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Warming shifts soil microbial communities and tropical tree seedling mortality

Yu Liu[1,2] | Fangliang He[1,3]

[1]ECNU-Alberta Joint Lab for Biodiversity Study, Tiantong National Station for Forest Ecosystem Research, School of Ecology and Environmental Sciences, East China Normal University, Shanghai, China

[2]Shanghai Institute of Pollution Control and Ecological Security, Shanghai, China

[3]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

Correspondence
Fangliang He
Email: fhe@ualberta.ca

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Abstract

Plant–soil feedback (PSF), regulated by both mycorrhizae and soil-borne pathogens, is a primary mechanism maintaining high tree species diversity in the tropics. But how warming actually affects PSF is not well understood. We conducted a field warming experiment to test PSF on seedling mortality of two tree species: a rhizobia-associated tree (*Ormosia semicastrata*, Fabaceae) suffering from host-specific soil-borne pathogens and an ectomycorrhizal fungi-associated tree (*Cyclobalanopsis patelliormis*, Fagaceae) with low susceptibility to soil-borne pathogens. Soil fungi from the warming versus control seedling plots were identified by molecular sequencing. Results showed that the elevated temperature lowered seedling mortality of *O. semicastrata*, but had no effect on *C. patelliormis* seedlings. This indicates that warming weakened the negative PSF on *O. semicastrata*, presumably due to the observed decrease of the relative abundance of plant-pathogenic fungi and increase of ectomycorrhizal fungi but did not affect the PSF on *C. patelliormis*. The differential warming effects on seedling mortality of species with different microbial associations affords an example showcasing how the change in soil-borne microbes in response to global warming would, in turn, through PSF, alter tropical tree species composition and diversity. This study helps shed mechanistic light on the debate of biodiversity change as driven by climate change.

KEYWORDS
biodiversity change, ectomycorrhizal fungi, global warming, Janzen–Connell effect, plant-pathogenic fungi, plant–soil feedback

INTRODUCTION

Direct adverse impacts of global warming on tropical forests, including decelerated plant growth due to high respiration costs (Feeley et al., 2007; Vlam et al., 2014) and increased tree mortality (Aleixo et al., 2019) attributed to high risk of hydraulic failure (Adams et al., 2017), have well been documented. However, an increasing number of studies have recently shown that global warming and its concomitant drought can also alter the interaction between pathogens and their host trees, for example, by increasing the load of infectious diseases (Anderson et al., 2004) or changing the severity of plant diseases (Bachelot et al., 2020; Swinfield et al., 2012). Any change in environmental conditions due to climate change can potentially affect disease severity as predicted by the framework of the classic plant disease triangle (Liu & He, 2019; Romero et al., 2021). Therefore, predicting the net response of forest tree species to global warming requires quantification of not only the direct

responses of tree species (e.g., ecophysiological stress; Adams et al., 2017), but also indirect responses such as those associated with changing natural enemies (e.g., pathogens and herbivores) (Bachelot et al., 2020; Liu & He, 2019; Thompson et al., 2010). This is particularly true for soil-borne pathogenic microbes, which form the most important biotic interactions with plant roots (Wardle et al., 2004) and play a major role in maintaining plant diversity in tropical forests via a negative plant–soil feedback (PSF) (Mangan et al., 2010; Schroeder et al., 2020).

Primarily driven by soil-borne microbes (Mariotte et al., 2018), PSF occurs due to changes in soil microbes induced by the presence of plants, which in turn influence plant performance (Bever et al., 1997). PSF can be either positive or negative (Kandlikar et al., 2019; Liu & He, 2019), with the direction and magnitude depending on the relative influence of beneficial (e.g., ectomycorrhizal fungi, EcM fungi) (Corrales et al., 2018) and antagonistic microbes (e.g., plant-pathogenic fungi) on plant species as well as the effect of climate (Liu & He, 2019). The factors that cause (negative) PSF can drive conspecific negative density- or distance-dependent effects, by which seedlings at high density or in the proximity of conspecific adults would suffer high mortality from attacks of host-specific enemies (pathogens and herbivores). This process was first independently reported by Janzen (1970) and Connell (1971) and has since been known as the Janzen-Connell (JC) effect. The JC effect is a type of net negative PSF, important to maintaining biodiversity in the tropics (Bell et al., 2006; Mangan et al., 2010). Its strength is typically estimated based on the mortality of seedlings or relative growth rate of seedlings inflicted by host-specific enemies.

Recently, we found that warming intensified the negative PSF concurrent with increased relative abundance of plant-pathogenic fungi in a temperate forest (Liu & He, 2021). This occurs because, in the temperate zone, low temperature in the winter is a risk factor. Thus, any warming would likely decrease overwintering mortality of fungal pathogens (also see Pfender & Vollmer, 1999). In the tropics, however, the warming effect could be opposite because tropical temperatures are already on the upper limit for many microorganisms, further increase in temperature could push pathogens out of the thermal tolerance zone (Bachelot et al., 2020; Liu & He, 2019; Thompson et al., 2010). As such, the role of the JC effect in maintaining tropical plant diversity can be potentially weakened by global warming (Bachelot et al., 2020). However, the response of PSF to global warming is more than the response of the pathogen-based JC effect. To fully understand warming effects on PSF, it is necessary to also include other types of microorganisms because the differential responses of different microorganisms

(e.g., antagonistic versus beneficial microbes) to warming can change the net PSF (Liu & He, 2019).

In this study, we conducted a 3 year warming experiment using open-top chambers (OTCs) to test how seedlings of *Ormosia semicastrata* f. *litchiifolia* (Fabaceae) and *Cyclobalanopsis patelliormis* (Fagaceae), with contrasting nutrient-acquisition strategies via soil-borne microbes, responded to elevated temperature in a tropical forest. Because of their potential differences in susceptibility to soil pathogens, we expected the performance of the two tree species would be different in response to elevated temperatures. For the rhizobia-associated species (*O. semicastrata*), the seedling survival (as mediated by PSF) is expected to vary significantly if warming alters soil pathogenic fungi. The survival could be decreased or increased, depending on the response of plant-pathogenic and/or EcM fungi to warming. In contrast, for the ectomycorrhizal fungi-associated species (*C. patelliormis*), no or a weak warming effect on the seedling survival is expected, possibly due to the Hartig net of EcM fungi protecting the host roots from pathogen attack (Albornoz et al., 2017).

METHODS

Study site and species

The study site was located in a tropical montane rain forest in Jianfengling Nature Reserve in Hainan Island, China (Appendix S1: Figure S1a), adjacent to a 60-ha stem-mapping plot established in 2012 (18°53′ N, 108°43′ E) (Xu et al., 2015). The region has monsoon climate. The site has an average annual temperature of 19.8°C, with summer temperature (June–August) of 27.5°C, and receives annual precipitation ranging 1300–3700 mm, with a dry season from November to March and a wet season from April to October (Xu et al., 2015). The two tree species selected for this study were *O. semicastrata*, a rhizobia-associated species, susceptible to host-specific soil-borne pathogens (Li et al., 2009) and *C. patelliormis*, an EcM fungi-associated species with low susceptibility to infestation of soil-borne pathogens (Appendix S1: Section S1.1).

Field experiments

The experiments were conducted for 3 years (early April 2016 to early September 2018). Three adult individuals of the two focal species with similar diameter at breast height were selected. At 1, 10, and 20 m distances from a selected adult, an OTC was set up to passively warm the soil by capturing radiation (Appendix S1: Figure S1b,c).

A control plot was established next to each OTC. Each OTC (and the control plot) was planted with two-week-old seedlings of three tree species. They were the focal species of that OTC (*O. semicastrata* or *C. patelliormis*, depending on the parent trees under which OTCs were placed), a congeneric of this focal species, and the other focal species (*C. patelliormis* or *O. semicastrata*) (Figure S1b). The congeneric species (*O. pinnata* for *O. semicastrata* and *C. hui* for *C. patelliormis*) were used for testing whether soil-borne pathogens were specific to their host trees (the focal species). The seedlings (germinated in a greenhouse) of these species were transplanted to two columns; one column (consisting of three 40 × 40 cm quadrats) was randomly selected for pesticide treatment, while the other was treated with the same amount of double distilled water (Appendix S1: Figure S1b and Section S1.2). There were 54 seedlings (9 seedlings/quadrat x 3 quadrats/column x 2 columns) in each OTC (or a control plot) (Figure S1b).

Soil sampling and amplicon sequencing of soil fungi

One soil core from each treatment combination (i.e., one column, consisting of three 40 × 40 cm quadrats; Appendix S1: Figure S1b) were collected in June 2018 for analyzing fungal composition. Surface soil samples (0–10 cm in depth) were collected from the interstices between the transplanted seedlings in each column (bulk soils instead of rhizosphere soils were collected because it was not feasible to trace the roots of the seedlings that died in the first 2 years). The collected soil samples were immediately shipped in dry ice boxes to Magigene Technology Ltd. (Guangzhou, China) laboratory to extract DNA for Illumina amplicon sequencing (see sequencing steps and blasting sequences to OTUs in Appendix S1: Section S1.4). According to the FUNGuild database (Nguyen et al., 2016), the fungal OTUs were grouped as plant-pathogenic fungi (421 OTUs), EcM fungi (392 OTUs), etc. (Appendix S1: Section S1.4) (https://doi.org/10.6084/m9.figshare.13378946).

Statistical analyses

Analysis of seedling mortality

In this study, seedling mortality was monitored over 3 years (24 time points of measurement), and the survival time analysis was conducted to estimate differences in seedling mortality of the two focal tree species under experiment treatments. The hazard ratios (HRs) of seedling mortality under different treatments (i.e., warming, distance-to-adult, and pesticide treatment) were modeled using the Cox proportional hazard (PH) model. HRs measure the relative risk of mortality. An HR larger than one indicates increased mortality risk for given a treatment compared to the control. The Cox model was estimated using the *coxph* function in the R *survival* package (http://survival.r-forge.r-project.org/) and the three adults for each of the two focal species were treated as a "cluster" to account for the possibility of intra-cluster data correlation (i.e., seedlings under the same adult may have similar mortality than those under different adults) (Williams, 2000). In addition to this survival time analysis, we also quantified seedling survival ratios using the widely adopted method of Bever et al. (1997) that compares seedling survival of focal tree species in conspecific soil and the survival of seedlings of the same species in heterospecific soil at the end of the experiment (Appendix S1: Figure S2). Because the qualitative results of both analyses were the same, in this study, we only report the results of the survival time analysis (i.e., Cox's PH models). Because survival analysis employs seedling mortality data throughout the whole experiment, it is more powerful in inferring PSF than Bever's method, which only counts seedling survival at the end of experiment.

Treatment effects on relative abundances of plant-pathogenic and EcM fungi

To quantify the treatment effects on the relative abundances of plant-pathogenic and EcM fungi, negative binomial generalized linear models (GLMs) were used to estimate the treatment effects on their relative abundances. Here, the relative abundance of a fungal guild (pathogenic fungi or EcM fungi) was the proportion of the guild relative to all fungi in a treatment combination at the end of the experiment. This relative abundance was presumed to be responsible for seedling mortality. In estimating the GLMs, the total sequence counts of fungal OTUs in each soil core were included as "weights" in the *glm.nb* function of R package MASS. To control the variation in the relative abundances of the two fungal guilds among the three selected adults of each tree species, the identities of the three adults were included as an independent (character) variable in the negative binomial models.

RESULTS

Hazard ratios of seedling mortality under treatments

The results of Cox's PH models for the 3 year seedling mortality indicate that the HR of *O. semicastrata* seedling
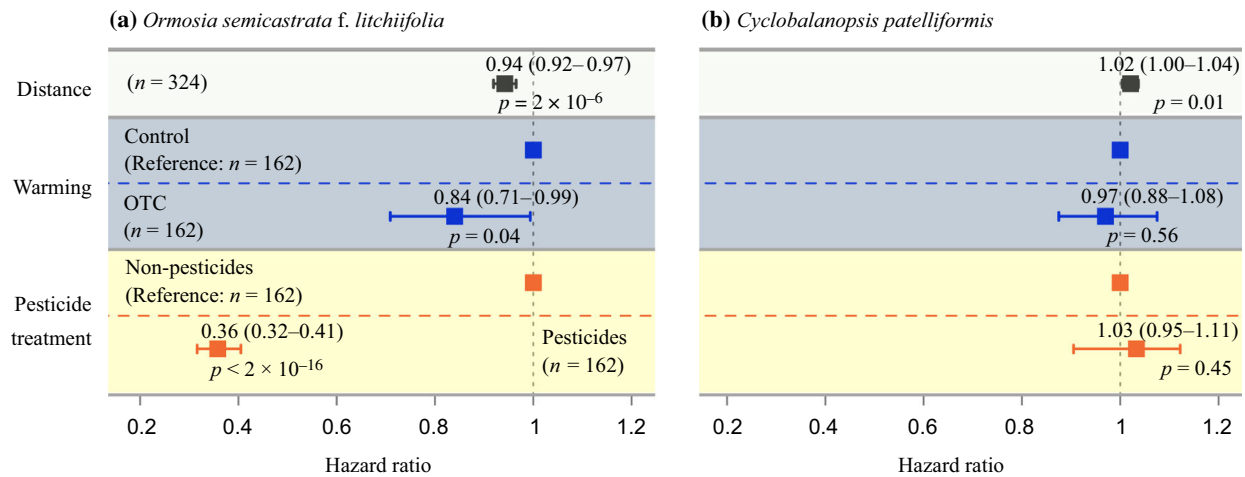
(a) *Ormosia semicastrata* f. *litchiifolia*

(b) *Cyclobalanopsis patelliformis*

FIGURE 1 Hazard ratios (relative risk) of seedling mortality of (a) *Ormosia semicastrata* f. *litchiifolia* and (b) *Cyclobalanopsis patelliformis*. The effects of experimental factors (distance to the parent tree, with pesticides versus without pesticides, and open-top chamber [OTC] warming versus control) on seedling mortality were estimated from Cox's proportional hazard models for seedling survival times. A hazard ratio >1 indicates an increased hazard of seedling mortality under a treatment versus control. The number of seedlings per treatment is *n*.

mortality, i.e., the risk of mortality under warming, was significantly less than 1 with 95% confidence interval (CI) of HR = 0.71–0.99, $p = 0.04$ (Figure 1a), while warming had no significant effect on the HR of *C. patelliormis* seedling mortality (95% CI of HR = 0.88–1.08, $p = 0.56$; Figure 1b). Additionally, the HR of *O. semicastrata* seedling mortality significantly decreased with increasing distance from their parent trees (95% CI of HR = 0.92–0.97, $p = 2 \times 10^{-6}$; Figure 1a) and with pesticide treatment (95% CI of HR = 0.32–0.41, $p < 2 \times 10^{-16}$; Figure 1a). In contrast, seedlings of *O. pinnata* (the congeneric species) and *C. patelliformis*, planted together beneath *O. semicastrata* parent trees (Appendix S1: Figure S1b), did not respond to pesticide treatment (Appendix S1: Figure S3). Furthermore, the mortality HR of *C. patelliormis* seedlings significantly increased with distance from their parent trees (95% CI of HR = 1.00–1.04, $p = 0.01$; Figure 1b), and pesticides had no effect on *C. patelliormis* seedling mortality (95% CI of HR = 0.95–1.11, $p = 0.45$; Figure 1b), nor on the congeneric species *C. hui* seedlings (Appendix S1: Figure S3). Worth to note warming did not also significantly affect the pathogen-induced seedling mortality of *O. semicastrata* beneath *C. patelliormis* parent trees (Appendix S1: Figure S4).

Relative abundance of EcM/pathogenic fungi under treatments

Warming significantly decreased the relative abundance of plant-pathogenic fungi in the soils under the two focal tree species ($z = -80.2$, $p < 2 \times 10^{-16}$ and $z = -682.0$, $p < 2 \times 10^{-16}$, respectively; Table 1), but increased that of EcM fungi of the two species ($z = 530.4$, $p < 2 \times 10^{-16}$ and

TABLE 1 Estimated coefficients (with SE in parentheses) of the negative binomial linear models for modeling the responses of the abundance of plant-pathogenic fungi to the three experimental treatments (open-top chamber warming versus control, pesticides versus without pesticides, and distance to the parent trees).

Effects	Coefficient	z	P (>|z|)
O. semicastrata			
Intercept	5.19 (1.84×10^{-3})	2813.9	$<2 \times 10^{-16}$
Warming	−0.07 (9.12×10^{-4})	−80.2	$<2 \times 10^{-16}$
Pesticide	−0.09 (9.17×10^{-4})	−102.9	$<2 \times 10^{-16}$
Distance	−0.03 (6.44×10^{-5})	−513.9	$<2 \times 10^{-16}$
Adult	0.21 (5.75×10^{-4})	373.3	$<2 \times 10^{-16}$
C. patelliformis			
Intercept	4.86 (1.56×10^{-3})	3109.3	$<2 \times 10^{-16}$
Warming	−0.63 (9.20×10^{-4})	−682.0	$<2 \times 10^{-16}$
Pesticide	−0.27 (9.21×10^{-4})	−293.2	$<2 \times 10^{-16}$
Distance	0.05 (5.64×10^{-5})	976.3	$<2 \times 10^{-16}$
Adult	0.15 (5.74×10^{-4})	260.8	$<2 \times 10^{-16}$

Note: The model coefficients estimated the treatment effects. In the models, adults were also included as an independent variable to control for the variation in the relative abundance of plant-pathogenic fungi among the three adults of each focal species.

$z = 293.7$, $p < 2 \times 10^{-16}$, respectively; Table 2). As expected underlying the JC effect, the relative abundance of pathogenic fungi decreased with the increasing distance from the adults of *O. semicastrata* ($z = -513.9$, $p < 2 \times 10^{-16}$; Table 1), and the relative abundance of EcM fungi decreased with distance from the adults of *C. patelliormis* ($z = -1034.6$, $p < 2 \times 10^{-16}$; Table 2). Pesticide treatment decreased the relative abundance

T A B L E 2 Estimated coefficients (with SE in parentheses) of the negative binomial linear models for modeling the responses of abundance of ectomycorrhizal fungi to three experimental treatments (open-top chamber warming versus control, pesticides versus without pesticides, and distance to the parent trees).

Effects	Coefficient	z	$P(>|z|)$
O. semicastrata			
Intercept	$9.57\ (3.37 \times 10^{-3})$	2840.6	$<2 \times 10^{-16}$
Warming	$0.88\ (1.67 \times 10^{-3})$	530.4	$<2 \times 10^{-16}$
Pesticide	$0.67\ (1.68 \times 10^{-3})$	397.6	$<2 \times 10^{-16}$
Distance	$-0.01\ (1.18 \times 10^{-4})$	-58.1	$<2 \times 10^{-16}$
Adult	$0.18\ (1.05 \times 10^{-3})$	171.7	$<2 \times 10^{-16}$
C. patelliformis			
Intercept	$9.55\ (2.38 \times 10^{-3})$	4006.8	$<2 \times 10^{-16}$
Warming	$0.41\ (1.41 \times 10^{-3})$	293.7	$<2 \times 10^{-16}$
Pesticide	$-0.28\ (1.41 \times 10^{-3})$	-199.2	$<2 \times 10^{-16}$
Distance	$-0.09\ (8.57 \times 10^{-5})$	-1034.6	$<2 \times 10^{-16}$
Adult	$0.20\ (8.77 \times 10^{-3})$	226.9	$<2 \times 10^{-16}$

Note: The model coefficients estimated the treatment effects. In the models, adults were also included as an independent variable to control for the variation in the relative abundance of ectomycorrhizal fungi among the three adults of each focal species.

of pathogenic fungi ($z = -102.9$, $p < 2 \times 10^{-16}$; Table 1), but increased the relative abundance of EcM fungi under the adults of *O. semicastrata* ($z = 397.6$, $p < 2 \times 10^{-16}$; Table 2), which may be responsible for the decreased seedling mortality of *O. semicastrata* at pesticide treatment (95% CI of HR = 0.32–0.41, $p < 2 \times 10^{-16}$; Figure 1a). However, changes in the relative abundance of pathogenic and EcM fungi under warming and pesticide treatment had no effect on *C. patelliormis* seedling mortality (95% CI of HR = 0.88–1.08, $p = 0.56$ and 95% CI of HR = 0.95–1.11, $p = 0.45$, respectively; Figure 1b).

DISCUSSION

Although the magnitude of global warming in the tropics is lower than that in high latitudes (Deutsch et al., 2008), warming could have more severe deleterious impacts on species in the tropics than those in the temperate and boreal because of low tolerance of tropical species to temperature change (Deutsch et al., 2008; Khaliq et al., 2014). Rising temperatures in the tropics are directly responsible for tree growth reduction (Feeley et al., 2007), increased tree mortality (Aleixo et al., 2019), and species range shift (Khaliq et al., 2014). Besides these direct effects, global warming could also have many consequential indirect effects (Liu & He, 2019; Pugnaire et al., 2019), of which the

warming effect on PSF is critical not only to maintaining tropical tree diversity (Mangan et al., 2010; Schroeder et al., 2020) but also to regulating soil carbon cycling (Nottingham et al., 2020). However, it has not been well understood how warming may affect PSF and how that could, in turn, affect tropical biodiversity. Our study shows that warming decreased the risk of seedling mortality of the rhizobia-associated *O. semicastrata* but had no effect on that of the EcM fungi-associated *C. patelliormis* seedlings (Figure 1). Such differential effects of elevated temperature on the mortality of heterospecific seedlings is new to the literature on the PSF regulating tropical tree diversity and could have important implications to understanding climate impacts on tropical tree diversity and shed mechanistic light on the debate of biodiversity change (Gonzalez et al., 2016; Vellend et al., 2013). Biodiversity change driven by changes in land use and climate does not have to involve the net loss (or gain) of species; change occurs if the abundances of constituent species shift (Dornelas et al., 2014).

Although the individual roles of mycorrhizal fungi and pathogenic fungi in regulating plant diversity have well been appreciated (Bell et al., 2006; Corrales et al., 2018; Liu et al., 2012; van der Heijden et al., 1998), increasing evidence has shown what matters to biodiversity maintenance is the net (interactive) effect of beneficial and antagonistic fungi (Liu & He, 2019; Merges et al., 2018; Schroeder et al., 2020). Our study shows that elevated temperature decreased the relative abundance of plant-pathogenic fungi (Table 1) while increased the abundance of EcM fungi (Table 2). This temperature-mediated trade-off between the two fungal guilds would inevitably alter the net outcome of PSF, depending on the relative magnitude between the positive PSF induced by beneficial microbes (e.g., EcM fungi) versus the negative PSF inflicted by antagonistic microbes (e.g., plant-pathogenic fungi) (Tables 1 and 2). This is consistent with previous observations that the decreased abundance of plant-pathogenic fungi and the increased abundance of EcM fungi could alleviate the negative PSF (Chen et al., 2019). The warming-weakened negative PSF observed in this study is not surprising because the summer temperature of 27.5°C in our study area (Xu et al., 2015) is already higher than the optimal temperature (20°–25°C) for pathogen reproduction (Pfender & Vollmer, 1999) and an increase in temperature of 0.89°C (Appendix S1: Figure S1c) would make the temperature suboptimal to pathogens. Our finding is consistent with that of Bachelot et al. (2020). However, different from tropical forests, we recently showed that a small increase in temperature in a temperate forest intensified negative PSF due to increased abundance of plant-pathogenic fungi (Liu & He, 2021). The effect of climate change on fungi is particularly pronounced because fungi have been observed

to be especially sensitive to temperature change (Alster et al., 2018). As such, a weakened negative PSF (the JC effect) under even moderate warming in the tropics could result in a decline in tropical tree species diversity.

The rhizobia-associated *O. semicastrata*, susceptible to host-specific soil-borne pathogens (Li et al., 2009), experienced a weakened negative PSF under warming due to the decreased abundance of plant-pathogenic fungi (and the increased abundance of EcM fungi, which could lead to decreasing the abundance of pathogenic fungi). Together with the warming effect disappearing after pesticide treatment, *O. semicastrata* was found to have the highest seedling survival in the combination of warming and pesticides (Appendix S1: Figure S2). However, different from the sensitiveness of *O. semicastrata* to the differential changes of the two fungal guilds under warming, seedling mortality of the EcM fungi-associated *C. patelliormis*, having low susceptibility to soil-borne pathogens, was unaffected by warming. This is possibly because EcM fungi can form Hartig nets around the roots of their host species that develop a line of defense against soil-borne pathogens (Segnitz et al., 2020). Once Hartig nets have been formed around the roots, the EcM fungi-associated tree species may no longer be sensitive to the change in load levels of plant-pathogenic and EcM fungi.

Seedling mortality of the rhizobia-associated *O. semicastrata* was significantly increased in the immediate proximity of the parent trees (Figure 1a; Appendix S1: Figure S3) consistent with a previous finding for the same species (Li et al., 2009) and other tropical tree species (Augspurger, 1983; Bell et al., 2006), possibly due to the accumulation of fungal pathogens under the decreased concentration of antifungal compounds in the soil close to leguminous species (Latz et al., 2012). In agreement with the prediction of the JC hypothesis, our study showed that the relative abundance of plant-pathogenic fungi decreased with increasing distance from *O. semicastrata* parent trees (Table 1), and these pathogens seemed to be very specific to *O. semicastrata* as they had no detectable effects on seedling mortality of congeneric *O. pinnata* and *C. patelliormis* (Appendix S1: Figure S3). In contrast, there was a decreased HR of seedling mortality of the EcM fungi-associated *C. patelliormis* in the immediate proximity of the parent trees (Figure 1b), consistent with the positive PSF or the "inverse" JC effect in EcM fungi-associated tree species (Merges et al., 2018).

We would like to note two possible limitations of our study. One is that the functional classification of fungi by the FUNGuild database is considered coarse (Nilsson et al., 2019) although it is widely used to classify fungal guilds (Chen et al., 2019; Delgado-Baquerizo et al., 2020). By quantifying the responses of plant-pathogenic fungi and EcM fungi to warming, we attributed the decreased

seedling mortality of *O. semicastrata* (Figure 1a) to the decreased abundance of plant-pathogenic fungi (Table 1) and also the increased abundance of EcM fungi. We suggest future studies to quantify disease severity and mycorrhizal colonization in experimental seedlings under warming, and explicitly measure host–pathogen and host–mutualist interactions. The other is that the warming simulation of OTCs also dried soils (Appendix S1: Figure S5), a well-recognized side effect of warming experiments (Hollister & Webber, 2000). The good news is that these dual effects of OTCs happen to follow the typical climate pattern in the tropics, i.e., the increase in temperature simultaneously reduces precipitation (or increases drought) (Bachelot et al., 2020; Malhi et al., 2008). Although no correlation between the change in OTC soil moisture and the soil temperature was detected in our study (Appendix S1: Figure S5), changes in pathogen-induced seedling mortality under warming could be magnified because of the high moisture preference of plant-pathogenic fungi (Romero et al., 2021; Swinfield et al., 2012). In addition, although it is important to investigate different responses of tree species associated with different soil microbes to warming for truly understanding the effect of global warming on net PSF, the findings of this study should be heeded cautiously as this study only included one focal tree species per each microbial association. The generality of the findings of this study remains to be fully tested.

CONCLUSIONS

Our 3 year OTC warming experiment shows that the effects of global warming on seedling performance of tropical trees is not simply positive or negative, but depends on the change in soil pathogens and soil mutualists. Our results indicate that warming benefits rhizobia-associated host tree species possibly due to the reduced relative abundance of soil pathogens and the increased relative abundance of soil mutualists in the tropics, while there is no detectable effect on EcM fungi-associated tree species. The differential warming effects on seedling mortality of tree species with different microbial associations afford an example showing that global warming could decrease the mortality of species with certain biological traits while impede those without, thus leading to change in tropical tree composition under climate change (Johnson et al., 2018). This finding adds an explanation why change in community composition has been so widely observed and is a major pattern of biodiversity change (Dornelas et al., 2014; Hillebrand et al., 2018).

AUTHOR CONTRIBUTIONS

Fangliang He and Yu Liu conceived the study. Yu Liu conducted the experiments; and Yu Liu and Fangliang

He jointly conducted data analysis, result interpretation, and manuscript writing.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data and R code (Liu, 2021) are available in Figshare at https://doi.org/10.6084/m9.figshare.13378946.

ORCID
Yu Liu https://orcid.org/0000-0001-9869-2735
Fangliang He https://orcid.org/0000-0003-0774-4849

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SUPPORTING INFORMATION

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