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Heavier summer downpours with climate change revealed by weather forecast resolution model

Results and Discussion

Decomposition models: Using a simple exponential decay model modified by a Q_{10} temperature function, we illustrate how local-scale decomposition data can lead to model projections that differ from the conventional approach of determining a single *k* value from site means for a given litter and decomposition stage[1]. Using our observations for individual wood blocks, we calculated decay rate constants (*k*) for each block decomposing at each site using the formula:

$k = -e(M / 100)$

where *M* is the percentage of initial mass after 1 year. Assuming a Q_{10} temperature function we calculated the combination rate constants and Q_{10} values that best fit the observed *k* values using single-decomposer (i.e. one *k*-value) and two-decomposer (i.e. two *k*-values) models using the gnls function in the "nlme" package in R (a statistical freeware program)[2]. For the two-decomposer model we assumed wood blocks with a final C:N ratio <250 had been colonized by wood-rot fungi that facilitated "fast" decomposition of wood. Such "fast" decomposers might group with non-unit restricted fungi that can forage with hyphal aggregations such as cords from one piece of wood across the forest floor to another, and so transfer energy and nutrients from another part of the environment to expedite the decomposition rate of a new wood resource[3-5]. Conversely, we assumed that wood blocks with final C:N ratios >250 had been colonized by "slow" wood-rot fungi which might be grouped with unit-restricted fungi, which might colonize by spores and so in general take longer to decompose a new wood resource because they do not translocate exogenous resources to the wood blocks. We made these post-hoc classifications to illustrate the influence of using one vs. multiple *k* values – for the decomposer community – on model outcomes, but the classifications were informed by our data analysis. Specifically, the residuals from our single *k*-value analysis were positively skewed and inversely correlated with wood C:N, suggesting that the wood blocks could be binned into two *k*-value classes.

We estimate that the rate constant is 0.056 y^{-1}, with a Q_{10} of 4.08, for the single-decomposer model (model (a) in Table S3). If we instead assume that two decomposer communities better characterise site-level variation we calculate decay rates of 0.114 y^{-1} and 0.051 y^{-1}, for fast and slow decomposers, respectively, with a common Q_{10} of 3.58 (model (b) in Table S3). Parameter estimates for both models align well with estimates for fungal-mediated decomposition of a common wood substrate from previous work[6], but the Q_{10} estimate from the two-decomposer model (b) is better constrained and this more complex model better predicts observed rates of mass loss across all samples ($r^2 = 0.47$, compared to 0.19 for the single-decomposer model). Further, in Table S4 we show the potential for projected woody-debris stocks to differ markedly between single- and two-decomposer models for sites with different mean climates, and also the influence of assuming a changing relative abundance of “fast” and “slow” wood decomposers. Specifically, under the two-decomposer framework, the abundance of fast and slow decomposers exerts substantive control over site-level woody debris stocks (Table S4) and therefore obviously wood decomposition rates. As such, developing empirical relationships between environmental drivers and the relative abundance of different wood-rot communities would be critical to project responses to environmental perturbations across scales (see text of the main manuscript). We emphasise that this example is only meant to illustrate how well-replicated experimental datasets can be used to add greater process-level understanding and insight into local controls within Earth system models; certainly, to estimate woody-debris stocks one would want to account for decreasing *k*-values as wood quality becomes more recalcitrant and as decomposition progresses to later stages[1].

Cross-site comparisons: Our field study design does not address explicitly the validity of using cross-site relationships between decomposition rates and correlated explanatory variables to project how varying these explanatory variables at a single location will affect decomposition. It is certainly feasible that within vs. cross-site relationships differ given, for example, ecotypic differences in climate responses between the same species at different locations[7]. As such, there are concerns about using cross-site relationships to inform predictive global change science, yet cross-site relationships are being used to inform predictive models, including for decomposition processes[8]. We therefore explored the validity of using our cross-site data to project decomposition rates.

There was not enough within-site variation in temperature to ask whether the temperature relationship in our wood decomposition data set was common both within and across sites. However, fungal colonization and mass loss varied similarly within and across sites (Fig. 3), permitting us to investigate whether there was evidence for a common relationship between fungal colonization and wood mass loss across each site using a post-hoc analysis. First, we used Maximum Likelihood model comparisons to ask whether wood decomposition was best fit by a model that included only fungal colonization (common slope, common intercept), fungal colonization plus site (common slope, different intercepts), fungal colonization by site (different slopes, common intercept) or fungal colonization plus site and their interaction (different slopes, different intercepts). The model that best described our data had a common slope but different intercepts (i.e. Fungal colonization + Site). Commensurate with this finding, plotting the univariate regressions between wood mass loss and fungal colonization for each site revealed that, although the slopes for each site were similar, intercept increased as site latitude decreased (Fig. S1). These results appear consistent with our full LMM analysis. That is, presumably the higher temperatures (Table S1, Fig. 3) and increasing termite abundances (Table S1, King et al.[9]) as one moves north to south promotes decomposition rates; that is, for the same amount of fungal colonization, mass loss rates are higher in more southerly locations. Note also that fungal colonization explains less of the variation (i.e. lower r^2) in mass loss at the more southerly sites (Fig. S1). Our results therefore emphasise the necessity of observing multiple controlling variables to explain decomposition rates across sites and, at the same time, the need to account for site-level context dependencies in decomposition rates.

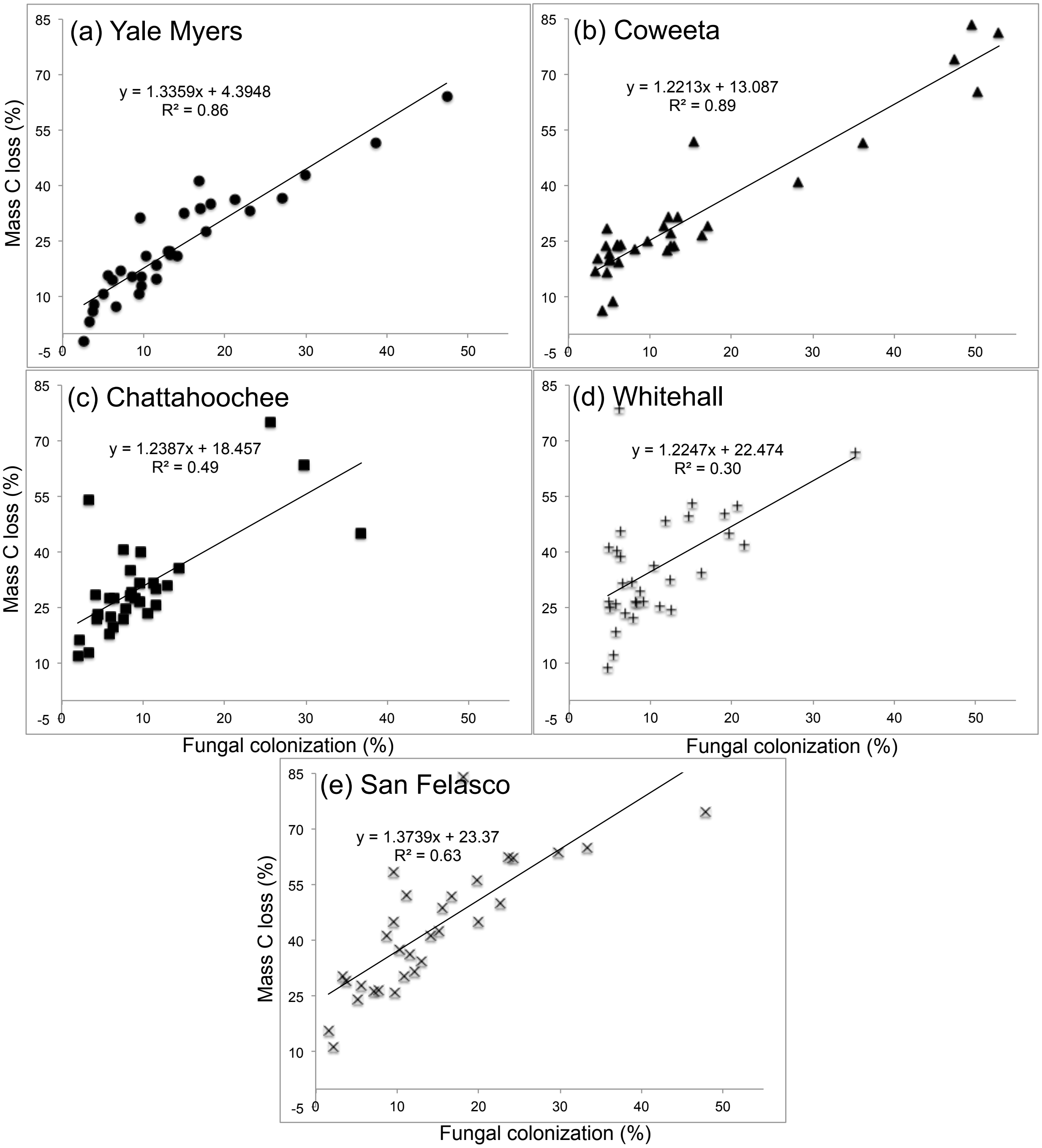

Figure S1 │ Decomposition of wood blocks has a common relationship (similar slopes) with fungal colonization, but unique intercepts, across five sites spanning a regional climate and ecological gradient in eastern U.S. temperate forest. Decomposition is expressed as the proportion of wood carbon lost from the initial carbon mass of a common wood substrate. Data points (a-e) represent mass C loss observations for individual wood blocks (*n* = 32 or 31 per site) and are plotted against fungal colonization (%). Shown are the site-specific regression relationships between wood carbon loss and fungal colonization from the coolest (a) to warmest site (e). The full data set is best described by a model that uses a common slope but site-specific intercepts (see Supplementary Results and Discussion text).

Table S1 │ Climate, biota, and wood mass loss for each of the five locations across the regional gradient for eastern U.S. temperate forest stretching from Connecticut in the north (YMF) to Florida in the south (SNF).

	North		Location		*South*
Variable	YMF	CWT	CNF	WHF	SNF
MAT (°C)	9.4	12.5	14.6	15.6	20.5
MAP (mm)	1264	1375	1427	1262	1202
CDI (unitless)	0.03	0.76	0.91	0.91	1.22
Soil temperature (°C)	12.3 ±0.3	18.3 ±0.7	20.3 ±0.5	21.5 ±0.6	23.4 ±0.5
Soil moisture (%)	19.1 ±4.5	17.0 ±4.7	10.6 ±2.2	12.0 ±2.3	9.16 ±3.3
Mass fungi C (%)	14.1 ±10.2	15.3 ±15.1	9.84 ±7.8	10.8 ±6.7	14.3 ±10.0
Termites (g block^{-1})	0	0	0.047±0.160	0.161±0.342	0.111±0.319
Ants (g block^{-1})	0.372±0.456	0.322±0.333	0.055±0.133	0.079±0.145	0.061±0.284
Blocks w/ termites (#)	0/32	0/32	6/31	10/32	10/31
Blocks w/ ants (#)	18/32	20/32	11/31	13/32	10/31
Mass C loss (% block)	23.2 ±14.7	31.8 ±19.5	30.7 ±13.7	35.7 ±15.1	43.0 ±17.3

Values are means ±SD from the wood blocks at each location, where *n*=31 or 32. Exceptions are mean annual temperature and precipitation (MAT, MAP), which are sourced by location from the National Climatic Data Center (NCDC; www.ncdc.noaa.gov) for the period 1981-2010, and the Climate Decomposition Index (CDI) calculated from the monthly NCDC data. Sites are Yale Myers Forest (YMF), Coweeta Hydrologic Laboratory (CWT), Chattahoochee National Forest (CNF), Whitehall Experimental Forest (WHF) and San Felasco State Park (SNF).

Table S2 │ Coefficients, *P* and r^2 values for the minimally-adequate (i.e. lowest AIC), linear mixed model for mass carbon loss of wood blocks. Mean coefficients, their SD and *P* values are estimated using an MCMC sampling approach; and r^2 values are shown for the full model and for significant univariate relationships, using a method that retains the random effects structure. Statistically significant ($P<0.05$) coefficients for the retained variables are shown in bold.

Variables	Coefficient	*P* value	r^2
Mass loss model			*0.75*
Intercept	-27.9 ± 16.10	0.0010	na[1]
Soil temperature	**2.05 ± 0.643**	0.0001	0.28
Soil moisture	0.268 ± 0.4424	0.2206	na
Fungal colonization	**1.24 ± 0.1488**	0.0001	0.73
Termite biomass	**9.01 ± 6.466**	0.0064	0.27
Ant biomass	3.03 ± 5.122	0.2408	na

[1] na: not applicable

Table S3 │ Parameter estimates, and their associated uncertainty, for the observed wood decomposition data applied to (a) single-decomposer (one *k*-value) and (b, c) two-decomposer (two *k*-value) models. Model fit was estimated using AIC, where lower relative values indicate less information loss. Models with AIC values within ± 2 units of each other (i.e. models b and c) are commonly considered to have equal fit[10]. We therefore selected the two-decomposer model with fewer parameter estimates (i.e. model b) to compare to the single-decomposer model. The comparison illustrates the potential for parameter estimates, developed from studies with high within-site replication (versus using site means), to influence projections of decomposition rates and organic matter stocks. Model projections are given in Table S4 and elaborated in the text of the Supplementary Results and Discussion. Parameter estimates are mean ± 95% confidence intervals.

Fit and parameter estimates	Model		
	(a)	(b)	(c)
AIC	-19.8	-84.6	-83.1
k_1 (y^{-1})	0.056 ± 0.040	0.114 ± 0.058	0.132 ± 0.078
Q_{10} for k_1 (unitless)	4.08 ± 2.18	3.58 ± 1.35	3.20 ± 1.43
k_2 (y^{-1})	na[1]	0.051 ± 0.092	0.040 ± 0.164
Q_{10} for k_2 (unitless)	na	na[2]	4.29 ± 4.71

[1] na: not applicable

[2] A Q_{10} estimate common to both k_1 and k_2 is given in the row "Q_{10} for k_1"

Table S4 │ Steady-state woody debris stocks estimated from model simulations with constant woody inputs in either a cool (5ºC) or warm (15ºC) site, assuming either a single rate constant (*k* value) for decomposition or two rate constants. Rate constants and Q_{10} values for the two models are given in Table S2 for models (a) and (b) where, conceptually, the decomposer community is considered to function as a homogenous unit (the conventional approach) or as multiple decomposer communities under different local-scale controls, respectively. All simulations received wood inputs of 100 g C m^{-2} y^{-1} and at steady state (i.e. wood C inputs = wood C decomposition losses) it follows that pool size = inputs / (k*Q_{10}). The two-*k* model had a fast and slow rate constant and stocks are determined assuming two classes of decomposer fungi represented by these rate constants (fast and slow). Shown are wood pool values from model scenarios where the proportion of fast decomposers is varied from 0 to 100%. These stock values are then compared (% difference) to the steady-state pool sizes for the single *k*-value (i.e. decomposer) model for both the cool and warm sites. The analysis is illustrative of the potential difference in model outcomes when parameter estimates (e.g. *k*-values) are derived from mean (single-*k* model) vs. local-scale data (two-*k* model).

Site Mean Annual Temperature	Single-*k* model	Two-*k* model				
		0% fast	25% fast	50% fast	75% fast	100% fast
5ºC stock (g C m^{-2})	3575	3727	2839	2293	1922	1655
15ºC stock (g C m^{-2})	877	1043	794	641	538	463
5ºC difference (%)	na[1]	4.2	-20.6	-35.9	-46.2	-53.7
15ºC difference (%)	na	18.9	-9.4	-26.8	-38.7	-47.2

[1] na: not applicable

Methods

Study sites

Our research was conducted at five locations spanning ~12° latitude in the eastern U.S. in temperate, second-growth, hardwood forest. From north to south, we worked at the following locations: (1) Yale Myers Forest (YMF), Tolland County, Connecticut (41°57’N 72°07’W; 750-1025 m elevation); (2) Coweeta Hydrologic Laboratory (CWT), Macon County, North Carolina (35°03'N, 83°25’W; 750-1025 m elevation); (3) Chattahoochee National Forest (CNF), Habersham County, GA (34º30’N, 83°29’W, 315-450 m elevation); (4) Whitehall Experimental Forest (WHF), Clarke County, GA (33º53’N, 83°21’W; 150-240 m elevation); (5) San Felasco State Park, Alachua County, Florida (29°43’N 82°26W; 43-52 m elevation). Dominant tree genera across our study locations include oak (*Quercus*), hickory (*Carya*) and maple (*Acer*). The subterranean termite *Reticulitermes flavipes*, which feeds primarily on downed wood, occurs as the sole or dominant termite species throughout our study range and is highly abundant at our three most southern sites[9]. *Aphaenogaster picea* is the dominant forest-floor nesting ant in our two northernmost sites. The diversity and abundance of ants nesting in the woody debris is much greater at the more southern locations[9].

Experimental design

At each study location, 70-m transects were established on two north- and two south-facing slopes (except at YMF, where slopes face east-west). Wooden blocks were placed on the forest floor at 10-m intervals along each transect. There were eight blocks per transect, four transects per location, and five locations, giving 160 wood blocks (8 × 4 × 5 = 160). Our design captured both local- and broad-scale variation in climate by varying slope aspect (north- or south-facing), slope position (transects ran from wetter downslope to drier ridge habitat), and location (northern to southern sites). Although CWT is ~6° latitude from both the most northern (YMF) and southern (SNF) location, the higher elevation makes it more ecologically and climatologically similar to YMF. Blocks were placed in the field in May 2011 and retrieved after 13 months. We chose this time-scale because previous, single-site investigations of the decomposition of smaller diameter logs (i.e. logs <10 cm dia.) have shown substantive decay in approximately one year[11]. Smaller diameter dead wood can represent a substantial proportion of woody debris inputs into an ecosystem, with more than half of dead wood inputs represented by this size class[12].

Wood blocks (15 × 12 × 2 cm) consisted of untreated white pine, following a design similar to that used in other studies investigating decomposition of woody debris[13]. We used a common size and source for our wood blocks, following the design of other multi-site decomposition studies[1,14] where the intention was also to minimize variation in substrate quality within a specific litter type. Wood size and within litter-type variation does influence decomposition processes[15], and so minimizing this variation enables researchers to ascribe with greater certainty the role of other controls (e.g. climate and litter quality between species[1]) in generating variation in observed decomposition rates. For the same reason, we also followed the design of other multi-site decomposition studies and placed our wood blocks in the litter layer, recognizing that position (e.g. standing versus downed) of dead wood influences a range of variables, including microclimate, and so has a large influence on decomposition rates[15].

We chose pine wood as a litter because it occurred across all our sites but in low abundances (reflecting successional dynamics following agricultural abandonment in the late 19th or early 20th centuries), meaning we could eliminate local adaptation of the decomposer community to dominant hardwood-species[16]. Although brown-rot fungi are often considered the main cause of coniferous wood decay, they likely only represent a greater proportion of fungal decomposers in coniferous systems because they are better adapted than white-rot fungi to the short, colder and drier growing seasons of cold temperate and boreal biomes[17]. As such, using pine in our warm temperate sites is unlikely to have biased the decomposer community toward brown over white-rot fungi, with the former still being subordinate to white-rot fungi in all biomes[17]. Wooden blocks were large enough to detect termite colonization and were modified to permit ant nesting by creating nesting chambers, allowing us to assess how dominant soil animals in woody debris[9] and microbes together affected wood decay rates. Nesting chambers were created by routing 1.5 cm deep grooves into the wood with access via a 10 × 4 mm entrance between the wood and a 1.5 mm Plexiglas® acrylic plate. The wood blocks were placed Plexiglas side up for observation of ant colonies, but covered with ceramic tiles (16 × 16 cm) to block sunlight. We placed the blocks in contact with the surface soil and flush with the forest litter layers. All wood blocks were weighed prior to field placement, and four nests were retained to assess initial wood chemistry and moisture content.

Field measurements

Spot measurements of soil temperature and moisture are effective at resolving local and regional spatial variation in the microhabitat conditions experienced by organisms in forest understories[18]. We took one measurement of soil temperature at 5-cm depth, and three measures of volumetric soil moisture (Campbell Hydrosense™) to 12-cm depth, around each wood block in June, August and November 2011, and March, May and June 2012. At the same time we checked the wood blocks for termite and ant colonization, estimating the number of workers, brood and soldiers. Other soil fauna associated with woody debris were observed in nest chambers and below the wood blocks, including spiders, isopods and salamanders. Their abundances were miniscule in comparison to termites and ants, mirroring the pattern observed for natural woody debris across the locations[9], and no other wood-nesting or wood-consuming fauna (e.g. wood-boring beetles) were observed.

Wood chemistry, faunal and microbial measures

Wood blocks were retrieved into plastic freezer bags, returned to the lab and placed at 5ºC overnight. Plexiglas plates, ants, termites, midden material and other fauna were removed from the blocks and fauna stored at -20ºC. Only termites and ants were commonly encountered: these fauna were sorted into workers, soldiers, brood, alates and queens. Fauna were enumerated, dried at 65ºC to constant mass, and then weighed. Wood blocks were weighed immediately after fauna and other materials had been cleaned from their surfaces. They were then drilled into from their underside with a 9.5-mm bit in a regular 5 × 6 array. The sawdust created by drilling was thoroughly mixed, half placed at -80ºC for fungal biomass determinations, and the other half dried at 65ºC for total carbon determinations. Drilled wood blocks were re-weighed, dried at 65ºC to constant mass, and weighed again. Dried sawdust was ball-milled to a fine powder and analysed for carbon and nitrogen using a Costech ESC 4010 Elemental Analyser (Costech Analytical Technologies Inc., Valencia, CA). Fungal biomass carbon in the wood blocks was estimated from ergosterol concentrations, assuming a conversion factor of 3.8 mg ergosterol per g fungus, and a carbon concentration of 47.2% in fungal biomass (following[19,20]).

Initial masses of the wood blocks had a mean value of 108.64 g and a SD of 12.40 g. We accounted for the differences in initial carbon contents resulting from the variance in starting mass of the wood blocks. Mass loss was expressed as percentage carbon loss, relative to the initial carbon content of each wood block. Wood blocks had initial moisture contents of 4.54±0.370%, carbon contents of 47.41±1.510%, nitrogen contents of 0.07±0.008% (mean±SD, n=4) and a mean C:N ratio of 672.

Data analysis

We fitted linear mixed models (LMMs) to investigate wood mass loss. Transect was fit as a random factor because clustering replicates by location and transect could introduce spatial autocorrelation[21]. The LMMs were fit assuming a Gaussian error distribution ("identity" link function) and the Laplace approximation in the "lme4" package for the "R" statistical program[2]. The first step in our analysis was to select the form of the variables. We had multiple time points for soil temperature and moisture, and fungal biomass vs. percentage colonization, as well as presence-absence, abundance and biomass of fauna. Variables were selected for the lowest AIC score when evaluated as a single explanatory variable for mass loss[10]. The best form of each explanatory variable was: the mean per wood block replicate of the temporal soil temperature and moisture observations, fungal colonization, and termite and ant biomass. Hence each wood block was associated with unique environmental data representing its immediate surroundings.

We constructed LMMs that included one to all five of the explanatory variables and used lowest AIC to determine which model structure to retain. In the mean model, ant and termite biomass had no influence on decomposition rates when tested with univariate regression and so, given the limited degrees of freedom of the mean data (n = 5 vs. 158), were dropped from the analysis. Note that in the mean model, mean decomposition was assessed as a function of mean soil temperature and mean fungal colonization at each location. Using mean soil temperature, as opposed to MAT or CDI, then ensured our observations of temperature and microbial activity were conducted at the same spatial scale (i.e. per wood block). Two-way interaction terms between the explanatory variables were included in all initial models, but were removed if not significant. Variance inflation factors of <2.0 indicated that collinearity was low among model variables.

The F-statistic is not considered accurate for the “lme4” package[22], so we used a Markov Chain Monte Carlo (MCMC) approach to estimate coefficients and *P*-values for retained parameters in the minimally-adequate (or best-fit) LMMs. All reported *P*-values are quasi-Bayesian, rather than the classical frequentist *P*-values, but retain the same interpretation. We considered coefficients with $P<0.05$ significant and coefficients with $P<0.10$ marginally significant[23]. We standardized model coefficients using a z-transformation in which we subtracted the mean and divided by the standard deviation for all independent model variables[24], though response variables were not standardized. The approach gives model coefficients that describe the standardized slopes which, unlike partial correlation coefficients, are comparable in magnitude within models because variables are expressed in common units[25]. An additional advantage of this analytic approach is that centring our independent variables makes main effects interpretable even when involved in interactions, thus allowing us to compare the relative effect size among variables that include both interaction and main effects[25]. The use of standardized model coefficients in ecology is growing for these reasons (e.g. Uriate et al.[26]).

Variance explained by the explanatory variables was also estimated by calculating r^2 values for the minimally-adequate LMMs following Nakagawa and Schielzeth[27] to retain the random effects structure. Calculation of r^2 values is common practice in modelling decomposition and typically these values are calculated for the fit between the response variable and a single explanatory variable. Where multiple variables provide the best model fit, calculating r^2 values for single explanatory variables ignores the fact that some of the variation explained by the single factor is caused by other explanatory model variables. With this caveat in mind, we calculated the r^2 values for each significant explanatory variable to facilitate comparison with other regional-scale decomposition experiments, but represent relationships in the figures based on the multivariate model.

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