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**Fungi and bacteria trade-off mediates drought-induced reduction in
wood decomposition**

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Abstract

Climate change has considerably increased the frequency and intensity of drought events over the past decades, potentially influencing organic matter (e.g., deadwood) decomposition. Although previous studies have quantified the effects of microclimate and wood traits on deadwood decomposition, how wood microbes regulate effects of drought intensity on deadwood decomposition remains elusive. In this study, a field drought experiment was conducted with three throughfall exclusion levels (i.e., control, -35% and -70% rainfall treatments) in a subtropical forest to probe relative importance of microclimate, wood traits, and microbial biomass on wood decomposition. Our results showed that the -35% and -70% rainfall treatments significantly decreased wood CO₂ efflux by 28.27% and 47.49%, respectively. Drought-induced decreases in wood CO₂ efflux were mainly mediated by wood microbial biomass, especially wood fungi biomass. Specifically, structural equation model suggested that the dominant wood microbial communities in regulating wood CO₂ efflux shifted from bacteria to fungi with increasing drought intensities. Our findings highlight the crucial role of wood microbial community with the trade-off between fungi and bacteria on deadwood decomposition in response to drought, which should be seriously considered to decode forest C cycle -climate feedback in the future research.

Keywords: wood CO₂ efflux, drought intensity, microbe, microclimate

1. Introduction

The intensification of the hydrological cycle induced by climate change is projected to have **higher** frequency and intensity of drought (Hinojosa et al., 2019). Consequently, high-intensity drought may increase tree mortality, and then stimulate deadwood production as well as decomposition (Piao et al., 2009; Zhou et al., 2022). As an important carrier of C and nutrient cycling in forest ecosystems (Bradford et al., 2016; Bani et al., 2018, Bai et al., 2022), forest deadwood stores about 73 Pg C globally, accounting for 8% of the world's forest C storage (Martin et al., 2021; Seibold et al., 2021). Deadwood decomposition, as the main pathway for plant C returning to the atmosphere, was estimated to account for about 15-25% of soil C release and 115% of fossil fuel emissions (Pan et al., 2011; Seibold et al., 2021). Therefore, drought-induced changes in deadwood CO₂ efflux may have a vital impact on forest C cycle (Dusenge et al., 2019). As we know, drought significantly **decreases** litter and wood decomposition (Brischke and Alfredsen, 2020; Hu et al., 2020; Xie et al., 2020), and the decreased magnitude largely changed with drought intensity as evidenced by different studies at the globe (Doughty et al., 2015; Hu et al., 2018). However, how different drought intensities affect deadwood decomposition under similar microclimate conditions remains unclear.

Deadwood decomposition is generally affected by microclimate, wood traits, and decomposer organisms simultaneously (Bradford et al., 2014). Previous studies showed that climate factors, especially temperature and precipitation, strongly influenced wood decomposition (Bradford et al., 2016; Hararuk et al., 2020; Piasczyk et al., 2022).

Specifically, wood decomposition rate increased exponentially with temperature in regions which are not restricted by precipitation (Herrmann and Bauhus, 2013). The optimum wood moisture content generally facilitates wood decomposition due to increased microbial activity under high wood humidity, while the excessive one with the anaerobic condition might inhibit wood decomposition (Forrester et al., 2012; Rowland et al., 2013; Joly et al., 2019; Piaszczyk et al., 2022). Wood traits (i.e., wood species, wood diameter, and nutrient contents) have been shown to play a dominant role in deadwood CO₂ efflux globally, surpassing the effects of climates (Hu et al., 2018, Bai et al., 2022). For example, tree species with relatively denser, thicker and nutrients-limited traits (e.g., low wood nitrogen and phosphorus) tend to have a slower wood decomposition rate than those softer, thinner and nutrient-sufficient species (Weedon et al., 2009; Oberle et al., 2020). However, under different drought stresses, how wood traits and climate jointly regulate wood decay is still largely unknown (Weedon et al., 2009; Hu et al., 2018; Tláškal et al., 2021).

In addition to the microclimate and wood traits, microbes, as the dominators in wood decomposition, convert wood detritus into atmospheric CO₂ and release essential nutrients for plant growth (Weedon et al., 2009; Glassman et al., 2018; Hararuk et al., 2020). Past studies suggested that both wood-inhabited bacteria and fungi considerably drive deadwood decomposition, which were susceptible to the changed surrounding environment (Glassman et al., 2018; Lustenhouwer et al., 2020). Under drought pressure, fungi with slow turnover rate are considered as the main contributors of the resistant substrates, while fast-growing bacteria are more effective in fragile organic

matter degradation (Kaiser et al., 2014). Yet, much less is known about how microbes, wood traits and microclimate jointly regulate deadwood CO₂ efflux and their relative importance under different drought intensities, hampering us to better predict future C cycle - climate feedback.

The subtropical forests in China, with high wood productivity and species diversity, have a significant impact on the global C sink (Guo et al., 2014; Wan et al., 2015). In this area, climate change-induced increase in extreme drought events remarkably threatens wood decomposition, potentially affecting regional C budgets. Herein, we conducted a field drought experiment with three throughfall exclusion levels (i.e., control, -35% and -70% rainfall treatments) to probe how different-intensity drought affects wood decomposition. We further applied structure equation model (SEM) analysis to reveal the potential influence and the relative importance of microbial communities, wood traits, and climate factors on wood CO₂ efflux under different drought intensities. Specifically, we aimed to examine the following two questions: 1) how different-intensity drought influences deadwood CO₂ efflux, traits and microbial composition; and 2) what was the relative importance of microbial community, climate and wood traits in determining wood decomposition under different drought intensities.

2. Materials and Methods

2.1 Site description

The experiment was conducted at the Zhejiang Tiantong Forest Ecosystem National Observation and Research Station (29°48'N, 121°47'E), Ningbo, China (Fig. S1). The

study area has a subtropical monsoon climate with an average annual precipitation of 1374 mm, in which 80% of the precipitation occurs in the growing season from March to October. The mean annual temperature is 16.2 °C with a maximum of 28.2 °C in July and a minimum of 4.2 °C in January (1978-2016, China Climatological Survey in Tiantong, Zhejiang; Zhou et al., 2020). The soil is an Acrisol and soil pH ranged from 4.4 to 5.0. The soil classification belongs to clay loam, with 6.8% sand, 55.5% silt, and 37.7% clay (Liu et al., 2019).

2.2 Experimental design

For our throughfall reduction experiment, we used the grooved transparent plastic plates (“V” shape) to exclude throughfall from a proportion of the plot area (Fig. S1). In July 2013, the plates were evenly placed 2 m above the plots and supported by frames made of galvanized steel pipes every about 2.5 m (Hu et al., 2020). Controlling the troughs covering the plot area resulted in an even reduction in rainfall of about 35% and 70%. Therefore, the experimental treatments were conducted as (a) an ambient control (CK), (b) 35% rainfall reduction (-35% rainfall), and (c) 70% rainfall reduction (-70% rainfall) with three replications, leading to 9 plots in total. The sample plot size is 25 m × 25 m, with similar geological conditions, soil properties and plant species. Each plot is set at least 5 m away from each other and no measurements were conducted in the buffer zone in this area to minimize artifacts related to plot establishment (Zhou et al., 2020).

Deadwood samples were obtained from six tree species that are locally dominant in

the subtropical forests of Southern China. Three tree species of *Michelia maudiae* Dunn, *Castanopsis fargesii* Franch, and *Schima superba* Gardn. et Champ. belong to angiosperms and three other tree species of *Cunninghamia lanceolate* (Lamb.), *Pseudolarix amabilis* (J. Nelson) Rehder, and *Cryptomeria japonica* var. *sinensis* Miquel are gymnosperms (Hu et al., 2020). In addition to that *Castanopsis* were non-plantation tree species, other wood samples were collected from an even-aged plantation evergreen forest at the same stand. Decomposition experiments began in November 2014, and each tree species had 9 stem sections with an initial mean wood length of 3.1 m. Each wood stem was then divided into three 1 m sections and the part far from the tree roots was selected for wood decay experiments, since wood decomposition among three 1 m sections was consistent and it is easy to find this wood part for six tree species (Hu et al., 2020; Fig. S2). Thus, 9 stems of each species, with a mean wood diameter of 12.9 ± 0.26 cm (including bark), were randomly placed in the 9 experimental plots and we have $6 \times 9 = 54$ stems in total.

2.3 Wood CO₂ efflux

For wood decomposition measured by wood CO₂ efflux, one respiration collar was installed on the wood surface using a PVC pipe (10 cm in diameter and 5 cm in height), which bound the pipes with stem samples and were tightened with aluminum wire. We then used a silicone sealant near the top-center of one stem section in each of the plots in March 2015. Thus, each plot contained six PVC collars for wood CO₂ efflux measurements.

The LI-COR 6400 infrared gas analyzer (LI-COR inc, Lincoln, NE, USA) was used to measure the CO₂ efflux of deadwood in the field experiment at monthly intervals from January 2018 to December 2018. Wood CO₂ efflux was calculated as the increment of CO₂ concentration in the system volume per unit of wood surface per unit of time and counted by an exponential regression of CO₂ concentration over time (Guo et al., 2014; Zhou et al., 2018). We measured wood CO₂ efflux on a sunny morning from 9:00-11:00 am in the middle of each month, because the mean CO₂ efflux during these periods is closely related to the 24-hour average rate (Guo et al., 2014).

2.4 Microclimate

Wood temperature was measured using a portable temperature sensor for LI-COR 6400 at the time of CO₂ efflux measurement. We cut a wedge-shaped sample on the original thick disks and oven-dried at 70 °C to a constant mass, and then recorded the wet and dry weights. The wood moisture content was calculated as the following equation: Wood moisture content = (wood wet mass (g) - wood dry mass (g))/wood dry mass (g).

2.5 Wood traits

In August 2018, we cut 5 cm thick discs from each stem and placed them in black bags for chemical analysis. Wood samples were obtained after mixing by drilling 15 points in discs through an electric drill with an 8 mm drill bit to extract sawdust and sterilized with ethanol before obtaining the next sample (Fig. S2). Samples were stored

at 4 °C for the further analyses. Total carbon (C) and nitrogen (N) concentrations of deadwood were measured using a CN analyzer (Elementar Vario MAX, Germany). Deadwood phosphorus (P) was determined using the Mo-Sb colorimetric method (Russell et al., 2015; Kahl et al., 2017). The deadwood properties were calculated by multiplying the concentrations by wood density (g/cm^3), which could better represent the nutrient lost during the deadwood decomposition (Russell et al., 2015). Wood C/N ratio was calculated via C density divided by N density.

The solid-state ^{13}C nuclear magnetic resonance spectroscopy (^{13}C NMR) was used to assess the C molecular structure during wood decay process. The NMR spectrum was obtained at a frequency of 100.59 MHz and magic angle spinning of 5 kHz. Single contact times of 0.5 ms were applied, with a recycle delay of 1.5 s and a Lorentzian line broadening function of 20 Hz was applied to all spectra. Chemical shift values were referenced externally to hexamethyl benzene at 132.1 ppm, which is equivalent to tetramethyl silane at 0 ppm. Spectra were divided into seven regions representing different chemical environments of a ^{13}C nucleus. These regions were alkyl-C (0-45 ppm), N-alkyl C (45-60 ppm), O-alkyl-C (60-90 ppm), acetal C (90-110 ppm), aromatic-C (110-145 ppm), phenolic-C (145-160 ppm) and carboxyl-C (160-185 ppm).

The relative area of each region (as a percentage of total area) was measured by the integration of the spectral regions. Wood stable C/labile C was calculated as the ratio of lignin C (Alkyl + N-Alkyl + Aromatic + Phenolic) to cellulose C (O-alkyl + Acetal) (Popescu et al., 2013; Hu et al., 2020).

2.6 *Wood microbial community*

Fungi, bacteria and total microbial biomass were characterized by PLFA analyses method, and a detailed description of the PLFA could be found in Wan et al (2015). In short, the lipids in 3 g wood fresh samples were extracted with a one-phase mixture of chloroform, methanol, and citric acid buffer (1:2:0.8, v/v/v). Chloroform, methanol, and citric acid buffer were added to the silica-filled solid-phase extraction column to separate the phospholipids. The resulting amount of PLFAs in the samples was calculated based on the peak areas of the internal standards PLFA 19:0. The area determined by GC-FID was used to calculate the abundance of PLFA markers and expressed as nmol PLFAs per gram of dry wood. Methylated phospholipids were analyzed using a gas chromatograph (GC; 6890N, Agilent, USA) equipped with a flame ionization detector (FID; 19091B-102, Agilent, USA). The fungi/bacteria ratio was calculated as the ratio of 18:2 ω 6,9 plus 18:1 ω 9 to the sum of all bacterial lipids (i15:0, a15:0, i16:0, i17:0, a17:0 16:1 ω 7c, cy17:0, 18:1 ω 7c, cy19:0) (Bray et al., 2012; Hu et al., 2017; Zhou et al., 2020).

2.7 *Statistical analysis*

Two-way ANOVA was used to evaluate effects of tree species, treatment, and their interaction on wood CO₂ efflux, wood traits (i.e., N, P density, C/N and stable/labile C), and wood microbes (i.e., wood bacteria and fungi biomass, fungi/bacteria, and Gram-positive bacteria/Gram-negative bacteria (GP/GN)). We used the liner regression model to assess the relationships between wood microbes, wood traits, and wood CO₂ efflux

under control and drought treatments with the *car* package. Repeated measures ANOVA was used to determine effects of drought treatment, time and their interaction on wood CO₂ efflux, wood temperature and moisture content. Variation partition analysis (VPA) was applied to determine effects of microclimate, microbial community, and wood traits on wood CO₂ efflux under different drought intensities by “*vegan*” package. Data in the conceptual diagram was evaluated from the VPA results. The coefficient of determination for *model microclimate* was equal to $a+d+g+e$; that for *model traits* was equal to $b+d+g+f$; and that for microbial community was equal to $e+c+g+f$. Here a is effect of microclimate on deadwood decomposition; b is effect of wood traits; c is effect of wood microbial community; d is the combined effects of microclimate and wood traits; e is the combined effects of microclimate and wood microbial community; f is the combined effects of wood traits and wood microbial community; g is the combined effects of microclimate, wood traits and wood microbial community on deadwood decomposition (Hu et al., 2020; Supplemental Method 1). A correlation matrix was run to explore the relationships between wood temperature, moisture, wood microbe and traits using the “*corrplot*” package.

Structure equation modeling (SEM) was applied to assess the direct and indirect effects of wood microclimate, traits, and microbial community in explaining the variation in wood decomposition using the package “*lavaan*”. First, we established a prior model that showed the rationale behind the direct and indirect associations from temperature, moisture, wood traits and microorganisms with wood decomposition (Bradford et al., 2016; Bani et al., 2018; Supplemental Method 2). Second, we used the

random forest method to detect the relative importance of these factors that had a vital impact on wood decomposition with the package “*rfPermute*”. We found that wood fungi biomass, N density, and stable C/labile C were the most significant factors in influencing wood decomposition under different drought intensities (Fig. S6). Third, the optimal model was chosen to present the multivariate effects of the concerned variables using the lowest Akaike's information criterion (AIC) values among different models. Mardia's test was used to ensure that the skewness or kurtosis was appropriate for assuming multivariate normality. Model estimation was achieved based on the maximum likelihood method, and the fit statistics included the *P*-value of the model (*P*) and Chi-square (χ^2). We examined the normality and heteroscedasticity for data as well as all bivariate relationships for signs of nonlinearities. All statistical analyses were performed in R software v. 3.6.1 (R Core Team, 2019).

3. Results

3.1. Deadwood CO₂ efflux under drought

During the study period, the -35% and -70% rainfall treatments significantly decreased wood moisture content by 22.94% and 43.51%, respectively (Table 1, Fig. S3). Similarly, deadwood CO₂ efflux was also reduced significantly by rainfall reduction, but the effects varied with tree species and drought intensity (Fig. 1). Specifically, the average deadwood CO₂ efflux was $1.86 \pm 0.15 \mu\text{mol m}^2 \text{s}^{-1}$ (Mean $\pm$ SE) in the control. The -35% and -70% rainfall treatments significantly decreased deadwood CO₂ efflux by 28.27% and 47.49 %, respectively (Fig. 1). Among six tree

species, *C. fargesii* had the greatest inhibition of drought on wood CO₂ efflux by 33.95% under the -35% rainfall and *C. lanceolata* by 50.60% under the -70% rainfall treatment (Figs. 1B and D). The smallest decreases in wood CO₂ efflux induced by drought were observed in *P. amabilis*, with 19.53% and 40.02% under the -35% and -70% rainfall treatments, respectively (Fig. 1F). Deadwood CO₂ efflux displayed significant positive correlations with both wood temperature and moisture under both -35% and -70% rainfall treatments (Fig. S4).

3.2. Effects of drought intensity on microbial community

Both drought treatments and tree species significantly influenced wood fungi and bacteria PLFAs contents (Fig. 2). On average, the -70% rainfall treatment significantly decreased fungi and bacteria biomass by 20.64% and 16.46%, respectively. Tree species *C. fargesii* had the highest fungal biomass and fungi/bacterial ratio, while *C. lanceolata* had the lowest ones (Fig. 2). Rainfall reduction and tree species exhibited a significant interaction on Gram-positive bacteria/Gram-negative bacteria (GP/GN), while no effect was found for fungi, bacteria biomass and fungi/bacteria.

Drought-induced change in wood fungal biomass was positively correlated with deadwood CO₂ efflux in both control and rainfall reduction treatments, while positive correlation between wood bacterial biomass and deadwood CO₂ efflux was only observed in the control (Fig. 3). In addition, wood fungi/bacteria and GP/GN were also positively associated with deadwood CO₂ efflux under both control and -70% rainfall treatments (Fig. 3).

3.3. Effect of drought intensity on wood traits

Wood traits (i.e., N density, C/N, and stable C/labile C) did not differ among the different drought intensity treatments (Table 2, Fig. S5). Drought-induced change in wood N density was positively correlated with deadwood CO₂ efflux, while stable C/labile C exhibited negative correlations under the control, -35% and -70% rainfall treatments (Figs. 4A and D). Under the -70% rainfall treatment, P density was positively but C/N was negatively related to deadwood CO₂ efflux (Figs. 4B and C). On average, wood CO₂ efflux was positively correlated with wood N density, but negatively with wood C/N and stable C/labile C (Fig. 4). Wood fungi and fungi/bacteria were correlated negatively with wood stable C/labile C ($P < 0.01$, Fig. 5A).

3.4. Linking wood microclimate, traits and microbial community to wood CO₂ efflux

Wood microbes could explain 62% of deadwood CO₂ efflux, whereas microclimate and wood traits jointly explained 38% under the control (Fig. 5B). The effect of microclimate on deadwood CO₂ efflux decreased, whereas the effect of microbial biomass increased with increasing drought intensities (Figs. 5C and D). Structural equation model (SEM) analysis showed that wood microclimate, fungi, bacteria, N density and stable C/labile C jointly mediated deadwood CO₂ efflux, but their roles varied with drought intensity (Fig. 6). Specifically, wood bacteria biomass was positively correlated with deadwood CO₂ efflux in the control, while there were no correlations under both the -35% and -70% rainfall treatments. By contrast, wood fungi

biomass exhibited positive relationships with deadwood CO₂ efflux under the -35% and -70% rainfall treatments. The positive effects of wood moisture content on wood bacteria increased significantly with increasing drought intensity. Wood N was positively correlated with deadwood CO₂ efflux and the correlation coefficient was smaller in rainfall reduction treatments compared to the control (Fig. 6).

4. Discussion

4.1. Drought-induced suppression in deadwood CO₂ efflux

Understanding effects of drought on deadwood CO₂ release is crucial for better predicting the climate - C cycle feedback in the future (Hinojosa et al., 2019; Martin et al., 2021; Seibold et al., 2021). In this study, drought significantly decreased deadwood CO₂ efflux in subtropical forests (Fig. 1), which was closely related to drought-induced reduction in wood moisture content ($R^2=0.65$; Figs. 2 and S3). A prior wood decomposition study in temperate forests of the southern Appalachians, USA, illustrated that wood moisture content could explain 75% of the deadwood mass loss (Bradford et al., 2021). Under water stress, drought might decrease water and mineral nutrient diffusion rates, and thereby suppressing microbial activity (Kahl et al., 2017; Xie et al., 2020), resulting in a reduction in deadwood decomposition. Our findings align with some earlier studies conducted in temperate and (sub)tropical forests (Liu et al., 2013; Rowland et al., 2013; Bradford et al., 2021), but contradict a study from a central European forest with high water table (Piaszczyk et al., 2022). This discrepancy may likely result from the high-moisture boggy habitat with anaerobic conditions, in

which wood decomposition was considerably inhibited due to limited microbial and enzymatic activity (Brischke and Alfredsen, 2020). Under light or moderate drought conditions, wood decomposition may be accelerated due to improvement of water condition to benefit microbial growth (Griffin, 1977; Bradford et al., 2021).

In our study, we found that wood CO₂ efflux was interactively affected by tree species and drought (Table 2), largely resulting from the significant differences in N, P and stable/labile C contents among tree species (Weedon et al., 2009; Kahl et al., 2017). Drought had a stronger inhibition effect on deadwood CO₂ efflux for angiosperm trees (i.e., *C. fargesii*, *S. superba*, and *C. carlesii*) than that for gymnosperm trees (i.e., *C. lanceolate*, *C. fortune*, and *P. amabilis*; Fig.1), which was consistent with a global meta-analysis and our prior study (Weedon et al., 2009; Hu et al., 2020). Generally, angiosperms tend to have lower lignin and higher N concentrations than gymnosperms, making them more susceptible to microbial decomposition (Kahl et al., 2017; Prescott and Vesterdal, 2021). Additionally, angiosperms exhibited a lower moisture sensitivity than gymnosperms (Hu et al., 2020), potentially leading to a more sensitive response to moisture deficiency in angiosperms. These distinctions in substrate availability and traits between angiosperms and gymnosperms trees may result in greater CO₂ release from angiosperms under drought.

4.2. Regulation of drought intensity in deadwood decomposition

Distinct changes in deadwood decomposition induced by different-intensity drought might largely result from differential responses of plants physiological traits, especially

plant growth and mortality in forest ecosystems (Malik et al., 2020; Martin et al., 2021). Our results showed that wood CO₂ efflux for all tree species gradually decreased as drought intensity increased (Fig. 1). In particular, the -35% rainfall treatment induced a lower effect on deadwood CO₂ efflux compared to that by the -70% rainfall treatment, because the former caused less damage to wood pores and fewer tree die-off or microbial dormancy than the -70% rainfall treatment (Fig. 2; Bani et al., 2018). Conversely, a previous study suggested that mass loss was greater under light drought than that under moderate drought (Xie et al., 2020). These differences were likely due to the regulation of local microclimate (especially moisture) on microbial community composition under varying degrees of drought stress (Figs. 5B-D; Herrmann and Bauhus, 2013).

Microorganisms may perform distinct responses and adaptations to different-intensity drought (Herzog et al., 2019; Brischke and Alfredsen, 2020). In our study, there were no obvious changes in wood fungi and bacteria biomass under the -35% rainfall treatment (Fig. 2), suggesting that moderate drought had the limited effects on microbial activity and resulted in only a slight reduction in wood decomposition. However, the -70% rainfall treatment significantly lowered wood fungi and bacteria biomass (Fig. 2), and then reduced the activity of decomposers during extreme drought, which may be attributed to slower microbial growth and increased microbial mortality under moisture deficiency during periods of microbial dormancy (Pereira et al., 2019). As previously mentioned, wood moisture content plays a crucial role in controlling the variability of wood decomposition, especially in severe drought (Rowland et al., 2013).

Optimal moisture content for wood decay is generally considered to be 25-30% (Griffin 1977), whereas wood decay will be greatly inhibited when moisture falls below 20% (Griffin, 1977; Bradford et al., 2021). Since the reduction in wood moisture content under the -70% rainfall was twice of the -35% rainfall treatment (Fig. S3), less deadwood CO₂ efflux was released under the severe drought (i.e., -70% rainfall, Fig.1).

Wood fungi had a stronger positive correlation with wood N under the -70% compared to the -35% rainfall treatments (Fig. 6). This tighter connection may relate to substrate and nutrient availability, which could be the primary limiting factors for microbial metabolism during severe drought (Figs 5B-D; Malik et al., 2020; Zhou et al., 2020). These findings indicate that the decreases in wood CO₂ efflux and microbial biomass exhibited synchronicity when suffering different drought intensities.

4.3. Drought-induced fungi and bacteria trade-off in deadwood decomposition

Environmental conditions were crucial in [shaping the relations](#) between wood fungi and bacteria, subsequently influencing deadwood decomposition (Hu et al., 2017; Bani et al., 2018). In our study, we observed a significant reduction in the biomass of both wood fungi and bacteria under the -70% rainfall treatment (Figs. 2 and 5). Competition for resources among microorganisms induced by drought stress could also lead to shifts of the microbial community involved in wood decomposition.

[Our SEM results showed](#) that the direct effect of bacteria on deadwood CO₂ efflux was stronger under the control compared to rainfall reduction treatments, while fungi dominated wood decomposition with increasing drought intensities (Figs. 6 and 7). This

suggested the existence of a crucial trade-off between fungi and bacteria in subtropical deadwood decomposition (Hu et al., 2017; Tláskal and Baldrian, 2021). Previous research has illustrated that fungi tend to be more drought-tolerant than bacteria in wood decomposition (Pereira et al., 2019). For instance, brown-rot fungi can decompose wood by occupying the empty lumen inside wood cells when the moisture content drops below 20% (Griffin, 1977). White-rot fungi typically exist as latent spores in living sapwood, developing mycelium and initiating decomposition when the moisture content in dead cells drops (Boddy, 1994). Therefore, wood fungi were likely to be more responsible for wood decomposition when suffering extreme drought.

The relative importance of microbial decomposer, climate and wood traits in wood decomposition remains debated under environmental stress, which blurred the accuracy of the model in predicting climate-biosphere feedback (Bradford et al., 2016). Our findings shed light on this issue by revealing that, under varying drought intensities, wood microbial community had the most significant influence on deadwood CO₂ efflux compared to climate and wood traits (Figs. 5B-D and 7). This can be attributed to the ingenious adaptability of microorganisms in maintaining osmotic balance by using cellular machinery when suffering surrounding environmental change (Lebre et al., 2017).

5. Implications for future experiments

Our experiments mainly focused on the influencing factors of wood decomposition at the late decomposition stage (i.e., the 4th year) under drought. We thus did not show

the initial wood traits for different tree species here, which were investigated at the beginning of the experiment (Hu et al., 2020). To further refine the regulatory mechanisms affecting wood decomposition under drought, we may need to have more drought intensities to examine linear or nonlinear responses. Forest C balance is simultaneously affected by global climate change, such as altered precipitation, climate warming, elevated CO₂ and N deposition (Doughty et al., 2015). Multiple global change factors may interactively affect the diverse ecosystem functions such as C storage (Zhou et al., 2019). It is essential to carry out more interactive decomposition experiments of climate change related to drought, which may fully understand the role of wood decomposition in global change mitigation. Furthermore, the SEM analysis could provide insights to emphasize the direct and indirect effects of microclimate, wood traits, and microbial biomass on deadwood decomposition.

Our experiment revealed that wood microbes override the effects of microclimate and wood traits on wood decomposition (Fig. 7). However, this study only measured wood bacteria and fungi biomass to examine drought-induced changes in microbial community. It's important to distinguish the specific microbial taxa and understand their functions within the microbial community under different-intensity drought. Further research employing microbial sequencing data is essential to gain deeper insights into how microbial community mediates wood decomposition under drought.

6. Conclusions

Deadwood CO₂ release is crucial for terrestrial C cycling as well as nutrient

turnover under climate change. Our results showed that the drought-induced inhibition on deadwood CO₂ efflux increased with increasing drought intensities, suggesting the critical role of drought intensity in exploring responses of ecosystem C processes to climate change. In addition, wood microorganisms were dominant in influencing wood decomposition compared to microclimate and wood traits, which verified the necessity of microbial processes in the development of woody C decomposition models. Furthermore, microbial community for wood decomposition shifted from bacteria to fungi as drought intensity increased. Our findings emphasize the importance of wood microbial community with the fungi and bacteria trade-off on deadwood decomposition under different intensity drought, which should be deliberated to understand forest C cycle - climate feedback in future research.

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Figure Legends

Figure 1 Monthly variation and the annual mean value of wood CO₂ efflux of six tree species in rainfall reduction treatments (A-F). Error bars represent the mean standard error. Different lowercase letters denote significant differences at $P < 0.05$ among rainfall reduction treatments. CK, control; -35% Rainfall, 35% Rainfall reduction treatment; -70% Rainfall, 70% Rainfall reduction treatment.

Figure 2 Mean phospholipid fatty acids (PLFA) of fungi (A), bacteria (B), fungi/bacteria (C) and GP/GN ratio (D) of different tree species in rainfall reduction treatments. Error bars represent the mean standard error. Different capital and lowercase letters denote significant differences at $P < 0.05$ among rainfall reduction and tree species treatments. Species: wood tree species; Treatment included CK, -35% and -70% rainfall levels; Species×Treatment: the interaction effects of wood and drought treatments. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; ns: not significant.

Figure 3 Relationships between (A) fungi, (B) bacteria, (C) fungi/bacteria, (D) GP/GN and mean deadwood CO₂ efflux in rainfall reduction treatments. ns: not significant.

Figure 4 Relationships between N density (A), P density (B), C/N (C), stable C/labile C (D) and mean deadwood CO₂ efflux in rainfall reduction treatments. ns: not significant.

Figure 5 Correlation analysis of mean deadwood CO₂ efflux, wood microbial community and wood traits (A) and the contribution of climate condition, wood microbial community and wood traits to wood decomposition under (B) control, (C) 35% rainfall reduction and (D) 70% rainfall reduction treatments. Note: Tw, wood temperature; Mw, wood moisture; F/B, fungi/bacteria, N, wood nitrogen density; P, wood phosphorus density. Red and blue circles indicated the positive and negative relation, respectively. Circle size is positively correlated with correlation coefficient and zeros have not been displayed. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

Figure 6 Structure equation models (SEM) outlining the influence of wood microclimate, traits and microbial community on wood decomposition and the standardized total effects under control (A and B), -35% Rainfall (C and D) and -70% Rainfall (E and F) treatments. Solid single-headed arrows in blue and red indicate the significant positive and negative relationships respectively. Dashed arrows are nonsignificant effects. The width of the arrow is the strength of the relationship. The standardized path coefficient is displayed beside the arrows, which reflect the effect size of the relationship.

Figure 7 Potential mechanisms of drought intensity effects on deadwood CO₂ efflux. The diagram showed that wood bacteria, fungi, nitrogen content and stable carbon/labile carbon regulated deadwood CO₂ efflux under 100% (CK) to -35% and -70% rainfall treatments. Line thickness corresponds to the relative size of CO₂ efflux. The number near the circle represented the contribution of deadwood CO₂ efflux under different drought intensities, and next to the wood is the decline percentage of deadwood CO₂ efflux under -35% and -70% rainfall treatments. Circles of different sizes represented microbial biomass under different drought intensities.

Figure 1

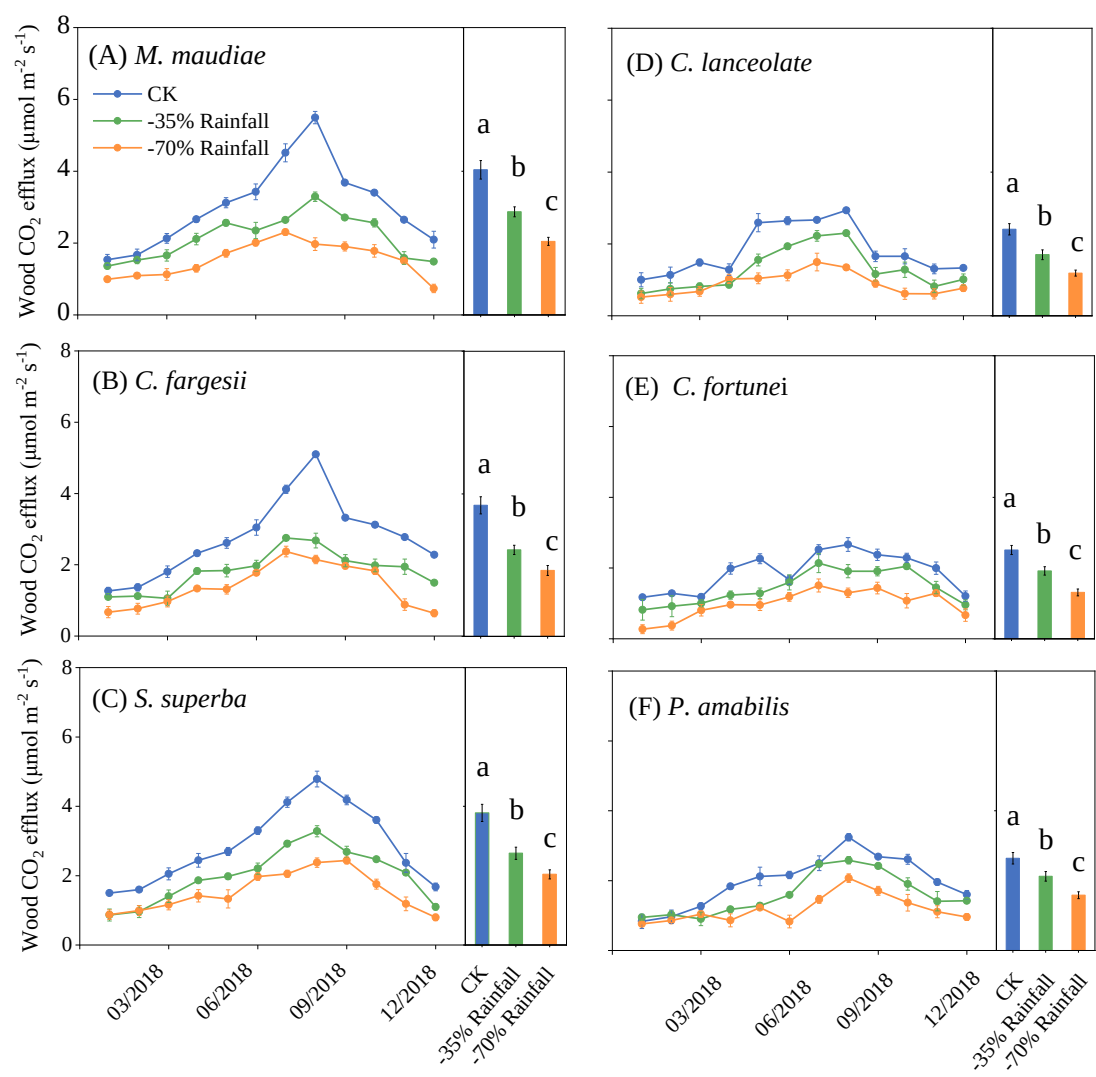


Figure 2

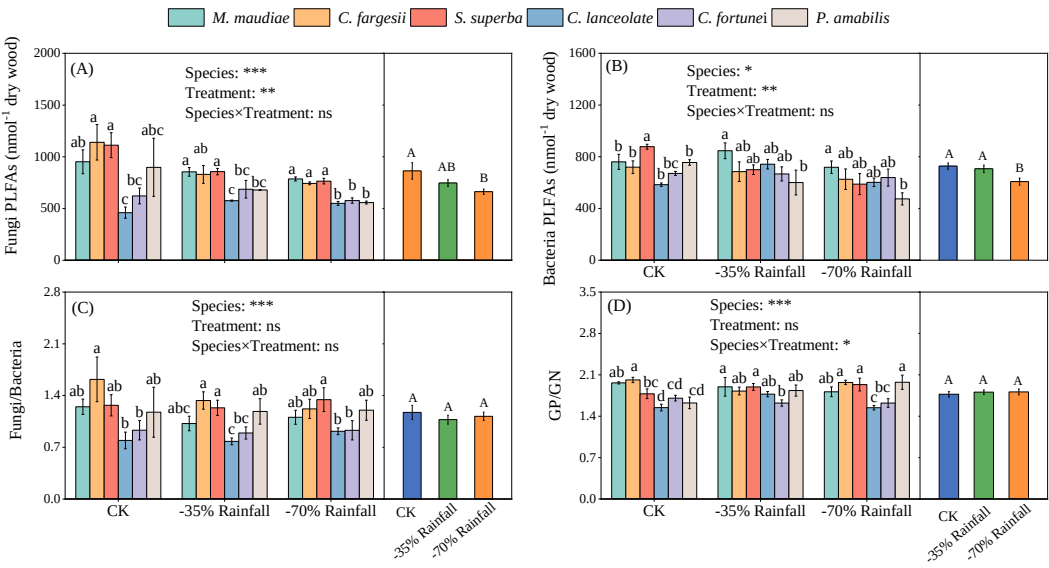


Figure 3

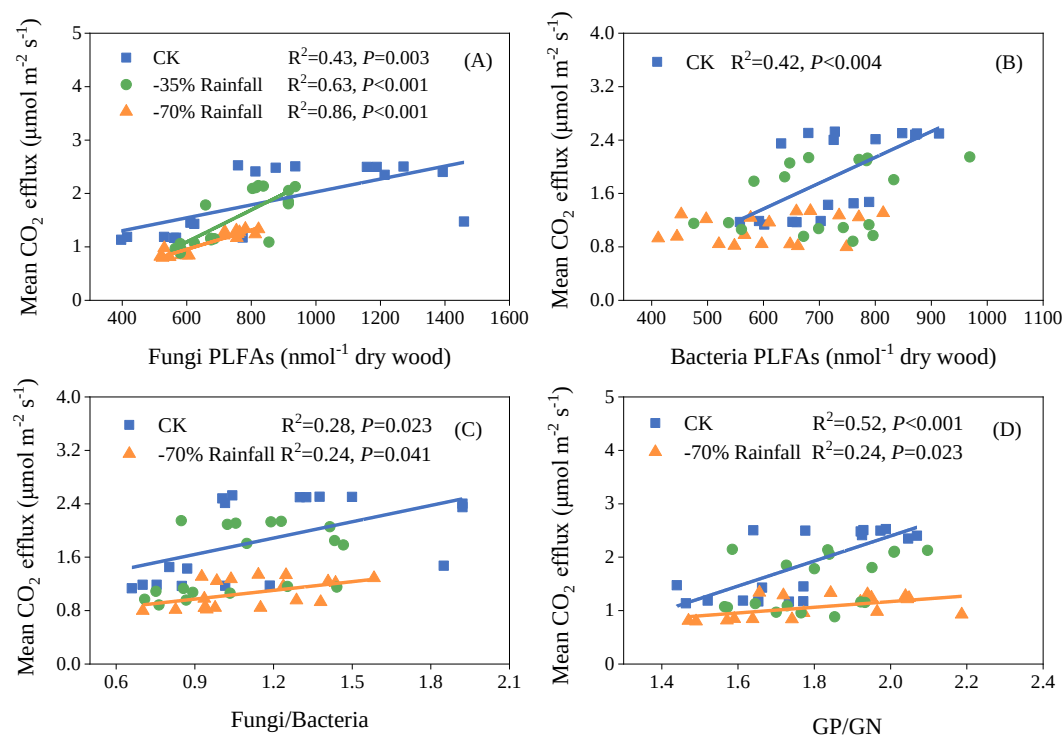


Figure 4

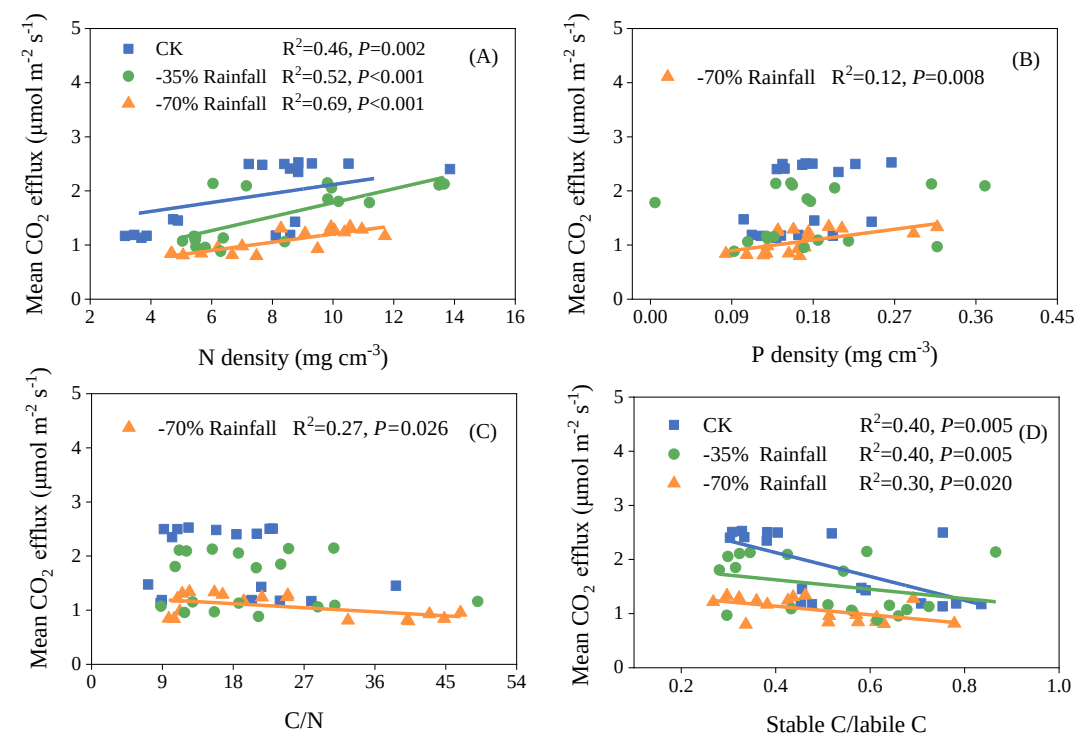


Figure 5

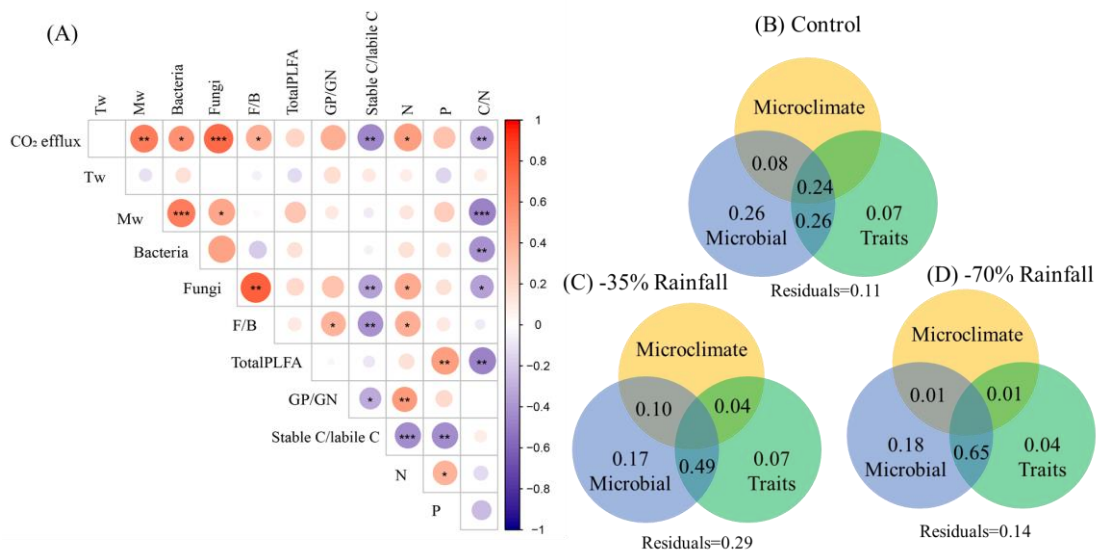


Figure 6

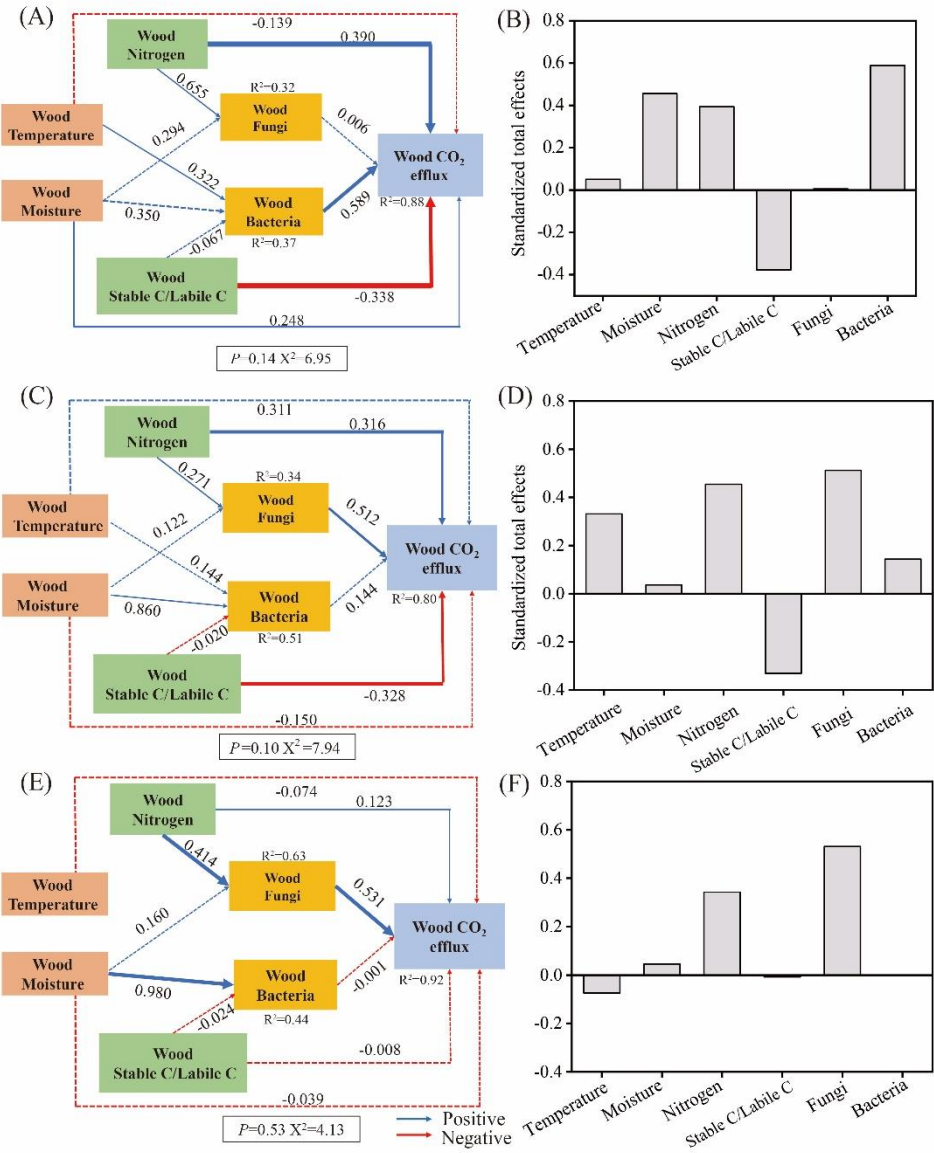


Figure 7

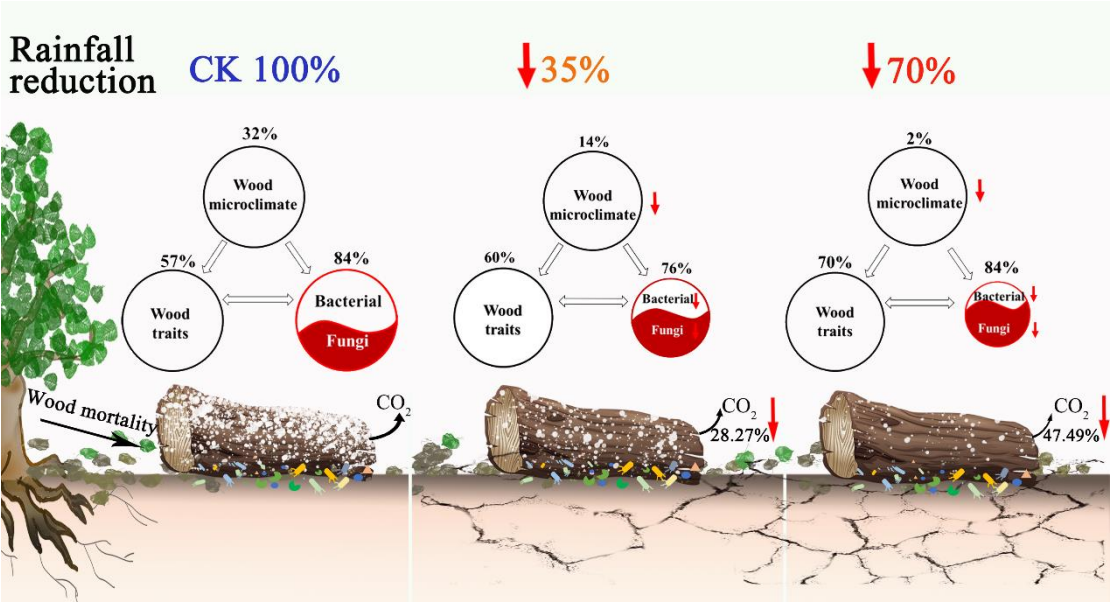


Table1 Results of repeated measures ANOVA for effects of rainfall reduction treatment (treatment) and sampling time (time) on wood CO₂ efflux, wood moisture and temperature.

Dependent variables	Factors	Df	Sum Sq	Mean Sq	F value	P value
Wood temperature	Treatment	2	37.10	18.57	8.64	<0.001
	Time	22	632.50	28.75	13.37	<0.001
	Treatment*Time	11	33297.00	3027.00	1005.00	<0.001
Wood moisture	Treatment	2	0.31	0.16	1482.49	<0.001
	Time	22	0.06	0.003	25.12	<0.001
	Treatment*Time	11	0.01	0.001	57.29	<0.001
Wood CO ₂ efflux	Treatment	2	140.49	70.25	718.44	<0.001
	Time	22	21.87	0.99	10.170	<0.001
	Treatment*Time	11	222.34	20.21	39.80	<0.001

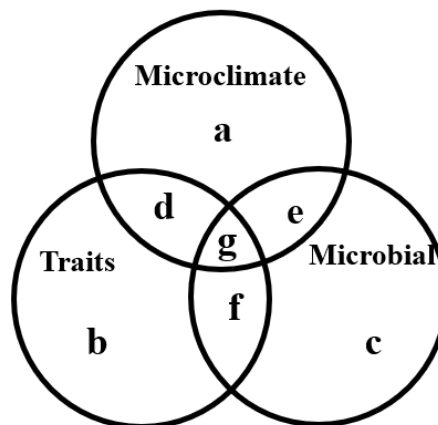
Table 2 The overall effects of tree species, drought intensities treatments and their interactions on wood mean CO₂ efflux, fungi, bacterial biomass, F/B(Fungi/Bacterial), GP/GN, N, P density, C/N and stable C/ labile C, as estimated by two-way ANOVAs.

Dependent variables		Species	Treatments	Species*Treatments
Mean CO₂ efflux	Sum Sq	10.19	5.75	1.62
	P value	<0.001	<0.001	<0.001
Fungi PLFAs	Sum Sq	114944331	36646219	35050397
	P value	<0.001	0.003	ns
Bacterial PLFAs	Sum Sq	15799989	14733106	18495379
	P value	0.011	0.001	ns
F/B	Sum Sq	1.75	0.08	0.39
	P value	0.002	ns	ns
GP/GN	Sum Sq	0.78	0.02	0.42
	P value	<0.001	ns	0.036
N density	Sum Sq	212.9	7.39	10.86
	P value	<0.001	ns	ns
P density	Sum Sq	0.07	0.0001	0.03
	P value	0.001	ns	ns
C/N	Sum Sq	1244	379	332
	P value	ns	ns	ns
Stable C/labile C	Sum Sq	0.58	0.01	0.18
	P value	<0.001	ns	ns

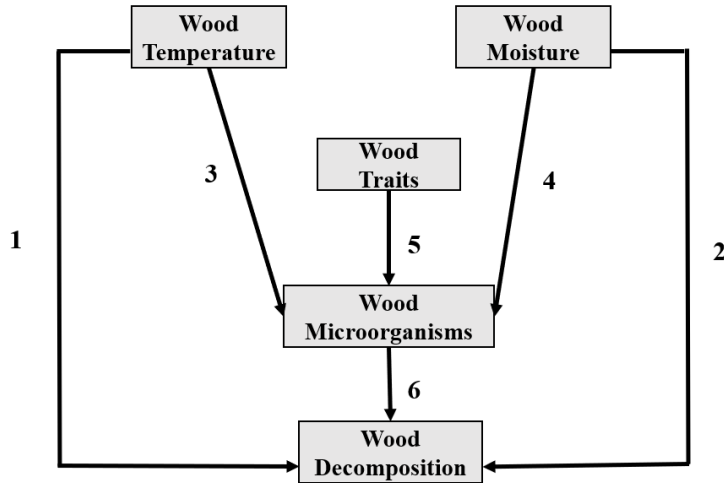
Supplemental information

Supplemental Method

1. Detailed procedures of variance partitioning of wood microclimate, traits and microbial community. The coefficient of determination for Model Microclimate was equal to $a+d+g+e$; that for Model Traits was equal to $b+d+g+f$; and that for microbial community was equal to $e+c+g+f$. Here a is effect of microclimate on deadwood decomposition; b is effect of wood traits; c is effect of wood microbial community; d is the combined effects of microclimate and wood traits; e is the combined effects of microclimate and wood microbial community; f is the combined effects of wood traits and wood microbial community; g is the combined effects of microclimate, wood traits and wood microbial community on deadwood decomposition.



2. A prior model showing the rationale behind the direct and indirect associations from temperature, moisture, wood traits, microorganisms with wood decomposition.



#	Rationale	References
1	Wood decomposition generally increased with increasing wood temperature.	Herrmann and Bauhus, 2013
2	wood moisture content is crucial in controlling the variability of wood decomposition.	Rowland et al., 2013
3	Microorganisms survive and function under appropriate temperature conditions	Herrmann and Bauhus, 2013; Yang et al 2022
4	Microbial taxa are only able to function as decomposers in a specific moisture content.	Zhou et al., 2020; Lebre et al., 2017
5	Microorganisms have a specific preference for substrate utilization.	Kahl et al., 2017; Prescott and Vesterdal, 2021
6	Wood-inhabited bacteria and fungi considerably drive deadwood decomposition.	Lustenhouwer et al., 2020

Appendix

Figure S1 Map of experimental site and illustration of the three rainfall reduction treatments (control, -35% rainfall and -70% rainfall treatments) in this study (see Zhou et al., 2020).

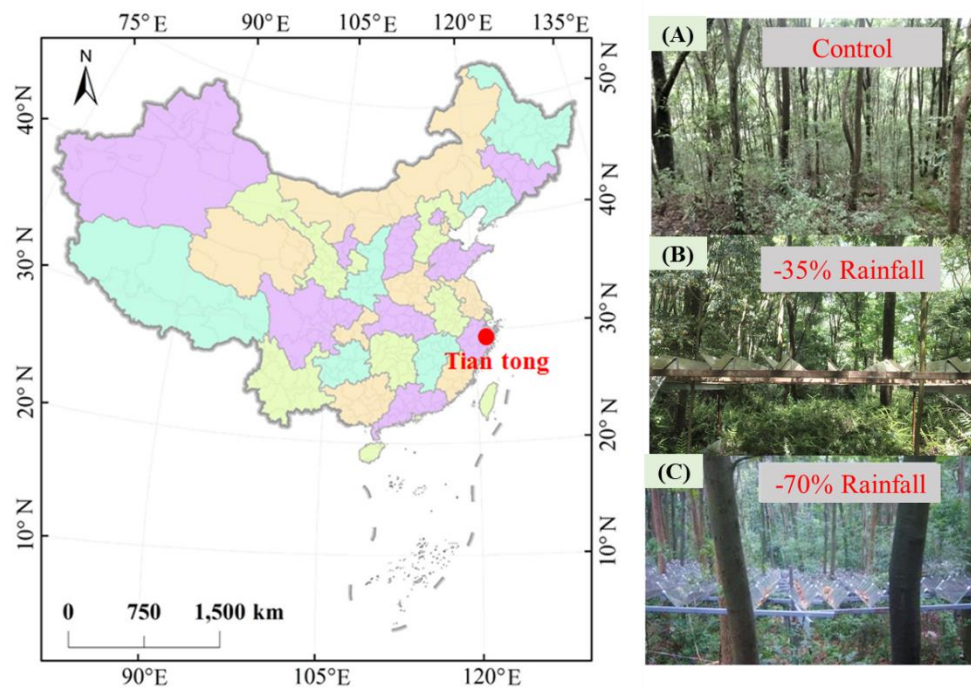
Figure S2 Sampling design for a wood disc collected from deadwood. Drill holes are made randomly to extract sawdust for further lab analyses (see Material and methods).

Figure S3 Wood moisture content under different drought intensities. Different lowercase letters indicate significant differences between treatments.

Figure S4 Relationship of mean wood CO₂ efflux, wood temperature (a) and wood moisture (b) of angiosperm and gymnosperm wood subjected to different rainfall reduction treatments (n=648). Each data point represents the annual mean of 12 repeated measurements. Slopes of relationships were significantly different ($P < 0.05$). Abbreviation, CK: control; -35% Rainfall: 35% rainfall reduction treatment; -70% Rainfall: 70% rainfall reduction treatment. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; ns: not significant.

Figure S5 Wood N density (A), P density (B), C/N (C) and stable C/labile C (D) of angiosperm and gymnosperm wood in rainfall reduction treatments. Error bars represent the mean standard error. Different lowercase letters denote significant differences at $P < 0.05$ among tree species. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; ns: not significant.

Figure S6 Relative important factors of wood microclimate, traits and microbial communities on wood CO₂ efflux under control (a), -35% rainfall (b), -70% rainfall treatments (c).



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777 **Figure S1**

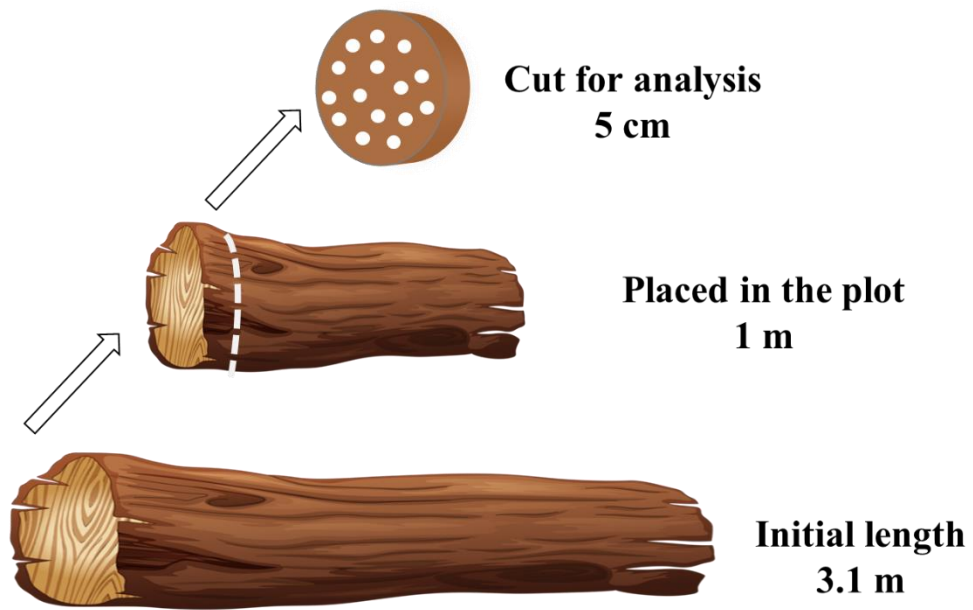
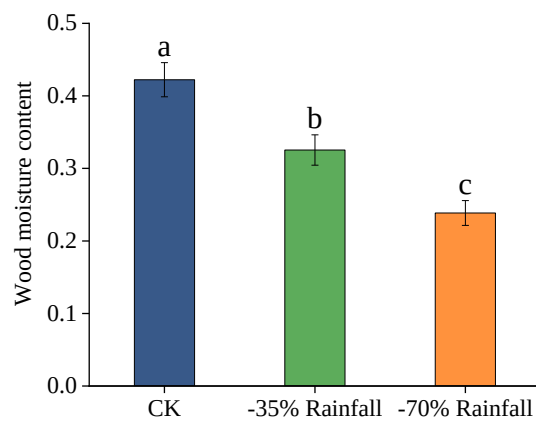


Figure S2

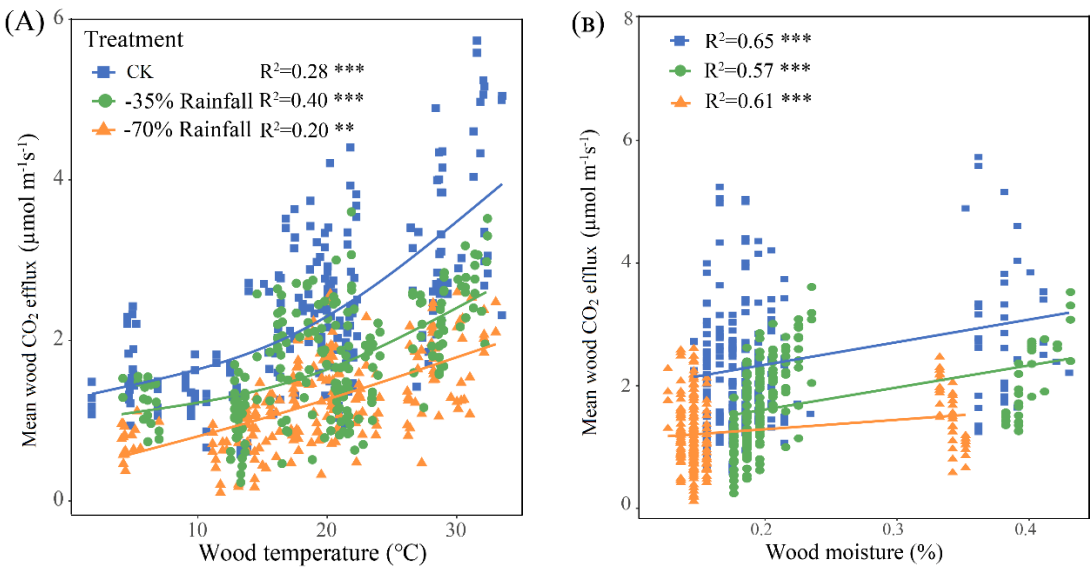


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783 **Figure S3**

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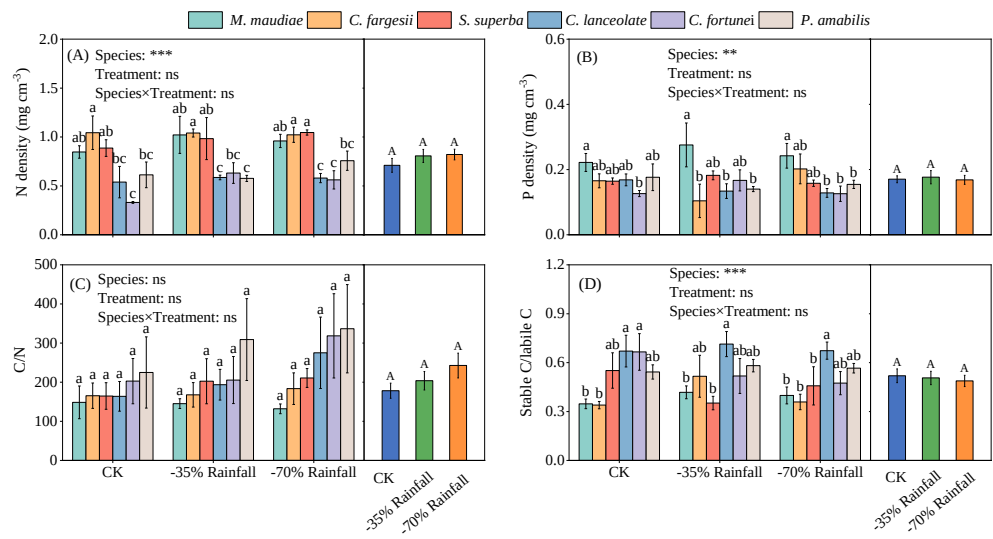
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Figure S4

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791 **Figure S5**

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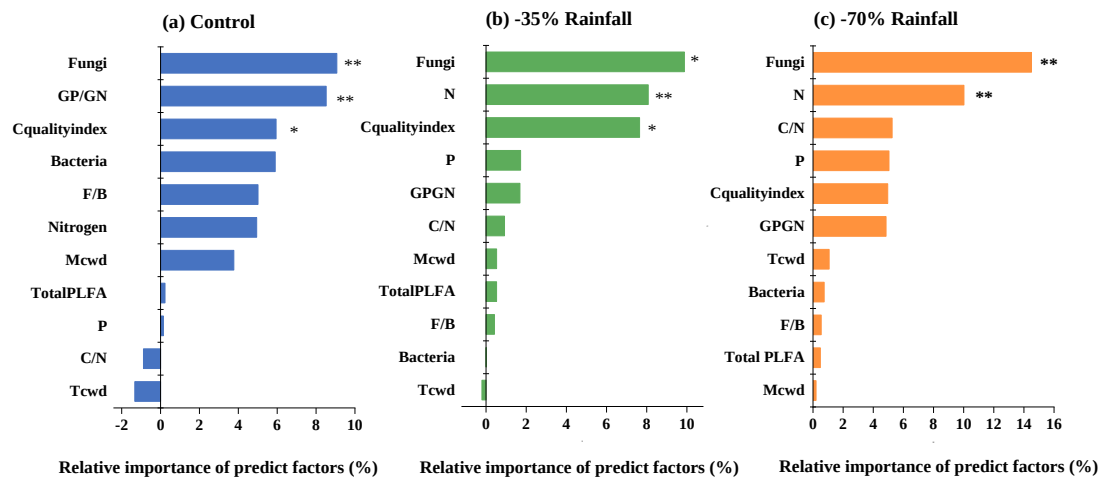


Figure S6