25% and 60% of the sample size for each plant species.

2.4 | Construction of phylogenies

For each of the 45 focal species, four sequences including *rbcL*, *matK*, *ITS1*, and *5.8S* were obtained from GenBank. Sequences from *Lithocarpus lohangwu* were not found in GenBank and we used the sequences from congeneric relatives as a proxy. We also used two early-diverging gymnosperm species, *Abies alba* and *Cycas rumphii*, to serve as the outgroup. Sequences were aligned using ClustalX2 and FASconCAT was used to concatenate the aligned sequences into a super matrix (Kück & Meusemann, 2010; Larkin et al., 2007). Smart Model Selection was used to determine the best-fit nucleotide substitution model (Anisimova & Gascuel, 2006; Guindon & Gascuel, 2003). A maximum likelihood phylogenetic tree was constructed using PHYML 3.0 with a BIONJ starting tree (Guindon & Gascuel, 2003). We rooted the phylogeny by Archaeopteryx (Zmasek & Eddy, 2001) and ran BLAST to identify whether there were problematic sequences that lead to long branches and wrong positions (Altschul, Gish, Miller, Myers, & Lipman, 1990). After eliminating and replacing the problematic sequences, we removed the two species in the outgroup and then obtained a final molecular phylogeny for the 45 species (Supporting Information Figure S2).

The alignment of the representative sequences of the pathogenic OTUs was performed by PASTA (Kivlin & Hawkes, 2016; Mirarab et al., 2015). The phylogenetic tree of all these pathogenic OTUs was then built using the RAxML v8.0 algorithm (Stamatakis, 2014) under a maximum likelihood model with a GTR plus Gamma nucleotides substitution model of evolution (100 bootstrap replicates).

2.5 | Measuring the plant species phylogenetic distinctiveness

Phylogenetic distinctiveness is a measure of species uniqueness in a phylogenetic tree and is also called evolutionary distinctiveness (Jetz et al., 2014; Redding, Dewolff, & Mooers, 2010). Two metrics, fair-proportion (Isaac, Turvey, Collen, Waterman, & Baillie, 2007) and equal-splits (Redding & Mooers, 2006), are commonly used to quantify phylogenetic distinctiveness. In this study, we used the fair-proportion (Isaac et al., 2007) because it was reported to be simpler and has greater information (Vellend, Cornwell, Magnuson-ford, & Mooers, 2011; Veron, Davies, Cadotte, Clergeau, & Povaine, 2017). Specifically, a plant species with a lower phylogenetic distinctiveness indicates that it has more close relatives, whereas a higher phylogenetic distinctiveness indicates that the plant species is less likely to share internal branches with other species.

2.6 | Statistical analyses

To test for significant differences in the composition of the pathogen communities between plant species, we partitioned the variance in a Bray–Curtis dissimilarity matrix by using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with 999 permutations.

We quantified the host specificity of the pathogens based on the pathogen prevalence of 529 individuals from 45 plant species. Pathogenic OTUs that were detected in only one single plant species were considered to be specialists for these 45 selected plant species. The observed number of specialists in each plant individual was used to assess the richness of specialists. Additionally, the number of OTUs that attack 2, 3, 4…45 plant species was calculated. For each of these multi-host pathogenic OTUs, the phylogenetic host breadth was measured by the standardized effect size of mean pairwise phylogenetic distance (SES.MPD) of the plants it attacks. Negative values of SES.MPD indicate that the pathogenic OTUs are more likely to attack closely related plants, and they are thus considered to be phylogenetic specialists (Poulin, Krasnov, & Mouillot, 2011) for these 45 plant species. As a consequence, we calculated the richness of specialists and phylogenetic specialists in each sample. In addition, the observed number of pathogenic OTUs in each sample was used to measure the richness of the total pathogen community, and other indexes including Shannon and Simpson were also calculated to assess the diversity of the total pathogen community.

The Mantel test with the Spearman method was performed to assess the association between plant species phylogenetic distance and the Bray–Curtis dissimilarity of the pathogen communities. Furthermore, a *ParaFit* with global and individual tests (Legendre, Desdevises, & Bazin, 2002) was performed to examine whether there was a non-random plant–pathogen association network.

Linear mixed-effects models were used to relate the richness of specialists to plant species abundance and relate the richness of phylogenetic specialists to plant species phylogenetic distinctiveness. Plant life stage and species name were treated as random effects, and the richness of specialists and phylogenetic specialists as well as the DBH of each plant individual were fixed effects. Similarly, linear mixed-effects models were also used to relate the richness of the total pathogen community to plant species abundance and phylogenetic distinctiveness, respectively, instead using the richness of the total pathogen community and the DBH of each plant individual as fixed effects. The statistical significance of these fixed effects was estimated by Satterthwaite's approximations. To interpret the standardized effect sizes of these fixed effects on a comparable

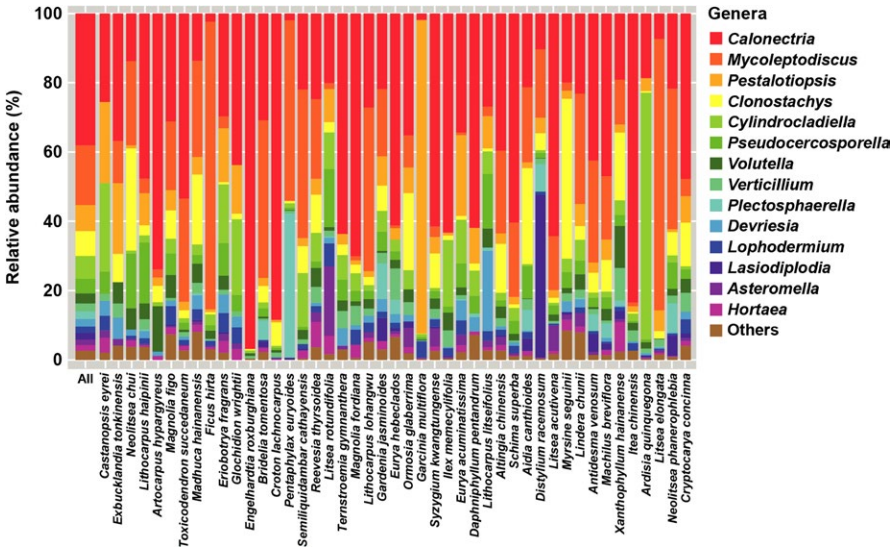

FIGURE 1 Relative abundance of pathogenic genera across the 45 plant species. Only the 14 genera that each occupied more than 1% of all pathogen sequences are shown. Others include 41 genera. The leftmost bar shows the relative abundance of each genus when considering all samples together. From left to right, plant species were ranked from rare to abundant according to their abundances in the plot

scale, all of the independent and dependent variables were *Z*-score standardized before building the linear mixed-effects models. The variation in sample sizes among the different plant species should not bias our results because all analyses were conducted at the plant individual level. Moreover, to further confirm that our conclusions are not biased by the variation in sample sizes across plant species and the threshold used to define the effective plant–pathogen associations, the linear mixed-effects models were repeated considering only the plant species with 10–15 sampled individuals and when other thresholds, including 25% and 60%, were used to define the effective plant–pathogen associations.

Finally, the above analyses were repeated for the data from the three plant life stages but only plant species names were used as random effects in the linear mixed-effects models. All statistical analyses were carried out in the R statistical computing environment (R Core Team, 2016).

3 | RESULTS

3.1 | Overall characteristics of the pathogen community

A total of 8,302,376 quality-filtered sequences were detected across the 529 root tip samples from the 45 plant species in the study plot, with an average of 15,699 ± 10,360 (mean ± *SD*) sequences and a range of 3,216–66,059 sequences per sample. After rarefying each sample to 3,000 sequences and removing the pathogenic OTUs that occurred in less than half of the sampled individuals of all 45 plant species, 158 OTUs representing 17 orders, 23 families, and 55 genera were retained and identified as putative plant fungal pathogens (Supporting Information Table S2).

For all the sequences that were assigned to pathogens, we found that the relative abundance of each of 14 genera was more than 1%. *Calonectria*, *Mycoleptodiscus*, and *Pestalotiopsis* represented the three most dominant genera and occupied 38.03%, 17.30%, and 7.49% of all pathogen sequences respectively (Figure 1). The relative abundances of the different pathogenic lineages varied considerably across the different plant species. Specifically, plant species identity explained a significant amount of the variation (28.23%) in the pathogen community composition (PERMANOVA test, $p < 0.05$).

3.2 | Host specificity of pathogens

When all plant individuals were considered, 38.61% of the pathogenic OTUs were found to attack only a single plant species and were regarded as specialists (Figure 2a). The proportion of these specialists at the sapling, juvenile, and adult stages was 29.23%, 17.39%, and 15.85% respectively (Figures 2b–d). The number of OTUs decreased as the number of plant species they attack increased, and this pattern was consistent when our analyses were restricted to each of the three plant life stages (Figure 2). Moreover, 24.68% of the pathogenic OTUs were found to attack multiple closely related plants (i.e., plants with negative SES.MPD) (Figure 2a). These pathogenic OTUs with phylogenetically clustered host breadths were identified as phylogenetic specialists, and their proportions of the total number of pathogenic OTUs were found to be 19.23%, 20.29%, and 18.29% at the sapling, juvenile, and adult stages respectively (Figures 2b–d). Taken together, these results showed that most of the pathogens only attacked a limited number of plants and the host breadths of most multi-host pathogens were phylogenetically clustered regardless of plant life stage (Figure 2).

3.3 | Plant–pathogen associations

The pairwise plant species phylogenetic distance and the dissimilarity of the total pathogen community were significantly positively correlated, suggesting that closely related plant species exhibit similar pathogen community compositions (Table 1). This correlation was found to be significant at both the sapling and juvenile stages while becoming non-significant at the adult stage (Table 1).

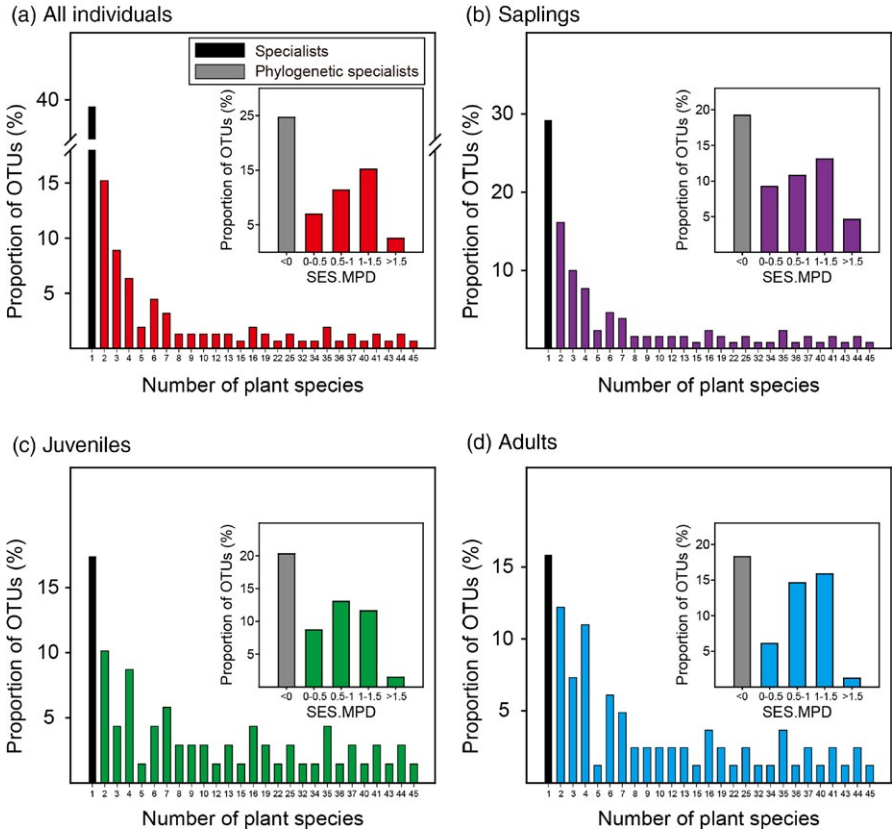

FIGURE 2 The host breadths of the pathogenic OTUs. The proportions of OTUs change with increases in the number and SES.MPD of the plant species they attack. These patterns are shown for (a) all individuals, (b) saplings, (c) juveniles, and (d) adults. Black bars show the proportion of specialists, and grey bars show the proportion of phylogenetic specialists

TABLE 1 Mantel tests (Spearman's rank correlation coefficient ρ and p-values) show the relationship between plant species phylogenetic distance and dissimilarity of the total pathogen community

	All individuals	Saplings	Juveniles	Adults
ρ	**0.17**	**0.24**	**0.11**	0.04
P	**0.03**	**0.03**	**0.02**	0.84

Note. Significance of the statistic is evaluated by Spearman method with 999 permutations and bold numbers indicate significant rank correlation.

Furthermore, the plant–pathogen association network was found to be significantly non-random for all individuals and for individuals at both the sapling and juvenile stages (Figures 3a–c), implying that plants at earlier life stages and their pathogens are more likely to occupy corresponding positions in their respective phylogenetic trees. However, this phylogenetic congruence network was non-significant at the adult stage (Figure 3d). Taken together, our results showed that closely related plant species were more likely to share the same pathogens when considering all plant individuals, but this pattern was only significant at earlier plant life stages (Figure 3).

3.4 | Relating pathogen richness to plant species abundance and phylogenetic distinctiveness

The results from the linear mixed-effect models showed that the richness of specialists is not correlated with plant species abundance across multiple plant life stages (Figure 4a). Rather, the richness of the phylogenetic specialists was found to be negatively correlated with plant species phylogenetic distinctiveness (standardized effect size $b = -0.12$, $p < 0.05$, $R^2 = 0.08$; Figure 4b), and this correlation was strongest at the sapling stage ($b = -0.13$, $p < 0.05$, $R^2 = 0.09$), weaker at the juvenile stage ($b = -0.08$, $p < 0.05$, $R^2 = 0.06$) and becoming non-significant at the adult stage ($b = -0.14$, $p > 0.05$, $R^2 = 0.04$).

Moreover, the richness of the total pathogen community was positively correlated with plant species abundance ($b = 0.23$, $p < 0.05$, $R^2 = 0.14$; Figure 4c), implying that abundant plant species are more likely to harbour or be attacked by a greater number of pathogens, while plant species rarity appears to provide some escape from pathogens. This result was consistent when we performed a univariate linear correlation analysis between the richness of the total pathogen community and plant species abundance (Pearson's $r = 0.32$, $p < 0.05$). When our analyses were restricted to the three plant life stages, we found that the correlation between the richness of the total pathogen community and plant species abundance was strongest at the sapling stage ($b = 0.19$, $p < 0.05$, $R^2 = 0.12$) and slightly weaker at both the juvenile ($b = 0.13$, $p < 0.05$, $R^2 = 0.09$) and adult stages ($b = 0.06$, $p < 0.05$, $R^2 = 0.04$).

Our subsequent analyses showed that the richness of the total pathogen community was negatively correlated with plant species phylogenetic distinctiveness ($b = -0.20$, $p < 0.01$, Figure 4d). Notably, the lack of a relationship between plant species abundance and

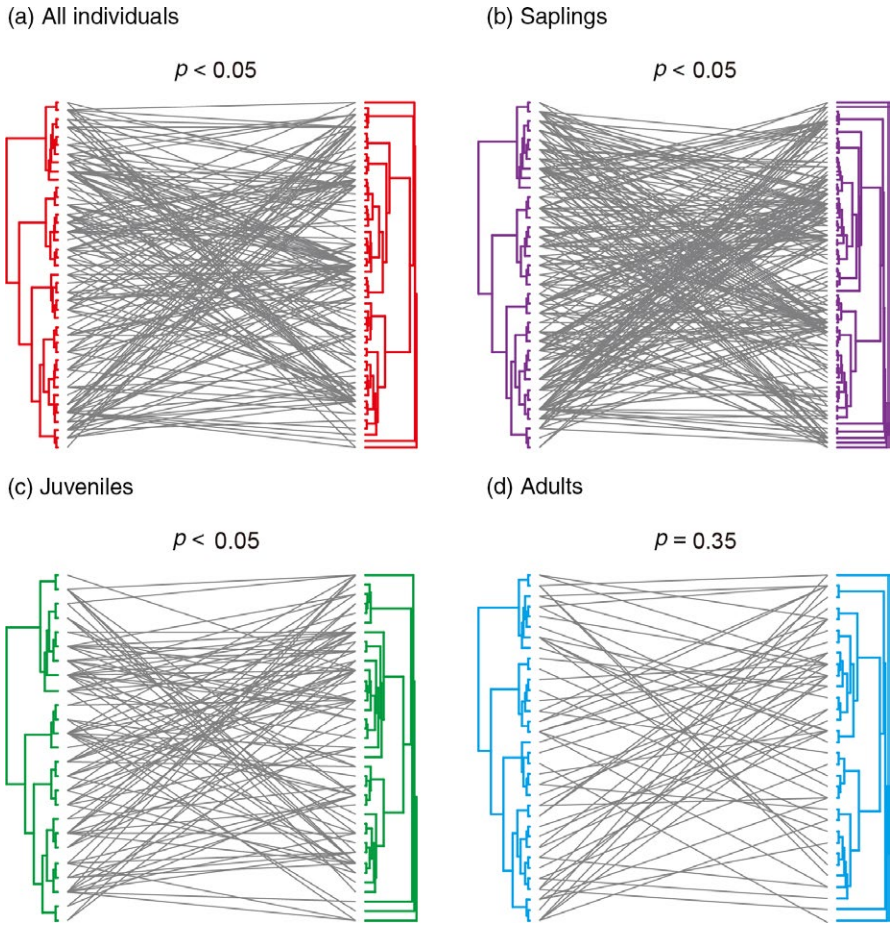

FIGURE 3 Plant–pathogen association networks. For each panel, plant and pathogen phylogenies are on the left and right respectively. Lines connecting tips on the phylogenies were inferred from the observed existence of the root-associated pathogenic OTUs within plants. This plant–pathogen association network is shown for (a) all individuals, (b) saplings, (c) juveniles, and (d) adults. Only the significant connections according to the individual *ParaFit* test are shown. *P* values indicate the significance of the global *ParaFit* test

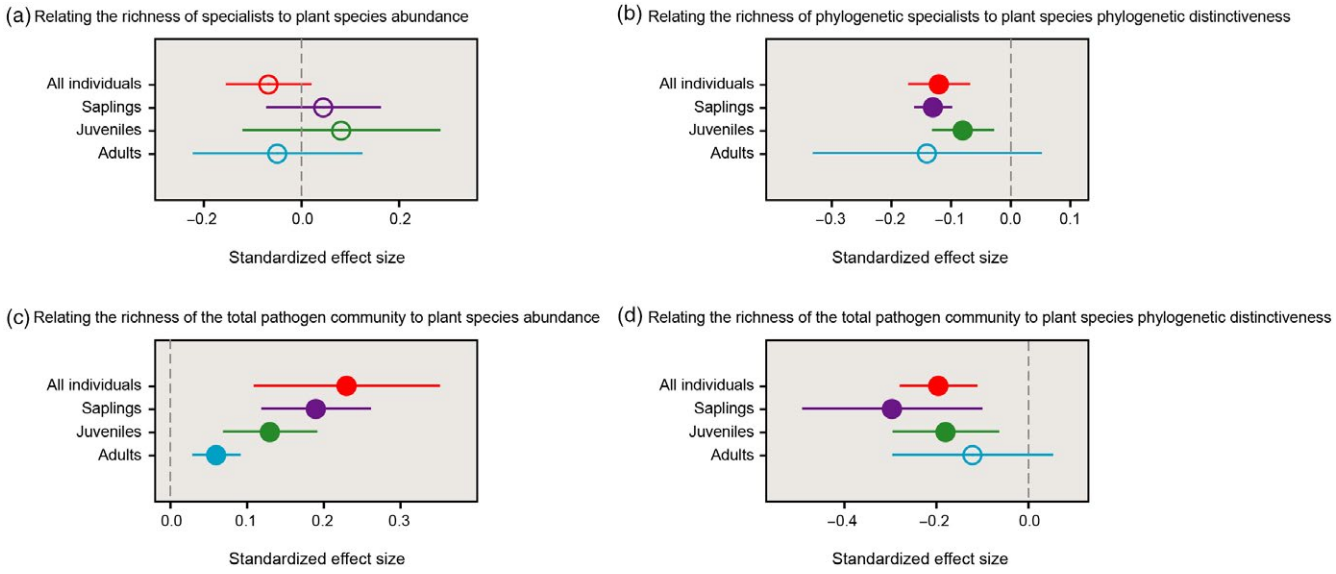

FIGURE 4 Relating pathogen richness to plant species abundance and phylogenetic distinctiveness across multiple plant life stages. (a, c) Filled circles with positive values (standardized effect sizes with 95% confidence intervals plotted as bars) indicate that rare plant species suffer less from pathogens, while negative values indicate that rare plant species are more susceptible to pathogens. (b, d) Filled circles with negative values indicate that phylogenetically distinct plant species suffer less from pathogens

phylogenetic distinctiveness ($r = -0.01$, $p = 0.95$) indicated that this result was not driven by their confounding effects. Thus, plant species that are distantly related to other species are attacked by fewer pathogens, whereas more pathogens appear to attack plant species that have more close relatives. We further validated this conclusion by performing a univariate linear correlation analysis between the

richness of the total pathogen community and plant species phylogenetic distinctiveness ($r = -0.24$, $p < 0.05$). Furthermore, we found that the correlation between the richness of the total pathogen community and plant species phylogenetic distinctiveness was also strongest at the sapling stage ($b = -0.30$, $p < 0.05$, $R^2 = 0.09$), weaker at the juvenile stage ($b = -0.18$, $p < 0.05$, $R^2 = 0.04$), and becoming non-significant at the adult stage ($b = -0.12$, $p > 0.05$, $R^2 = 0.02$). All of the above conclusions were consistent when other indexes, including Shannon and Simpson diversity, were used to measure the diversity of the total pathogen community (Supporting Information Table S3), when only considering plant species with 10–15 sampled individuals (Supporting Information Tables S4 and S5) and when other thresholds were used to define the effective plant–pathogen associations (Supporting Information Tables S6 and S7).

4 | DISCUSSION

A fundamental goal in forest ecology is to uncover the mechanisms that regulate the commonness and rarity of plant species (Bachelot & Kobe, 2013; Bachelot, Kobe, & Vriesendorp, 2015; Comita et al., 2010; Johnson et al., 2012; Preston, 1948). Furthermore, how the phylogenetic structure of plant communities is maintained has attracted increasing interest because plant species in a forest are frequently found to be non-randomly distributed in their phylogenies (Liu et al., 2012; Webb, Gilbert, & Donoghue, 2006). In this study, we attempted to provide some potential insights into the roles of pathogens in determining both plant species abundance and phylogenetic structure by relating pathogen richness to plant species abundance and phylogenetic distinctiveness and further highlighted the changes in these correlations across multiple plant life stages.

In contrast to previous findings that the susceptibility to pathogens leads to plant species rarity (Comita et al., 2010; Johnson et al., 2012; Mack & Bever, 2014; Mangan et al., 2010), our results support that rare plant species in our study plot exhibited less diverse root-associated pathogen communities because we observed a positive relationship between the richness of the total pathogen community and plant species abundance. A possible implication of our results is that the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970) could be important in explaining the plant species abundance pattern in our study plot. The Janzen–Connell hypothesis states that natural enemies such as pathogens disproportionately kill seedlings in higher conspecific density stands (Connell, 1971; Janzen, 1970). Therefore, abundant plant species are more likely to attract pathogens because of their higher conspecific densities (Parker et al., 2015). In contrast, rare plant species might tend to experience infrequent conspecific interactions and thus they are less susceptible to pathogens, which would allow for the persistence of rare plant species (Fricke & Wright, 2017; Yenni et al., 2012). However, we are not able to rule out the possibility that some rare plant species could suffer more from pathogens if their abundance was higher than their equilibrium (Chisholm & Muller-Landau, 2011). For example, *Ormosia glaberrima*, which accounted for only 0.62% of the plant individuals in our study plot, was found to be less likely to be affected by pathogens when it was at low densities but suffered strong pathogen effects when it was at high densities (Liu et al., 2015). Therefore, a more realistic test of the Janzen–Connell hypothesis is to explore how pathogen richness and its effects on plant demography vary along a gradient of conspecific plant density.

Our results showed that the richness of specialists was not related to plant species abundance. Two reasons potentially account for this. First, specialists are commonly identified as key agents for regulating plant species population density (Connell, 1971; Janzen, 1970), whereas they might not be sufficient to provide negative feedback for maintaining plant species abundance and diversity (Chesson & Kuang, 2008; Sedio & Ostling, 2013; Stump, 2017; Stump & Chesson, 2015). Our results coincide with recent findings that abundant and rare plant species host similar numbers of specialized enemies (Bachelot, Uríarte, Thompson, & Zimmerman, 2016; Schroeder et al., 2018). Second, specific root traits (Snapp, Kirk, Román-Avilés, & Kelly, 2003) or the root exudates (Wu et al., 2008; Zhang, Wang, Yao, Yan, & He, 2012) of plant species serve as resources or cues that attract specialists with species-specific preferences. Thus, the richness of specialists might not vary with plant species abundance when the trait values and the concentrations of the root exudates are determined by the physiology of plants but not necessarily related to plant species abundance. Notably, our results showed that the proportion of specialists when considering all plant individuals was higher than the proportion at any particular plant life stage, implying that each specialist is specific to each life stage of their hosts to some extent. Specifically, the higher proportion of specialists at the seedling stage indicates that more specialists tend to attack the seedlings of their hosts.

Our results showed that the roots of the phylogenetically distinct plant species in our study plot exhibited a lower richness of both phylogenetic specialists and the total pathogen community. Phylogenetic specialists are more likely to be able to infect closely related plant species than distantly related ones (Gilbert & Webb, 2007), and thus phylogenetically distinct plant species tend to escape control from phylogenetic specialists. Additionally, the positive association between plant species phylogenetic distance and the dissimilarity of the total pathogen community and the significant phylogenetic congruence signal in the plant–pathogen association network indicate that closely related plant species are more likely to share a similar total pathogen community (Gilbert & Webb, 2007; Parker & Gilbert, 2004; Wapshere, 1974). As a consequence, phylogenetically distinct plant species also escaped control from the total pathogen community. Moreover, the plant community in our plot was found to be comprised of species that are more distantly related than would be expected by chance (Liu et al., 2012), perhaps because both the phylogenetic specialists and the total pathogen community limit the coexistence of closely related plant species. By extension, this phylogenetic overdispersed pattern indicates that the root-associated pathogens might potentially enhance the phylogenetic diversity of the

plant communities by limiting the population growth of plant species with many close relatives.

Furthermore, we found that the correlation between the richness of the phylogenetic specialists and plant species phylogenetic distinctiveness and the correlations between the richness of the total pathogen community and plant species abundance and phylogenetic distinctiveness were stronger at earlier plant life stages than at later plant life stages. Notably, neither the richness of the phylogenetic specialists nor the total pathogen community was related to plant species phylogenetic distinctiveness at the adult stage. A probable reason is that plant defence and tolerance increased over the lifetime of the plant (Boege & Marquis, 2005). Plant individuals at earlier life stages, such as the sapling and juvenile stages, were more susceptible to natural enemies (García-Guzmán & Heil, 2014; Gilbert, Hubbell, & Foster, 1994). Another reason is that pathogen infections are related to conspecific density (Liu et al., 2015), and thus, the higher density of plants at earlier life stages (Nathan & Muller-Landau, 2000) might attract more infections from pathogens.

While we showed that pathogen richness was associated with both plant species abundance and phylogenetic distinctiveness, two limitations should be noted in this study. First, although massively parallel sequencing provides opportunities to open the "black box" of the pathogen community, this OTU-level identification of pathogens is fundamentally different from the morphological species-level identification of isolated pathogen strains (Gilbert & Webb, 2007). It is possible that OTUs that are found to be specialists based on the genetic threshold defining OTUs might actually belong to generalists when defined morphologically, and thus, the proportion of specialists would be lower. Second, the effects of plant species abundance and phylogenetic distinctiveness on plant species population growth were not tested in this study because of the lack of dynamic temporal data to fully assess plant recruitment and mortality, especially that caused by pathogens. As a consequence, we suggest that characterizing the pathogen community and monitoring the plant demography should be implemented in parallel in multiple natural ecosystems to clearly reveal the roles of pathogens in maintaining the taxonomic and phylogenetic diversity of the plant community.

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AUTHORS' CONTRIBUTIONS

Y.C., P.J., M.W.C., and W.S. developed and framed research questions; P.J., Y.Q., X.J., and Z.W. collected the data used in this analysis; Y.C., P.J., X.L., and P.W. analysed the data; Y.C. and P.J. wrote the first draft of the manuscript and all authors contributed to discussing the results and editing the manuscript.

DATA ACCESSIBILITY

Data are deposited in figshare at https://doi.org/10.6084/m9.figshare.6948977.v1 (Chen et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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