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Microbial Life History Mediates the Drought-Induced Decrease in Wood Decomposition in Subtropical Forests

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ABSTRACT

Progressive intensification of drought regimes worldwide threatens wood decomposition - a critical biogeochemical process in forest carbon cycling. However, the interactions between microbial strategies, wood traits and microclimate in regulating wood decomposition remain poorly understood under drought conditions. In a throughfall exclusion experiment (control 35% and 70% rainfall reduction) across 12 tree species, we found that drought-induced reductions in wood CO_2 efflux rates were primarily driven by wood traits (density and carbon reduction) and shifts in fungal *K*/*r*-strategies. Coarse wood debris with higher Basidiomycota and lower Ascomycota abundance decomposed faster. Significant positive correlations were observed between fungal *K*/*r*-strategies and wood CO_2 efflux under control, 35%, and 70% rainfall reduction, while bacterial strategies showed no correlation. Our findings highlight the greater drought sensitivity of fungi than bacteria, emphasising their critical role in forest carbon dynamics and informing carbon models to improve the prediction of climate-biosphere feedback in the changing world.

1 | Introduction

Decomposition is a key process in which dead plant tissues break down and are transformed into bioavailable organic forms (Bradford et al. 2016; Joly et al. 2023). This process involves two simultaneous pathways: a portion of plant residues is incorporated into the soil, while another fraction is released into the atmosphere as an exogenous carbon (C) source (Prescott and Vesterdal 2021). Globally, deadwood decomposition is estimated to release approximately 10.9 billion tons of CO_2 into the atmosphere each year (Seibold et al. 2021), which is pivotal for global forest C balance and nutrient recycling.

Human activities such as forest management and fossil fuel combustion have substantially altered natural water cycles, triggering more intense and frequent droughts (Xu et al. 2019). Drought generally reduces plant productivity and CO_2 uptake by limiting photosynthesis. However, drought can also increase tree mortality and woody debris accumulation, potentially enhancing CO_2 emissions through wood decomposition (Chen, Vogel, et al. 2022). Previous studies have primarily assessed wood decomposition using the mass loss method (Glassman et al. 2018; Guo et al. 2021), but the magnitude of wood-derived CO_2 emissions under different drought intensities remains unclear.

Wood decomposition is generally regulated by climate, substrate quality and decomposer activity (Zhang et al. 2008; García-Palacios et al. 2013; Bradford et al. 2016). Plant species-specific wood structure and chemical composition, such as wood traits (e.g., wood density and nutrient concentrations), explain about 30%–50% of decomposition rates at global scales (Cornwell et al. 2008; Hu et al. 2018). These interspecific differences in wood traits, shaped by both phylogenetic legacy and environmental filtering over evolutionary timescales, serve as crucial indicators of plant function and ecosystem diversity, leading to non-synchronous decomposition rates (Sardans et al. 2021; Rowland et al. 2013; Weedon et al. 2009). For instance, tree species with resource-acquisition strategies, which have a low C/N and lignin/N ratios, tend to have faster decomposition rates than those with conservative strategies (Aerts 1997; Chave et al. 2009; Canessa et al. 2021). Additionally, different kinds of wood traits exhibit divergent trajectories during decomposition. For example, physical characteristics (e.g., wood porosity and water-holding capacity) gradually increase over time, while wood density and structural stability progressively decrease (Guo et al. 2021; Maillard et al. 2021). While the regulatory influence of wood traits on decomposition is well documented, how drought alters these traits and subsequently shapes decomposition processes remains unclear.

In the past decades, microbial communities are increasingly recognised to be critical in understanding decomposition processes, with recent advances in molecular tools and analytical methods (Bani et al. 2018; Glassman et al. 2018; Maillard et al. 2022). For example, microbial communities mediate both direct and indirect effects of climate on decomposition, challenging traditional paradigms that focused solely on abiotic drivers (Bradford et al. 2017). In the context of climate change, drought reshapes decomposition dynamics through moisture limitation, inducing divergent effects with inhibition, acceleration or nonlinear changes (Joly et al. 2019; Lee et al. 2014; Piaszczyk et al. 2022). These effects likely result from the interaction between wood traits and different substrate-dwelling microbes in response to drought. Shifts in microbial substrate preferences and the proportion of microbial communities associated with different life-history strategies (*r*- or *K*-strategists) strongly impact deadwood structural stability and the rate of CO_2 release (Malik et al. 2020; Zeng et al. 2022). Generally, microbes with *r*-strategists thrive in environments with rich labile C due to their rapid growth rates, whereas those with *K*-strategists are more efficient with low-availability C sources in more stable environments (Chen, Jing, et al. 2022). The ratio of fungal and bacterial oligotroph (representing *K*-strategists) to copiotroph (representing *r*-strategists) taxa is commonly used to evaluate microbial life history strategies based on 16S rRNA and ITS sequencing (Zeng et al. 2022). Fungal and bacterial communities exhibit distinct sensitivities to environmental changes and tree species (Malik et al. 2020; Martiny et al. 2017). Therefore, understanding how microbial communities interact with wood traits and the microclimate to influence wood decomposition is crucial under varying drought intensities.

Subtropical forests play a crucial role as significant sinks for global CO_2 concentration (Jiang et al. 2023). However, climate models predict a continuous drying in the subtropics, potentially impacting forest productivity and tree mortality. Therefore, it is essential to gain a comprehensive understanding of the effects of different drought intensities on deadwood decomposition across various tree species in the subtropics. In this study, we conducted a deadwood decomposition experiment involving 12 tree species under a gradient of drought intensity (CK: control, D1: 35% rainfall reduction treatment, and D2: 70% rainfall reduction treatment) in a subtropical forest. Our aims were to address the following two questions: (1) How does wood decomposition vary under different drought intensities? (2) How do microbial strategies, wood traits and microclimate interact to regulate deadwood decomposition? We hypothesised that: (1) drought-induced reductions in wood moisture would significantly reduce wood CO_2 efflux with greater effects in the D2 treatment relative to the D1 one; and (2) microbial *K*/*r*-strategists interacted with wood traits and microclimate would influence wood decomposition, and fungal *K*/*r*-strategists would be more important than bacterial ones due to fungi's greater resilience to moisture limitations.

2 | Materials and Methods

2.1 | Study Sites

The experimental site was conducted at Tiantong National Forest Ecosystem Observation and Research Station (29°48′ N, 121°47′ E) in Zhejiang province, China. The study area has a subtropical monsoon climate with an average annual temperature of 16.2°C and rainfall of 1374 mm in recent decades. The soil in the study site is Acrisol based on the FAO soil classification, with 55.5% silt, 37% clay and 6.8% sand (Zhou et al. 2020). In the study area, the vegetation is a subtropical evergreen broadleaf forest, with *Michelia maudiae* Dunn, *Castanopsis fargesii* Franch and *Schima superba* Gardn. et Champ as the dominant tree species (Jiang et al. 2023).

2.2 | Experimental Design

Rainfall reduction experiments were established in July 2013 using a randomised complete block design with three blocks (Figure S1). The three blocks have similar topography (i.e., elevations, slope and aspect), site properties and plant species. Treatments included control (CK), 35% rainfall reduction (D1) and 70% rainfall reduction (D2) with three replications. Each treatment is randomly set in these three blocks on a total of nine 25 m × 25 m plots (Figure S1). The grooved transparent plastic plates ("V" shape) were used to exclude the canopy precipitation and fixed at a height of 2.5 m above the ground (Hu et al. 2020). Each sample plot was enclosed with 2.5 mm thick PVC plates and inserted to a depth of 2 m below ground to exclude disturbance from lateral movement of water. Buffer zones were set at a minimum distance of 5 m between each plot. Footpaths have been constructed in the sample plots to avoid the impact of human activities as far as possible (Zhou et al. 2020).

Deadwood samples from 12 tree species in subtropical forests were collected and randomly placed in 9 treatment plots (3 drought treatments × 3 replications) in September 2020. Thus, a total of 108 logs (12 species × 9 plots) were randomly put down in study sites for decomposition experiments. The average length of the deadwood stems was 1.5 m (including bark) and the average diameter was 14.3 ± 0.34 cm. Deadwood species included *Sassafras tzumu* (Hemsl.) Hemsl, *Phoebe chekiangensis* C. B. Shang, *M. maudiae*, *Liriodendron chinense* (Hemsl.) Sarg, *Liquidambar formosana* Hance, *Castanopsis carlesii* (Hemsl.) Hayata, *Castanopsis sclerophylla* (Lindl.) Schottky, *Quercus chenii* Nakai, *Cyclobalanopsis gracilis*, *Acer elegantulum* Fang & P. L. Chiu, *S. superba* and *Kalopanax septemlobus* (Thunb.) Koidz, with about 40–60 years (Table S1). All tree species were Angiosperms and the life form is macrophanerophytes. Moreover, these selected 12 species are dominant in subtropical forests, representing a range of wood traits and ecological strategies, which allowed us to examine how different tree species respond to drought intensities. Additionally, these species span different tree families in this area, such as Lauraceae, Fagaceae and Magnoliaceae, ensuring the diversity of functional traits (Table S1). In November 2021, we collected 5 cm thick discs from the distal ends of each stem. The discs were collected freshly, with no visible signs of decomposition at the time of sampling. They were then homogenised by mixing wood bark, sapwood and heartwood to form composite samples. These samples were subsequently placed in black bags and stored for chemical analysis.

2.3 | Wood CO_2 Efflux

To measure deadwood decomposition, a respiration collar with a diameter of 10 cm and a height of 5 cm was placed on the top-center of each deadwood sample, and it was secured with aluminium wire. The gap between each collar and the sample was sealed with silicone glue. We regularly checked, re-sealed with silicone glue and reinforced the aluminium wire every month since September 2020. Thus, one respiration collar was placed on each log, with one log per tree species at each plot, totalling 12 collars per plot and 108 collars across all plots.

Wood decomposition rate was detected in the field using a portable LI-COR 8100 infrared gas analyser (LI-COR Inc., Lincoln, NE, USA) at the middle of each month from November 2020 to November 2021. All debris such as plant litter was removed from the respiration collar prior to measurement. Measurements were taken between 9:00–11:00 am on a sunny day (Hu et al. 2020), and each measurement was taken approximately every 3 days. The annual cumulative wood respiration (CWR) was calculated by using the trapezoidal area method as Equation (1).

$$\mathrm{CWR} = \sum \frac{1}{2} \times \frac{\left(\mathrm{WR_m} + \mathrm{WR_{m+1}}\right) \times \mathrm{t} \times 12}{1{,}000{,}000} \tag{1}$$

where the CWR is the cumulative wood respiration ($\mathrm{g\,C \cdot m^{-2} \cdot yr^{-1}}$), $\mathrm{WR_m}$ and $\mathrm{WR_{m+1}}$ are the wood respiration ($\mathrm{\mu mol \cdot m^{-2} \cdot s^{-1}}$) measured in month m and month $m+1$, t is the total number of days in month m. 12 indicates the molar mass of CO_2-C ($\mathrm{g \cdot mol^{-1}}$) and 1,000,000 is the time conversion coefficient.

To explore effects of different drought intensities on wood CO_2 efflux amongst 12 tree species, drought effects were calculated as follows (Asensio et al. 2024):

$$\text{Drought effect} = \left(\left(\mathrm{M_d} - \mathrm{M_c}\right) / \mathrm{M_c}\right) \times 100\,\% \tag{2}$$

$$\text{Drought effect variance} = 100 \times (\mathrm{e}\ (\ln \mathrm{VR}) - 1) \tag{3}$$

where $\mathrm{M_d}$ and $\mathrm{M_c}$ are the mean values of wood CO_2 efflux in drought and control plots, respectively. $\mathrm{VR} = (\mathrm{SD_d})^2/\mathrm{N_d}\ (\mathrm{M_d})^2 + (\mathrm{SD_c})_2/\mathrm{N_c}\ (\mathrm{M_c})^2$. $\mathrm{SD_d}$ and $\mathrm{SD_c}$ are the standard deviations in the drought and control plots; $\mathrm{N_d}$ and $\mathrm{N_c}$ are the sample numbers in the drought and control plots.

During wood CO_2 efflux measurements, a thermocouple probe integrated with the LI-COR 8100 system was used to measure wood temperature at the depth of 1 cm in the wood surface. A wedge-shaped section was removed from the original thick discs, oven-dried at 70°C until a constant mass was reached, and weighed to determine dry mass. Wood moisture content was calculated as the difference between wet mass and dry mass, divided by the dry mass.

2.4 | Wood Traits

A 5-cm thick disc wood was cut from each sample in November 2020 and 2021, and a part of wood was overdried and smashed for the determination of wood traits. We measured wood density ($\mathrm{g\,cm^{-3}}$) as the ratio of dry mass (g) to volume ($\mathrm{cm^3}$). The volume was determined using the water displacement method, where the sample was submerged in water, and the displaced water volume was recorded. Wood carbon (C) and nitrogen (N) concentration of initial and after one year of decomposition was determined using a CN analyser (Elementar Vario MAX, Germany). Wood phosphorus (P) concentration was determined by the Mo-Sb colorimetry method. We multiplied the C, N and P concentrations by wood density ($\mathrm{g \cdot cm^{-3}}$), which was considered to better characterise the absolute C and nutrients loss during wood decay (Hu et al. 2020; Russell et al. 2015). Wood lignin concentration was determined by acidolysis-titration using UV spectrophotometry (Kahl et al. 2017). The method of anthrone-sulfuric acid colorimetry and visible spectrophotometry was used to determine cellulose and hemicellulose concentration in wood (Guo et al. 2021). Wood lignin/N ratio was calculated as wood lignin divided by N density.

After one year decomposition, the loss of wood density, C, N, P, lignin, cellulose, hemicellulose and lignin was calculated as follows:

$$\Delta\text{Wood traits} = \left(\mathrm{W_o} - \mathrm{W_i}\right) / \mathrm{W_i} \tag{4}$$

where $\mathrm{W_o}$ is the wood trait after decomposition, and $\mathrm{W_i}$ is the initial wood trait. Smaller values of ΔWood traits indicate greater losses of wood traits.

Principal component analysis (PCA) was used to create a new index to represent all wood traits, and the first axis explained 34.6% variance of wood traits (Table S4). We thus used PC1 in further correlation and SEM analyses.

2.5 | Wood Microbial Community

Wood samples were obtained from the wood discs and stored in a −80°C refrigerator in preparation for the determination of microbial community composition and structure after one year of decomposition. Wood bacterial communities were amplified and sequenced by the V4 region of the 16S rRNA gene using the specific primers 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACNVGGGTWTCTAAT-3′) (Chen, Jing, et al. 2022). We accessed wood fungal communities by the internal transcribed spacer (ITS) region with the primers ITS5-1737F (GGAA GTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC) (Huang et al. 2022). Microbial primers were synthesised by Invitrogen (Invitrogen, Carlsbad, CA, USA). The constructed amplicon library was sequenced PE250 using the Illumina Nova 6000 platform (Guangdong Magigene Biotechnology Co. Ltd. Guangzhou, China) and the sequences were clustered by operational taxonomic units (OTU). Constrained Principal Coordinate Analysis (CPCoA) was used to project the multidimensional characteristics of wood microbial composition onto a two-dimensional space, enabling the detection of differences in bacterial and fungal diversity between different treatments. To classify microbial life-history strategies, we categorised bacterial and fungal taxa as copiotrophs (*r*-strategists) and oligotrophs (*K*-strategists) based on sequencing data and microbial abundance based on methods from Li et al. (2021) and Zeng et al. (2022). The microbial strategies were quantified using the oligotroph to copiotroph ratio (O/C; Table S2). Additionally, we validated the classification by examining fungal functional groups using the ectomycorrhizal/saprotrophic ratio and the bacterial 16S rRNA operon copy number. Details of the classification criteria and computational methods are provided in the Supplementary Methods. Wood-decaying fungi abundance, including white rot fungi, brown rot fungi and soft rot fungi, were identified through the FUNGuild (Nguyen et al. 2016).

2.6 | Statistical Analysis

To assess drought intensity effects on wood CO_2 efflux, wood traits and microbial parameters, we used linear mixed models (LMM, *lme4* package) with drought treatment as a fixed effect and tree species and block as random effects. To evaluate differences in cumulative wood CO_2 efflux, wood microclimate, wood traits and microbial properties amongst tree species, we performed a one-way analysis of variance (ANOVA) followed by Tukey's post hoc test for multiple comparisons. ANOVA was conducted using the *aov* function and post hoc comparisons were performed using the *TukeyHSD* function in R (R Core Team 2023). Generalised linear models were used to examine the relationships between the loss of wood traits, wood microbial oligotroph/copiotroph ratios, and wood CO_2 efflux using package "*stats*". Considering the potential implications of studying the phylogeny of multiple tree species, we then used Bayesian phylogenetic linear mixed models to reveal the role of phylogeny in wood decomposition with 12 tree species under drought (Sardans et al. 2021). Drought treatment was set as a fixed factor, phylogeny and tree species were set as the random factors. Phylogeny aimed to explain the part of the variance by long-term evolutive distances amongst species, and species factor aimed to explain ancestry related explanations of variance not related with phylogenetic distances such as phenomenon's epigenetic evolution and convergent or divergent evolution. This test allows us to know the intra-species variance explanation in the random factors. Correlation analysis was conducted to explore the relationship between microbial strategies and changed wood traits with spearman method by "*corrplot*" package.

Furthermore, we used the Random Forest analysis to explore the main controlled factors of wood CO_2 efflux by '*rfPermute*' package, and the ranking method was ground on comparing the percentage increase in mean square error (% lncMSE). The variable was more important with the higher % lncMSE. To explore the relationship between wood CO_2 efflux and one of three impactor groups—wood microclimate (wood temperature, moisture), altered wood traits (ΔWood density, ΔC density, ΔN density, ΔP density, ΔCellulose, ΔLignin, ΔLignin/N), and wood microbial properties (microbial O/C, fungal and bacterial O/C, ECM/saprotrophic, *rrn* copy number, Shannon index, diversity, white rot, soft rot and brown rot)—while controlling other two factors, partial correlation analysis was conducted using the "*ppcor*" package in R.

Structural equation modelling (SEM) was conducted to evaluate the direct and indirect effects of microclimate, wood traits and wood microbial community strategies on regulating wood decomposition, as well as the standardised total effect (direct effects plus indirect effects) of each variable using the package "*lavaan*" (Rosseel 2012). Model indicators including *p*-values ($p > 0.05$), Root Mean Square Error of Approximation (RMSEA < 0.06), Chi-Square, and Comparative Fit Index (CFI) indices were used to assess the goodness of model fit. The optimal model was compared according to the minimum value of Akaike Information Criterion (AIC). All variables were checked for normality, and log transformation was conducted when necessary to satisfy the model's assumptions. All analyses were performed with R 4.3.2 (http://cran.r-project.org/).

3 | Results

3.1 | Wood CO_2 Efflux of 12 Trees Amongst Rainfall Reduction Treatments

On average, cumulative wood CO_2 efflux across all species was 1749.7, 1334.8 and 962.8 $g\,C \cdot m^{-2} \cdot yr^{-1}$ under the control, 35% rainfall reduction (D1), and 70% rainfall reduction (D2) treatments, respectively (Figure 1a). Under ambient conditions, the greatest amount of CO_2 efflux was released from the *L. formosana* at 3395.0 ± 37.6 (mean ± SE) $g\,C \cdot m^{-2} \cdot yr^{-1}$, which was about 5.5 times greater than the minimum from *P. chekiangensis* (622.5 ± 24.1) in 2021 (Figure S3). For drought effects, cumulative wood CO_2 efflux across all species was significantly decreased by 18.8% and 42.0% under the D1 and D2 treatments compared with the control, respectively (Figure 1b).

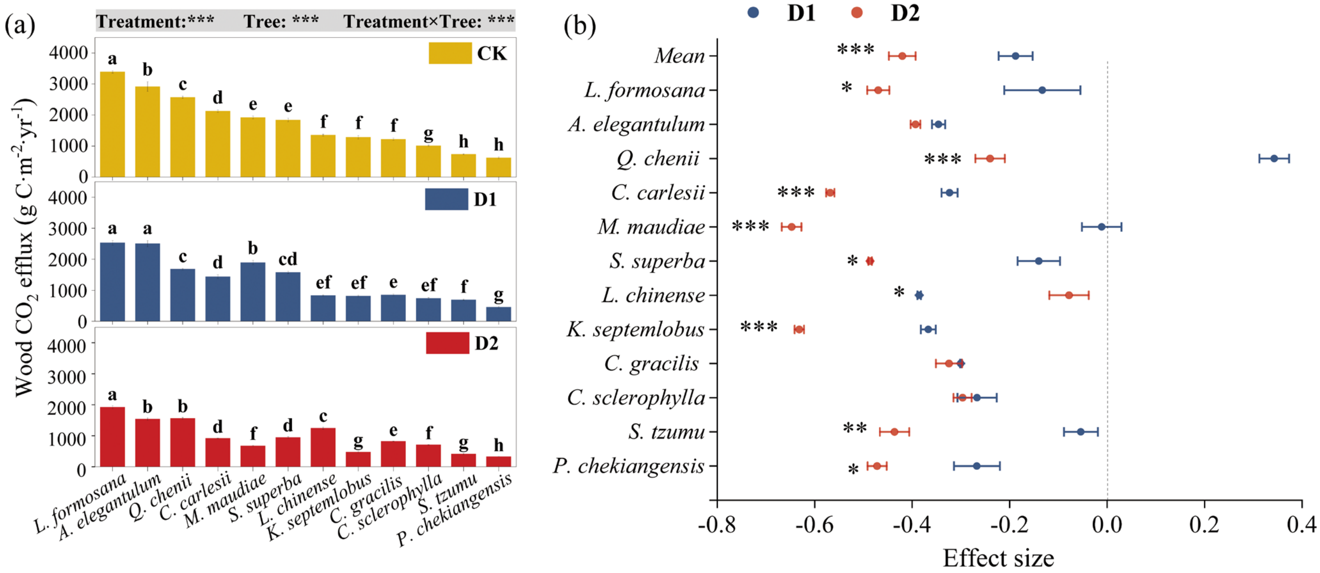

FIGURE 1 | Accumulative wood CO_2 efflux (a) and the drought effects (b) in different rainfall reduction treatments amongst 12 tree species. Error bars represent the mean standard error. Different lowercase letters denote significant differences at $p < 0.05$ among tree species. CK, control; D1, 35% rainfall reduction treatment; D2, 70% rainfall reduction treatment. Tree: Wood tree species; Treatment included CK, D1 and D2 rainfall reduction levels; Treatment × Tree: The interaction effects of wood and drought treatments and the same below. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Amongst 12 species, tree phylogeny, species and intraspecific factors explained 77.1% of the variation in wood CO_2 efflux for both control and drought conditions (Table S5). Phylogenetic signal analysis revealed weak phylogenetic signals for wood CO_2 emissions (Table S6). Wood moisture content decreased by 18.1% and 49.3% under the D1 and D2 treatments, respectively. The linear model showed that both wood moisture content and temperature had a positive relationship with wood CO_2 efflux (Figure S2).

3.2 | Microbial Life-History Strategy Under Two Drought Treatments

Microbial oligotroph/copiotroph (O/C) ratio represented microbial life-history strategy in this study. Drought significantly decreased microbial O/C ratio and fungal O/C ratio, but had no significant effects on bacterial O/C ratio (Figure 2). Wood CO_2 efflux had significant positive relationships with microbial and fungal O/C ratios (Figure 2). However, there was no significant linear relationship between bacterial O/C ratio and wood CO_2 efflux (Figure 2).

For the copiotroph taxa, Ascomycota abundance experienced an increase under drought treatments, exhibiting a negative correlation with wood CO_2 efflux. In contrast, Basidiomycota abundance, characterised as an oligotroph taxon, decreased under drought and was positively associated with wood CO_2 efflux, showing an opposite trend with Ascomycota (Figure 3b). Amongst 12 tree species, tree phylogeny, species and intraspecies variance factors explained a large amount of total variance of microbial (62.5%) and fungal O/C ratio (51.6%), but only 8.02% of bacterial O/C ratio. Wood-decaying fungi, particularly white rot and soft rot fungi, showed positive relationships with wood CO_2 efflux (Figure 3b).

3.3 | Wood Traits and Microbial Properties Under Different Drought Treatments

Drought slowed down the reduction in wood density, C, cellulose and P concentrations, while it stimulated the losses in wood N concentration and produced an increase in the lignin/N ratio (Figure S5). There were significant negative correlations of wood CO_2 efflux with the changes in wood density, C, cellulose, and P concentration, whereas changes in lignin and lignin/N ratio were positively correlated with wood CO_2 efflux (Figure 4a). Microbial and fungal O/C ratios had strong negative correlations with the drought-induced changes in wood density, C, and P density (Figure 4b). Amongst 12 tree species, phylogeny, species and intraspecies variance explained 70.9% of the variance in wood C loss (Table S5).

3.4 | Interactions of Wood Traits, Microbial Strategies and Microclimate on Wood CO_2 Efflux Under Drought

Drought-induced decrease in wood density was the primary factor explaining variations in wood CO_2 efflux, followed by wood moisture content (Figure 5a,b). Amongst microbial variables, microbial and fungal O/C ratios, ECM/saprotrophic fungi ratio, and the presence of wood decaying fungi significantly impacted wood decomposition (Figure 5a). Partial correlation analyses revealed that microbial and fungal O/C ratios had no significant correlation with wood CO_2 efflux without accounting for wood microclimate and wood trait properties. However, after controlling for wood microclimate, the bacterial O/C ratio showed a positive relationship with wood CO_2 efflux ($p < 0.05$, Figure 5b). In contrast, wood moisture content was always significantly correlated with wood CO_2 efflux whether or not controlling for wood microclimate, wood traits and wood microbial properties (Figure 5b).

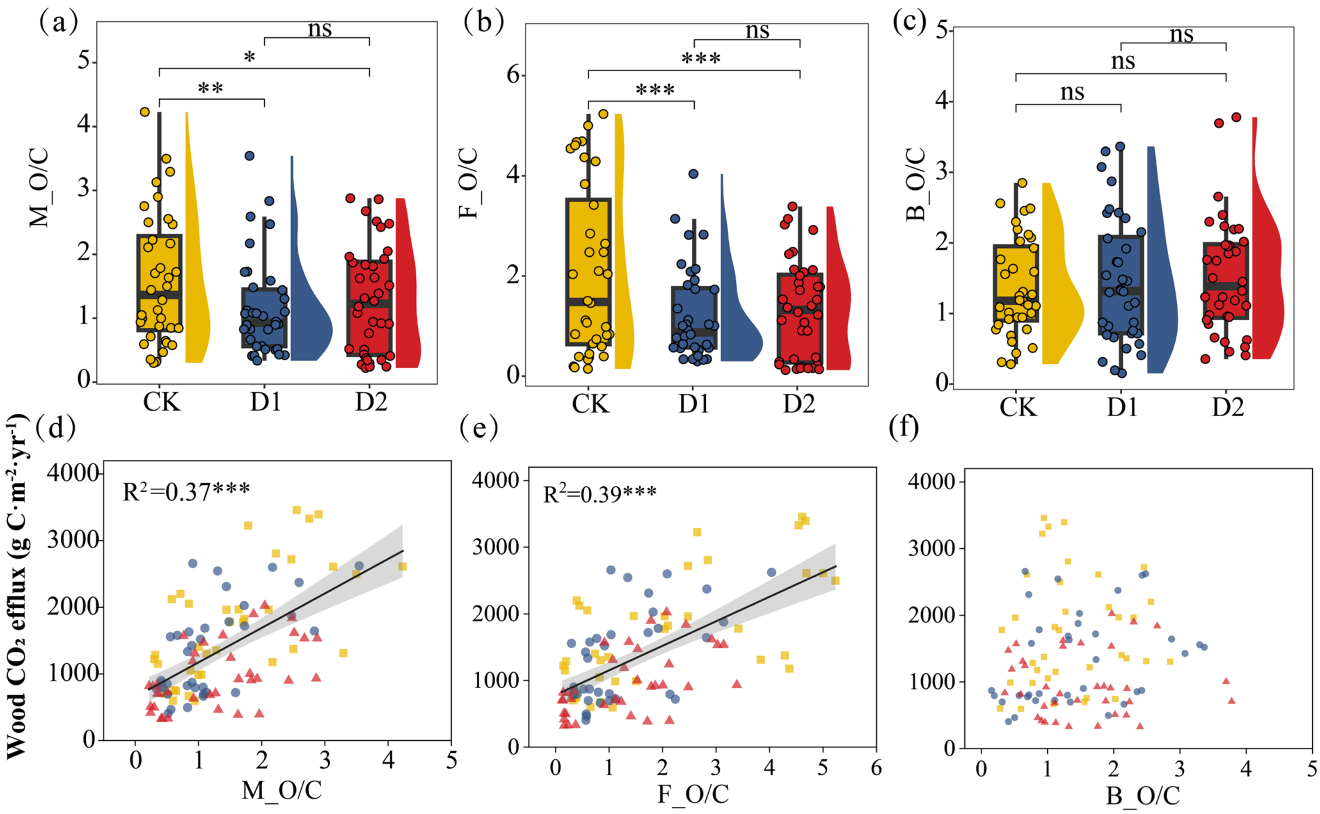

FIGURE 2 | Microbial (a), fungal (b) and bacterial (c) oligotroph: Copiotroph (O/C) ratio under different rainfall reduction treatments, and the relationships between microbial properties and wood CO_2 efflux (d–f). Different lowercase letters denote significant differences among tree species. CK, control; D1, 35% rainfall reduction treatment; D2, 70% rainfall reduction treatment. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant.

Results from structural equation model (SEM) showed that wood temperature, moisture content, wood traits, fungal O/C and bacterial O/C jointly mediated deadwood CO_2 efflux (Figure 6). Specifically, wood moisture had a direct effect and wood temperature had an indirect effect via wood traits and fungal O/C ratio on wood CO_2 efflux. Wood traits had negative relationships with fungal O/C ratio (−0.51) and cumulative wood CO_2 efflux (−0.47). Wood traits had very strong effects on wood CO_2 efflux. Both fungal and bacterial O/C ratios were positively correlated with wood CO_2 efflux, while the effect of fungal O/C ratio was higher than that of bacterial O/C ratio (Figure 6b).

4 | Discussion

Long-term drought-induced moisture deficit generally leads to a decrease in wood decomposition, impacting forest product-dependent industries, biodiversity, habitat structure and C sequestration (Hu et al. 2020). The microbial community is often considered a 'black box' in the C cycle models, and thus clarifying the microbial composition and life-style strategies may provide a better framework in decomposition models. In this study, we mainly considered drought-induced changes in wood traits and microbial community *r* and *K* strategies to disentangle how these variables mediate wood decomposition at different drought intensities.

4.1 | Responses of Wood Decomposition to Drought Intensity Amongst 12 Tree Species

Wood decomposition is intricately influenced by microclimatic conditions, including wood moisture and temperature (Figure S2). In this study, our results showed that drought significantly decreased wood decomposition, which supported our hypothesis (1) and the previous works in a tropical lowland rainforest with 26 deadwood species decomposition experiments (Rowland et al. 2013; Xie et al. 2020). Furthermore, deadwood decomposition rates decreased proportionally more under the D2 compared to the D1 treatments (Figure 1a). This pronounced reduction is mainly because extreme drought significantly lowers water availability at the wood-soil interface, leading to a stronger inhibition of microbial activity than moderate drought (Bani et al. 2018; Joly et al. 2019).

In our study, the magnitude of the drought effect on wood decomposition varied significantly amongst the 12 tree species, likely due to differences in wood moisture content and water-holding capacity (Figure 1a). Phylogenetic relationships amongst tree species play a significant role in how wood traits respond to drought across species (Table S5). This suggests that the reaction of different species to drought-induced changes in wood decomposition rates may be influenced by their evolutionary history, which shapes the physicochemical wood traits (Weedon et al. 2009).

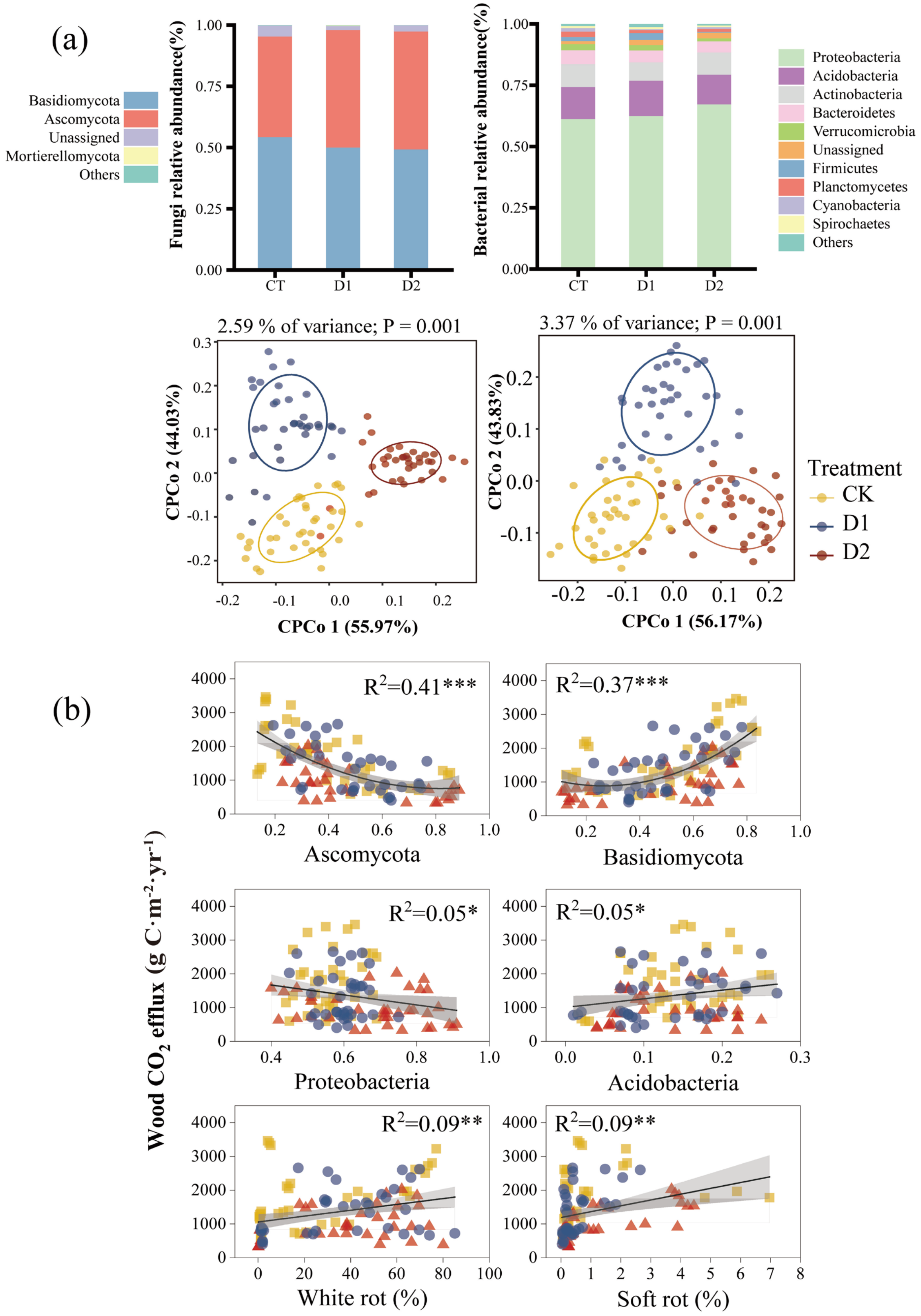

FIGURE 3 | Microbial composition and diversity of fungi and bacteria under rainfall reduction treatments (a) and relationships between wood CO_2 efflux and the significant fungal, bacterial phyla and wood decay fungi (b). CK, control; D1, 35% rainfall reduction treatment; D2, 70% rainfall reduction treatment. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

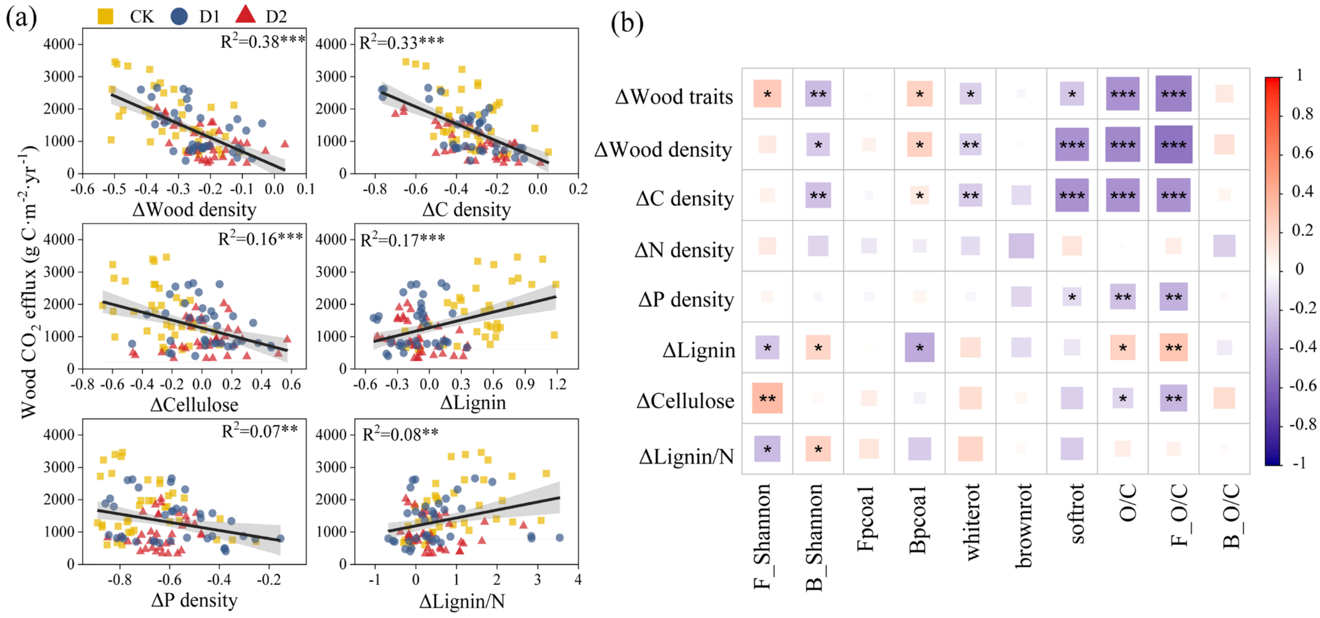

FIGURE 4 | Relationships of accumulative wood CO_2 efflux with ΔWood density, ΔC density, ΔCellulose, ΔLignin, ΔP density and ΔLignin/N in different rainfall reduction treatments (a). Correlation of microbial variables and wood traits (b). ns, Not significant. ΔWood traits, PC1 of all wood traits; B_O/C, Bacterial oligotroph/copiotroph; F_O/C, Fungal oligotroph/copiotroph, O/C, Microbial oligotroph/copiotroph. CK, control; D1, 35% rainfall reduction treatment; D2, 70% rainfall reduction treatment *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

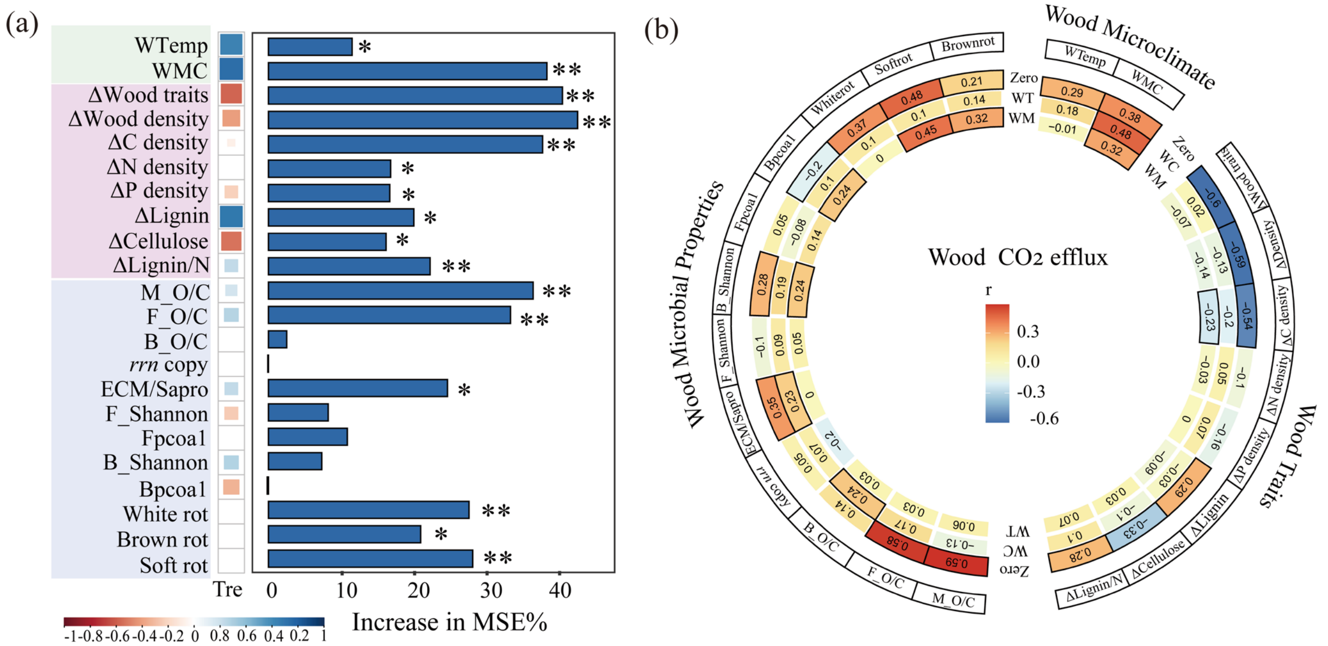

FIGURE 5 | Correlation analysis and relative importance of microclimate, changed wood traits and microbial properties in wood decomposition under different rainfall reduction treatments (a). Partial correlations between wood CO_2 efflux and three types of predicting factors under drought (b). The outermost circle shows the factors (i.e., wood microclimate, wood traits and wood microbial properties) and their respective correlations with wood CO_2 efflux. The colour of the fan shapes indicates the strength of the correlation coefficient, dark colours represent stronger correlation, with black frame line showing the significant correlation at $p < 0.05$. The variation in colour between the zero-order correlations (labelled as "Zero") and those with the factors under scrutiny reflects the extent to which the correlation between wood CO_2 efflux and the given factor is influenced by the controlled variable. A consistent colour between the controlled factor and the zero-order correlation suggests no dependency on the controlled variable. Conversely, a change in colour intensity, a decrease or an increase, indicates a loss or gain in correlation strength, respectively. B_O/C, bacterial oligotroph: Copiotroph ratio; ECM/Sapro, ectomycorrhizal/saprotrophic fungi ratio; F_O/C, fungal oligotroph: Copiotroph ratio; M_O/C, microbial oligotroph: Copiotroph ratio; *rrn* copy, the weighted average rRNA operon copy number of bacterial community; WC, wood microclimate; WM, wood microbial properties; WMC, wood moisture content; WT, wood traits; WTemp, wood temperature. *, $p < 0.05$; **, $p < 0.01$.

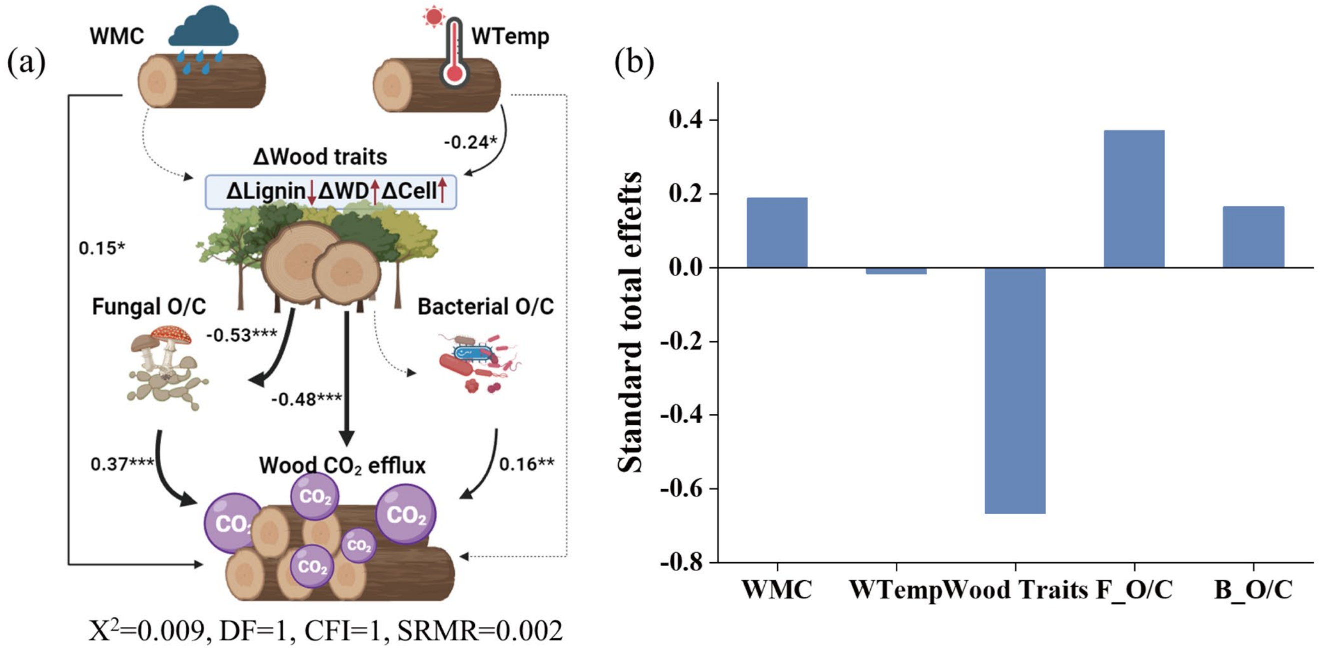

FIGURE 6 | Structure equation models (SEM) outlining the influence of wood microclimate, changes in wood traits, and microbial strategy on wood decomposition (Created with BioRender.com) (a) and the standardised total effects under rainfall reduction treatments (b). The solid black line indicates a significant correlation and the coefficient indicates positive or negative correlations. Dashed arrows indicated nonsignificant effects. The width of the arrow is the strength of the relationship. The standardised path coefficient is displayed beside the arrows, which reflect the effect size of the relationship. ΔCell, ΔCellulose; ΔWD, ΔWood density; B_O/C, bacterial oligotroph: Copiotroph ratio; F_O/C, fungal oligotroph: Copiotroph ratio; WMC, wood moisture content; Wtemp, wood temperature. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

4.2 | Relationships of Wood CO_2 Efflux With Wood Traits and Microbial Community Under Drought

Due to phylogenetic and environmental selection, there are significant differences in the initial traits amongst tree species (Sardans et al. 2021; Weedon et al. 2009), which may regulate wood trait responses to drought (Piaszczyk et al. 2022). Changes in wood density and C content, which reflect the compactness of the cellular structure and the quality of decomposable wood materials as microbial substrate, directly correlate with the advancement of decay (Figures 4a and 5). These changes in wood density serve as critical measures to accurately forecast the pace of the decomposition process through three primary mechanisms. First, a greater reduction in wood density over time reflects more intense activity by decomposers, including small fauna and microbes, which break down structural components and increase CO_2 emission (Weedon et al. 2009). Second, the larger decrease in deadwood density may improve microbial accessibility, allowing deeper colonisation and faster carbon release (Cornwell et al. 2008). Third, the decreased wood density could increase substrate and water permeability, improving oxygen diffusion and thereby facilitating organic matter decomposition (Piaszczyk et al. 2022). These reasons together may contribute to progressive and sustained changes in wood CO_2 efflux, where species with lower wood density exhibit greater C release. The breakdown of organic C-C bonds during wood decomposition releases C as CO_2 (Cornwell et al. 2008), contributing to a change in observed wood CO_2 efflux. The ensuing reduction in wood density enhances microbial colonisation by improving the penetrability of the wood's structure, consequently accelerating the decomposition process.

Microorganisms adapt to moisture stress through mechanisms such as metabolic slowdown, dormancy or mortality, depending on their physiological and genetic traits (Malik et al. 2020). In our study, drought significantly influenced microbial composition and diversity (Figure 3), echoing findings from a Mediterranean system study that highlighted microbial adaptations to moisture stress (Hueso et al. 2012). Drought weakened the correlations of wood decomposition with wood C loss and microbial O/C ratio (Figures 2 and 3), likely due to the decreased activity and abundance of C-decomposing microbes under water scarcity. Furthermore, we found a decline in microbial O/C ratio under different drought intensities (Figure S3), suggesting that water shortages induce cellular dehydration and oxygen stress, leading to protein dysfunction and microbial mortality with more negative effects on oligotrophic microbes (Manzanera 2021).

Fungal communities, mainly Ascomycota and Basidiomycota (Figure 3a), constitute over 90% of fungal diversity and are crucial in the process of wood decomposition (Lustenhouwer et al. 2020; Maillard et al. 2021). The abundance of Ascomycota had a negative relationship with wood CO_2 release, but Basidiomycota was positive (Figure 3b), which was consistent with another wood decomposition experiment conducted in a subtropical forest ecosystem, Ailao mountain, China (Huang et al. 2022). This observed pattern may be linked to the internal microbial competition dynamics, wherein Basidiomycota demonstrates the enhanced metabolic capacities compared to Ascomycota, especially in decomposing more recalcitrant C sources (Tláskal et al. 2021). The phylum Basidiomycota is a primary contributor to *K*-strategy microorganisms, specialising in the decomposition of lignocellulose through spore production and mycelium growth in moist habitats (Boddy 1994). Furthermore, the drought-induced decrease in wood moisture negatively affected wood-decaying fungi, primarily those in the Basidiomycota group (Figures 3 and S6), which carry out their vital role of breaking down wood structure, impeding these fungi from surviving. The higher drought sensitivity of fungi, especially Basidiomycota, than bacteria can be attributed to their reliance on extensive hyphal networks for nutrient and water transport, which are highly vulnerable to drought (Lustenhouwer et al. 2020). Additionally, the enzymatic activity of Basidiomycota, particularly ligninolytic enzymes, is strongly dependent on stable moisture conditions for substrate accessibility and catalytic efficiency (Boddy 1994).

4.3 | Regulation of Wood Microclimate, Traits and Microbial Strategies on Wood Decomposition Under Drought

The Bayesian phylogenetic results provide strong evidence that species-specific traits, shaped by their evolutionary history, significantly influence wood trait responses to drought (Table S5). Indeed, these findings indicate that differences in woody species result from the acquisition of various functional and adaptive traits encoded in their genomes. Structural and chemical compositions in wood are largely influenced by the phylogenetic background as well as the capacity to absorb water and other essential nutrients (Sardans et al. 2021). These findings highlight that the decomposition of wood is intricately governed by the combined effects of environmental drivers and species-specific genetic traits, which together determine its structural resilience and vulnerability to microbial degradation. For the close relationship between wood traits and microbial properties, we observed that tree species with higher microbial and fungal O/C ratios at the same time had a greater substrate destroyed, like the density and nutrient loss, causing more CO_2 release (Figure 4b). This intricate microbial balance between oligotrophs, with a reserved resource utilisation in scant nutrient settings, and copiotrophs, thriving in and swiftly exploiting nutrient-abundant niches (Zeng et al. 2022), crucially dictates the rate and intensity of wood breakdown and subsequent C release.

The trade-off between bacteria and fungi in relation to environmental adaptability has been a subject of on-going debate (Tláskal et al. 2021; Wang et al. 2021). Structural equation model (SEM) analyses showed fungal O/C ratio, rather than bacteria's one, exhibited a more pronounced effect on the decomposition process, highlighting their pivotal role in mediating wood C dynamics (Figures 2 and 6b). Although drought reduced fungal O/C ratios, this does not necessarily indicate a diminished fungal contribution to wood CO_2 efflux. Instead, it likely reflects shifts in fungal community structure or ecological strategies under moisture stress, with fungal taxa continuously dominating decomposition processes (Zhou et al. 2020; Lustenhouwer et al. 2020). The dominant role of fungi or bacteria in wood decomposition is shaped by the initial chemical properties of the substrate and changes in the dynamic traits that occur over time (figures 4b and S6; Canessa et al. 2021). In ecosystems like grasslands, bacterial communities might react more swiftly to disturbances (Glassman et al. 2018). *K*-strategist microbes, characterised by their slow growth, focus on breaking down complex, recalcitrant compounds, whereas *r*-strategist types rapidly utilise more accessible substances (Zeng et al. 2022). While fungi typically possess expansive mechanistic strategies for resource utilisation (Wang et al. 2021), our results indicate that drought stress impairs their decomposition activities despite their potential adaptability. These adaptive behaviours highlight the nuanced responses of microbial communities to environmental stressors and support theoretical models that emphasise the interplay between microbial functions and climatic influences in ecosystems (Glassman et al. 2018). Consequently, our findings highlight the need to incorporate microbial community-traits interactions to fully understand microbial roles in ecological processes, particularly nutrient cycling and ecosystem resilience in the face of climate change.

5 | Conclusions

Drought-induced decreases in wood moisture significantly reduced wood CO_2 efflux, with large variations amongst tree species, which were primarily regulated by substrate traits and microbial strategies. Moreover, changes in wood density emerged as a better predictor of deadwood C release, and the inhibition of fungal oligotrophic taxa was primarily attributed to drought-induced reductions in wood decomposition. Overall, our study highlights the crucial role of fungal strategies in wood CO_2 efflux under water stress, and emphasises the complex interaction of wood microclimate, traits and microbial properties on wood decomposition. These findings advance our understanding of the biotic and abiotic regulators of wood decomposition at different drought levels. A deeper comprehension of these microbial adaptation mechanisms enhances our capacity to forecast climate change impacts on forest ecosystems, providing critical insights to optimise conservation strategies and sustainable forest management protocols.

Author Contributions

S.J., Y.F. and X.Z. designed the study, and Y.F. and X.Z. supervised the research work. S.J. and Z.J. conducted the field experiment. S.J., X.W. and J.S. performed the data analyses. S.J. wrote the manuscript. S.J., G.Z., L.Z., J.S., Y.F., X.Z. and J.P. discussed the design, methods and results and edited the manuscript. All authors contributed substantially to the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data are available online in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.28731833.v1.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70133.

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Supporting Information

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