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Climate Change Drives Changes in the Size and Composition of Fungal Communities Along the Soil–Seedling Continuum of *Schima superba*

Xian Wu[1,2] | M. Derek MacKenzie[2] | Jiarong Yang[1,2] | Guoyu Lan[3] | Yu Liu[1,4]

[1]ECNU-Alberta Joint Lab for Biodiversity Study, Tiantong Forest Ecosystem National Observation and Research Station, School of Ecology and Environmental Sciences, East China Normal University, Shanghai, China | [2]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada | [3]Rubber Research Institute, Chinese Academy of Tropical Agricultural Sciences, Haikou, Hainan, China | [4]Shanghai Institute of Pollution Control and Ecological Security, Shanghai, China

Correspondence: Yu Liu (yuliu@des.ecnu.edu.cn)

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ABSTRACT

Plant microbiomes have a major influence on forest structure and functions, as well as tree fitness and evolution. However, a comprehensive understanding of variations in fungi along the soil–plant continuum, particularly within tree seedlings, under global warming is lacking. Here, we investigated the dynamics of fungal communities across different compartments (including bulk soil and rhizosphere soil) and plant organs (including the endosphere of roots, stems and leaves) of *Schima superba* seedlings exposed to experimental warming and drought using AccuITS absolute quantitative sequencing. Our results revealed that warming and drought significantly reduced the number of specific fungal amplicon sequence variants (ASVs) in the bulk soil and rhizosphere soil, respectively. Variations in fungal communities were mainly explained by compartments and plant organs, with the composition of endophytic fungal communities within leaves (primarily attributed to species gain or loss) being most influenced by climate change. Moreover, warming significantly reduced the migration of Ascomycota, soil saprotrophs, wood saprotrophs and yeasts from the bulk soil to the rhizosphere soil but increased that of plant pathogens from the roots to the stems. Drought significantly decreased the absolute abundances of Chytridiomycota, Glomeromycota and Rozellomycota, as well as the migration of ectomycorrhizal fungi from the bulk soil to the rhizosphere soil but increased that of plant pathogens. Warming could indirectly reduce leaf area by increasing the diversity of leaf pathogens. These findings have potential implications for enhancing the resilience and functioning of natural forest ecosystems under climate change through the manipulation of plant microbiomes, as demonstrated in agroecosystems.

1 | Introduction

Forests are substantial terrestrial carbon sinks, storing approximately 45% of terrestrial carbon (Bonan 2008) and accounting for 80% of global plant biomass (Chapin, Matson, and Vitousek 2011). With nearly half of Earth's natural forests lost due to human activities (Crowther et al. 2015), forests now face drastic challenges caused by global warming (IPCC 2023). Increasing temperatures can reduce the soil water content, escalating the frequency, duration and intensity of drought

(Samaniego et al. 2018). Drought, a defining characteristic of this century (Schwalm et al. 2017), is expected to coincide with a warming climate, ultimately diminishing forest resilience and curtailing carbon sequestration (Wolf and Paul-Limoges 2023). Under drought conditions, forests may change from being carbon sinks that absorb carbon dioxide to carbon sources that release it under future climate change (Brienen et al. 2015). Carbon emissions from forests could have considerable positive feedback effects on global climate change (Cox et al. 2000), exacerbating the climate crisis and posing a threat to forest health (Trumbore, Brando, and Hartmann 2015). However, while plant adaptation to climate change is primarily influenced by plant-associated microbiomes (Trivedi et al. 2022), the responses of plant microbiomes to warming and drought in forest ecosystems remain largely unknown (Mishra, Hättenschwiler, and Yang 2020).

A multitude of microbes residing in various compartments (e.g., rhizosphere soil) and plant organs (including endosphere of roots, stems and leaves) collectively form the plant microbiomes (Turner, James, and Poole 2013; Vandenkoornhuyse et al. 2015). These microbiomes play vital roles in enhancing plant growth and nutrient uptake (Hardoim et al. 2015), defending against pathogens (Vannier, Agler, and Hacquard 2019) and improving plant resilience to environmental stresses (Trivedi et al. 2020). Endophytes have been shown to have a positive impact on the stress resistance of trees (Blumenstein et al. 2015; Rodriguez and Redman 2008). The distinction of microbial communities within the root endosphere and within the rhizosphere soil likely arises from the host selection of unique microbial consortia capable of penetrating and thriving in the host environment (Gottel et al. 2011). Understanding the variability in host-selected microbiomes, from soil to plant organs, is essential for comprehending how microbiomes influence plant health (Cregger et al. 2018).

The structure and functions of plant microbiomes undergo changes in response to abiotic stresses and environmental stimuli, such as climate change (Lata et al. 2018; Rodriguez and Redman 2008). Plants may actively cooperate with microbes as a defence mechanism (Durán et al. 2018; Lau and Lennon 2012), leading to the enrichment of specific microbes that enhance plant stress tolerance (Trivedi et al. 2020, 2021). Given that the manipulation of plant microbiomes hold significant potential for reducing greenhouse gas emissions (Singh et al. 2010), many national and international policy agencies have identified enhancing plant productivity in response to climate change through the strategic manipulation of plant microbiomes as a top priority (Trivedi et al. 2020). In particular, plant microbiome engineering has emerged as a strategy to combat drought stress in agroecosystems (Ali et al. 2022), where most of the related research has focused on root-associated microbiomes (Santos-Medellin et al. 2021; Xu et al. 2018) due to the essential roles of roots in nutrient and water uptake from the soil. However, there is a lack of understanding of plant microbiomes in forest ecosystems compared to those in farmland ecosystems (Mishra, Hättenschwiler, and Yang 2020; Terhonen et al. 2019), despite the crucial roles that forests play in combating climate change (Bonan 2008). Some studies have emphasised the positive roles of microbiomes in assisting trees in coping with drought (Khan et al. 2016; Zhang, Zhang, and Huang 2014), suggesting the potential for enhancing forest stability through microbiome interventions. Bridging this knowledge gap is critical for enhancing forest resistance and resilience to global warming through the manipulation of tree microbiomes, as demonstrated in agroecosystems (Trivedi et al. 2022).

The response of forests to climate change is largely mediated by microbes, particularly fungi and bacteria (Baldrian, López-Mondéjar, and Kohout 2023). Fungi, which are known to exhibit a stronger host preference than bacteria (Chen et al. 2022; Tedersoo et al. 2010), are more closely associated with plants (Gan et al. 2022) and play a pivotal role in forest ecosystems. The majority of terrestrial plant species form symbiotic relationships with mycorrhizal fungi (van der Heijden et al. 2015), which in turn has a profound impact on bacterial communities within plant organs (Akyol et al. 2019; Poosakkannu, Nissinen, and Kytöviita 2017). In times of climate change–cased environmental stress, such as drought, the impact on these relationships may become increasingly profound. Drought can directly affect plant physiology, such as decreasing the hydraulic conductance (Choat et al. 2018), and also indirectly influence plant health by altering the dynamics of the fungal communities (Schimel 2018). At present, the proliferation of pathogens associated with climate change is regarded as a significant threat to forest health worldwide (Singh et al. 2023; Trumbore, Brando, and Hartmann 2015). For instance, elevated temperatures have amplified the susceptibility of American chestnut to infections caused by the fungal pathogen *Phytophthora* spp., leading to severe tree mortality events across North America (Gustafson et al. 2022). Moreover, the expansion of *Phytophthora cinnamomi*, exacerbated by global warming, is likely to exert a substantial detrimental effect on native plant populations across various regions around the world (Rigg, McDougall, and Liew 2018; Thompson, Levin, and Rodriguez-Iturbe 2014). Therefore, it is crucial to understand how climate change affects fungal communities in forest ecosystems.

Here, we conducted a pot experiment involving six distinct treatments (warming and/or drought) within two climatic chambers to investigate the alterations in fungal communities. This study encompasses both bulk soil and rhizosphere soil, as well as various plant organs, including the endosphere of roots, stems and leaves of *Schima superba* seedlings. As a representative broadleaf evergreen tree species widely distributed in the subtropical forests of southern China, this focal tree species plays a dominant role in our study region (Kong et al. 2023). It acts as a foundational element that influences both the composition and characteristics of the local community (Yu et al. 2020). Due to its exceptional fire resistance, this species is widely recognised as a preferred option for afforestation in firebreaks (Li et al. 2023; Zhang et al. 2013). Additionally, wood of this species is used in furniture making and in construction owing to its high hardness (Zhang et al. 2019). In a previous study involving seven tree species, which was also one part of the current research, it was observed that climate change exerted the most significant impact on the composition of fungal communities within the rhizosphere soil of *S. superba* (Wu et al. forthcoming; Figure S1). In this study, we used absolute abundances to measure the size

of fungal communities associated with *S. superba*, and our primary objective was to (i) explore how climate change influences fungal community composition along the soil–tree seedling continuum and its relative contribution to variations in fungal communities in each compartment and plant organ; (ii) assess whether fungal community size decreases in response to increasing compartment (as well as plant organ) effects and identify indicators along the soil–tree seedling continuum; and (iii) investigate how climate change affects the migration of fungi from soil to aerial plant organs.

2 | Materials and Methods

2.1 | Seed Collection and Germination

We collected seeds of *S. superba* within a 25-ha (500 × 500 m) stem-mapped forest plot (centred on 27°45′43″ N, 119°11′53″ E) located in Baishanzu Nature Reserve, Zhejiang Province, China. As an integral component of the Forest Global Earth Observatory (ForestGEO) network (https://forestgeo.si.edu/), this plot serves as a critical node in the global monitoring of forest ecosystem dynamics. To ensure that the seeds were devoid of surface contaminants and to minimise the potential for pathogen infection, we used a comprehensive surface sterilisation process. This involved immersion in 70% ethanol for 1 min, followed by 3% sodium hypochlorite for 3 min, followed by 1 more minute in 70% ethanol. The seeds were then rinsed with ion-free water to remove any chemical residues and then air-dried before being stored in a refrigerator at 4°C. In April 2022, we initiated the germination of these seeds in trays filled with sterilised sand in a climate chamber. The chamber was programmed to provide 16 h of daylight, with a light intensity of 20 klx. The temperature regime in the chamber was maintained at 21°C/15°C (light/dark), and the relative humidity was approximately 65%.

2.2 | Soil Mixture and Seedling Transplanting

In June 2022, we collected soil samples from the 0–20-cm depth under adult individuals of *S. superba* within the Baishanzu forest plot. Then, we carefully passed them through a sterilised 2-mm sieve to eliminate any visible debris such as stones and roots. We also collected common background forest soil to minimise the potential impact of differences in soil physicochemical properties among the selected tree species. This soil was also sieved through a 2-mm mesh and subjected to gamma-radiation sterilisation at a dosage of 25 KGray (Zhengjiang Zhengshi Irradiation Technology Co. Ltd., Zhengjiang, China) (McNamara et al. 2003). For each pot (18 cm diameter × 19 cm height), we created a soil mixture that consisted of 20% (by volume) alive in situ soil as inocula, 50% gamma-sterilised background forest soil and 30% gamma-sterilised substrate soil (simulating the addition of nutrients from litters in the field) totalling 3.5 L. This specific composition was designed to ensure that the dynamics of the microbial communities would be influenced by the biotic characteristics of the inoculant, rather than by abiotic factors. A single seedling, approximately 2 weeks of age, was transplanted into the centre of each pot. We took care to replace any seedlings that perished or showed signs of poor growth due to transplant shock within the initial week, ensuring the health and viability of our experimental plants.

2.3 | Experimental Manipulations

The experiment had a 2 × 3 factorial design with two levels of temperature, including no warming and elevated (+3°C), which we chose based on projected global increases of between 2.7°C and 3.2°C by the end of this century (UNEP 2021, 2022). We also examined three levels of drought intensity, including no drought, moderate drought and severe drought. This led to a total of six treatment combinations: (a) a control without warming and drought (CK); (b) moderate drought without warming (D1); (c) severe drought without warming (D2); (d) warming alone (W); (e) moderate drought combined with warming (WD1); and (f) severe drought in conjunction with warming (WD2) (Figure S1). The pot experiment was conducted in two climate chambers, each designed to simulate distinct climatic conditions. We set the temperature to 21°C/15°C (light/dark) for the no-warming chamber and 24°C/18°C (light/dark) for the warming chamber while ensuring a uniform light intensity (20 klx), a consistent photoperiod (16/8 h light/dark) and relative humidity (~65%) across both chambers. We simulated the precipitation conditions in the climate chambers based on field monitoring data from the Baishanzu forest plot over 6 years (2016–2021) before the experiment commenced (Table S1; Supplementary Methods). In this study, drought conditions were simulated by reducing the frequency of watering. Specifically, the soil moisture regime was manipulated by watering the pots every 3 days for the control treatment, once a week for the moderate drought treatment and every 2 weeks for the severe drought treatment. The soil gravimetric moisture content of the pots was calibrated to sustain 70% of their water holding capacity with each watering. It was detected that both warming and drought could substantially reduce the moisture content of potted soil prior to each watering event (Figure S1). This drought treatment design reflects the projected alterations in precipitation patterns under global climate change scenarios, where reductions in rainfall frequency are expected to be accompanied by increases in the intensity of rainfall events (Shortridge 2019; Zhang et al. 2021). Each treatment was replicated 10 times, resulting in a total of 60 pots. During the initial acclimatisation period of the first 2 weeks, all pots received uniform watering and were watered 3–4 times per week. After this uniform watering phase, the pots were subjected to the gravimetric watering regime to maintain the targeted moisture levels throughout the experiment.

2.4 | Pot Harvesting

Given the limited resistance of seedlings to persistent drought stress, potted seedlings were harvested after 20 weeks of the pot experiment to ensure an adequate supply of alive seedlings for subsequent analyses. Given the relatively high costs associated with absolute quantitative sequencing and the constraints imposed by limited funding, we randomly selected five pots with alive seedlings per experimental treatment, thereby ensuring a representative and reliable dataset for subsequent analyses. To establish a one-to-one correspondence between each soil sample and the seedling within the same pot, we opted against creating

a composite sample for the five selected samples. This approach facilitated comparative analyses among individual specimens. Subsequently, we carefully extracted the seedlings, rhizosphere soil and bulk soil (see below).

2.5 | Soil and Seedling Sample Processing

First, seedlings were removed from their pot and carefully shaken by hand to ensure that any loosely bound soil particles around the roots were completely removed while taking care not to damage the roots. Next, each root was placed in a 500-mL beaker, and the soil particles adhering to the roots were rinsed with phosphate-buffered saline (PBS) and transferred to a 50-mL tube. This process allowed us to obtain rhizosphere soil. Subsequently, the collected rhizosphere soil samples were centrifuged at 8000 rpm for 10 min. The resulting pellet was then stored at −80°C for genomic DNA extraction. We passed the bulk soil samples through a sterilised 2-mm sieve to remove visible roots. Each sample was divided into three subsamples: one for molecular analysis (stored at −80°C), another for the analysis of soil physicochemical properties (air- or oven-dried) and the third for measurements of ammonium (NH_4^+-N) and nitrate (NO_3^--N) contents (stored at 4°C). For the extraction of endophytic DNA from plant organs, approximately 5 g of plant tissue, including roots, stems and leaves, was processed separately following a previously described method for surface sterilisation (Gao et al. 2021). It is important to note that the sterilisation procedure utilised sodium hypochlorite and effectively removed approximately 98% of the microbes on the exterior of plant organs (Richter-Heitmann et al. 2016), precluding the characterisation of the plant surface–associated fungal communities. The treated plant samples were frozen at −80°C until DNA extraction. Overall, each sample of the soil–tree seedling continuum was systematically divided into two compartments (the bulk soil and rhizosphere soil) and three plant organs (the endosphere of roots, stems and leaves).

2.6 | DNA Extraction and Fungal ITS rRNA Gene Amplification

All samples from different compartments and plant organs were selected for fungal identification using the AccuITS absolute quantification sequencing method (Yang et al. 2023). This method allowed us to determine the absolute abundance of fungi accurately and reliably. Genomic DNA from each sample was extracted using the FastDNA SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA, USA) following the manufacturer's instructions. The integrity of the extracted DNA was assessed through gel electrophoresis, and the concentration and purity were quantified using a Qubit 3.0 spectrophotometer (Thermo Fisher Scientific, USA). To achieve absolute quantification, spike-in internal standards with known gradients of copy numbers were added to the experimental DNA samples (Smets et al. 2016). This allowed for back-normalisation and calculation of the absolute abundances of all community members. The primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′) were used to amplify the ITS1 hypervariable regions (Luan et al. 2020). The PCR reaction mixture contained 1 μL of 10× Toptaq Buffer, 0.8 μL of 2.5 mM dNTPs, 0.2 μL of each primer (10 μM), 0.2 μL of Toptaq DNA Polymerase and 1 μL of template DNA and ddH_2O to a final volume of 10 μL. The PCR programme was as follows: 94°C for 2 min, followed by 25–27 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s and elongation at 72°C for 1 min, with a final extension at 72°C for 10 min (ABI 2720 Thermal Cycler, Thermo Fisher Scientific, USA). All amplification reactions were performed in triplicate, and the PCR products were gel-purified using VAHTS DNA Clean Beads (Vazyme, China). The purified amplicons were subjected to paired-end sequencing (2 × 250 bp) on the Illumina NovaSeq platform at Genesky Biotechnologies Inc. (Shanghai, China).

The raw sequencing data were processed in QIIME2 (Bolyen et al. 2019). Adaptor and primer sequences were trimmed using the Cutadapt plugin. Quality control and assignment of amplicon sequence variants (ASVs) were performed using the DADA2 plugin (Callahan et al. 2016). Taxonomic assignments of ASV representative sequences were performed using the UNITE database (version 9.0) (Nilsson et al. 2019) for ASVs. Spike-in sequences were identified, and reads were counted. A standard curve was generated for each sample based on the read-counts versus spike-in copy number. The absolute copy number of each ASV in each sample was calculated using the corresponding read-counts. The spike-in sequences, which are not part of the sample flora, were removed from the subsequent analysis. Fungal absolute abundances were expressed as copies per gram of freeze-dried soil or plant tissue. In total, there were 8890 fungal ASVs in 150 samples (six treatments × five replicates × (two compartments + three plant organs)).

2.7 | Statistical Analyses

All statistical analyses were conducted using R (version 4.3.2). To assess the effects of experimental warming and drought on fungal communities, we examined the richness, absolute abundance, number of specific ASVs within each compartment and plant organ, and number of shared ASVs across compartments and plant organs. The percentage increase or decrease in the number of specific or shared ASVs was quantified by calculating the ratios of the difference in the number of specific or shared ASVs between warming and non-warming conditions (as well as between drought and non-drought conditions) to the number of that under non-warming condition (as well as under non-drought condition). We conducted two-way ANOVAs (MacFarland and Yates 2021) to test the effects of warming and drought on fungal communities in a full two-factorial design, ensuring that the assumptions of normality and homoscedasticity were met. When necessary, the data were log-transformed to achieve normality (West 2022). In cases where these assumptions were not satisfied, we employed the non-parametric Scheirer–Ray–Hare test as an alternative (Mangiafico 2024). The effects of warming, drought and compartments (as well as plant organs) on fungal absolute abundances were modelled using generalised linear models (GLMs) via the *glm* function from the *stats* package. To elucidate the relationships between fungal community composition and soil properties, we utilised the *mantel_test* function from the *linkET* package (Huang 2021). Moreover, indicator species analysis was conducted using the *multipatt* function from the

indicspecies package (De Cáceres and Legendre 2009). Fungal functional groups, that is, ectomycorrhizal fungi (EMF), plant pathogens, soil saprotrophs, wood saprotrophs, litter saprotrophs, mycoparasites and yeasts, were categorised based on the FungalTraits database (Põlme et al. 2021).

Fungal β-diversity was quantified using the Bray–Curtis distance matrices and visualised through principal coordinate analysis (PCoA) (Gao et al. 2020). To assess the significance of fungal community dissimilarity under different treatments along the soil–tree seedling continuum, we used PERMANOVA as implemented in the *adonis2* function (with the argument *by = margin*) in the *vegan* package (Oksanen et al. 2022). We then disentangled the separate effects of species turnover (which is defined as the extent of changes in species composition along predefined gradients; Anderson et al. 2011; Vellend 2001) from changes in species richness among treatments on each compartment and plant organ using the *beta.pair* function in the *betapart* package (Baselga et al. 2023). Note that species turnover is different from species loss (which refers to the absence of some species from certain sites; Baselga 2009) and species dispersion (which refers to the unidirectional movement of individuals away from their place of birth; Levin et al. 2003; Tamme et al. 2014). In these analyses, we partitioned the total β-diversity into two indices, where β_{BTU} is the turnover component of the Bray–Curtis dissimilarity and β_{BNE} is the species gain or loss component of the Bray–Curtis dissimilarity.

Causal path modelling was used to explore the direct and indirect effects of warming and drought on the seedling traits, using the *lavaan* R package (Rosseel 2012). The first principal coordinate deprived from the PCoA conducted on the relevant Bray–Curtis dissimilarity matrix, using the *vegan* package (Oksanen et al. 2022), was employed to represent the fungal community structure. All predictors were standardised to have a mean of 0 and an SD of 1. Support for the causal path models was evaluated with the following criteria: a non-significant Chi-square test ($p > 0.05$), goodness-of-fit index > 0.90 and root-mean-square error of approximation < 0.08 (Schermelleh-Engel, Moosbrugger, and Müller 2003). Partial least-squares path modelling was used to evaluate the direct and indirect effects of climate change on fungal communities, using the *plspm* R package (Sanchez, Trinchera, and Russolillo 2024).

A source-tracking analysis was employed to estimate the potential sources of the fungal communities in each compartment and plant organ. Specifically, the first step in developing a source model of the plant microbiome involves establishing an a priori model based on known sources and relationships among fungi present in different compartments and plant organs (Xiong et al. 2021). Subsequently, the model was examined using SourceTracker (Knights et al. 2011) based on the Bayesian approach with default parameters. To provide a deeper understanding of how warming and drought influence the distribution and abundance of fungal species, we introduced two novel metrics: the species abundance loss (SAL) and the species relative migration ratio (SRMR). These indices were designed to quantify the directional changes in fungal communities in response to our experimental treatments. The SAL was calculated as the difference in absolute abundance between the lower and upper compartments or plant organ of the soil–tree seedling continuum, which reflects the loss of fungal species in the lower compartment or plant organ as they migrate upward. The SRMR was the ratio of the absolute abundance of fungi in the upper compartment or plant organ to that in the lower compartment or plant organ. This calculation provided a measure of the relative migration or movement of fungal species from the lower to the upper compartment or plant organ, indicating the colonisation status of the species. The effects of warming and drought on both the SAL and SRMR along the soil–tree seedling continuum were also tested by two-way ANOVAs.

3 | Results

3.1 | Climate Change Significantly Decreases the Number of Specific ASVs in the Bulk Soil and Rhizosphere Soil

Our results showed that the rhizosphere soil had the greatest number of specific ASVs and the greatest fungal richness (Figures S2 and S3). Warming and drought significantly decreased the number of specific ASVs (as well as fungal richness) in the bulk soil (specific ASVs: 39.67%; richness: 30.33%; $p < 0.001$) and rhizosphere soil (specific ASVs: 18.30%–25.88%; richness: 14.37%–17.49%; $p < 0.01$), respectively (Figure 1a; Figure S4). The number of shared ASVs between the bulk soil and rhizosphere soil also decreased significantly in response to warming (24.19%, $p < 0.01$; Figure 1a). Moisture and available phosphorous (AP) were the strongest soil variables influencing fungal communities in both the bulk soil and rhizosphere soil (Figure 1b). Total nitrogen (TN, $p < 0.05$) and total phosphorus (TP, $p < 0.01$) also significantly affected the fungal communities in the bulk soil and rhizosphere soil, respectively (Figure 1b). Moreover, drought significantly decreased moisture (21.44%–29.25%, $p < 0.01$) but significantly increased the content of TP (5.28%–11.24%, $p < 0.001$) and AP (67.31%–82.31%, $p < 0.001$; Figure S5). Warming also significantly increased the TP content (4.99%, $p < 0.05$; Figure S5).

3.2 | Climate Change Exerts the Most Pronounced Influence on Fungal Community Composition Within the Leaf Endosphere

PCoA coupled with PERMANOVA indicated that the variations in fungal communities were mainly explained by compartments and plant organs ($R^2 = 0.12$, $p = 0.001$), followed by warming ($R^2 = 0.02$, $p = 0.002$) and drought ($R^2 = 0.02$, $p = 0.003$) (Figure 2a). Hierarchical clustering analysis revealed clear and separate clustering among the bulk soil, rhizosphere soil, roots, stems and leaves (Figure 2b). There was a significant difference in fungal communities between the soil (including bulk soil and rhizosphere soil) and the endosphere (including the endosphere of roots, stems and leaves) (Figure S6). Within each compartment and plant organ, the intensity of the climatic effects on the fungal community varied (Figure 2c). We found a dominant influence of climatic treatments on leaf fungi ($R^2 = 0.46$, $p = 0.001$), followed by rhizosphere soil ($R^2 = 0.31$,

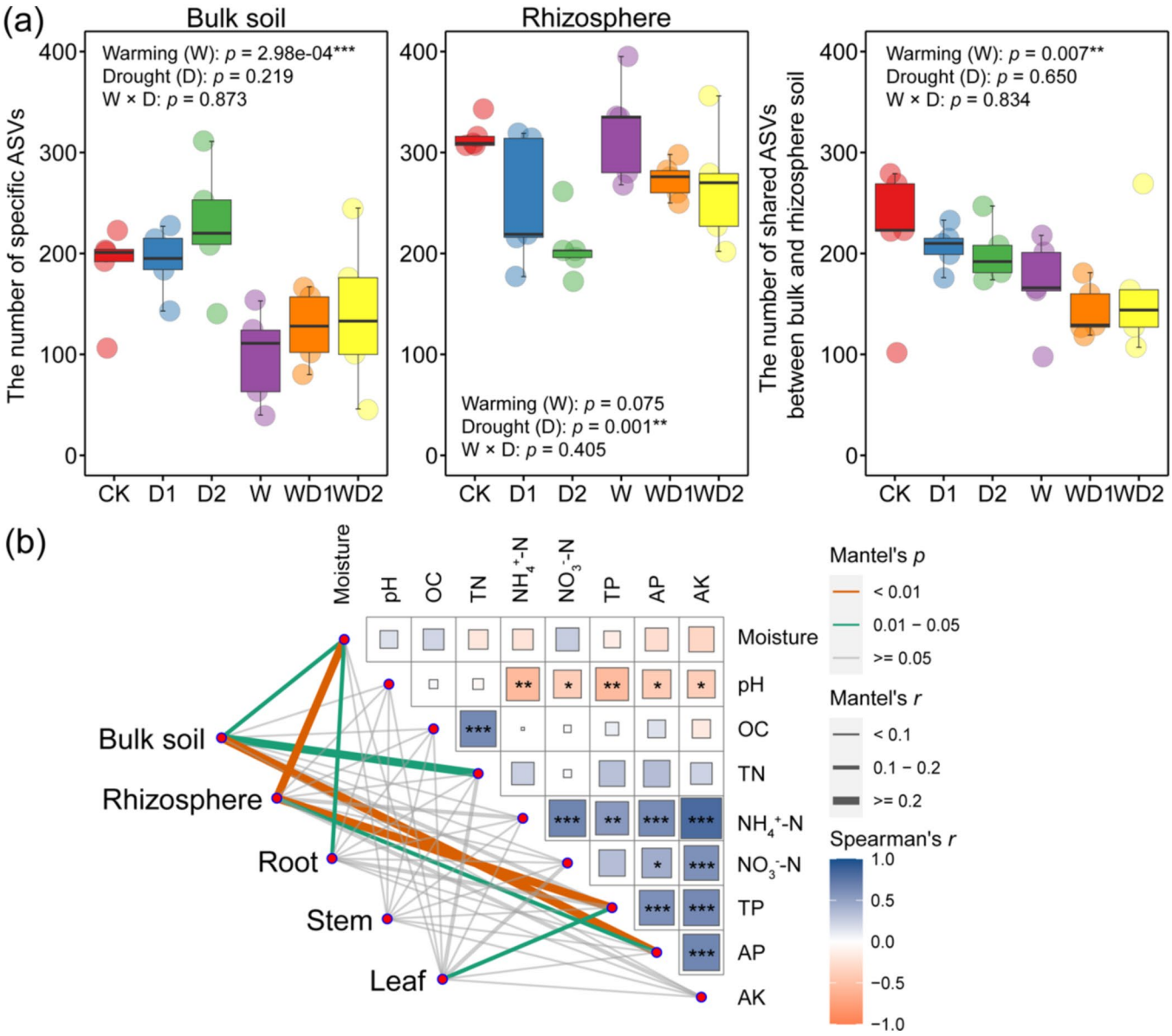

FIGURE 1 | Climate change significantly decreases the number of specific and shared ASVs in the bulk soil and rhizosphere soil. (a) The number of specific and shared ASVs in the bulk soil and rhizosphere soil under different treatments. Boxplots are shown, where the thick horizontal line shows the median, boxes represent the first and third quartiles and whiskers represent either the minimum and the maximum values of the data or 1.5 times the interquartile range of the data. Asterisks indicate significant results from the two-way ANOVA. ***$p < 0.001$ and **$p < 0.01$. The small circles represent the raw data points, which are horizontally jittered to avoid overlap. CK, neither warming nor drought; D1, moderate drought alone; D2, severe drought alone; W, only a 3°C increase in temperature; WD1, moderate drought plus warming; WD2, severe drought in conjunction with warming. (b) Relationships of the fungal community composition in each compartment and plant organ with soil properties. Edge width corresponds to Mantel's *r* value, and the edge colour denotes the statistical significance. ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$. Pairwise correlations of these variables are shown with a colour gradient denoting Spearman's correlation coefficient. AK, available potassium; AP, available phosphorous; NH_4^+-N, ammonium nitrogen; NO_3^--N, nitrate nitrogen; OC, organic carton; TN, total nitrogen; TP, total phosphorus. [Colour figure can be viewed at wileyonlinelibrary.com]

$p = 0.001$), bulk soil ($R^2 = 0.26$, $p = 0.001$), stems ($R^2 = 0.19$, $p = 0.041$) and roots ($R^2 = 0.19$, $p = 0.135$) (Figure 2c; Figure S7). Specifically, the fungal community compositions in the rhizosphere soil (warming: $R^2 = 0.10$, $p = 0.001$; drought: $R^2 = 0.12$, $p = 0.006$) and leaves (warming: $R^2 = 0.22$, $p = 0.001$; drought: $R^2 = 0.13$, $p = 0.011$) were significantly affected by both warming and drought (Figure S7). Warming also notably altered the fungal community compositions in the bulk soil ($R^2 = 0.08$, $p = 0.005$) and roots ($R^2 = 0.06$, $p = 0.032$) (Figure S7). Moreover, the shifts in community composition among treatments in the bulk soil, rhizosphere soil, roots and stems were primarily attributed to species turnover, while the differences in the leaves were mainly due to species gain or loss (Figure 2d). The partial least-squares path modelling result showed that climate change not only directly affected fungal communities (standardised direct coefficient = −0.55) but also indirectly affected fungal communities by altering plants (standardised indirect coefficient = −0.16) (Figure S8).

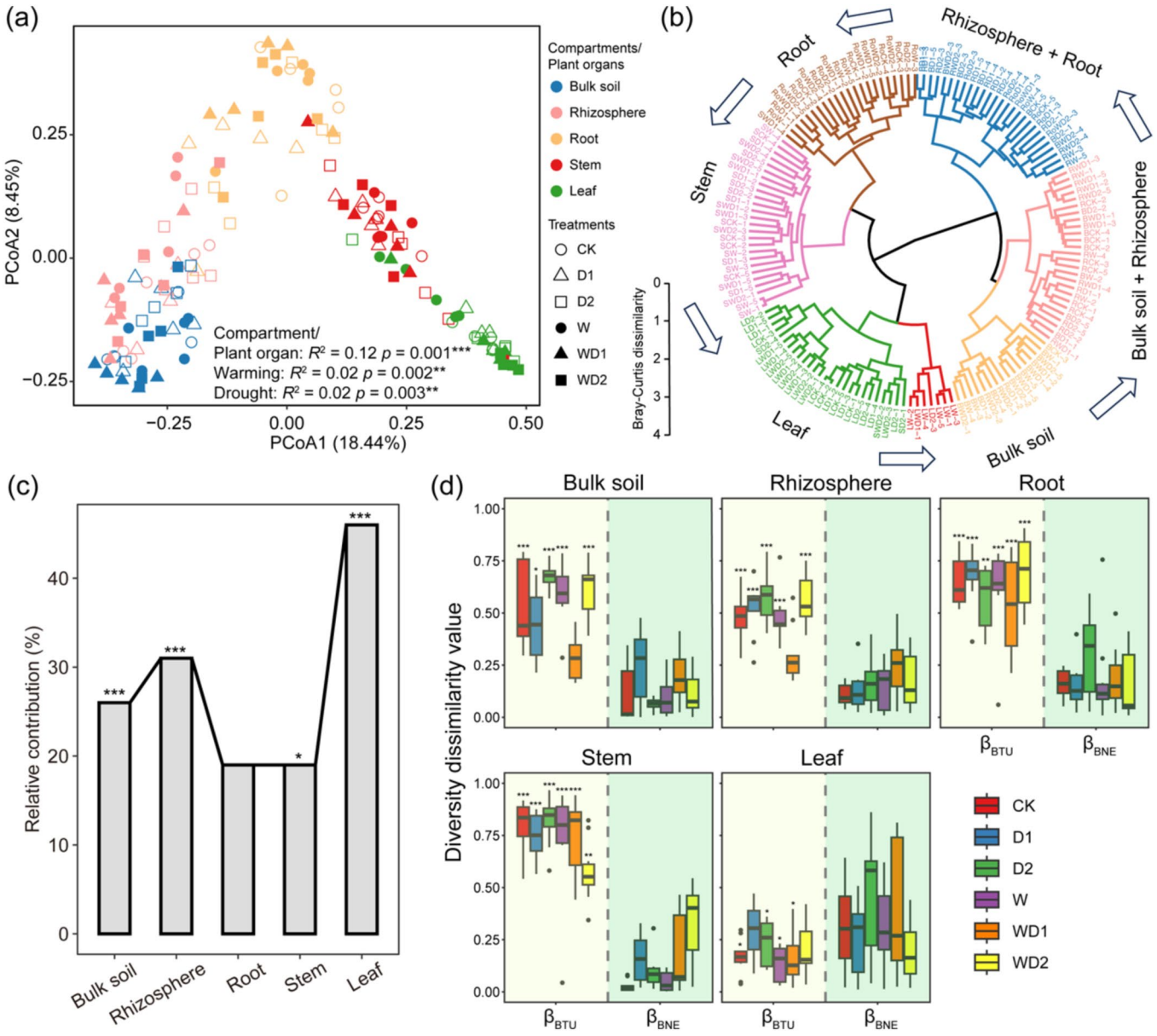

FIGURE 2 | Variations in the fungal β-diversity along the soil–tree seedling continuum under different treatments. (a) Principal coordinate analysis (PCoA) ordinations of the Bray–Curtis dissimilarity matrices with permutational analysis of variance (PERMANOVA), showing a significant association of the fungal community composition with compartments and plant organs ($R^2=0.12$), warming ($R^2=0.02$) and drought ($R^2=0.02$). ***$p<0.001$ and **$p<0.01$. (b) Hierarchical clustering based on the Bray–Curtis distances of fungal ASVs from all samples ($n=150$). Samples were clustered according to Ward.D2 method. (c) Contributions of treatments to the variations in fungal communities in each compartment or plant organ based on PERMANOVA. ***$p<0.001$ and *$p<0.05$. (d) Partitioning of the total β-diversity (Bray–Curtis index) among treatments into the components of species turnover (β_{BTU}) and species loss or gain (β_{BNE}) along the soil–tree seedling continuum. Boxplots are shown, where the thick horizontal line shows the median, boxes represent the first and third quartiles and whiskers represent either the minimum and the maximum values of the data or 1.5 times the interquartile range of the data. Asterisks indicate significant differences between β_{BTU} and β_{BNE} under the same treatment according to *t*-test. ***$p<0.001$, **$p<0.01$ and *$p<0.05$. CK, neither warming nor drought; D1, moderate drought alone; D2, severe drought alone; W, only a 3°C increase in temperature; WD1, moderate drought plus warming; WD2, severe drought in conjunction with warming. [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Climate Change Significantly Alters the Absolute Abundance of Fungal Phyla

On the soil–tree seedling continuum, Basidiomycota and Ascomycota were the most dominant groups in the belowground and aboveground parts, respectively (Figure 3a). Overall, compartments and plant organs ($p=7.85e\text{-}14$), rather than climate factors (warming: $p=0.53$; drought: $p=0.27$), significantly affected the total fungal absolute abundance (Figure 3a). Specifically, the total fungal absolute abundance was significantly decreased from the bulk soil to the leaves (Figure 3b). Only the total fungal absolute abundance in the rhizosphere soil ($p=0.009$) and leaves ($p=0.008$) was significantly decreased in response to warming and the interaction of warming and drought, respectively (Table S2). The abundances of Chytridiomycota ($p=5.62e\text{-}03$), Glomeromycota ($p=5.53e\text{-}03$) and Rozellomycota ($p=0.02$) were significantly negatively affected by drought (Table S3). Moreover, warming significantly decreased the absolute abundance of

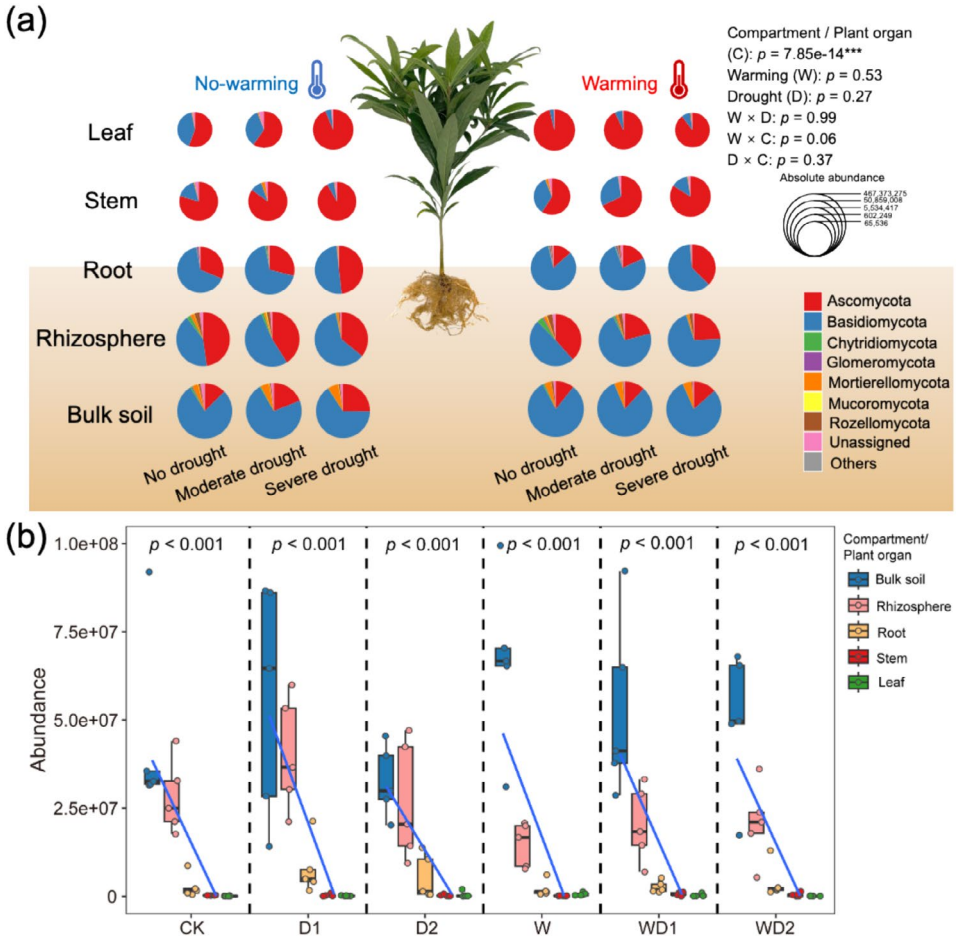

FIGURE 3 | Fungal community composition and total absolute abundance along the soil–tree seedling continuum. (a) Fungal community composition at the phylum level along the soil–tree seedling continuum under different treatments. Asterisks depict significant results from generalised linear models. ***$p < 0.001$. Statistical significance is based on Wald type II χ^2 tests ($n = 150$). The circle size is proportional to the fungal absolute abundances. Different colours indicate different fungal phyla. (b) The total fungal absolute abundance decreased significantly from the bulk soil to the leaves under different treatments. Boxplots are shown, where the thick horizontal line shows the median, boxes represent the first and third quartiles and whiskers represent either the minimum and the maximum values of the data or 1.5 times the interquartile range of the data. CK, neither warming nor drought; D1, moderate drought alone; D2, severe drought alone; W, only a 3°C increase in temperature; WD1, moderate drought plus warming; WD2, severe drought in conjunction with warming. [Colour figure can be viewed at wileyonlinelibrary.com]

Ascomycota in the rhizosphere soil ($p = 1.53e\text{-}04$) and roots ($p = 0.044$) (Figure S9). To further ascertain which microbial taxa were responsible for the observed community differences among compartments and plant organs, we used species indicator analysis to discover significant associations between microbial taxa and compartments (as well as plant organs). The full lists of indicators and their corresponding indicator values can be found in Table S4, which revealed 58 indicator genera in the bulk soil, 40 in the rhizosphere soil, 4 in the roots, 52 in the stems and 11 in the leaves.

3.4 | Climate Change Drives Changes in Specific Functional Groups

Different functional groups of various compartments and plant organs respond differently to climate change. For example, warming significantly reduced the absolute abundance of EMF in the bulk soil (38.45%, $p = 0.02$) and that of plant pathogens (66.17%, $p = 0.02$), soil saprotrophs (70.85%, $p = 3.52e\text{-}05$) and yeasts (78.79%, $p = 0.003$) in the rhizosphere soil but significantly increased that of mycoparasites (213.23%, $p = 0.01$) and yeasts (291.61%, $p = 0.004$) in the leaves (Table S5). Drought significantly reduced the absolute abundance of EMF in the rhizosphere soil (53.74%–82.92%, $p = 0.002$) but significantly increased that of mycoparasite in the bulk soil (89.82%–91.43%, $p = 0.04$) (Table S5). Furthermore, warming led to a significant increase in the richness and phylogenetic diversity of leaf plant pathogens, and specific pathogens existed only in specific climatic treatments (Figure 4a,b). Most notably, causal path modelling results showed that there was an indirect causal pathway between warming and leaf area mediated by pathogen phylogenetic diversity (Figure 4c), but no mediating role of pathogens was observed in other compartments and plant organs (Figure S10).

3.5 | Climate Change Significantly Influences the Migration of Fungi From Soil to Plant Organs

The findings, derived from the source model of plant microbiome, suggest that plant-associated fungal communities

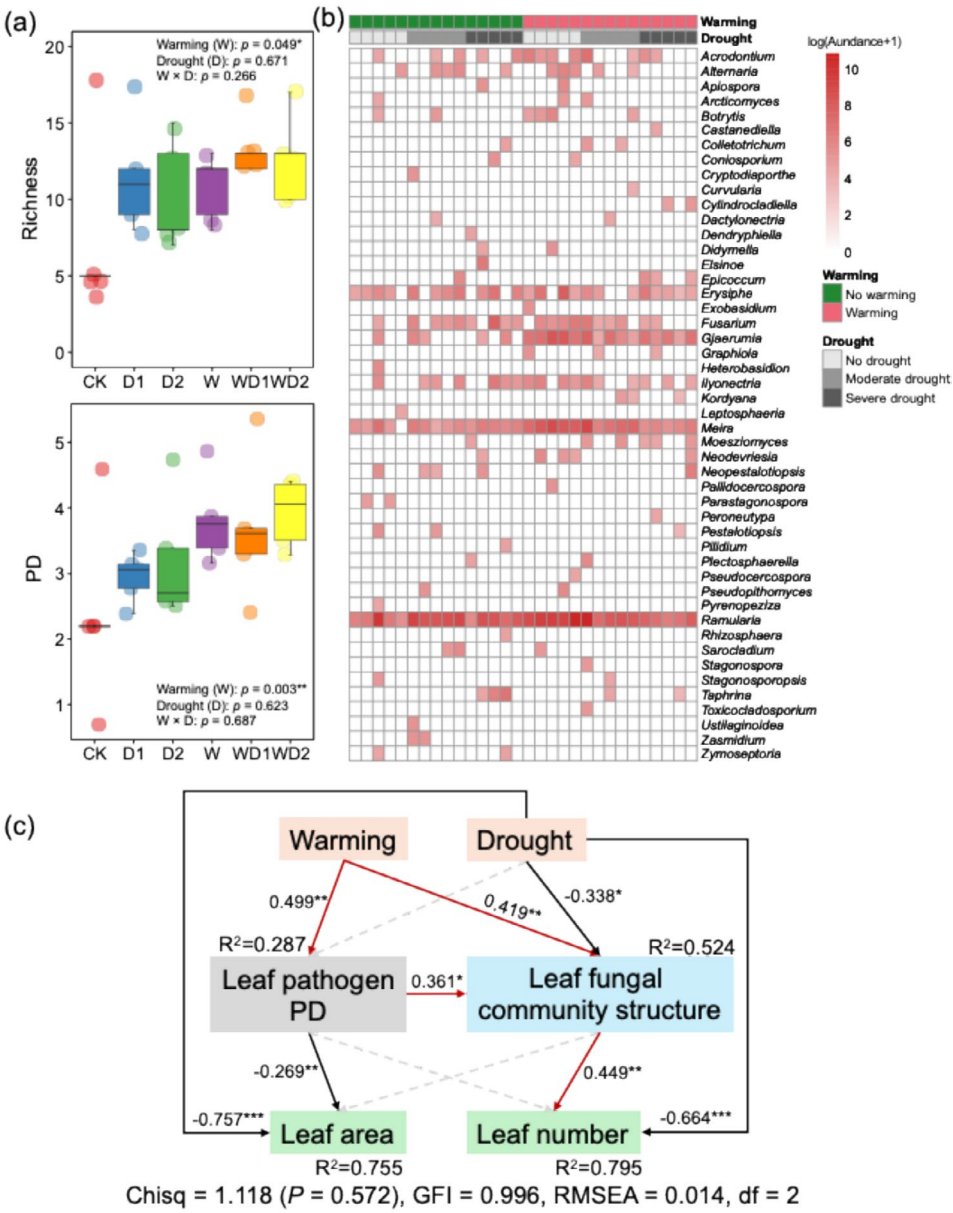

FIGURE 4 | Effects of warming and drought on the leaf plant pathogens and seedling traits. (a) Effects of warming and drought on the richness and PD (Faith's phylogenetic diversity) of plant pathogens in the leaves. Boxplots are shown, where the thick horizontal line shows the median, boxes represent the first and third quartiles and whiskers represent either the minimum and the maximum values of the data or 1.5 times the interquartile range of the data. Asterisks indicate significant results from the two-way ANOVA. $^{**}p < 0.01$ and $^{*}p < 0.05$. The small circles represent the raw data points, which are horizontally jittered to avoid overlap. CK, neither warming nor drought; D1, moderate drought alone; D2, severe drought alone; W, only a 3°C increase in temperature; WD1, moderate drought plus warming; WD2, severe drought in conjunction with warming. (b) The absolute abundance of plant pathogens (at genus level) in the leaves under different treatments. (c) Effects of warming and drought on leaf area and leaf number mediated by plant pathogens and fungal community structure. Solid and dashed arrows represent significant and non-significant relationships, respectively. Red and black arrows indicate positive and negative relationships, respectively. Values adjacent to arrows represent standardised path coefficients. R^2 donates the proportion of variance explained for each variable. Significant levels of each predictor are $^{***}p < 0.001$, $^{**}p < 0.01$ and $^{*}p < 0.05$. [Colour figure can be viewed at wileyonlinelibrary.com]

predominantly originated from bulk soil and underwent a progressive filtration process through different compartments and plant organs (Figure S11). Specifically, the rhizosphere soil, root endosphere and leaf endosphere exhibited a high proportion of taxa that were selectively retained from a nearby fungal species pool, with known source values exceeding 91% (Figure S11). Warming significantly increased and decreased the fungal SAL and SRMR (particular in Ascomycota and wood saprotrophs migrating from bulk soil to rhizosphere soil, $p < 0.01$; and Basidiomycota migrating from stems to leaves, $p < 0.05$), respectively (Table 1; Tables S6 and S7). Moreover, warming also significantly decreased the SRMR of soil saprotrophs ($p < 0.001$) and yeasts ($p = 0.006$) migrating from bulk soil to rhizosphere soil but increased that of plant pathogens ($p = 0.038$) migrating from roots to stems (Table 1; Tables S6 and S7). Although drought did not significantly affect the SAL and SRMR based on total fungal abundance (Table 1), it did affect the migration of different fungal groups (Tables S6 and S7). For example, drought

TABLE 1 | Treatment effects on the species abundance loss (SAL) and the species relative migration ratio (SRMR) along the soil–tree seedling continuum based on two-way ANOVA.

Compartment/plant organ			Warming (W)	Drought (D)	W × D
Bulk soil ↓ Rhizosphere	SAL	F	5.133	0.389	0.099
		$pr(>F)$	**0.033**	0.682	0.906
	SRMR	F	6.832	0.155	0.191
		$pr(>F)$	**0.015**	0.857	0.827
Rhizosphere ↓ Root	SAL	F	6.057	0.876	0.503
		$pr(>F)$	**0.021**	0.429	0.611
	SRMR	F	0.554	0.806	0.387
		$pr(>F)$	0.464	0.459	0.683
Root ↓ Stem	SAL	F	0.762	1.092	1.089
		$pr(>F)$	0.391	0.352	0.353
	SRMR	F	0.549	0.455	2.201
		$pr(>F)$	0.466	0.640	0.133
Stem ↓ Leaf	SAL	F	3.949	0.066	0.020
		$pr(>F)$	0.070	0.937	0.889
	SRMR	F	0.859	0.579	5.064
		$pr(>F)$	0.363	0.568	**0.015**

Note: Significant effects ($p < 0.05$) are given in bold.

notably increased and decreased the SAL ($p = 0.049$) and SRMR ($p = 0.002$) of the EMF migrating from the bulk soil to the rhizosphere soil, respectively (Table S7). Additionally, the SRMR of plant pathogens ($p = 0.035$) migrating from the bulk soil to the rhizosphere soil significantly increased in response to drought (Table S7).

4 | Discussion

4.1 | Effects of Climate Change on Fungal Communities Vary Across Different Compartments and Plant Organs

The nutrient-rich environment of bulk soil and rhizosphere soil serves as a magnet for a lot of microbes, rendering these habitats one of the most vibrant compartments (Raaijmakers 2015). In this study, soil fungi exhibited greater vulnerability to climate fluctuations than that of endophytic fungi (Figure 1a; Figure S4). This distinction is underscored by the observed alterations in soil characteristics due to climate change (Figure S5), which have been identified as predictive indicators of soil fungi (Figure 1b). The reduction in fungal richness attributed to warming is predominantly governed by the soil microclimate, which exerts a significant filtering effect on the pre-existing fungal taxa present within bulk soil. Drought-induced reductions in soil moisture curtail the mobility of nutrients and the supply of substrate to microbes, and they simultaneously enhance soil aeration (Manzoni, Schimel, and Porporato 2012). However, the dual impacts of drought may collectively contribute to the decline in fungal richness within the rhizosphere soil (Figure S4). Moreover, drought can induce changes in root exudation profile, which in turn affects the composition and structure of microbial communities indirectly (Zhalnina et al. 2018).

Unlike rhizosphere colonisation, the establishment of endophytic competence necessitates specific traits and intricate interactions between the soil-borne fungi of the rhizosphere and the host plant immune system (Turner, James, and Poole 2013). Due to their stress tolerance, endophytic fungal communities within aboveground organs may exhibit a greater degree of coexistence (Whipps et al. 2008). Although this can explain why endophytic fungal richness is not affected by climate change (Figure S4), climate-induced changes in plant immunity, such as the suppression or even collapse of effector-triggered immunity (Cheng, Zhang, and He 2019; Desaint et al. 2021), may precipitate dysbiosis within the endophytic microbiome (Trivedi et al. 2022), thereby exacerbating disease progression in various plant pathosystems (Cheng, Zhang, and He 2019).

Our findings elucidate the pronounced influence of climate change on the leaf endophytic fungal community composition (Figure 2c; Figure S7), which is distinct from that observed for α-diversity (Figure S4), suggesting that the adaptive capacity of leaves to climate change is intricately linked to the presence of particular fungal taxa within the endophytic community. For example, specific pathogens existed only in specific climatic treatments (Figure 4b), which implies that the overall diversity of fungal communities may not be as critical as the presence of specific, functionally significant fungal species in determining the response of leaves to changing climatic conditions. In this study, we detected an increase in the pathogen diversity within the leaves under warming,

as evidenced by the data obtained from absolute quantitative sequencing (Figure 4a), but no disease symptoms were observed on the leaves throughout the duration of the 20-week experiment. Leaves are immediately subjected to increased temperatures, whereas soil serves as a mitigating factor, postponing the effects of the temperature increase on the rhizosphere (Hoefle et al. 2024). Additionally, the role of certain fungal endophytes in modulating stomatal conductance on the leaf surface is well documented (Arnold and Engelbrecht 2007). For instance, *Beauveria bassiana*, an entomopathogenic fungus known to reside as an endophyte, has been shown to enhance stomatal conductance in response to drought stress (Ferus, Barta, and Konôpková 2019).

4.2 | Habitat Selection Effects on Fungal Communities

The pronounced effects of compartments and plant organs on the fungal community composition observed herein for *S. superba* (Figure 2a) have also been documented in previous studies involving *Populus deltoides* and *Populus trichocarpa* × *deltoides* (Cregger et al. 2018), as well as *Salix purpurea* and *Salix miyabeana* (Tardif et al. 2016). This can be attributed to factors such as habitat selection (i.e., the specific microenvironments of different compartments and plant organs), which forces fungi to adopt unique adaptation strategies (Dastogeer et al. 2020; Vorholt et al. 2017). Environmental filtering has emerged as a selective force influencing fungal communities in these compartments and plant organs (Cregger et al. 2018). Varied exposures to environmental conditions contribute to the diverse physicochemical properties observed in these compartments and plant organs (Fitzpatrick et al. 2020). For instance, fungal communities in bulk soil and rhizosphere soil are predominantly influenced by moisture and AP (Figure 1b), while those in roots and leaves are shaped primarily by the mechanical properties of the organs and the nutrient supply from the host plant as reported previously (Mercado-Blanco 2015). In other words, soil predictors play a minimal role in explaining the community composition of endophytes. Each compartment or plant organ harbours a highly distinctive microbial community, and the presence of obligate endophytes-specific taxa that reside within the endosphere (Figure S2)—may depend strictly on the plant microenvironment for survival (Hardoim, van Overbeek, and Elsas 2008).

A marked decrease in fungal richness and absolute abundance was noted during the transition from soil to endophytic environments (Figure 3b; Figure S3), indicating the strict requirements for fungal specialisation to thrive within plant organs. This specialisation means that many fungi cannot colonise plant organs, allowing only a few fungi, capable of sustaining a symbiotic relationship with their host plant, to dominate the endophytic communities. This pattern of colonisation is likely due to the strong selectivity of the host plant and increased host specificity at the soil–root interface (Trivedi et al. 2020), which serves as a selective barrier that restricts endophytic colonisation to certain fungal groups. According to co-evolution theory, plants attract beneficial microorganisms by emitting signalling molecules and then exerting selective pressure through their immune systems and by providing specific nutrients and habitats (Cordovez et al. 2019; Foster et al. 2017). Rhizodeposition and root exudation by the host plant in the root zone enhance the chemoattraction and colonisation of the rhizosphere soil, thereby fostering the development of unique and diverse rhizosphere microbiomes (Bais et al. 2006). This also explains why rhizosphere soil had the highest fungal richness and the greatest number of specific ASVs (Figures S2 and S3). Additionally, rhizodeposition contributes to the selection of specific endophytic assemblages, with substrate-driven selection in the rhizosphere continuing to influence the composition of the endospheric community (Cregger et al. 2018).

4.3 | Indicator Sensitive to Climate Change and Compartments as Well as Plant Organs

Our study identified the drought-sensitive fungal phyla, including Glomeromycota, Chytridiomycota and Rozellomycota (Table S3). The decrement in Glomeromycota due to drought is particularly alarming, given that their role in forming extensive hyphal networks, which facilitate nutrient uptake and enhance soil water retention (Pauwels, Graefe, and Bitterlich 2023). Chytridiomycota, predominantly water-film inhabiting organisms reliant on zoospores for dispersal, are particularly susceptible to drought (Volk 2013). The effects of reduced precipitation on the less characterised Rozellomycota warrant further investigation. In light of these findings, it is imperative to continue monitoring and studying the responses of these critical fungal groups to drought, which will inform future management strategies.

We characterised a diverse array of indicators within different compartments and plant organs, and many of these are plant pathogens. For instance, indicator groups in the bulk soil, including *Erysiphe*, *Moesziomyces*, *Acrodontium*, *Ganoderma* and *Teratosphaeria* (Table S4), may have detrimental effects on plant hydraulic performance and drought tolerance (Oliva, Stenlid, and Martínez-Vilalta 2014), as evidenced by reduced stomatal conductance (Hajji, Dreyer, and Marçais 2009). Moreover, they can lead to the induction of tyloses that obstruct water transport, resulting in decreased xylem conductance (Yadeta and Thomma 2013). In the rhizosphere soil, Leotiomycetes encompasses numerous plant pathogens (Walker et al. 2011), potentially exerting a profound impact on plant health. Likewise, woody plant organs become more susceptible to pathogens under drought stress (Jactel et al. 2012). In the stem, we detected *Pestalotiopsis*, a genus known to harbour plant pathogen responsible for various aerial plant diseases (Maharachchikumbura et al. 2014). This pathogen is known to cause leaf lesions and can spread into the stems (Chen et al. 2012), further impacting the plant health and functionality. Conversely, we also observed beneficial impacts of certain fungi, such as *Paraphoma* in the stem, which has been shown to boost plant growth, especially under water-deficient conditions (He et al. 2021; Li et al. 2019). This is achieved through the improvement of total biomass, nutrient concentration and antioxidant enzyme activities in the host plants (He et al. 2021; Li et al. 2019).

4.4 | Effects of Climate Change on the Migration of Fungi From Soil to Aerial Plant Organs

Elucidating the potential sources and environmental processes shaping plant microbiomes is crucial for understanding the

intricate interactions among plants, soil and microbes (Zhang et al. 2017). Soil acts as a reservoir, providing the initial inoculum for root microbiome development, the rhizosphere serves as a nurturing environment and the endosphere is a restricted microbial habitat (Vandenkoornhuyse et al. 2015). In this study, it was detected that bulk soil serves as the primary reservoir for fungi present in plant organs (Figure S11), corroborating previous findings reported in *Populus tremula*×*tremuloides* (Fracchia et al. 2024), *Arabidopsis* (Bai et al. 2015) and some crops (Xiong et al. 2021; Zarraonaindia et al. 2015). Generally, the adaptation of soil microbes to an endophytic lifestyle depends on their ability of soil microbes to penetrate the endodermis and pericycle, gain access to the xylem and achieve systemic colonisation (Compant, Clément, and Sessitsch 2010). Through a 30-day study monitoring the growth of *Populus tremula*×*tremuloides* seedlings, recent findings have revealed that the initial chemoattraction of the dominant members of the shoot microbes occurred in the rhizosphere, followed by their subsequent transit through roots to shoots (Fracchia et al. 2024). Furthermore, by tracking the infection process of rice by rhizobia tagged with green fluorescent protein, it has been demonstrated that these microbes initially colonised the surface of the rhizoplane (Chi et al. 2005). This was followed by endophytic colonisation within the roots and then ascended endophytic migration into the stems and leaves (Chi et al. 2005). Consequently, leaf endophytic fungi are inferred to be transported from roots to aboveground leaves through the internal plant tissue transmission (Xiong et al. 2021). Many endophytes spread systemically within plants via the xylem to various organs, including leaves, where they can influence water-transport-related traits and affect tree hydraulic functioning (Oliva, Stenlid, and Martínez-Vilalta 2014). For example, vascular wilt pathogens (e.g., *Ceratocystis* of stem indicator species; Table S4) can cause the formation of tyloses, which block water transport in xylem conduits (Oliva, Stenlid, and Martínez-Vilalta 2014; Yadeta and Thomma 2013). Moreover, it is important to recognise that, despite the absence of dispersal factors such as wind, insect visits and water splashing for plants grown in climate chambers, there remains a potential for fungal colonisation on stem epidermis and phylloplane through aerosols (Warren 2022). This may subsequently facilitate the colonisation of the endosphere within stems and leaves to a certain degree.

Climate change is expected to influence the community dynamic of plant microbiomes by altering the initial inoculum from bulk soil (Bazany et al. 2022; Santos-Medellin et al. 2021), as illustrated in Figure S12. Water is the basic transport medium for microbes (Tecon and Or 2017), and as the soil becomes drier due to the increasing temperature, the decrease in water potential leads to a sharp decline in microbial diffusion and mobility (Schimel 2018). In response to water limitation, plants have the capacity to recruit specific microbes from the surrounding environment to modulate the assembly of root-associated microbial communities (Fitzpatrick et al. 2018). Additionally, the rhizosphere can also select for the colonisation of specific microbes through changes in plant root exudates mediated by warming (Sasse, Martinoia, and Northen 2018). Ascomycota, renowned for their saprophytic decomposition prowess (Treseder et al. 2014), are pivotal in nutrient cycling. The observed reduction in the abundance of Ascomycota due to warming may be ascribed to enhanced carbon availability at the elevated temperature, thereby diminishing their proliferation and dominance (Zhong et al. 2023). Such warming-induced changes could culminate in a decelerated decomposition process of forest litter, with consequential impacts on organic matter accumulation and nutrient availability. Moreover, we found that Basidiomycota is the most dominant fungal phylum in the underground system of *S. superba*, contrasting with the findings in *Populus deltoides* and *Populus trichocarpa*×*deltoides* (Cregger et al. 2018), which may be attributed to the fact that specific tree species recruit specific dominant soil microbes under the guidance of root exudates (Berg and Smalla 2009).

Despite the fact that the prolonged drought treatment led to a gradual increase in seedling mortality, which necessitated the implementation of the pot experiment lasting only 20 weeks, this study effectively captured the initial and rapid ecological responses of microbial communities to climatic stress. Given previous research indicating potentially thermal adaptation in microbes following prolonged warming (Bradford et al. 2008), it is crucial to emphasise that long-term experiments are essential for gaining a comprehensive understanding of how microbial communities adapt to climate change over time, potentially maintaining the functions microbes fulfil in the soil–plant continuum.

In this study, absolute abundance profiles offer a more precise tool for delineating microbial community dynamics in the face of climate change. This is particularly significant given that relative sequencing data require cautious interpretation to avoid the misrepresentation of microbial population dynamics (Props et al. 2017), in which an increase in the relative abundance of certain microbes inevitably leads to a corresponding decrease in others. Moreover, addressing the mechanisms underlying the responses of microbiomes to climate change along the soil–tree seedling continuum is vital for developing strategies aimed at leveraging microbial power to improve forest health. Future studies are needed to revolve microbial biotechnology to sustainably enhance forest stability by harnessing the potential of microbiome-based products.

Author Contributions

X.W. and Y.L. designed and performed most of the experiments and data interpretation. J.Y. and G.L. helped with experiments and data interpretation. X.W. wrote the manuscript. M.D.M. and Y.L. critically revised the manuscript. Y.L. directed the study and critically revised the manuscript for important intellectual content. X.W. and Y.L. conceived the project, designed the experiments and directed the study. All authors read and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Raw sequence reads are deposited in the National Center for Biotechnology Information (NCBI) database: BioProject PRJNA1193141.

The data and scripts used in this study can be found at https://github.com/XianWu2024/Soil-tree-seedling-continuum.git.

Benefit-Sharing Statement

Benefits from this research will be gained from depositing our data and results on public databases.

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Supporting Information

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