


Traits drive global wood decomposition rates more than climate

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Abstract

Wood decomposition is a major component of the global carbon cycle. Decomposition rates vary across climate gradients, which is thought to reflect the effects of temperature and moisture on the metabolic kinetics of decomposers. However, decomposition rates also vary with wood traits, which may reflect the influence of stoichiometry on decomposer metabolism as well as geometry relating the surface areas that decomposers colonize with the volumes they consume. In this paper, we combined metabolic and geometric scaling theories to formalize hypotheses regarding the drivers of wood decomposition rates, and assessed these hypotheses using a global compilation of data on climate, wood traits, and wood decomposition rates. Our results are consistent with predictions from both metabolic and geometric scaling theories. Approximately half of the global variation in decomposition rates was explained by wood traits (nitrogen content and diameter), whereas only a fifth was explained by climate variables (air temperature, precipitation, and relative humidity). These results indicate that global variation in wood decomposition rates is best explained by stoichiometric and geometric wood traits. Our findings suggest that inclusion of wood traits in global carbon cycle models can improve predictions of carbon fluxes from wood decomposition.

KEYWORDS

carbon cycling, metabolic scaling theory, wood decomposition, wood diameter, wood nitrogen

1 | INTRODUCTION

Forests contain ~360 Pg of carbon (C) in plant biomass, about 20% of which is stored in dead wood (Pan et al., 2011). Dead wood

biomass is predicted to increase with more frequent and intense climate extremes and disturbances (e.g., deforestation, storms, drought, heat waves, and fire) in the future (Pan et al., 2011; Reichstein et al.,

2013). Decomposition returns the C stored in dead wood to the atmosphere via microbial respiration. Thus, wood decomposition plays a critical role in regulating global C stocks and fluxes (Bradford et al., 2014; Harmon et al., 1986; Hoppe et al., 2015). However, the mechanisms driving global variation in decomposition rates are still not fully understood (Cornwell et al., 2009; Harmon et al., 1986), which makes it difficult to predict terrestrial C cycle feedbacks under projected global change scenarios.

Most decomposition studies at broad spatial scales have viewed climate as the primary control on decomposition rates (Berg et al., 1993; Harmon et al., 1986; Moore et al., 1999), with wood traits having only a secondary influence (Bradford, Berg, Maynard, Wieder, & Wood, 2016; Harmon et al., 1986). However, the relative importance of climate variables and wood traits has been a subject of recent debate (Cornwell et al., 2008, 2009; Zhu et al., 2017). Some studies have shown that variation in decomposition rates were influenced by stoichiometric, geometric, and structural wood traits (van der Wal, de Boer, Smant, & van Veen, 2007; van Geffen, Poorter, Sass-Klaassen, van Logtestijn, & Cornelissen, 2010; Weedon et al., 2009). It has also been suggested that the colonization of microorganisms and wood nutrient content, rather than climate, explained much of the variation in decomposition rates (Bradford et al., 2014; Cornwell et al., 2008; Vitousek, Turner, Parton, & Sanford, 1994). However, most studies have been conducted at plot or regional scales, and thus considered relatively limited ranges of variation in climate and wood traits. There is therefore a need to evaluate the relative influence of climate and traits on global variation in wood decomposition rates.

To evaluate the relative influences of these drivers, we combine metabolic and geometric scaling theories to link hypothesized climate and trait drivers with wood decomposition rates (Supporting Information Appendix S1), and assess the hypothesized relationships using a global compilation of climate, wood trait, and decomposition data (Supporting Information Appendix S2). Metabolic scaling theory (MST) predicts that decomposition rates will vary with temperature and elemental stoichiometry due to their influence on the biochemical kinetics of decomposition (Allen, Gillooly, & Brown, 2005; Brown, Gillooly, Allen, Savage, & West, 2004; Follstad Shah et al., 2017). Geometric scaling theory (GST) suggests that decomposition rates will vary with wood size and shape due to the scaling of the surface areas that decomposers colonize with the volumes that they consume (McMahon & Kronauer, 1976; Niklas, 1994, 1995; Schmidt-Nielsen, 1984). Assuming the influences of these factors are multiplicative, variation in decomposition rates can be evaluated using a single common expression:

$$k = k_1 e^{-E/k_B T} P^{\alpha_P} h^{\alpha_h} l_{as}^{\alpha_{l_{as}}} e^{\alpha_D} N^{\alpha_N} D^{\alpha_D}, \quad (1)$$

where the annualized wood decomposition rate k (year⁻¹) has a power-law dependence on precipitation (P , mm), relative humidity (h , dimensionless), length of the active season (l_{as} , day/year, sum of days when daytime mean air temperature was >4°C; Pietikäinen, Pettersson, & Bååth, 2005), wood nitrogen content (N , g N/g M), and

wood diameter (D , cm), with scaling exponents α_P , α_h , α_h , $\alpha_{l_{as}}$, α_N , and α_D , respectively (Supporting Information Table S1). GST and MST predict that diameter-scaling exponents for idealized wood geometries will vary between -1 and -0.6 (Supporting Information Appendix S1). Decomposition rates have an exponential dependence on wood mass density (ρ , g/cm³) and a wood density coefficient (a , cm³/g). The influence of temperature (T , K) is characterized by a Boltzmann-Arrhenius relation with an apparent activation energy (E , eV) and Boltzmann's constant ($k_B = 8.617 \times 10^{-5}$ eV/K). Activation energies of ~0.65 eV have been hypothesized based on the enzyme kinetics of metabolism (Gillooly, Brown, West, Savage, & Charnov, 2001), whereas values of ~0.31–0.56 eV have been hypothesized based on microbial coenzyme kinetics (extracellular enzymes not enclosed within membranes of living cells; Sinsabaugh & Follstad Shah, 2012; Wang, Post, Mayes, Frerichs, & Sindhu, 2012; Follstad Shah et al., 2017). Finally, k_1 (year ^{$\alpha_{l_{as}}+1$} mm^{- α_P} day^{- $\alpha_{l_{as}}$} cm^{- α_D} gN^{- α_N} gM ^{α_N}) is a decomposition normalization constant. The formalizations of the above hypotheses in Equation (1) are consistent with a “Fermi approach” for developing intentionally concise and efficient “zeroth order” theory against which complexities can be later evaluated (Harte, 2002; Marquet et al., 2014).

Although MST considers instantaneous rates, wood decomposition does not occur continuously through time at all sites across the globe. As decomposition rate constants k are quantified at an annual time resolution, their magnitudes are confounded by variation in active season length among study sites. By definition, when all else is equal, sites with longer active seasons will have larger values of k . We thus rewrite Equation (1) to give a more instantaneous decomposition rate during the active season (k/l_{as} ; day⁻¹), such that

$$\frac{k}{l_{as}} = k_2 e^{-E/k_B T} P^{\alpha_P} h^{\alpha_h} e^{\alpha_D} N^{\alpha_N} D^{\alpha_D}, \quad (2)$$

where k_2 is another decomposition normalization constant (day⁻¹ mm^{- α_P} gN^{- α_N} gM ^{α_N} cm^{- α_D}) that accounts for other potential drivers that are not considered here (e.g., wood water content, wood nutrient content, etc.).

Here we evaluate support for the hypotheses formalized in Equations (1) and (2) using a new globally distributed dataset for climate, wood traits, and wood decomposition rates. These data fill the climate space occupied by terrestrial woody plants across the world, and thus span global ranges in both temperature and precipitation (Figure 1a, b). Our objectives were to (a) assess the global activation energy and diameter-scaling exponent of wood decomposition and (b) examine the relative importance of climate and wood traits on wood decomposition rates.

2 | MATERIALS AND METHODS

2.1 | Data collection, compilation, and calculations

We searched the literature for decomposition rates of wood (defined as woody plant tissues of any size including “twigs” and “fine woody

debris”) using the ISI Web of Science database and the keywords “(woody debris OR twigs) AND (decomposition OR decaying OR processing)” (1900–2016). To avoid bias, papers meeting the following criteria were selected: (a) decomposition of wood was measured on the surface of the soil (not buried in the soil or hung in the air); (b) either a decomposition rate constant or change in mass or wood density over a known period of time was reported; and (c) wood traits (initial wood N content, wood diameter, and wood density) were recorded in the experiment. Papers that did not meet these three criteria were excluded.

On the basis of the above criteria, we compiled a dataset that consists of 191 observations from 83 sites and 142 tree species (Supporting Information Appendix S2). These sites fill the climate space occupied by terrestrial woody plants across the globe, and thus span global ranges in both temperature and precipitation (Figure 1; Supporting Information Figure S1). Data were extracted from the main text, tables, and/or digitized graphs of primary references. Authors were contacted if it was clear that the desired data had been collected but not reported in the paper. Information extracted from each paper included location (i.e., latitude, longitude and country), study duration (including beginning and ending dates), species names, the approach to quantifying decomposition (direct or chronosequence), initial wood density, decomposition rate constant or percent mass/density loss, and initial litter chemistry (% C, N, C/N). We obtained decomposition rates as fitted k values, the decay constant in the single negative exponential decay model (Equations S1–S2 in Supporting Information Appendix S1, Olson, 1963). When only mass- or density-loss data were reported, we estimated k via regression of Equation S1. For cases in which initial wood densities were not provided (<15% of our dataset), we filled the data from the Global Wood Density Database (Chave et al., 2009) based on both tree species and location. For cases in which wood diameters were not provided (<13% of our dataset), these data were imputed via predictive mean matching (PMM) using the “mice” package in the statistical software R 3.4.3 (R Core & Team, 2017).

Climate data for each site were obtained from the Twentieth Century Reanalysis Project, a global one-half degree resolution gridded climate dataset (Compo et al., 2011). For each site where decomposition data were available, we obtained climate time series at a 3-hr resolution based on bilinear interpolation. Climate data were then truncated and averaged so they corresponded to the time period when the decomposition experiments were conducted. This helps minimize error arising from scale mismatch of data (Michaletz, 2018; Michaletz, Cheng, Kerckhoff, & Enquist, 2014; Michaletz, Kerckhoff, & Enquist, 2018). Temperature, precipitation, and relative humidity were calculated as both annual and active season values. We defined the length of active season for wood decomposition as the sum of days when mean daily air temperature was $>4^{\circ}\text{C}$, as microbial growth and enzyme activity almost ceases at air temperatures $<4^{\circ}\text{C}$ (Pietikäinen et al., 2005). Mean annual temperature ($^{\circ}\text{C}$) was calculated as the 12-month average of mean monthly air temperatures, whereas microbial active season temperature ($^{\circ}\text{C}$) was calculated as the average across microbial active season days only.

Temperature was also expressed as the Boltzmann factor exponent $1/k_{\text{B}}T$, where k_{B} is the Boltzmann constant ($8.617 \times 10^{-5} \text{ eVK}^{-1}$) and T is temperature (K). The Boltzmann factor exponent was also calculated as annual and active season averages $\langle 1/k_{\text{B}}T \rangle_{\text{ma}}$ and $\langle 1/k_{\text{B}}T \rangle_{\text{as}}$, respectively. Mean annual precipitation P_{ma} (mm) was taken as the 12-month sum of mean monthly totals, mean annual relative humidity h_{ma} (%) was taken as the mean of mean monthly values, mean active season precipitation P_{as} (mm) was taken as the sum of mean daily totals in the active season, and mean active season relative humidity h_{as} (%) was calculated as the mean of mean daily values in the active season.

To explore global patterns of decomposition rates, we divided tree species into different tree taxa and functional groups (angiosperms and gymnosperms), leaf life span (evergreen and deciduous), and divided the globe into different regions (tropical, temperate, and boreal regions). The tropical region was defined between 23.5°S – 23.5°N ; the temperate region was 23.5°N – 50°N and 23.5°S – 50°S ; and the boreal region was 50°N – 66.5°N (Spurr & Barnes, 1980).

2.2 | Statistical analyses

We used three distinct analyses to evaluate the hypotheses in Equations (1) and (2). First, consistent with many previous studies (Berg et al., 1993; Harmon et al., 1986; Moore et al., 1999), we used bivariate ordinary least squares (OLS) regression to characterize relationships between annual decomposition rates k and each covariate in Equation (1). As an additional test, we used orthogonal distance regression (ODR), which minimizes residual variation in both the x - and y -dimensions and is less biased than OLS in estimates of the functional relationship between two variables subject to error (Warton, Wright, Falster, & Westoby, 2006). We fitted ODR using the package “pracma” in R. Results of bivariate analyses can be compared directly to those of previous studies. However, as they do not account for correlated variation among independent variables, we cannot draw firm conclusions regarding the correct strength of these relationships and the relative importance of hypothesized drivers.

Second, to evaluate the relative importance of each hypothesized driver while accounting for correlated variation among all covariates, we used multiple regression to fit Equation (1) to data for annual decomposition rate constant (k) and fit Equation (2) to data for active season decomposition rates (k_{as}) and climate variables. Active season data are more appropriate than annual data for evaluating the metabolic kinetics of decomposition, as they consider only the time periods during which decomposition actually occurs, and thus better correspond to predictions of MST for instantaneous rates (Michaletz et al., 2018). Functional forms for precipitation-, relative humidity-, wood N -, and wood density-dependence of k in Equation (1) were assessed using partial residual plots (Supporting Information Table S1) obtained using `crPlots()` from the R package “car.” To evaluate potential collinearity problems that may arise from relationships between model covariates (Ryan, 1997), we calculated variance-inflation factors (VIFs) for each covariate in each model using `vif()` from

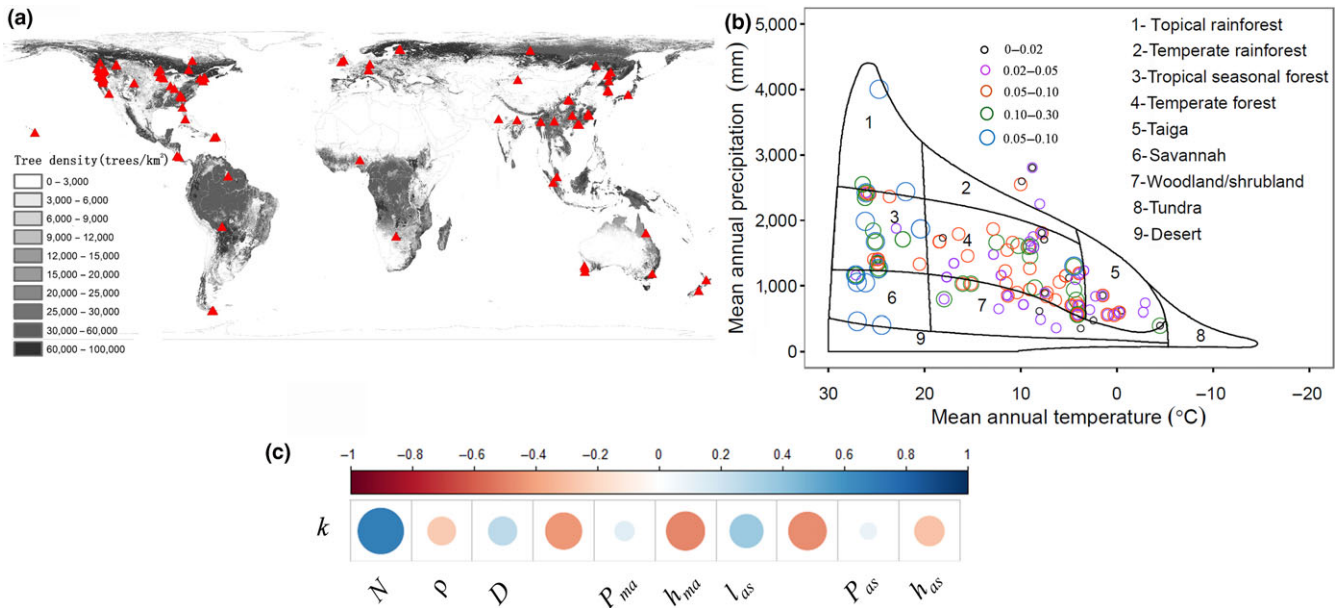


FIGURE 1 Variation in wood decomposition rates at 191 sites spanning global climate gradients. (a) Geographical distribution of the sites where data were available in forest distribution map (Crowther et al., 2015). (b) Variation in annualized wood decomposition rates (k , year⁻¹) in relation to mean annual temperature and mean annual precipitation. All major terrestrial plant biomes are shown (Whittaker, 1970). Circle size and color represent classes of decomposition rates. (c) Correlations between annualized wood decomposition rates (k , year⁻¹) and variables of climate and wood traits by multiple regression. Positive correlations are displayed in blue and negative correlations in red color. Color intensity and the size of the circle are proportional to the correlation coefficients. Variable names: k , wood decomposition rate (year⁻¹); N , wood N content (g N/g M); D , wood diameter (cm); ρ , wood mass density (g/cm³); $\langle 1/k_B T \rangle_{ma}$, averaged annual temperature (eV⁻¹); P_{ma} , mean annual precipitation (mm); h_{ma} , mean annual relative humidity (%); l_{as} , length of the active season (d); $\langle 1/k_B T \rangle_{as}$, averaged active season temperature (eV⁻¹); P_{as} , active season precipitation (mm); and h_{as} , active season relative humidity (%)

the package “car” in R. VIFs for all covariates were lower than 4 (Supporting Information Table S2), far less than the threshold of 10 above which collinearity may adversely affect regression results (Dormann et al., 2013; Ryan, 1997). As k/l_{as} and $\langle 1/k_B T \rangle_{as}$ are nonindependent, their shared term l_{as} may give rise to spurious correlations (Brett, 2004), but this was not observed in our data (Supporting Information Table S3). Partial regression statistics were obtained using *modelEffectSizes()* from the R package “lmSupport,” and partial regression plots were prepared with data from *avPlots()* of the “car” package. Partial regression plots show the correct strength of the relationship between the dependent variable and each independent variable while controlling for the influence of all other independent variables included in the model; plotted variables are residuals, so the slope and variance equal the partial estimates from the multiple regression model.

Multiple regression analyses were performed on 191 data points from 83 sites, where 37 sites (45% of all sites) included two or more data points. In these cases, multiple observations within sites had the same climate data but different wood trait data, which may bias results to reflect variation in traits rather than climate. To evaluate the potential impact of this on our results, we re-ran multiple regressions after randomly selecting one wood sample from each site, and repeated this process 500 times. As a further test, we used classification and regression trees (CART) to examine the relationships between wood decomposition rates, climate variables, and wood

traits for the entire set of 191 data points using the packages “rpart” and “rpart.plot” in R. The ANOVA method was used to divide the data into progressively smaller groups that maximized homogeneity within the groups while minimizing the residual variance. The model was fitted using the one standard error rule and then pruned to minimize the estimated error (De’ath & Fabricius, 2000).

Third, we used linear mixed-effects models (LMMs) to assess the relative importance of wood traits and climate variables on decomposition rates. LMMs are appropriate for macroecological datasets that comprise multiple observations from the same site and the same species, as in our dataset. The complete model (Equation (2)) was fitted to the entire database as well as data subsets (i.e., angiosperms versus gymnosperms; deciduous versus evergreen; tropical regions versus temperate regions) using LMM from the R package “lme4.” The first step in our analysis was to select the form of the variables. Based on partial residual results (Supporting Information Table S1), temperature, wood density, and wood diameter were best characterized as exponential functions, whereas precipitation, relative humidity, and wood N were best characterized by power laws. Then variables were selected for the lowest AIC score when evaluated as a single explanatory variable for wood decomposition rates. We constructed LMMs that included one to all six of the explanatory variables and used lowest AIC to determine which model structure to retain (Supporting Information Table S4). Both spatial location (i.e., actual site) and tree

species (i.e., individual species) were used as random (intercept) terms in LMMs, as our dataset contains multiple observations for some sites and species. To examine the relative effect size (defined here as the parameter estimate and confidence interval obtained from the LMM) of each predictor on decomposition rate, each predictor variable was Z-score transformed. These transformed data were then used in the LMM analyses, which gave the parameter estimates. In addition, we used two sets of LMMs to assess the relative importance of climate and wood traits on decomposition rates. First, we compared the r^2 values of submodels that include only climate (temperature, precipitation, and relative humidity) or traits (wood N, diameter, and density) to evaluate their relative importance (circle areas in Figure 3b). Second, we used the difference in r^2 values of the full model and the submodels to consider the combined effects of climate and traits on decomposition rates (areas in circles that were not overlaid with other circles in Figure 3b). We then compared r^2 values and AIC scores in LMMs with all fixed effects and LMMs with only climate or wood traits for the entire database and subdatabase (Supporting Information Table S5). We calculated r^2 values to estimate variance explained by the explanatory variables for the minimally adequate LMMs, which follows Nakagawa and Schielzeth (2013) to retain the random effects structure. On the basis of this method, we calculated the r^2 values for each significant explanatory variable to represent relationships on the multivariate model.

3 | RESULTS

Three sets of analyses were consistent with expectations from metabolic scaling theory (MST) and geometric scaling theory (GST), showing that wood traits (not climate) were the strongest statistical predictors of global variation in wood decomposition rates. First, bivariate ordinary least squares regression (OLS) and orthogonal distance regression (ODR) suggested that both climate variables and wood traits were important predictors of global variation in annualized decomposition rates (Figure 1c and Supporting Information Figure S3; Table 1 and Supporting Information Table S6). Wood decomposition rates increased exponentially with average active season temperature $\langle 1/k_B T \rangle_{as}$ ($r^2 = 0.31$, $p = 2.00 \times 10^{-16}$). The estimated activation energy E was 0.68 eV, with a 95% confidence interval (95% CI) of 0.54–0.83 (Table 1) that included the value of 0.65 eV hypothesized for respiration (Allen et al., 2005; Brown et al., 2004), but excluded the range of ~ 0.31 – 0.56 eV hypothesized for kinetics of microbial coenzymes (Follstad Shah et al., 2017; Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012). Some of the variation in wood decomposition rates was explained by active season length ($r^2 = 0.16$, $p = 6.72 \times 10^{-9}$) and the active season relative humidity ($r^2 = 0.07$, $p = 2.01 \times 10^{-3}$), whereas almost none of the variation was explained by the active season precipitation ($r^2 = 0.03$, $p = 0.05$). Wood traits were generally stronger predictors of decomposition rates, which increased with wood N content ($r^2 = 0.40$, $p = 2.00 \times 10^{-16}$) and wood density ($r^2 = 0.09$, $p = 2.27 \times 10^{-5}$), and decreased with wood diameter ($r^2 = 0.18$, $p = 1.171 \times 10^{-9}$).

Second, multiple regression models (Figure 2 and Supporting Information Table S3; the same general results were obtained for annual data in Supporting Information Figure S4) showed that most of the explained variation in wood decomposition rates (full model adjusted $r^2 = 0.59$) was accounted for by two wood traits: N content (partial $r^2 = 0.25$; Figure 2d) and diameter (partial $r^2 = 0.20$; Figure 2e). In contrast to bivariate analyses (Figure 1c; Supporting Information Figure S3), average active season temperature $\langle 1/k_B T \rangle_{as}$ (partial $r^2 = 0.09$; Figure 2a) and relative humidity (partial $r^2 = 0.07$; Figure 2c) accounted for only minor amounts of the explained variation in decomposition rates, whereas active season precipitation (partial $r^2 = 0.00$; Figure 2b) and wood density (partial $r^2 = 0.00$; Figure 2f) accounted for none of the explained variation. The estimated activation energy of $E = 0.30$ eV (Supporting Information Table S3) had a 95% CI of 0.16–0.43 that excluded the value of 0.65 eV hypothesized for respiration (Allen et al., 2005; Brown et al., 2004) but were more consistent with the range ~ 0.31 – 0.56 eV for microbial coenzyme kinetics (Follstad Shah et al., 2017; Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012). The diameter-scaling exponent (α_D) was estimated as -0.35 with a 95% CI of -0.45 to -0.25 that did not include the values predicted by GST and MST for idealized wood geometries. The same general conclusions were obtained from 500 multiple regressions based on randomly selecting a single wood sample for each site, showing that these results were not an artifact of having multiple observations within some sites (Supporting Information Figure S5). Regression tree analyses also identified wood N as the most important driver of decomposition rates (Supporting Information Figure S6).

Third, linear mixed-effects models (LMM) also showed that wood traits were better predictors of variation in decomposition rates than climate variables (Figure 3). In contrast to multiple regression, LMMs did not assume independence among observations, so it was more appropriate for datasets with multiple observations from a single site (as was the case for some of our data). Wood traits (N content, diameter, and density) explained 49% of the variation in global normalized decomposition rates, whereas climate variables (temperature, humidity, and precipitation) explained only 21% (Figure 3b). Wood decomposition rates increased with N content and decreased with diameter (Figure 3a). These same general results were obtained for various subsets of taxa (Supporting Information Figure S7), leaf life spans (Supporting Information Figure S8) and climate regions (Supporting Information Figure S9).

In summary, estimated coefficients (exponents and activation energies) varied between bivariate (OLS) and multivariate (multiple regression and LMM) regression approaches (Table 1). However, results from multiple regression and LMM were statistically indistinguishable, and better characterized the correct relationship between decomposition rates and each covariate as they controlled out the influence of other covariates. All analyses (Table 1) were consistent in suggesting that wood traits were stronger predictors of global variation in wood decomposition rates than climate variables. Wood N was the most important variable on controlling decomposition rates in three sets of analyses.

TABLE 1 Coefficients, 95% confidence interval (95% CI), and r^2 values for ordinary least squares regression models, multiple regression models, and linear mixed-effects models for global wood decomposition rates

Variables	OLS			Multiple regression			LMM		
	Coefficient	95% CI	r^2	Coefficient	95% CI	r^2	Coefficient	95% CI	r^2
$\langle 1/k_B T \rangle_{as}$	-0.68	-0.83 to -0.54	0.31	-0.30	-0.43 to -0.16	0.09	-0.27	-0.34 to -0.10	0.18
P_{as}	0.31	0.00 to 0.61	0.02	-0.10	-0.33 to 0.13	0.00	-0.07	-0.09 to 0.15	0.00
h_{as}	-1.72	-2.61 to -0.82	0.07	-1.21	-1.87 to -0.55	0.07	-1.13	-0.29 to -0.05	0.11
l_{as}	1.27	0.86 to 1.69	0.16	-	-	-	-	-	-
N	0.79	0.65 to 0.93	0.40	0.50	0.37 to 0.62	0.25	0.48	0.28 to 0.48	0.37
D	-0.45	-0.59 to -0.31	0.18	-0.35	-0.45 to 0.25	0.20	-0.37	-0.44 to 0.24	0.29
ρ	2.22	1.21 to 3.23	0.09	-0.27	-0.96 to 0.43	0.00	-0.31	-0.15 to 0.05	0.00

4 | DISCUSSION

Global variation in wood decomposition rates was consistent with predictions from both MST and GST. The activation energy of $E = 0.68$ eV (Table 1; 95% CI = 0.54–0.83) estimated with bivariate regression included the value of 0.65 eV hypothesized for respiration (Allen et al., 2005; Brown et al., 2004). While using multiple linear regression to fit Equation (2) to active season decomposition rates (k_{as}) and driver variables (Figure 2 and Supporting Information Table S4), the estimated activation energy of $E = 0.30$ eV (95% CI = 0.16–0.43) was significantly lower than the value of 0.65 eV (Allen et al., 2005; Brown et al., 2004), but largely overlapped with the range of $E = 0.31$ –0.56 eV hypothesized for extracellular enzymes important for the acquisition of N and P and the degradation of cellulose and lignin (Follstad Shah et al., 2017; Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012). As bivariate analyses did not account for the correlated variation among independent variables, we drew firm conclusions regarding the correct strength of these relations and the relative importance of the hypothesized drivers with multiple regression. This implies that rate-limiting reactions in wood decomposition may be constrained by stoichiometric imbalance, low moisture availability and activation energies of key enzymes for the degradation of macromolecular constituents such as lignin and cellulose (Cornwell et al., 2009; Hu et al., 2017).

Diameter-scaling exponents were also consistent with predictions based on the idealized wood particle geometries from four scaling models: geometric similarity theory (Niklas, 1995), elastic similarity theory (McMahon & Kronauer, 1976; Niklas, 1995), stress similarity theory (Niklas, 1995), and the West-Brown-Enquist (West, Brown, & Enquist, 1999) network theory. These predictions originate from different optimality theories for length-to-diameter geometry in woody plant stems and branches. It is important to consider these various idealizations as length-to-diameter geometries vary spatially (Bertram, 1989) and temporally (Niklas, 1995) within individuals, reflecting spatial and temporal variation in constraints on scaling of plant form and function. In our study, the diameter-scaling exponent (α_D) was estimated as -0.35 , which was significantly lower than GST and MST predictions for idealized wood geometries that ranged between -1 and -0.6 (see Supporting Information Appendix S1). These

differences arose because broken, decomposing wood particles were shorter than that expected for idealized geometries, meaning that the scaling of length with diameter departs from idealized optimality assumptions. For example, if wood particle length scales with the $\frac{1}{4}$ power of diameter, then k_{as} will scale with the -0.34 power of diameter, which is approximately equal to our empirically fitted value of $\alpha_D = -0.35$ (Supporting Information Appendix S1).

Our bivariate and multiple regression results showed that wood traits were better predictors of global variation in decomposition rates than climate variables (Figures 1c, 2 and 3). Wood traits explained more than twice as much variation in decomposition rates than did climate (Figure 3b). Furthermore, wood N content and diameter (not temperature or precipitation) were the most important drivers of decomposition rates (Figures 2 and 3a). This suggests the traditional view of climate as the dominant driver of decomposition at broad spatial scales may be an artifact of plot- or regional-scale analyses based on relatively limited ranges of climate variables and wood traits. Bradford et al. (2014) suggested that local-scale controls should be the primary control on C dynamics of decaying wood in response to environmental change. Similarly, Zhu et al. (2017) found that traits rather than climate variables were the optimal factors for predicting C stocks and fluxes of dead organic matter. Wood traits involved in C quality and nutrient availability strongly influence microbial community on decomposition processes (Manning, Rosemond, Gulis, Benstead, & Kominoski, 2018; van der Wal et al., 2007). These traits also influence how microbial community composition might respond to changes in the environment (e.g., warming and drought; Lavorel & Garnier, 2002; Matulich & Martiny, 2015), whereas microbial taxa determine microbial decay capacity and decomposition rates (Hu et al., 2017). Therefore, wood traits may play a dominant role in determining the microbial taxa for wood decomposition across global climate gradients.

Wood N content and diameter were the most important traits controlling global normalized decomposition rates (Figures 2, 3). N is expected to limit decomposition because degradative enzymes needed N-rich conditions (C:N ratios is $\sim 3:1$) for wood decay (Sternner & Elser, 2002), whereas C:N ratios in wood were much higher (most between 200 and 1,200:1). Low N availability of wood may

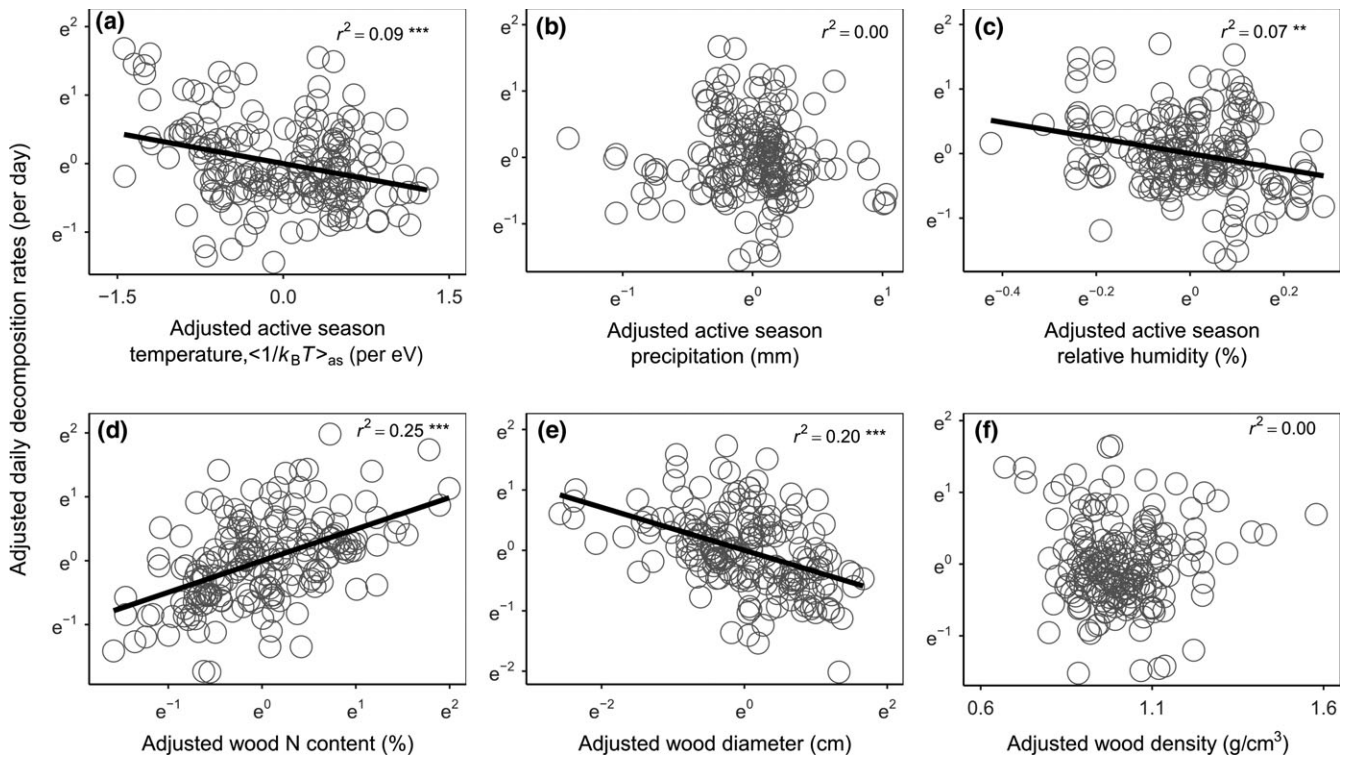


FIGURE 2 Partial regression plots illustrating relationships between active season wood decomposition rates and individual covariates from Equation (2) at 191 globally distributed sites. Plots show the relation (slope and variance) between decomposition rates and each covariate while controlling for the influence of all other model covariates. (a) Mean active season temperature; (b) Mean active season precipitation; c, Mean active season relative humidity; (d) Wood N content; (e) Wood diameter; (f) Wood density; (e) mathematical constant (~2.718). ** and *** indicate significant correlation between wood decomposition rates and the corresponding variable at $p < 0.01$ and $p < 0.001$, respectively. There were no significant linear relationships between active season decomposition rate and active season precipitation, and wood density

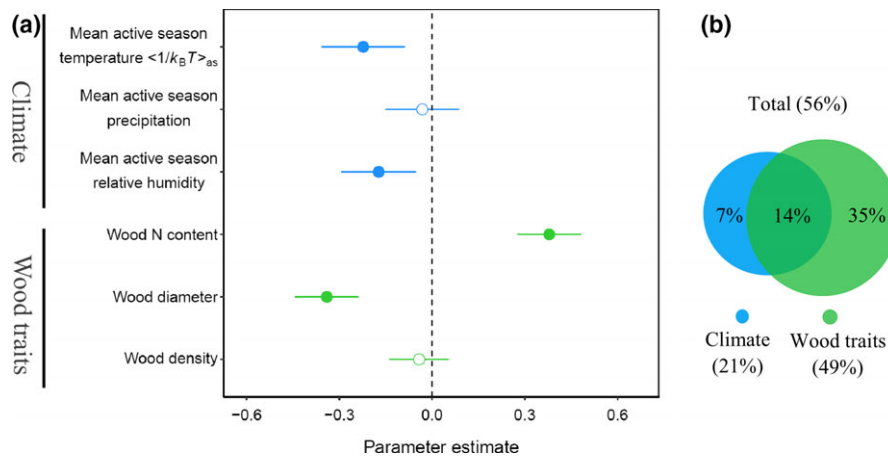


FIGURE 3 Relative importance of climate and wood traits on controlling global wood decomposition rates ($n = 191$). (a) Model-averaged effect size of the predictors on active season wood decomposition rates (based on Z-scores with linear mixed-effects models) at the global scale. (b) Percentage of variations in active season decomposition rates explained by climate, wood traits, and both climate and wood traits at the global scale. Points denote average estimates, and lines denote 95% confidence intervals. Filled circles indicate significance at $p < 0.05$. Climate variables in skyblue; wood traits in green

divert microbial energy investment away from lignocellulase synthesis and toward N acquisition (Sinsabaugh, Hill, & Follstad Shah, 2009). Microbial composition has also been observed to interact more strongly with changing N availability and less with changing

moisture or temperature (Matulich & Martiny, 2015), indicating N availability was more important than temperature for wood decomposition rates. The size effect on wood decomposition (i.e., large-diameter wood decompose more slowly than small-diameter wood) is

a logical consequence of a decrease in surface area to volume ratio with an increase in diameter (van Geffen et al., 2010), which affects microbial and macrodecomposer accessibility to the substrate (Cornwell et al., 2009; van der Wal et al., 2007). In addition, heartwood is usually the most decay resistant component and its proportion increases with wood diameter (Harmon et al., 1986), and moisture content and water flux in the substrate decreases with wood diameter (Cornwell et al., 2009), so the overall decay rate should decrease with wood size. In our study, wood density was an unimportant trait for predicting variations in decomposition rates, which was consistent with the finding from Weedon et al. (2009), who suggested that wood chemistry drove differences in decomposition rates between gymnosperms and angiosperms rather than wood density.

As was the case with many global datasets (Follstad Shah et al., 2017; Michaletz et al., 2018; Weedon et al., 2009), our data are heavily biased toward temperate regions, whereas tropical regions were underrepresented relative to their importance for the global C cycle (Malhi, Doughty, & Galbraith, 2011; Taylor et al., 2017). Although the majority of our sites were located in a relatively small proportion of the total land area on earth (North America, East Asia, and Europe; Figure 1a), the sites did fill the climate space occupied by terrestrial woody plants, and thus spanned global ranges in both temperature and precipitation (Figure 1b). Indeed, for these sites, MAT varied from -4.5 to 27.2°C , and MAP ranged between 354 and 4,005 mm, which covered most forest distribution areas in the world (Supporting Information Figure S1). The range of temperature and precipitation across our study sites was comparable to many other global surveys for plants, animals, and phytoplankton, and are broad enough to characterize general patterns of climate effects on ecological communities (Zhou et al., 2017). Nevertheless, our conclusions should be re-evaluated in future studies that used large, high-quality observational, and experimental datasets.

Understanding wood decomposition rates under global change is important for modeling the C cycle feedbacks to climate (Bradford et al., 2014; Cornwell et al., 2009). Our work based on both MST and GST highlights the importance of wood traits for wood decomposition across global climate gradients. This challenges the conventional view that climate is the dominant driver of decomposition rates at broad spatial scales. This perspective provides the basis for parameterization of most Earth system models (Oleson et al., 2013). If the wood traits such as N or size change under future climates, Earth system models that are parameterized with climate–decomposition relationships only can lead to decomposition rate projections that substantively differ from models that explicitly consider the potential changes in wood traits. Our study suggests that current wood decomposition models can be substantially improved by incorporating relationships between traits such as resources and physical property in wood and wood decomposition rates in combination with climate factors.

Wood traits have already been shown to be useful parameters in decomposition models (Cornwell et al., 2009). For example, the use of wood chemical composition, especially lignin to N ratio, as a criterion for dividing the material into soil organic C pools with different

decay rates seems to be a good approach in temperate and boreal ecosystems (Cornwell et al., 2009). In our study, because wood N content is the most important trait controlling global decomposition rates (Figures 2, 3), we suggest that difference of initial wood nutrient concentrations related with tree taxa can be incorporated in models based on the biochemical kinetics of decomposition (Allen et al., 2005; Follstad Shah et al., 2017; Sinsabaugh & Follstad Shah, 2012). This would enable the models to represent the known trait-based differences in wood decay rates that are probably not related to temperature and moisture (Zell, Kändler, & Hanewinkel, 2009). Our analyses suggest wood diameter is the second most important trait influencing decomposition rates (Figures 2, 3), which reduces the surface area to volume ratio governing microbial decomposition rates. Wood size is not included in most decomposition models (e.g., CLM 4.5 (Oleson et al., 2013) and CENTURY (Parton, Stewart, & Cole, 1988), but see LPJ (Smith, Prentice, & Sykes, 2001)) based on the “big leaf” approximation. The development of next generation of demographic models (Fisher et al., 2018) allows explicit representation of tree size and thus more explicit simulation of size impact on wood decomposition. Finally, we want to point out that, by fitting models derived from physicochemical processes to observations collected over environmental gradients, we can potentially inform parameter values that control wood decomposition rate in global wood decomposition models.

In conclusion, our study combined MST and GST to link multiple hypothesized drivers to global variations in wood decomposition rates. Using multiple approaches to fit our theory to data spanning global climate gradients, we have shown that global variation in wood decomposition was consistent with predictions from both MST and GST. Our compiled data conformed to power laws as predicted by both theories. Additionally, multiple regression and mixed model estimates of the activation energies for wood decomposition were statistically indistinguishable from expectations for the kinetics of extracellular enzymes that are important for microbial decomposition. Furthermore, diameter-scaling exponents estimated using three regression approaches were all consistent with how the scaling of length with diameter in decomposing wood particles departs from idealized optimality assumptions. We have also shown that wood traits were stronger predictors of variation in wood decomposition rates than climate variables. Diameter and wood N content were the most important traits controlling global normalized decomposition rates. Specifically, wood diameter influenced the relationship between the surface area on which microbial decomposers reside to the volume of the wood that they consume, resulting in a decrease in decomposition rates with wood diameter (Cornwell et al., 2009; van der Wal et al., 2007; van Geffen et al., 2010). The importance of wood N potentially originates from the relatively low nutrient availability of most dead wood. The observed increase in wood decomposition rates with N content has important implications for assessing effects of N deposition on wood decomposition rates. Although wood traits are key drivers of variation in decomposition rates, they are not included in most Earth system models, and most models have only one single coarse wood debris pool for wood

decomposition (e.g., the Community Land Model; Oleson et al., 2013). Our results suggest that inclusion of wood traits in these models will improve global change predictions.

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AUTHOR CONTRIBUTION

Z-Hu, STM, XZ, and CX designed the study; Z-Hu compiled data; STM developed theory; Z-Hu, STM, DJJ, and CX performed analyses; Z-Hu and STM wrote the first draft, and all other authors contributed to the revision and discussions of the results.

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SUPPORTING INFORMATION

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

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