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Traits mediate drought effects on wood carbon fluxes

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Abstract

CO_2 fluxes from wood decomposition represent an important source of carbon from forest ecosystems to the atmosphere, which are determined by both wood traits and climate influencing the metabolic rates of decomposers. Previous studies have quantified the effects of moisture and temperature on wood decomposition, but these effects were not separated from the potential influence of wood traits. Indeed, it is not well understood how traits and climate interact to influence wood CO_2 fluxes. Here, we examined the responses of CO_2 fluxes from dead wood with different traits (angiosperm and gymnosperm) to 0%, 35%, and 70% rainfall reduction across seasonal temperature gradients. Our results showed that drought significantly decreased wood CO_2 fluxes, but its effects varied with both taxonomical group and drought intensity. Drought-induced reduction in wood CO_2 fluxes was larger in angiosperms than gymnosperms for the 35% rainfall reduction treatment, but there was no significant difference between these groups for the 70% reduction treatment. This is because wood nitrogen density and carbon quality were significantly higher in angiosperms than gymnosperms, yielding a higher moisture sensitivity of wood decomposition. These findings were demonstrated by a significant positive interaction effect between wood nitrogen and moisture on CO_2 fluxes in a structural equation model. Additionally, we ascertained that a constant temperature sensitivity of CO_2 fluxes was independent of wood traits and consistent with previous estimates for extracellular enzyme kinetics. Our results highlight the key role of wood traits in regulating drought responses of wood carbon fluxes. Given that both climate and forest management might extensively modify taxonomic compositions in the future, it is critical for carbon cycle models to account for such interactions between wood traits and climate in driving dynamics of wood decomposition.

KEYWORDS

carbon quality, CO_2 fluxes, metabolic theory, moisture availability, temperature sensitivity, wood decomposition, wood nutrients

1 | INTRODUCTION

Dead wood contains 10%–20% of the carbon stored in the biomass of the world's forests (Pan et al., 2011), and its decomposition releases 7%–14% of total assimilated CO_2 back into the atmosphere (Chambers, Schimel, & Nobre, 2001; Odum, 1970). Dead wood stocks are predicted to increase in response to more frequent and intense future climate extremes and climate-driven disturbances (McDowell et al., 2018; Reichstein et al., 2013; Seidl et al., 2017), and decomposition of these stocks is expected to strongly alter forest carbon balance (Zhu et al., 2017). Estimates of the global carbon budget are currently subject to large uncertainties, because climate effects on wood decomposition are not well understood and only roughly integrated into carbon cycle models (Bradford, Berg, Maynard, Wieder, & Wood, 2016; Cornwell et al., 2009).

Over several decades, climate (e.g., temperature and moisture) was thought as the dominant factor influencing wood decomposition rates (Berg et al., 1993; Meentemeyer, 1978; Wall et al., 2008). However, this view has been challenged by recent studies, suggesting that decomposition rates were strongly influenced by wood traits that characterize initial substrate quality (Cornwell et al., 2009; Hu et al., 2018). In particular, initial wood nitrogen and phosphorus content and carbon quality (e.g., relative quantities of lignin carbon and cellulose carbon) have been shown to exert strong controls over wood decay rates (Hu et al., 2017; Kahl et al., 2017). Unfortunately, the effects of climate and wood traits on wood decomposition have generally been studied separately, with little emphasis given to their combined effects. Studies on how climate and wood traits interact to affect wood decomposition are now needed (Zanne et al., 2015) in order to better understand and predict the magnitude of CO_2 fluxes in response to climate change.

Drought is an increasingly important climate-driven disturbance that alters carbon cycle components by decreasing moisture availability (IPCC, 2014). Reduced moisture generally inhibits wood decomposition rates (A'Bear, Jones, Kandeler, & Boddy, 2014; Harmon et al., 1986), because saprotrophic fungi are important decay agents and require adequate moisture to produce extracellular enzyme and then break down dead wood (Rajala, Peltoniemi, Pennanen, & Mäkipää, 2012). It has been further suggested that drought effects on decomposition rates may be constrained by low nutrients (Alster, German, Lu, & Allison, 2013). For example, the moisture sensitivity of litter decomposition under drought was higher in nitrogen-fertilized than non-fertilized plots (Allison et al., 2013). However, it is not well understood how drought effects on wood CO_2 fluxes may vary with wood chemical traits. Previous studies of wood decomposition in drought mostly comprised reciprocal transplants (e.g., across climatic gradients) and lab experiments (Berg et al., 1993; Bradford et al., 2017; Russell et al., 2015). These studies could not isolate trait effects independent of climate due to covariation of traits and climate, nor did they reflect realistic environmental conditions. While the frequency and intensity of droughts are predicted to increase (Dai, 2013), few studies have used experimental rainfall reductions to examine drought effects on wood decomposition in real forest environments.

Long-term records show that droughts are associated with higher temperatures (IPCC, 2014). Higher temperatures are expected to increase rates of wood microbial metabolism, but the magnitudes of these increases are unclear and the temperature sensitivity of wood decomposition is not well understood (Cross, Hood, Benstead, Huryn, & Nelson, 2015). Metabolic scaling theory (MST) hypothesizes that wood decomposition rates will ultimately be governed by the kinetics of microbial biochemistry (Brown, Gillooly, Allen, Savage, & West, 2004; Gillooly, Brown, West, Savage, & Charnov, 2001). Building on this hypothesis, Follstad Shah et al. (2017) showed that temperature sensitivity of leaf decomposition varies among plant genera that differ in leaf traits and litter quality. Litter quality makes a key control on temperature sensitivity of decomposition, where the decomposition of low-quality litter (i.e., litter low in nutrient concentrations and high in recalcitrant compounds) is more sensitive to temperature compared with high-quality litter (Davidson, Janssens, & Luo, 2006; Fierer, Craine, McLauchlan, & Schimel, 2005). Compared with leaf litter, dead wood generally includes much lower nutrient concentrations and higher complex carbon compounds (Pietsch et al., 2014). While many studies have considered the temperature sensitivity of leaf litter decomposition, that of wood decomposition and how it is influenced by traits remains largely unstudied.

In two of our earlier studies, we tested the relative influence of climate and traits on wood decomposition rates. We showed that traits drive decomposition rates more than climate (Hu et al., 2018), and that trait effects on microbial community composition and function changes through time (Hu et al., 2017). These underscore the need to understand how wood traits will influence climate effects on wood microbial metabolism and decomposition. Here, we examined the influence of initial wood traits on wood CO_2 fluxes for six tree species (three angiosperms and three gymnosperms) in response to rainfall reduction and seasonal temperature variation in a subtropical forest. We hypothesize that: (H1) wood traits regulate drought effects on wood CO_2 fluxes by controlling moisture sensitivity of wood decomposition, and (H2) the temperature sensitivity of wood decomposition rates will vary with wood traits.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

A wood decomposition experiment was conducted at Tiantong National Station for Forest Ecosystem Research (29°48′N, 121°47′E), Zhejiang Province, China. The site has a subtropical monsoon climate with a hot, humid summer (June–October) and a short, mild winter (January–February). The mean annual temperature and precipitation are 16.2°C and 1,374.7 mm, respectively, with most rainfall occurring in spring and summer. Soils belong to red and yellow types, and soil texture is mainly sandy to silty clay loam Ferric Acrisol according to the FAO/UNESCO classification. The vegetation is a subtropical evergreen broadleaf forest, and common tree species include *Castanopsis fargesii* Franch., *Schima superba* Gardn, and *Castanopsis carlesii* (Hemsl.) Hayata.

In July 2013, we established a rainfall reduction experiment consisting of transparent concave polycarbonate troughs ("V" shape) that drain and exclude precipitation from a proportion of the plot area (see below). Each trough was 27 m long, 0.3 m wide, and 0.15 m high. The trough structure is similar to that described by Bu et al. (2018). Troughs were attached with self-tapping metal screws to horizontal rails ~2 m above the ground that were supported by vertical posts every ~2.5 m. The experiment consisted of four treatments: (a) 35% rainfall reduction, (b) 70% rainfall reduction, (c) a "disturbance" control comprising inverted troughs that excluded 0% of precipitation, and (d) an ambient "control" without troughs. Each treatment had three replicates, resulting in 12 plots in total. The size of each plot was 25 m × 25 m (625 m^2), and plots were spaced at least 5 m apart. Rainfall reduction was accomplished by the aforementioned troughs that covered 35% or 70% of the total plot area. A trench up to 2 m depth was excavated around the perimeter of each plot, and PVC segregation boards were placed inside with 0.5 m above the ground to prevent subsurface and overland flow of water into the plots.

Dead wood samples were obtained for six tree species that are dominant in the subtropical forests of southern China (Table S1). Three species were angiosperms (*C. fargesii*, *S. superba*, and *C. carlesii*) and three species were gymnosperms (*Cunninghamia lanceolate*, *Pseudolarix amabilis*, and *Cryptomeria fortunei* Hooibrenk). All wood samples were obtained from even-aged plantation trees growing in the same stand, except for *Castanopsis* which were non-plantation forest trees. Twelve stems of each species were felled in November 2014, and one 3.1 m section (including bark) was obtained from each stem. Two 5 cm thick disks were cut from both ends of each stem section (Figure S1), placed in black plastic bags, and transported to the laboratory for analysis. Twelve stem sections of each species were then randomly selected and placed into the 12 experimental plots. Each stem section was then further divided into three 1 m sections. The two end sections were kept for the experiment, and the middle section was removed out of the plot for other experiments not relevant to the current study. In total, the experiment comprised 6 × 12 × 2 = 144 stem sections. In March 2015, we installed one respiration collar (PVC pipe, 11 cm diameter × 5 cm height) using a silicone sealant near the top-center of one stem section in each of the plots. The mean diameters of these stem sections were 12.4 ± 0.16 cm and 13.9 ± 0.21 cm for angiosperms and gymnosperms, respectively.

2.2 | Wood density measurements

For each disk, a wedge-shaped piece (one-eighth of the total disc) was excised and separated into sapwood, heartwood, and bark (Figure S1). The volume of each component was measured using Archimedes' water displacement method. All samples were then oven-dried at 70°C for 3 days, and the density of each segment was calculated as dry mass per unit volume (g/cm^3).

2.3 | Wood carbon and nitrogen density

We analyzed the chemistry of bark, sapwood, and heartwood from each stem disk. Bark samples obtained from each disk were ground into a fine powder using a ball mill. Sapwood and heartwood samples were obtained using an electric drill with an 8 mm drill bit that was sterilized with ethanol between samples; each wood sample comprised at least 15 drill holes. Samples were stored at 4°C until further analyses. The carbon and nitrogen concentrations were determined from the milled subsamples with an LECO CHN-2000 analyzer (LECO Corp.). As suggested by Russell et al. (2015), % carbon or nitrogen may be confounded by changes in wood volume over time. We calculated carbon and nitrogen density (g/cm^3) by multiplying the concentrations by the wood density in bark, sapwood, and heartwood. The carbon: nitrogen ratio was calculated as carbon concentration divided by nitrogen concentration.

2.4 | Wood NMR spectroscopy

We used solid-state ^{13}C nuclear magnetic resonance spectroscopy (^{13}C-NMR) with cross-polarization and magic-angle spinning (CPMAS) to assess the carbon structure of dead wood. Combined with CPMAS, ^{13}C-NMR is a powerful analytical method for producing a high-resolution spectrum with minimum alteration of sample integrity (Baldock et al., 1997). Milled samples of the replicates for each tree species were combined into a single sample for analyses. The NMR spectrum was obtained at a frequency of 100.59 MHz, magic angle spinning of 5 kHz, a contact time of 2 ms, and recycle delay of 2.5 s on a Varian Unity Inova400 spectrometer (Varian Inc.). A Lorentzian line broadening function of 20 Hz was applied to all spectra. Standard chemical shift (0 ppm, tetramethylsilane) values were referenced externally to hexamethyl benzene at 132.1 ppm. Spectra were divided into seven regions representing different chemical environments of a ^{13}C nucleus. These regions were alkyl-carbon (0–45 ppm), N-alkyl-carbon (45–60 ppm), O-alkyl-carbon (60–90 ppm), acetal-carbon (90–110 ppm), aromatic-carbon (110–145 ppm), phenolic-carbon (145–160 ppm), and carboxyl-carbon (160–185 ppm). The relative area of each region (as a percentage of total area) by each carbon type was measured by integration of the spectral regions. Because cellulose has a less complex structure and a lower carbon content (44% vs. 67%) than lignin, the wood carbon quality index was characterized as the ratio of lignin carbon (Alkyl + N-Alkyl + Aromatic + Phenolic) to cellulose carbon (O-alkyl + Acetal; see Hu et al., 2017). A higher carbon quality index indicates a lower carbon quality.

2.5 | Measurements of wood CO_2 fluxes and microclimates

Dead wood CO_2 fluxes (F_w) were measured in the field using an LI-COR 6400 infrared gas analyzer (LI-COR Inc). At the time of measurement, headspace air was circulated by a pump from the chamber to the analyzer with an airflow rate of 1.5 L/min, and CO_2 concentrations were logged every second for 2 min. The CO_2 flux was calculated by an exponential regression of CO_2 concentration over time. The measurement data during the first 15 s were discarded to avoid artifacts resulting from closing the chamber. Wood CO_2 flux was calculated as CO_2 concentration increment in the system volume per unit of wood surface per unit of time (Guo, Chen, Xie, Yang, & Yang, 2014). Wood CO_2 flux was measured in each collar with a respiration chamber at monthly intervals from October 2015 to December 2016, because wood CO_2 fluxes from April to September 2015 were too small to be measured with an LI-COR 6400. Measurements were obtained between 09:00 and 11:00 a.m. in the middle of the month during rain-free days, because mean CO_2 fluxes during these periods are strongly correlated with the 24-hourly mean rate (Guo et al., 2014). For each survey, we randomly assigned the order in which the collars were measured and the entire survey took 3–4 days to complete. Collars were checked monthly and resealed when needed.

At the time of CO_2 flux measurement, wood temperature was measured at approximately 3 cm depth using a Model SK-250WP thermometer (Sato Keiryoki Mfg. Co. Ltd), and volumetric soil moisture within the 0–12 cm layer was recorded using a time-domain reflectometry unit (Model TDR300, Spectrum Technologies Inc.) near each stem section. Wood moisture content was measured in each bole every 3 months during the measurement period. For determination of wood moisture content, a 1 cm disk was obtained from the end of each sample using a chain saw, and a wedge-shaped piece (one-eighth of the total disk) was then removed. The total mass of each wedge was weighed on a portable electronic scale (Ohaus Model CT6000). All samples were then oven-dried at 70°C to a constant mass before the measurement of dry mass. Wood moisture content (%) was calculated as ((wet wood mass − dry wood mass)/(dry wood mass)) × 100. To estimate wood moisture content for each month, we used soil moisture data measured for each month with regression equations based on the 3 month data for wood moisture content and soil moisture content (Table S2). A micrometeorological weather station installed at the study site provided daily air temperature and precipitation data (Figure S2). Based on Jiang et al. (2019), the throughfall (mm) in each plot was calculated as precipitation × 60% × (1-rainfall reduction (%)).

2.6 | Statistical analyses

We used linear mixed-effects models (LMMs) to determine the effect of taxonomic group (angiosperm or gymnosperm) on initial wood chemical properties (i.e., wood density, carbon and nitrogen density, carbon/nitrogen ratio, and carbon structure), separately for bark, sapwood, and heartwood. Accordingly, we used the taxonomic group as the only fixed-effects term and tree species as the random-effect term. LMM was also used to examine the effects of rainfall reduction treatments on wood microclimates (i.e., wood moisture and temperature) and CO_2 flux. The treatment, taxonomic group, and their interactions were used as fixed-effect terms. The random-effect terms were the individual wood samples (hereafter wood ID) nested in tree species, which could influence the intercepts and slopes of wood microclimates and CO_2 fluxes against water treatment. LMMs were subjected to a model selection based on the likelihood ratio test (LRT) and Akaike's information criterion (AIC; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Before model selection, all the fixed-effect terms were included in LMM. Then, the LRT was applied to assess whether the random term can be retained. Once all the random-effect terms were significant after they sequentially deleted the most nonsignificant random terms, the optimal fixed effects were selected based on the AIC scores and the final model structure was obtained. The “lme4” package in R was used to run these LMMs and the “lmerTest” package was used to test the model coefficients by using the Satterthwaite approximation.

In order to test the hypothesis (H1) that wood traits mediate drought effects on wood CO_2 fluxes, we used LMM to evaluate the effect of taxonomic group on the reduction of wood CO_2 fluxes (or wood moisture content and temperature). The reduction of wood CO_2 fluxes (or wood moisture content and temperature) was calculated as the difference between control and the 35% or 70% rainfall reduction treatment. As there was no statistical difference in CO_2 fluxes between the “disturbance” and control treatments, we assumed the disturbance caused by the installation of experimental infrastructure could be ignored. We also used LMM to test the effect of taxonomic group on moisture sensitivity of wood CO_2 fluxes. We calculated the linear relationship of wood CO_2 fluxes and wood moisture contents across different rainfall reduction treatments. The slope of this model is the moisture sensitivity of CO_2 fluxes. The tree species were considered as the random term, which could influence both the intercepts and slopes of the linear relationships.

The same model selection procedure mentioned above was used to determine the final model structure. The data were the annual mean values of 12 repeated measurements on dead wood, which would overcome the temperature effects during the measurement period. Tukey's HSD post hoc test was used to determine the statistical difference of moisture sensitivity between angiosperms and gymnosperms. Tukey's HSD post hoc test was conducted using the "multcomp" package.

In order to test the hypothesis (H2) that wood traits play a key role in the temperature sensitivity of wood CO_2 fluxes, we used LMM to test for an effect of taxonomic group on temperature sensitivity. The temperature sensitivity of wood CO_2 fluxes can be characterized by the Arrhenius relationship, such that

$$\ln\left(F_{\mathrm{w},T}\right) = \ln\left(F_{\mathrm{w},T_0}\right) + E\left(\frac{1}{k_B T_0} - \frac{1}{k_B T}\right), \qquad (1)$$

where F_{w,T_0} is a normalization constant, E (eV) is apparent activation energy, and k_B is the Boltzmann constant (8.617×10^{-5} eV/K), T is the temperature in Kelvin (K), and T_0 is a standard wood temperature. This normalization centers the temperature data on the standard temperature (Follstad Shah et al., 2017; Manning, Rosemond, Gulis, Benstead, & Kominoski, 2018), such that values of 0 on the *x*-axis represent rates at the standard temperature. We centered our data using the approximate mean annual wood temperature of our wood samples (T_0 = 17°C = 290.15 K). Temperature data were centered in this way in order to facilitate a comparison of mean CO_2 flux rates among tree taxonomic groups or treatments at a common and biologically relevant temperature. In the ln-transformed version of Equation (1), the slope is the activation energy (E). Larger values of E indicate larger sensitivities of wood CO_2 fluxes to wood temperature. For the comparisons of temperature sensitivity among treatment × taxonomic groups, we first regrouped the data into six groups (3 treatment levels × 2 taxonomic groups). Then, the ($1/k_\mathrm{B}T_0 - 1/k_\mathrm{B}T$), treatment and their interactions were considered as the fixed-effects terms, and tree species and wood ID were used as random-effect terms. As mentioned above, we used the same model selection procedure to determine the final model structure. Then, the Tukey's post hoc comparisons were used to test the differences of temperature sensitivity (slope of the linear relationships in Equation (1)) among treatment × taxonomic groups. In addition, we also took CO_2 flux for specific temperatures (WT) and for an increase in temperature of 10°C (WT_{+10}) to calculate Q_{10} values as F_w (WT_{+10})/F_w (WT), which enable comparison of our temperature sensitivity results to those reported as Q_{10} in previous studies.

Building upon our previous study (Hu et al., 2018), we used MST to link hypothesized environmental and trait drivers with wood CO_2 fluxes. All of the drivers considered in our MST were significant predictors of CO_2 fluxes in bivariate LMM analyses (Table S3). The normalization constant of CO_2 flux (F_{w,T_0}; Equation 1) can be unpacked to account for several biotic and abiotic variables that have been hypothesized to influence wood CO_2 fluxes. Specifically, the potential influences of wood temperature, wood moisture content (M), wood nitrogen density (N), and wood carbon quality index (C_q) on CO_2 fluxes can be expressed as:

$$\ln\left(F_{\mathrm{w},T}\right) = \ln\left(F_{\mathrm{w},T_1}\right) - E\left(\frac{1}{k_\mathrm{B} T_0} - \frac{1}{k_\mathrm{B} T}\right) + \alpha_\mathrm{M} \ln(\mathrm{M}) + \alpha_\mathrm{N} \ln(\mathrm{N}) + \alpha_{\mathrm{C_q}} \ln(\mathrm{C_q}), \qquad (2)$$

where α_M, α_N, $\alpha_{\mathrm{C_q}}$, and α_D are scaling exponents for wood moisture content, nitrogen density, and carbon quality index, respectively. Activation energies (E) have been hypothesized to be either ~0.65 eV (corresponding to the average values for respiration; Allen, Gillooly, & Brown, 2005) or ~0.31–0.56 eV (corresponding to values for extracellular enzymes that constrain rates of microbial metabolism; Sinsabaugh & Follstad Shah, 2012; Wang, Post, Mayes, Frerichs, & Sindhu, 2012).

Piecewise structural equation models (SEMs) were used to test how microclimates, wood traits, and their interaction affected wood CO_2 fluxes. We first used LMMs with Equation (2) to evaluate the relative importance of wood microclimates and traits on wood CO_2 fluxes, which enabled us to identify the best predictors for use in SEM. In order to be consistent with the above analyses, air and wood temperatures were taken as the centered values ($1/k_\mathrm{B}T_0 - 1/k_\mathrm{B}T$). Each predictor variable was standardized and *Z*-score transformed, and the parameter estimates and relative effect size (defined here as the parameter estimate and confidence interval obtained from the LMM) of each predictor on wood CO_2 fluxes were reported. Then, the potential paths in SEMs were based on a hypothetical model (Figure S3) that comprised the following hypotheses: (1) wood temperature was influenced by air temperature and wood moisture, and wood moisture was affected by air temperature and throughfall (moisture input); (2) wood age had an influence on wood diameter, wood nitrogen, and carbon quality, and wood diameter had an influence on wood nitrogen and carbon quality; (3) wood traits (wood nitrogen density and carbon quality) and microclimates (wood temperature and moisture) directly affect CO_2 fluxes; (4) interactions between wood traits and microclimates influenced CO_2 flux to test whether traits mediate climate effects on CO_2 flux. The interaction terms were regarded as fixed-effect terms in LMMs and SEMs (Cross et al., 2015). The above-mentioned model selection procedure was applied to determine the final model structure. To obtain the most parsimonious path model, we assessed the full model versus reduced models by the goodness-of-fit statistics. Then, we chose the final model with the lowest AIC score among alternative models. The SEMs were conducted using "piecewiseSEM" package (Lefcheck, 2016). All statistical analyses were performed in R v. 3.4.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Wood physical and chemical properties

The density of bark, sapwood, and heartwood was significantly higher in angiosperms than in gymnosperms ($p < .01$, Figure 1; Figure S4). Indeed, the bark density of angiosperms was almost

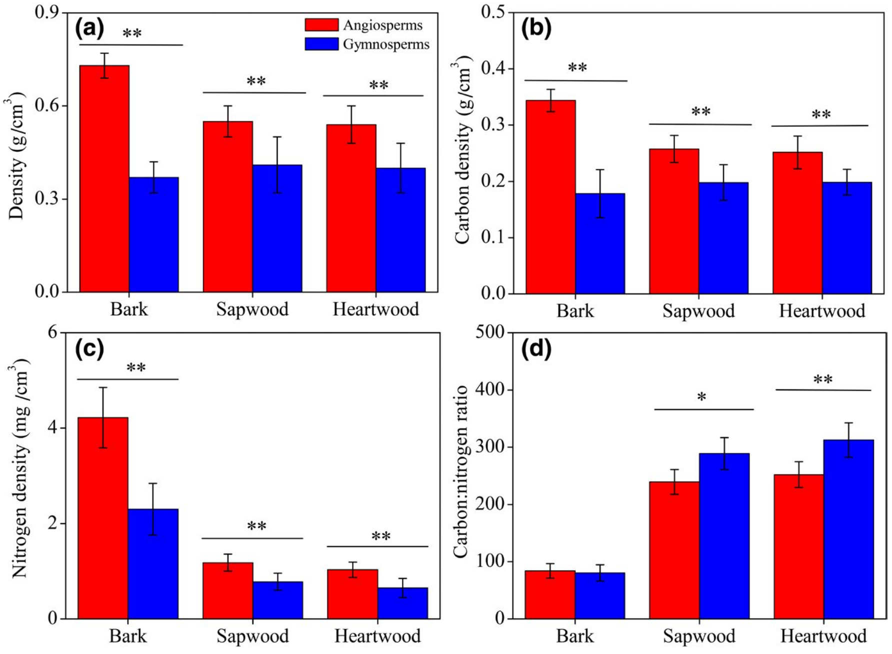

FIGURE 1 The initial wood density (a), carbon density (b), nitrogen density (c), and carbon: nitrogen ratio (d) of subtropical angiosperm and gymnosperm wood samples used in this study. Data are plotted as means (n = 18) and error bars are 1 *SE*. * indicates a significant difference at α = 0.05 and ** indicates a significant difference at α = 0.01 [Colour figure can be viewed at wileyonlinelibrary.com]

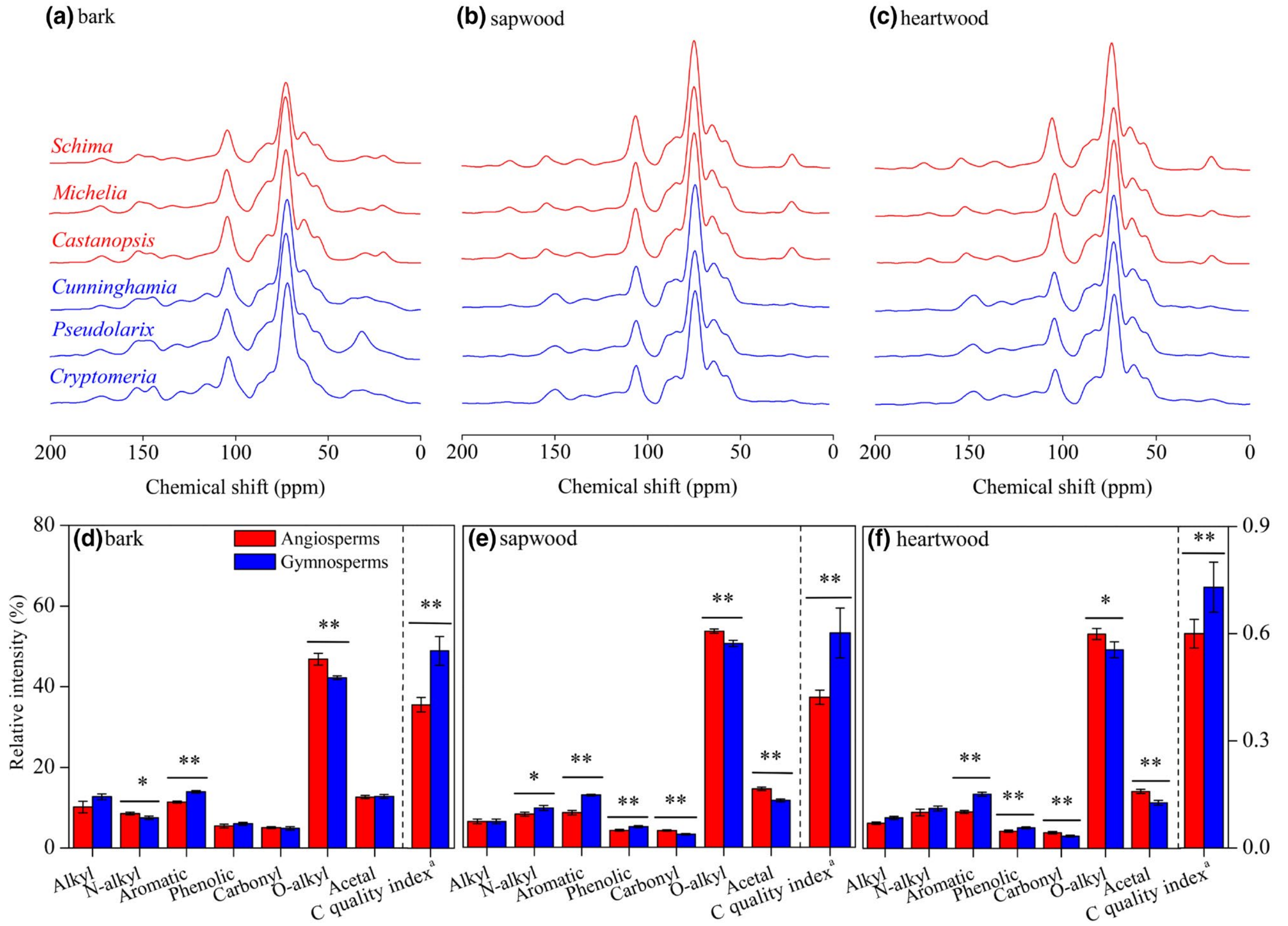

FIGURE 2 Solid-state ^{13}C-CPMAS-NMR spectra (a–c) and relative proportion (%) of initial chemical composition (d–f) of bark, sapwood, and heartwood from angiosperm and gymnosperm wood samples in a subtropical forest (a–c). For (d–f), plotted data are means (n = 3) and error bars are 1 *SE*. ^{a}(Alkyl + N-Alkyl + Aromatic + Phenolic)/(O-alkyl + Acetal). * indicates a significant difference at α = 0.05 and ** indicates a significant difference at α = 0.01 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Linear mixed-effects model results showing effects of rainfall reduction treatments on wood CO_2 fluxes, moisture contents, and temperature. Data were not ln-transformed in these models and the results of ANOVA analysis were consistent with the values shown in Figure 3a–c

Fixed-effect term	*NumDF*	*DenDF*	*F*	*p*
Wood CO_2 fluxes				
Treatment	2	1,286	90.6	<.001
Taxonomic group	1	4.0	22.8	<.01
Treatment × group	2	1,286	8.06	<.001
Wood moisture				
Treatment	2	102	152.5	<.001
Taxonomic group	1	102	16.9	<.001
Treatment × group	2	102	0.277	.759
Wood temperature				
Treatment	1	1,290	1.17	.311
Taxonomic group	1	1,290	0.013	.907
Treatment × group	1	1,290	0.0054	.995

Note: We reported *NumDF* (numerator degrees of freedom), *DenDF* (denominator *df*), *F* value, and *p* value for the fixed-effect term.

twice that of gymnosperms. Carbon and nitrogen density of bark, sapwood, and heartwood were also significantly higher in angiosperms than gymnosperms ($p < .01$). There was no significant difference for the carbon/nitrogen ratio of bark, but the carbon/nitrogen ratio of sapwood and heartwood was significantly lower in angiosperms than gymnosperms ($p < .05$).

The ^{13}C NMR spectra differed between angiosperms and gymnosperms in similar ways for bark, sapwood, and heartwood (Figure 2a–c), where carbon quality index (lignin carbon/cellulose carbon) was significantly higher in gymnosperms than in angiosperms ($p < .01$, Figure 2d–f). Specifically, the relative proportions of cellulose carbon signal for all three wood components were significantly higher in angiosperms than in gymnosperms ($p < .05$). The carbon quality index for all three wood components tended to be significantly lower in angiosperms than gymnosperms ($p < .05$). Furthermore, angiosperm wood was significantly younger with a significantly smaller diameter than gymnosperm wood (Table S1).

3.2 | Drought effects on wood microclimates and CO_2 fluxes

LMMs showed that rainfall reduction treatments significantly decreased wood moisture contents and CO_2 fluxes in both angiosperms and gymnosperms ($p < .01$), but had no significant effect on wood temperature ($p > .05$; Table 1 and Figure 3a–c, S5). The 35% rainfall reduction treatment caused larger reductions of wood CO_2 fluxes and moisture contents in angiosperms than gymnosperms (all $p < .01$, Table 2 and Figure 3d,e), but no significant difference was found in the 70% rainfall reduction treatment (all $p > .05$). There was no significant difference in CO_2 fluxes between upper bole and lower bole within the same tree species (data not shown).

3.3 | Moisture and temperature sensitivity of wood CO_2 fluxes

Wood CO_2 fluxes increased with wood moisture content in both angiosperms and gymnosperms (Figure 4). However, the coefficient was

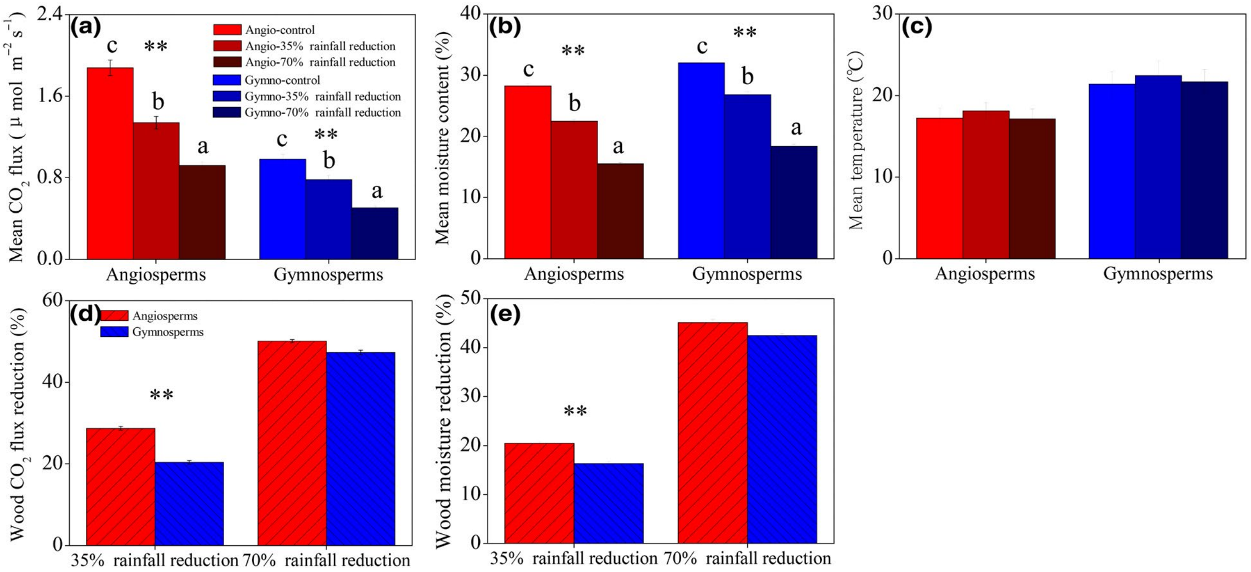

FIGURE 3 Mean CO_2 fluxes (a), moisture content (b), temperature (c), CO_2 flux reduction (d), and wood moisture reduction (e) of angiosperm and gymnosperm wood in rainfall reduction treatments. The wood CO_2 flux or moisture reduction was calculated as the difference of CO_2 fluxes or wood moisture between control and 35% or 70% rainfall reduction treatment. Plotted data are means ($n = 216$) and error bars represent 1 *SE*. * indicates a significant difference at $\alpha = 0.05$ and ** indicates a significant difference at $\alpha = 0.01$ [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results of tests for differences between angiosperms and gymnosperms in reduction of wood CO_2 flux and moisture content of samples subjected to 35% rainfall reduction treatment and 70% rainfall reduction treatment when compared with control. Data were not ln-transformed in these models and the results of ANOVA analysis were consistent with the values shown in Figure 3d,e

Treatment	Fixed-effect term	*NumDF*	*DenDF*	*F*	*p*
CO_2 flux reduction					
35% rainfall reduction	Taxonomic group	1	4	38.7	<.01
70% rainfall reduction	Taxonomic group	1	4	3.18	.149
Moisture reduction					
35% rainfall reduction	Taxonomic group	1	34	24.5	<.01
70% rainfall reduction	Taxonomic group	1	4	1.06	.361

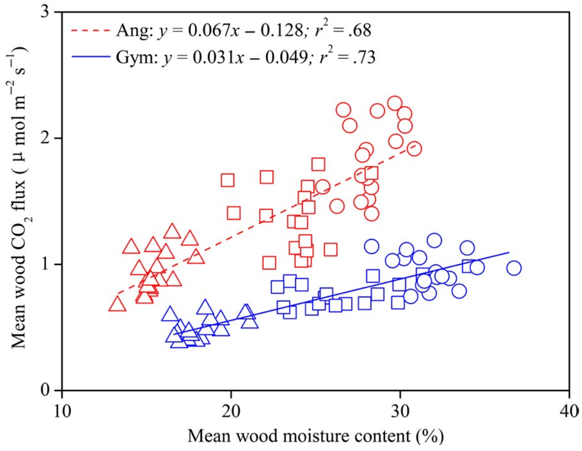

FIGURE 4 Relationship of CO_2 flux and moisture content of angiosperm and gymnosperm wood subjected to different rainfall reduction treatments (n = 108). Each data point represents the annual mean of 12 repeated measurements. Slopes of relationships were significantly different ($p < .01$, $F = 22.68$). Circular, control; square, 35% rainfall reduction treatment; triangle, 70% rainfall reduction treatment [Colour figure can be viewed at wileyonlinelibrary.com]

significantly greater in angiosperms than gymnosperms ($p < .001$), showing that CO_2 fluxes were more sensitive to moisture availability in angiosperms than gymnosperms. The moisture sensitivity of wood CO_2 fluxes was positively correlated with wood nitrogen density and negatively correlated with wood carbon quality index (Figure 5). Wood CO_2 fluxes were also positively correlated with temperature, showing high values in summer and low values in winter (Figure S6). The temperature sensitivity of wood CO_2 fluxes (activation energy, E) was statistically indistinguishable among the three treatments for both angiosperms and gymnosperms (all $p > .05$, Figure 6). The estimated E value was 0.50 eV (Q_{10} = 2.11; Figure S7) with a 95% confidence interval of 0.48–0.52 (Table 3) that excluded the hypothesized value of 0.65 eV for respiration (Brown et al., 2004; Gillooly et al., 2001), but was within the range ~0.31–0.56 eV for microbial ecoenzyme kinetics (Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012).

3.4 | Interaction effects between wood traits and microclimates

Wood nitrogen density was the best predictor of seasonal CO_2 fluxes, followed by wood temperature, carbon quality index, moisture content, and diameter (Figure S8). SEM showed that throughfall and air temperature ($1/k_BT_0 - 1/k_BT$) had direct positive effects on wood moisture content (r = .14 and .28, respectively; Figure 7). Air temperature ($1/k_BT_0 - 1/k_BT$) had a direct positive effect on wood temperature ($1/k_BT_0 - 1/k_BT$; r = .98). Wood temperature ($1/k_BT_0 - 1/k_BT$) had a direct negative effect (r = −.69) on wood CO_2 fluxes, while wood moisture had a positive effect (r = .31). Wood age had a direct positive effect on wood diameter (r = .48). Wood diameter had a direct negative effect on wood nitrogen (r = −.38) and a direct positive effect on wood carbon quality index (r = .41). Wood nitrogen (r = .67) had a direct positive effect on CO_2 fluxes, but the wood carbon quality index had a direct negative effect (r = −.53). Wood moisture and nitrogen had a significant interaction effect on wood CO_2 fluxes (r = .26), which increased with higher wood nitrogen and greater wood moisture contents. Wood moisture and nitrogen had a significant interaction effect on wood CO_2 fluxes (r = .26), which increased with higher wood nitrogen and greater wood moisture contents.

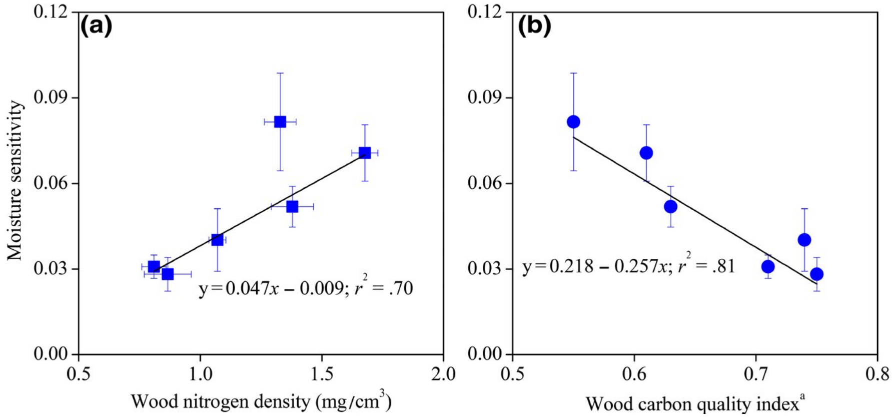

FIGURE 5 The relationships between moisture sensitivity of wood CO_2 fluxes and wood nitrogen density (a) and carbon quality index (b). Each data point represents a tree species. ^{a}(Alkyl + N-Alkyl + Aromatic + Phenolic)/(O-alkyl + Acetal) [Colour figure can be viewed at wileyonlinelibrary.com]

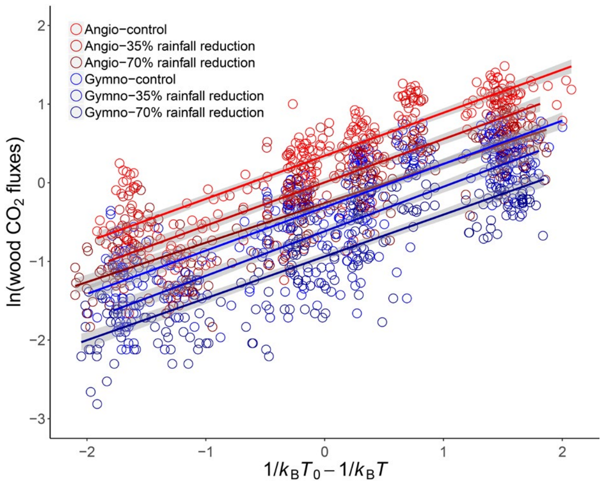

FIGURE 6 Modified Arrhenius plot showing linear mixed model fits of Equation (1) to data for temperature and CO_2 flux from wood subjected to three rainfall reduction treatments (n = 1,296). The x-axis is the inverse absolute temperature (T) in Kelvin (K) multiplied by the Boltzmann constant (k_B, 8.617×10^{-5} eV/K) and normalized by a standard wood temperature (T_0), 290.15 K or 17°C. Estimated activation energies E (shown by slopes) were not statistically different for taxonomic groups ($F = 0.65$; $p = .43$) or treatments ($F = 0.53$; $p = .60$). The shaded areas indicate 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Coefficients, 95% confidence interval (95% CI), and p values for linear mixed-effects model fits of Equation (2) for wood CO_2 fluxes

Variables	Coefficient	95% CI	p
$1/k_BT_0 - 1/k_BT$	0.50	0.48 to 0.52	<.001
Wood moisture	0.56	0.51 to 0.61	<.001
Wood nitrogen density	2.17	1.67 to 2.67	<.001
Wood carbon quality[a]	−3.14	−4.54 to −1.74	<.05

[a](Alkyl + N-Alkyl + Aromatic + Phenolic)/(O-alkyl + Acetal).

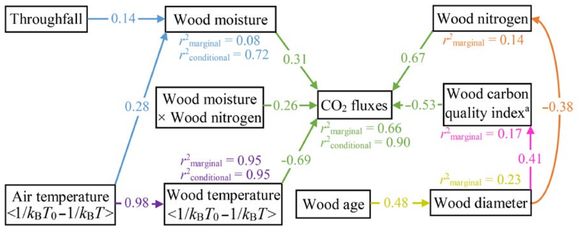

FIGURE 7 Piecewise structural equation model (SEM) outlining the influence of wood microclimates, traits, and their interactions on wood CO_2 fluxes (n = 1,296). Single-headed arrow represents a directional effect of one variable upon another. Numbers besides arrows show standardized coefficients (r). All fitted coefficients are significant at $\alpha = 0.05$. $r^2_{marginal}$ and $r^2_{conditional}$ represent the amount of variation of the variable explained by all paths from the fixed effects and both the fixed and random effects ("tree species" and "wood ID"). As the paths between wood diameter and wood nitrogen and carbon quality index were calculated from generalized linear models, only $r^2_{marginal}$ was provided. [a](Alkyl + N-Alkyl + Aromatic + Phenolic)/(O-alkyl + Acetal) [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Predicting ecosystem responses to extreme drought strongly depend on our understanding of the drought-induced effects on wood decomposition. Our results show that the effects of drought on wood CO_2 fluxes were different for angiosperm and gymnosperm wood. These fluxes were more inhibited by drought in angiosperms than gymnosperms because angiosperms had significantly higher moisture sensitivity than gymnosperms. Moisture sensitivity was positively correlated with wood nitrogen density and carbon quality, which were both higher in angiosperm wood. On the whole, the results supported our hypothesis (H1) that wood traits mediated wood CO_2 fluxes in response to drought. However, the temperature dependence of CO_2 fluxes was similar in angiosperms and gymnosperms, which is consistent with the MST hypothesis that these fluxes are ultimately controlled by the kinetics of microbial decomposition as characterized by the activation energy E, independent of wood traits. This result was inconsistent with hypothesis (H2), indicating that wood traits do not influence the temperature sensitivity of wood decomposition. Our results suggest that land surface models that predict wood decomposition must incorporate temperature and moisture effects along with their mediation by wood traits.

4.1 | Drought effects on wood CO_2 fluxes varied with traits

It is well established that water availability is the most important environmental constraint in wood decomposition due to that dead wood is dense compounds with a low water-holding capacity (Harmon et al., 1986). Our results showed that drought significantly decreased wood CO_2 fluxes, and this reduction was higher in angiosperms than in gymnosperms in the 35% rainfall reduction treatment (Figure 3). This difference of the drought-induced reduction was explained by the higher moisture sensitivity of wood carbon fluxes in angiosperms (Figure 4). We found that moisture sensitivity was positively correlated with wood nitrogen density and carbon quality (Figure 5), suggesting that higher substrate quality in angiosperms than gymnosperms resulted in larger drought-induced decrease in wood CO_2 fluxes. These findings are consistent with an earlier experimental study that reported increased drought effects on soil enzymatic activity as nitrogen addition increased litter quality (Alster et al., 2013). Furthermore, some limited evidence also showed a similar relationship between moisture sensitivity of heterotrophic respiration and nutrient availability in terrestrial decomposers (Chen Harmon, Griffiths, & Hicks, 2000; Manzoni, Schimel, & Porporato, 2012), supporting our finding on the role of moisture sensitivity and wood quality on wood decomposition.

Interaction effects among multiple global change drivers on ecosystem processes are universal (Li, Niu, & Yu, 2016; Luo et al., 2004), which can have complex and significant impacts on forest carbon cycling and storage. For example, moisture sensitivity of soil organic carbon (SOC) decomposition is highly determined by interaction effects of moisture availability and substrate quality on the microbial property (e.g., biomass and community composition; Manzoni et al., 2012). Similar to SOC decomposition, our SEM analysis also revealed a positive interaction between wood moisture and wood nitrogen (Figure 7), with high wood nitrogen density promoting CO_2 fluxes at a given wood moisture content. This likely reflects fundamental stoichiometric and environmental controls on the moisture sensitivity of wood microbial respiration rates (A'Bear et al., 2014). Angiosperm wood with higher nitrogen density and carbon quality benefits greater microbial growth and biomass compared with gymnosperm one (Kahl et al., 2017; Purahong, Wubet, Krüger, & Buscot, 2018). It indicates that more water is needed for microbial metabolism and further supports a higher decay rate in angiosperms (Herbst, Roberts, Rosier, Taylor, & Gowing, 2007; Hu et al., 2017). Under the drought treatment, microbial biomass may decrease since a portion of microbes would have been killed by desiccation (Hueso, García, & Hernández, 2012). Thus, microbial decomposition in angiosperms may be more inhibited under drought, especially with a higher reduction in wood moisture in angiosperms (Figure 3e). Substrate quality has a key control on microbial community structure and may also influence moisture sensitivity (Hu et al., 2017). Plant litter with high carbon quality (e.g., angiosperm wood) appears to favor bacterial more than fungal growth, while low-quality litter (e.g., gymnosperm wood) may produce the opposite relationship (Moore et al., 2004; Six, Frey, Thiet, & Batten, 2006). Since bacteria is typically more sensitive to drought than fungal communities (Allison et al., 2013; Manzoni et al., 2012), angiosperm wood with higher bacterial abundances may largely affected by drought compared to gymnosperm one. In addition, other traits such as wood age and size could also indirectly affect drought effects on wood CO_2 fluxes through controlling wood chemical composition (Figure 7). We found that wood age had a direct positive control on wood diameter. As wood diameter had a negative control on wood nitrogen and carbon quality, a lower substrate quality in gymnosperms may induce slower decomposition than that in angiosperms.

In this study, we have assumed that trait effects on wood decomposition are due primarily to shift in microbial activity or community composition induced by changes in wood moisture. Since microbes are the main decomposers of dead wood (Bradford et al., 2016; Cornwell et al., 2009), the roles of climate and wood traits on microbial community establishment are still being explored (Hu et al., 2017; Purahong et al., 2018). It deserves the further study to probe the microbial mechanisms of climate and trait effects on wood decomposition. In addition, we explored the effect of wood nitrogen and carbon quality on decomposition with the initial values, but wood nitrogen density and carbon quality could change with the decomposition and potentially affect our results. Due to the slow processes of wood decomposition, narrow change in nitrogen density and carbon quality may has neglectful impact in this 1 year study, but caution should be taken in the long-term research (Hu et al., 2017; Oberle et al., 2020).

4.2 | Drought effects on wood CO_2 fluxes varied with drought intensities

Our results showed that there was a significant difference in the reduction of CO_2 fluxes between wood types (angiosperm and gymnosperm) in 35% rainfall reduction treatment, but the insignificant difference was found in 70% rainfall reduction treatment (Figure 3d). This finding indicates that drought effects on wood CO_2 fluxes are not only dependent on wood traits but also on drought intensity. Drought generally limits the physiological performance of microbes and the diffusion of nutrients in the wood pore space, and therefore inhibits the microbial community to an important adaptive force (Hueso et al., 2012). The effect of drought is accounted for a potential decrease of microbial respiration through linear functions under optimum water conditions (Bauer, Herbst, Huisman, Weihermüller, & Vereecken, 2008). Past research by a meta-analysis found that there was a quasi-constant water-stress threshold when microbial activity effectively ceases, at a moisture content of about 20% in plant litter (Manzoni et al., 2012). In the present study, wood moisture contents dropped to a critically low level for 70% rainfall reduction treatment, with 16.2% and 17.7% for angiosperms and gymnosperms, respectively (Figure S5), which was below the water-stress threshold. Enzymes in decomposing litter have been shown to maintain residual activity to near air-dry conditions (Harmon et al., 1986). It is known that air-drying has detrimental effects in microbial community, since microorganisms not adapting to high water tension will die or be dormant (Hueso et al., 2012). Under extreme dry conditions, substrate and nutrient bioavailability may be the most limiting factor for microbial metabolism (A'Bear et al., 2014), because severe drought could reduce diffusion of soluble substrates, microbial mobility, and/or consequent access to substrates (Manzoni et al., 2012). Therefore, when wood moisture content was extremely low, wood CO_2 fluxes were only maintained at a low level for both taxonomic groups in this case. Consistent with previous studies (Allison et al., 2013; Harmon et al., 1986), this finding highlights that increasing drought intensity may alter the decomposition processes relying on nutrient availabilities. Thus, it is important to distinguish different drought effects varying with drought intensities, which could accurately represent microbial feedback in wood decomposition rate.

4.3 | Temperature sensitivity of wood CO_2 fluxes independent of traits

The temperature sensitivity of wood CO_2 fluxes was invariant with wood traits in this study, exhibiting a single activation energy (*E*) of 0.50 eV. Our estimate was slightly lower than the hypothesized value of 0.65 eV based on MST (Brown et al., 2004; Gillooly et al., 2001), but within the range of ~0.31–0.56 eV observed for kinetics of microbial ecoenzymes that degrade organic macromolecules (including lignin and cellulose; Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012) and the ranges of ~0.41–0.74 eV reported for respiration associated with several organism groups (Gillooly et al., 2001). This finding implies that wood CO_2 fluxes may be slightly less sensitive to temperature changes than those predicted by the MST that assumes steady-state resource supply (mainly soil respiration, but see Allen et al., 2005).

Our results were consistent with other studies of wood decay (Chen et al., 2000; Mackensen & Bauhus, 2003; Manning et al., 2018), but opposite to the reported variated temperature sensitivity on leaf litter decay (Fierer et al., 2005; Follstad Shah et al., 2017). Comparing with nutrient contents of leaf litter at the globe (Follstad Shah et al., 2017), carbon/nitrogen ratios of wood were extremely high (~251 vs. ~64). The nutrient limitation might be the main reason for the stable biochemical reactions in wood decay in response to temperature (Chambers et al., 2001; Mackensen & Bauhus, 2003). Recent advances in ecological stoichiometry and MST have initiated that there are lower nutrient thresholds and higher maximum values for microbial growth and activity when temperature elevates (Allen & Gillooly, 2009; Sterner & Elser, 2002). When nutrient supply rates are near optimal, strong interaction effects between nutrient and temperature appeared (Cross et al., 2015; Davidson et al., 2006), which increased nutrient-use efficiency at higher temperatures. Dead wood is primarily composed of recalcitrant compounds such as carbohydrates and lignin with limited nutrient (e.g., nitrogen) supplied from soils or atmosphere for decomposers (Cornwell et al., 2009). In particular, our samples focused more on lower nutrient concentrations at the early stages (the first 2 years) compared with woody debris at the later stages (Rinne et al., 2019). Thus, we found no significant interaction between wood nutrient and temperature (Figure 7), indicating their additive effects on wood CO_2 fluxes.

4.4 | Implication for wood decay models

Vegetation models have been extensively used to assess individual effects of global change drivers on decomposition rates over the past two decades (Bradford et al., 2017; Cornwell et al., 2009), by mostly parameterizing the decomposition constant as a function of temperature and moisture (e.g., OCN, Zaehle, and Friend, 2010) and by accounting for the carbon/nitrogen ratio between different plant function types (e.g., LPJ, Sitch et al., 2003; ORCHIDEE, Krinner et al., 2005; and CLM 4.5, Oleson et al., 2013). However, interactions between moisture and nutrient availability are not currently incorporated into the coupled carbon–climate models to date. As a result, it is expected that models will not be able to reproduce the different moisture sensitivities of wood decay between taxonomic groups as observed in our study. Moisture sensitivities of decomposition have already been proved to be crucial to capture the response of the net flux to drought in the CABLE model (Haverd et al., 2016). In our study, because a strong interaction between moisture and wood traits explained larger reductions of CO_2 fluxes in angiosperms than gymnosperms, we suggest that moisture sensitivity of wood decomposition can be incorporated in models based on linear functions described kinetic rate of decomposition (Bauer et al., 2008; Sinsabaugh & Follstad Shah, 2012). Although the subtropical tree species might have a narrow range for wood traits, the difference of wood nitrogen and carbon quality between angiosperms and gymnosperms was significant within bark, sapwood, and heartwood. These ranges are broad enough to characterize general patterns of traits effects on ecological communities (Weedon et al., 2009). Our study therefore points out the possibility to enable the development of next generation of vegetation models featured with forest demography (Fisher et al., 2018).

Meanwhile, our results have implications for studying the effects of climate change and varied tree species composition on forest carbon cycling. For example, large tracts of native evergreen broadleaved forests in many areas of subtropical China have been transformed into plantations due to the long-term human activities (Sheng et al., 2010). At present, plantations in this region account for about 63% of all forest plantations in China, and 72% of them are coniferous forests (Hou & Chen, 2008). Lower decomposition rates of gymnosperm compared with angiosperm wood have the potential to slow down the carbon release in this region. However, we should also note that drought decreases wood decomposition more in angiosperms than gymnosperms. Given an increased tendency for drought occurrence in the future climate, if we do not consider this difference, it will produce serious biases in modeling wood carbon fluxes. Furthermore, historical forest management since pre-industrial times in Europe has converted 27% of deciduous forest (as associated with an angiosperm dominance) into coniferous forest (Naudts et al., 2016). In order to mitigate climate change in the future, coniferous forests in northern and central Europe might have to be converted to deciduous forests (Luyssaert et al., 2018). Global vegetation models predict an increase in deciduous forests particularly at the southern edge of the boreal region (IPCC, 2014). The disturbances of wildfire have resulted in pioneer deciduous forest instead of coniferous forest in the first several decades in Canadian forests (Seidl et al., 2017). As the net effect of forest species change on wood carbon stock might be complex, these large-scale shifts in forest species composition will also render dead wood as carbon sources or sinks in forest ecosystems. Therefore, an urgent need to incorporate the trait-based approach for modeling wood turnover and forest carbon cycle on the vegetation feedback by global change.

In summary, our study was the first quantitative attempt to explicitly test for interaction effects of two dominant drivers, climate and wood traits, on wood carbon fluxes. There was a significant interaction effect between wood moisture and nitrogen, with moisture effect on wood CO_2 fluxes increasing at higher nitrogen availability. This further demonstrated that wood traits regulated drought effects on wood CO_2 fluxes, where drought-induced decreases in wood CO_2 fluxes were larger in angiosperms than gymnosperms. We also used MST to link wood chemical traits to temperature sensitivity (activation energy, *E*) of wood CO_2 fluxes, but found no significant interaction between wood temperature and substrate quality. The temperature sensitivity was unchanged by wood traits and was comparable to predictions based on the MST (Gillooly et al., 2001). Given the increasing frequency of drought globally and large-scale changes in tree species composition in future climate change (Weedon et al., 2009), interaction effects of climate and traits on wood decomposition should have important implications for wood decay models to more accurately quantify the pools and fluxes of dead wood in carbon cycling.

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CONFLICT OF INTEREST

All authors declare no conflicts of interest.

AUTHORS' CONTRIBUTION

Z.H., S.T.M., and X.Z. designed the study; Z.H., S.T.M., and H.Y.H.C. performed analyses; Z.H. wrote the first draft; Z.H., G.Z., and J.W. performed measurements; and all the other authors contributed to the revisions and discussions of the results.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are subject to restrictions, and may be available on request from the authors.

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REFERENCES

A'Bear, A. D., Jones, T. H., Kandeler, E., & Boddy, L. (2014). Interactive effects of temperature and soil moisture on fungal-mediated wood decomposition and extracellular enzyme activity. *Soil Biology and Biochemistry*, *70*, 151–158. https://doi.org/10.1016/j.soilbio.2013.12.017

Allen, A. P., & Gillooly, J. F. (2009). Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecology Letters*, *12*(5), 369–384. https://doi.org/10.1111/j.1461-0248.2009.01302.x

Allen, A. P., Gillooly, J. F., & Brown, J. H. (2005). Linking the global carbon cycle to individual metabolism. *Functional Ecology*, *19*(2), 202–213. https://doi.org/10.1111/j.1365-2435.2005.00952.x

Allison, S. D., Lu, Y., Weihe, C., Goulden, M. L., Martiny, A. C., Treseder, K. K., & Martiny, J. B. H. (2013). Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology*, *94*(3), 714–725. https://doi.org/10.1890/12-1243.1

Alster, C. J., German, D. P., Lu, Y., & Allison, S. D. (2013). Microbial enzymatic responses to drought and to nitrogen addition in a southern California grassland. *Soil Biology and Biochemistry*, *64*, 68–79. https://doi.org/10.1016/j.soilbio.2013.03.034

Baldock, J. A., Oades, J. M., Nelson, P. N., Skene, T. M., Golchin, A., & Clarke, P. (1997). Assessing the extent of decomposition of natural organic materials using solid-state ^{13}C NMR spectroscopy. *Soil Research*, *35*(5), 1061. https://doi.org/10.1071/S97004

Bauer, J., Herbst, M., Huisman, J. A., Weihermüller, L., & Vereecken, H. (2008). Sensitivity of simulated soil heterotrophic respiration to temperature and moisture reduction functions. *Geoderma*, *145*(1-2), 17–27. https://doi.org/10.1016/j.geoderma.2008.01.026

Berg, B., Berg, M. P., Bottner, P., Box, E., Breymeyer, A., de Anta, R. C., … de Santo, A. V. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: Some relationships with climate and litter quality. *Biogeochemistry*, *20*(3), 127–159. https://doi.org/10.1007/bf00000785

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., & Wood, S. A. (2016). Understanding the dominant controls on litter decomposition. *Journal of Ecology*, *104*(1), 229–238. https://doi.org/10.1111/1365-2745.12507

Bradford, M. A., Veen, G. F., Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., … van der Putten, W. H. (2017). A test of the hierarchical model of litter decomposition. *Nature Ecology & Evolution*, *1*(12), 1836–1845. https://doi.org/10.1038/s41559-017-0367-4

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Bu, X., Gu, X., Zhou, X., Zhang, M., Guo, Z., Zhang, J., … Wang, X. (2018). Extreme drought slightly decreased soil labile organic C and N contents and altered microbial community structure in a subtropical evergreen forest. *Forest Ecology and Management*, *429*, 18–27. https://doi.org/10.1016/j.foreco.2018.06.036

Chambers, J. Q., Schimel, J. P., & Nobre, A. D. (2001). Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry*, *52*(2), 115–131. https://doi.org/10.1023/a:1006473530673

Chen, H., Harmon, M. E., Griffiths, R. P., & Hicks, W. (2000). Effects of temperature and moisture on carbon respired from decomposing woody roots. *Forest Ecology and Management*, *138*(1-3), 51–64. https://doi.org/10.1016/S0378-1127(00)00411-4

Cornwell, W. K., Cornelissen, J. H. C., Allison, S. D., Bauhus, J., Eggleton, P., Preston, C. M., … Zanne, A. E. (2009). Plant traits and wood fates across the globe: Rotted, burned, or consumed? *Global Change Biology*, *15*(10), 2431–2449. https://doi.org/10.1111/j.1365-2486.2009.01916.x

Cross, W. F., Hood, J. M., Benstead, J. P., Huryn, A. D., & Nelson, D. (2015). Interactions between temperature and nutrients across levels of ecological organization. *Global Change Biology*, *21*(3), 1025–1040. https://doi.org/10.1111/gcb.12809

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*(1), 52–58. https://doi.org/10.1038/nclimate1633

Davidson, E. A., Janssens, I. A., & Luo, Y. (2006). On the variability of respiration in terrestrial ecosystems: Moving beyond Q_{10}. *Global Change Biology*, *12*(2), 154–164. https://doi.org/10.1111/j.1365-2486.2005.01065.x

Fierer, N., Craine, J. M., McLauchlan, K., & Schimel, J. P. (2005). Litter quality and the temperature sensitivity of decomposition. *Ecology*, *86*(2), 320–326. https://doi.org/10.1890/04-1254

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., … Moorcroft, P. R. (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, *24*(1), 35–54. https://doi.org/10.1111/gcb.13910

Follstad Shah, J. J., Kominoski, J. S., Ardón, M., Dodds, W. K., Gessner, M. O., Griffiths, N. A., … Zeglin, L. H. (2017). Global synthesis of the temperature sensitivity of leaf litter breakdown in streams and rivers. *Global Change Biology*, *23*(8), 3064–3075. https://doi.org/10.1111/gcb.13609

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*(5538), 2248–2251. https://doi.org/10.1126/science.1061967

Guo, J., Chen, G., Xie, J., Yang, Z., & Yang, Y. (2014). Respiration of downed logs in four natural evergreen broad-leaved forests in subtropical China. *Plant and Soil*, *385*(1-2), 149–163. https://doi.org/10.1007/s11104-014-2205-7

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S., Lattin, J., … Sedell, J. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, *34*, 59–234. https://doi.org/10.1016/S0065-2504(08)60121-X

Haverd, V., Smith, B., Raupach, M., Briggs, P., Nieradzik, L., Beringer, J., … Cleverly, J. (2016). Coupling carbon allocation with leaf and root phenology predicts tree–grass partitioning along a savanna rainfall gradient. *Biogeosciences*, *13*(3), 761–779. https://doi.org/10.5194/bg-13-761-2016

Herbst, M., Roberts, J. M., Rosier, P. T., Taylor, M. E., & Gowing, D. J. (2007). Edge effects and forest water use: A field study in a mixed deciduous woodland. *Forest Ecology and Management*, *250*, 176–186. https://doi.org/10.1016/j.foreco.2007.05.013

Hou, Y., & Chen, T. (2008). The strategic benefits of developing precious commercial tree species integrated with secondary forest management in China. *World Forest Research* (with abstract in English).

Hu, Z., Michaletz, S. T., Johnson, D. J., McDowell, N. G., Huang, Z., Zhou, X., & Xu, C. (2018). Traits drive global wood decomposition rates more than climate. *Global Change Biology*, *24*(11), 5259–5269. https://doi.org/10.1111/gcb.14357

Hu, Z., Xu, C., McDowell, N. G., Johnson, D. J., Wang, M., Luo, Y., … Huang, Z. (2017). Linking microbial community composition to C loss rates during wood decomposition. *Soil Biology and Biochemistry*, *104*, 108–116. https://doi.org/10.1016/j.soilbio.2016.10.017

Hueso, S., García, C., & Hernández, T. (2012). Severe drought conditions modify the microbial community structure, size and activity in amended and unamended soils. *Soil Biology and Biochemistry*, *50*, 167–173. https://doi.org/10.1016/j.soilbio.2012.03.026

IPCC. (2014). *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change*. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandre, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.). Cambridge, UK and New York: Cambridge University Press.

Jiang, M.-H., Lin, T.-C., Shaner, P.-J.-L., Lyu, M.-K., Xu, C., Xie, J.-S., … Yang, Y.-S. (2019). Understory interception contributed to the convergence of surface runoff between a Chinese fir plantation and a secondary broadleaf forest. *Journal of Hydrology*, *574*, 862–871. https://doi.org/10.1016/j.jhydrol.2019.04.088

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., … Gossner, M. M. (2017). Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecology and Management*, *391*, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012

Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., … Prentice, I. C. (2005). A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*, *19*(1). https://doi.org/10.1029/2003GB002199

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210x.12512

Li, Y., Niu, S., & Yu, G. (2016). Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: A meta-analysis. *Global Change Biology*, *22*(2), 934–943. https://doi.org/10.1111/gcb.13125

Luo, Y., Su, B. O., Currie, W. S., Dukes, J. S., Finzi, A., Hartwig, U., … Field, C. B. (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, *54*, 731–739. https://doi.org/10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2

Luyssaert, S., Marie, G., Valade, A., Chen, Y.-Y., Njakou Djomo, S., Ryder, J., … McGrath, M. J. (2018). Trade-offs in using European forests to meet climate objectives. *Nature*, *562*(7726), 259–262. https://doi.org/10.1038/s41586-018-0577-1

Mackensen, J., & Bauhus, J. (2003). Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*. *Soil Biology and Biochemistry*, *35*(1), 177–186. https://doi.org/10.1016/S0038-0717(02)00255-9

Manning, D. W. P., Rosemond, A. D., Gulis, V., Benstead, J. P., & Kominoski, J. S. (2018). Nutrients and temperature additively increase stream microbial respiration. *Global Change Biology*, *24*(1), e233–e247. https://doi.org/10.1111/gcb.13906

Manzoni, S., Schimel, J. P., & Porporato, A. (2012). Responses of soil microbial communities to water stress: Results from a meta-analysis. *Ecology*, *93*(4), 930–938. https://doi.org/10.1890/11-0026.1

McDowell, N. G., Michaletz, S. T., Bennett, K. E., Solander, K. C., Xu, C., Maxwell, R. M., & Middleton, R. S. (2018). Predicting chronic climate-driven disturbances and their mitigation. *Trends in Ecology & Evolution*, *33*(1), 15–27. https://doi.org/10.1016/j.tree.2017.10.002

Meentemeyer, V. (1978). Macroclimate the lignin control of litter decomposition rates. *Ecology*, *33*(1), 15–27. https://doi.org/10.2307/1936576

Moore, J. C., Berlow, E. L., Coleman, D. C., Ruiter, P. C., Dong, Q., Hastings, A., … Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, *7*(7), 584–600. https://doi.org/10.1111/j.1461-0248.2004.00606.x

Naudts, K., Chen, Y., McGrath, M. J., Ryder, J., Valade, A., Otto, J., & Luyssaert, S. (2016). Europe's forest management did not mitigate climate warming. *Science*, *351*(6273), 597–600. https://doi.org/10.1126/science.aad7270

Oberle, B., Lee, M. R., Myers, J. A., Osazuwa-Peters, O. L., Spasojevic, M. J., Walton, M. L., … Zanne, A. E. (2020). Accurate forest projections require long-term wood decay experiments because plant trait effects change through time. *Global Change Biology*, *26*(2), 864–875. https://doi.org/10.1111/gcb.14873

Odum, H. T. (1970). Summary: An emerging view of the ecological system at El Verde. In H. T. Odum & R. F. Pidgeon (Eds.), *A tropical rainforest: A study of irradiation and ecology and El Verde, Puerto Rico* (pp. 1191–1289). Washington, DC: US Atomic Energy Commission.

Oleson, K. W., Lawrence, D. M., Gordon, B., Flanner, M. G., Kluzek, E., Peter, J., … Feddema, J. (2013). *Technical description of version 4.5 of the Community Land Model (CLM). NCAR Technical Note NCAR/TN-503+STR* (420 pp.). Boulder, CO: National Center for Atmospheric Research.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., … Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Pietsch, K. A., Ogle, K., Cornelissen, J. H. C., Cornwell, W. K., Bönisch, G., Craine, J. M., … Wirth, C. (2014). Global relationship of wood and leaf litter decomposability: The role of functional traits within and across plant organs. *Global Ecology and Biogeography*, *23*(9), 1046–1057. https://doi.org/10.1111/geb.12172

Purahong, W., Wubet, T., Krüger, D., & Buscot, F. (2018). Molecular evidence strongly supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate forests. *ISME Journal*, *12*(1), 289–295. https://doi.org/10.1038/ismej.2017.177

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Rajala, T., Peltoniemi, M., Pennanen, T., & Mäkipää, R. (2012). Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. *FEMS Microbiology Ecology*, *81*(2), 494–505. https://doi.org/10.1111/j.1574-6941.2012.01376.x

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., … Wattenbach, M. (2013). Climate extremes and the carbon cycle. *Nature*, *500*(7462), 287–295. https://doi.org/10.1038/nature12350

Rinne, K. T., Peltoniemi, K., Chen, J., Peltoniemi, M., Fritze, H., & Mäkipää, R. (2019). Carbon flux from decomposing wood and its dependency on temperature, wood N_2 fixation rate, moisture and fungal composition in a Norway spruce forest. *Global Change Biology*, *25*, 1852–1867. https://doi.org/10.1111/gcb.14594

Russell, M. B., Fraver, S., Aakala, T., Gove, J. H., Woodall, C. W., D'Amato, A. W., & Ducey, M. J. (2015). Quantifying carbon stores and decomposition in dead wood: A review. *Forest Ecology and Management*, *350*, 107–128. https://doi.org/10.1016/j.foreco.2015.04.033

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., … Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*(6), 395–402. https://doi.org/10.1038/nclimate3303

Sheng, H., Yang, Y., Yang, Z., Chen, G., Xie, J., Guo, J., & Zou, S. (2010). The dynamic response of soil respiration to land-use changes in subtropical China. *Global Change Biology*, *16*(3), 1107–1121. https://doi.org/10.1111/j.1365-2486.2009.01988.x

Sinsabaugh, R. L., & Follstad Shah, J. J. (2012). Ecoenzymatic stoichiometry and ecological theory. *Annual Review of Ecology*, *Evolution*, *and Systematics*, *43*(1), 313–343. https://doi.org/10.1146/annurev-ecolsys-071112-124414

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., … Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*(2), 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Six, J., Frey, S. D., Thiet, R. K., & Batten, K. M. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal*, *70*(2), 555–569. https://doi.org/10.2136/sssaj2004.0347

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press.

Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-pelletier, V., Bignell, D. E., … Zou, X. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, *14*, 2661–2677. https://doi.org/10.1111/j.1365-2486.2008.01672.x

Wang, G., Post, W. M., Mayes, M. A., Frerichs, J. T., & Sindhu, J. (2012). Parameter estimation for models of ligninolytic and cellulolytic enzyme kinetics. *Soil Biology and Biochemistry*, *48*, 28–38. https://doi.org/10.1016/j.soilbio.2012.01.011

Weedon, J. T., Cornwell, W. K., Cornelissen, J. H. C., Zanne, A. E., Wirth, C., & Coomes, D. A. (2009). Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters*, *12*(1), 45–56. https://doi.org/10.1111/j.1461-0248.2008.01259.x

Zaehle, S., & Friend, A. D. (2010). Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, *24*(1). https://doi.org/10.1029/2009GB003521

Zanne, A. E., Oberle, B., Dunham, K. M., Milo, A. M., Walton, M. L., & Young, D. F. (2015). A deteriorating state of affairs: How endogenous and exogenous factors determine plant decay rates. *Journal of Ecology*, *103*(6), 1421–1431. https://doi.org/10.1111/1365-2745.12474

Zhu, J., Hu, H., Tao, S., Chi, X., Li, P., Jiang, L., … Fang, J. (2017). Carbon stocks and changes of dead organic matter in China's forests. *Nature Communications*, *8*(1). https://doi.org/10.1038/s41467-017-00207-1

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects modeling for nested data. In M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, & W. Wong (Eds.), *Mixed effects models and extensions in ecology with R* (pp. 101–142). Berlin: Springer.

SUPPORTING INFORMATION

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

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