Climate fails to predict wood decomposition at regional scales

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Decomposition of organic matter strongly influences ecosystem carbon storage[1]. In Earth-system models, climate is a predominant control on the decomposition rates of organic matter[2-5]. This assumption is based on the mean response of decomposition to climate, yet there is a growing appreciation in other areas of global change science that projections based on mean responses can be irrelevant and misleading[6,7]. We test whether climate controls on the decomposition rate of dead wood—a carbon stock estimated to represent 73 ± 6 Pg carbon globally[8]—are sensitive to the spatial scale from which they are inferred. We show that the common assumption that climate is a predominant control on decomposition is supported only when local-scale variation is aggregated into mean values. Disaggregated data instead reveal that local-scale factors explain 73% of the variation in wood decomposition, and climate only 28%. Further, the temperature sensitivity of decomposition estimated from local versus mean analyses is 1.3-times greater. Fundamental issues with mean correlations were highlighted decades ago[9,10], yet mean climate–decomposition relationships are used to generate simulations that inform management and adaptation under environmental change. Our results suggest that to predict accurately how decomposition will respond to climate change, models must account for local-scale factors that control regional dynamics.

Climate is traditionally thought to be the predominant control on decomposition rates at global and regional scales, with biotic factors controlling only local rates[2,4]. Biotic factors are divided into decomposer organisms, such as soil microbes, and the quality (for example, chemical composition) of the plant litter they decompose. Recent work suggests that litter quality may be more important than climate in controlling decomposition rates across biomes worldwide[3,11], but the influence of decomposer organisms is still assumed limited across broad climate gradients[12]. A core reason for this assumption is that climate is considered a primary control on the activity of decomposers. As such, across climate gradients, mean temperature and moisture availability are assumed to explain much of the variation in the activity of decomposer organisms and hence decomposition rates of organic matter. These climate–decomposition relationships are used to parameterize and evaluate Earth-system models[13]. It is therefore important to test the assumption that climate drives decomposer activities because proper understanding of these activities is needed to inform model projections such as carbon cycle–climate feedbacks[1,14].

Climate–decomposition relationships are typically developed from regional to global studies that use the mean response of decomposition to climate and litter quality drivers[2-5]. There is growing awareness in other areas of global change science that using mean responses masks the fine-scale variation required to understand effects of environmental change[6,7], although the importance of local-scale variation to ecological processes was acknowledged decades ago[9]. When fine-scale variation is considered to predict species responses, for example, local factors are of equal or more importance than climate factors in determining phenomena such as species distributions[6]. Local conditions also dictate the effects of broad-scale global change factors on ecosystem processes. For example, warming effects on ecosystem respiration rates, and tree growth responses to elevated atmospheric CO_2, depend on soil carbon and nitrogen availability, respectively[15,16]. Local-scale factors might therefore strongly mediate regional- to global-scale responses to environmental change. If so, it is conceivable that in broad-scale decomposition experiments the focus on mean decomposition rates[2,3,5,12,17] 'averages away' the role of local-scale factors in determining decomposer activity and hence organic matter decomposition rates. Using local-level variation—rather than location-level means—in decomposition experiments is then necessary to verify the conventional wisdom that climate is a primary control on decomposition rates at broad spatial scales.

Broad-scale decomposition experiments generally focus on the breakdown of foliar litters, leaving dead wood decomposition a critical uncertainty in carbon-cycle models. Global stores of dead wood are substantive; estimated at 73 ± 6 Pg C (ref. 8). For living wood carbon to be transformed to a longer-term carbon store in soils, it first passes through the dead wood pool[18]. The turnover rate and fate (for example, CO_2 versus soil carbon) of dead wood therefore influences the carbon balance of forests under global change[19,20]. Dead wood also stores plant nutrients and is a hotspot for nitrogen accumulation[21], making its decomposition dynamics a determinant of forest productivity. Local-scale processes do affect wood decomposition where, for example, rates of mass loss depend on the species of wood-rot fungi and hyphal grazing by soil invertebrates[22,23]. The influence of these local-scale variables on wood decomposition at regional scales, relative to climate, is uncertain given the paucity of regional-scale wood decomposition studies[24].

Here we investigate whether climate or other factors primarily control wood decomposition rates across a regional gradient in temperate forest. Regional decomposition experiments typically

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include few replicates of a single litter type per location and analyse the mean of these observations[2,3,5,12,17], precluding detection of the relative effect of local-scale controls. To overcome this limitation we had 32 observations for a standard wood substrate at each of five locations. We proposed (Hypothesis 1a) that if climate is a predominant control on decomposition then the decomposition rates of replicate wood blocks should cluster around the location-level means (Fig. 1a). Conversely, (Hypothesis 1b) if local-scale factors are the predominant control on decomposition rates then replicate values should broadly scatter around the location-level means (Fig. 1b). Fungi are the primary decomposers of dead wood[25] and so we estimated decomposer activity by measuring percentage fungal colonization of the wood blocks (Supplementary Methods), a metric equivalent to that used to estimate the functional role of mycorrhizal fungi[26]. If Hypothesis 1a holds, climate should largely explain fungal colonization and wood decomposition. If Hypothesis 1b holds, then fungal colonization (but not climate) should primarily explain wood decomposition rates. By using fungal colonization we explicitly recognize that local-scale controls—such as fungal grazers, density of dead wood as a source of wood-rot fungi, and nitrogen availability—probably vary both within and across locations. Our study was not designed to identify specific local-scale controls, but rather to test whether they need to be identified to inform the development of models used to project decomposition rates under changing climate.

Testing our competing hypotheses requires that climate data be broadly enough distributed to identify climate as the predominant control on mean rates of decomposition (as in Fig. 1a). We observed an ~11 °C difference in soil temperature, and mean annual temperature, between our most northern and southern sites (Supplementary Table 1). These temperature gradients are large enough to generate marked variation in decomposition rates due to climate[27]. Moisture availability is also an important control of decomposer activity[12,28] and, although we worked in a mesic biome, warmer sites had drier soils (Supplementary Table 1). Given this auto-correlation, we use only temperature in our mean statistical models but it functions, essentially, as an estimator of combined temperature and moisture effects on decomposition. We calculated the climate decomposition index for each location to verify this claim; the index is used in broad-scale decomposition studies as a combined metric of temperature and precipitation, where higher values represent more favourable conditions for decomposer activity[28]. Climate decomposition index values were positively correlated ($r = 0.98$) with mean soil temperature (Supplementary Table 1), highlighting that the latter was a robust estimator of climate effects on wood decomposition.

Using the mean model, there were significant ($P < 0.001$) positive effects of temperature and fungi, and a temperature × fungi interaction (Fig. 2), on wood mass loss. The interaction indicates that, for the same percentage of fungal colonization, mass loss rates are greater at warmer temperatures. The mean model explained 99.5% of variance in mass loss across the regional gradient. Temperature was the dominant driver of mass loss, with a standardized coefficient three-times greater than for fungi and the interaction (Fig. 2c). Hence, mean temperature was the predominant control on mean decomposition rates, confirming the expectations of the conventional decomposition paradigm. Indeed, temperature alone explained 84% of variance in mass loss. Collapsing within-location variance therefore recreates the strong regional-scale relationship of temperature with mass loss that is commonly reported in decomposition studies[2,3,5,12,17]. However, mean temperature did not explain mean fungal colonization ($r^2 = 0.098$), suggesting a disconnection in the causal chain of logic in the conventional wisdom that temperature is the primary control on microbial activity and hence decomposition rates. If
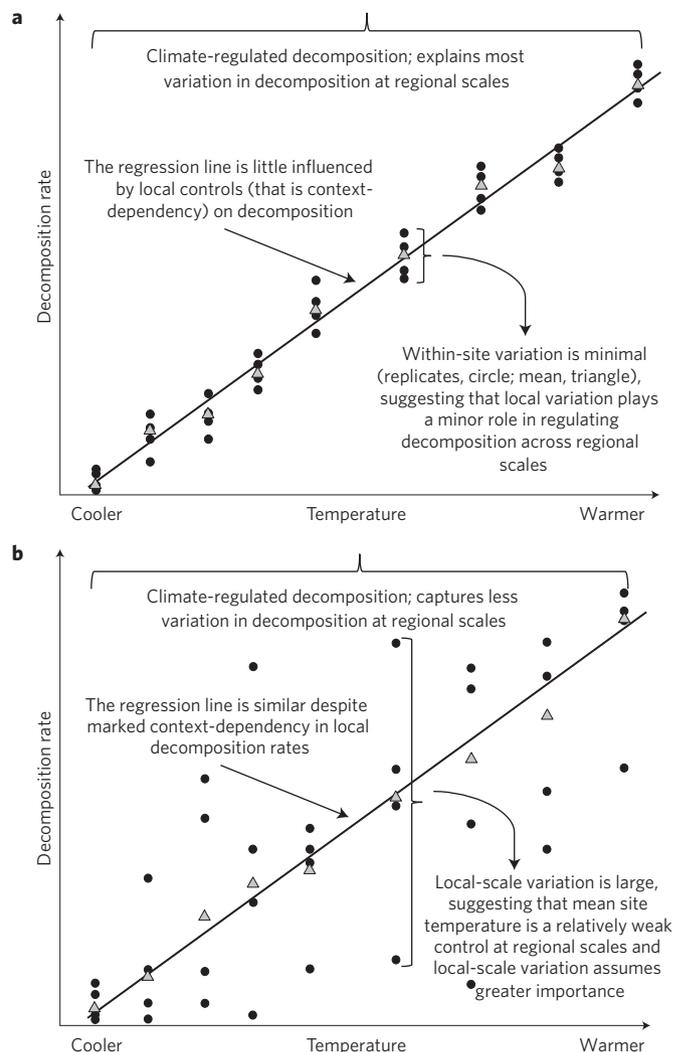

a

Climate-regulated decomposition; explains most variation in decomposition at regional scales

The regression line is little influenced by local controls (that is context-dependency) on decomposition

Within-site variation is minimal (replicates, circle; mean, triangle), suggesting that local variation plays a minor role in regulating decomposition across regional scales

Decomposition rate

Cooler   Temperature   Warmer

b

Climate-regulated decomposition; captures less variation in decomposition at regional scales

The regression line is similar despite marked context-dependency in local decomposition rates

Local-scale variation is large, suggesting that mean site temperature is a relatively weak control at regional scales and local-scale variation assumes greater importance

Decomposition rate

Cooler   Temperature   Warmer

Figure 1 | Competing conceptual models of relationships between decomposition and climate across regional to global gradients. a, The classical conceptual model where climate is the predominant control. **b**, A conceptualization where local-scale factors that affect decomposer activity are instead the predominant control on decomposition rates. Decomposition is represented as mass loss of plant litter, and climate as mean annual temperature. Decomposition rates and climate variables are, however, represented using various expressions, including rate constants (*k*) and functions that integrate mean monthly temperature and precipitation data. The representation of these variables affects the form of the relationship (for example, linear versus curvilinear) but the relationships are always positive, as depicted above. The classical decomposition paradigm, shown in **a**, posits that climate explains (and controls) variation in decomposition rates at regional to global scales because climate functions as the primary control on the activity of decomposer organisms. In contrast, an emerging idea in projecting ecological responses to global change, shown in **b**, suggests instead that local-scale controls on biotic activity generate local-level variation in process rates equal to or greater than broad-scale controls such as climate, highlighting the need to understand local context-dependency to project decomposition rates under changing environmental conditions.

climate is not then the primary control on microbial activity it calls into question using mean climate variables to make projections of decomposition rates. To explore the possibility that local-scale factors instead primarily control microbial activity (Hypothesis 1b), we investigate our data retaining the local-scale variation.
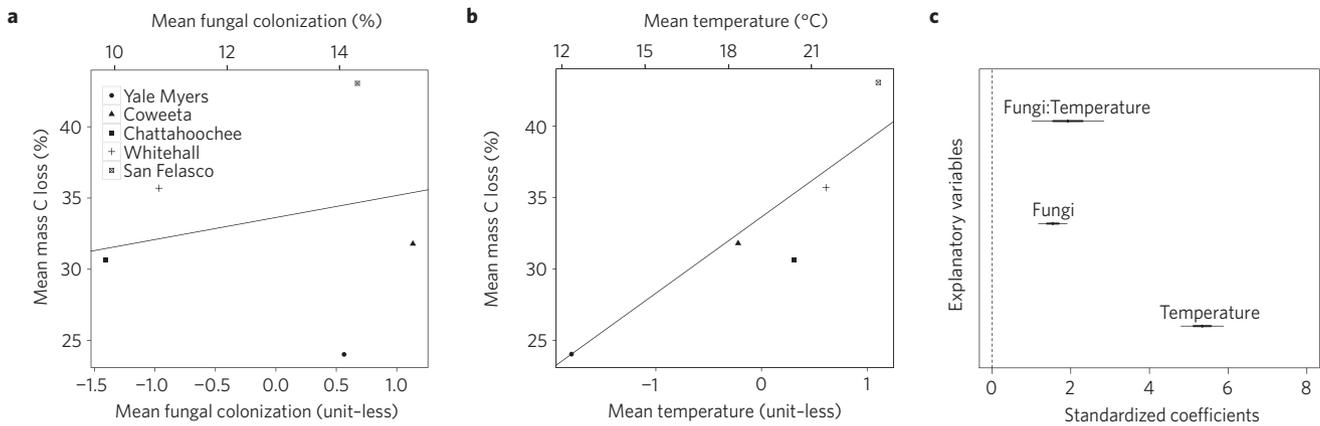
Figure 2 | Relationships between wood decomposition, climate and fungi when local-scale variation is collapsed into a mean value for each of the five locations across the regional gradient. a,b, Relationships between decomposition and the significant explanatory variables. **c**, Relative influence on decomposition of the explanatory variables retained in the best-fit model. Location-scale variation is generally collapsed into a mean value for global- and regional-scale decomposition studies; we do it here to evaluate changes in the interpretation of the dominant controls on mass loss compared with when local-scale variation is retained (Fig. 1). Decomposition is expressed as the proportion of wood carbon lost from the initial carbon mass of a common wood substrate. Data points (**a,b**) represent mean observations from 32 wood blocks placed at each of five locations ($n = 5$), and are plotted against the top x axis for fungal colonization (**a**; %) and temperature (**b**; °C) for comparison with Supplementary Table 1. Regression lines (**a,b**) are shown for significant main effects and are standardized (bottom x axis; unit-less) for the influence of the other variables in the full linear model, which retained soil temperature, fungi and their interaction (**c**; all significant at $p < 0.05$). Plotting the standardized variables (**a,b**) and coefficients (**c**), permits us to make a relative comparison of the influence of each variable and model term on mass loss despite the different scales on which the variables are measured (for example, temperature as degrees Celsius versus fungi as percentage colonization). The standardized coefficients reveal that temperature had the strongest influence on mass loss, and that fungi and the temperature × fungi interaction had similar and much smaller effects (**c**).

The assumption that climate is a predominant control on decomposition was not supported by the local-scale data. First, decomposition rates of individual wood blocks did not cluster around the mean location values (Fig. 3b), suggesting that local-scale factors are the predominant control on decomposition rates (Hypothesis 1b). Second, our local-scale statistical models supported the inference—contrasting with the mean analyses—that fungal colonization was a much better predictor of decomposition rates than temperature (Fig. 3). The best-fit local-scale model included moisture, which was not auto-correlated with temperature at the local scale, and soil animals, where termites and ants are the dominant macroinvertebrates in dead wood across our gradients[29] and may influence decomposition through wood consumption (termites) or inhibition of fungi (ants)[30].

The local-scale analyses revealed that mass loss increased significantly with higher temperatures, fungal colonization and termite biomass (Fig. 3 and Supplementary Table 2). Local-scale controls on microbial activity seemed to be the predominant driver of decomposition, with the standardized coefficient for fungal colonization being two-times larger than for temperature (Fig. 3d). As such, a change in fungal colonization affects mass loss twice as much as a change in temperature. The full model explained 75% of variance in mass loss, and fungal colonization alone explained 73% of the variance (Supplementary Table 2). In contrast, temperature explained only 28% of variance in mass loss (Supplementary Table 2). The conventional paradigm that climate is a predominant control on decomposition at broad spatial scales then seems to be an artefact of using location-level mean values in previous studies. Our data, along with recent studies on plant traits[3,11], suggest that a new decomposition paradigm should emphasize that litter quality and other local-scale controls instead predominate over climate as regulators of wood decomposition rates at broad spatial scales.

Issues with aggregating fine-scale data to model coarser-scale processes have long been appreciated in ecosystem ecology but largely focus on generating appropriate mean values[31]. In contrast, scientists concerned with topics such as species conservation are moving away from aggregation given an expectation that local-scale data reveal true controls on ecological processes[6,7]. Indeed, the need to understand the role of spatial scale in driving ecosystem processes is recognized as one of the most fundamental ecological questions[32]. At present, mean climate–decomposition relationships (for example, Fig. 2) are used to parameterize Earth-system models and hence inform simulations of phenomena such as carbon cycle–climate feedbacks[13]. Yet inferential issues with using mean data to deduce controls on local processes have been appreciated for decades, where the term 'ecological correlation' (or ecological fallacy) was coined to describe erroneous deductions from aggregated data[10]. Such fallacies become evident when we use our mean- versus local-scale temperature data to infer the temperature sensitivity of wood decomposition. For example, the slope coefficient for the univariate relationship between mean site temperature and mass loss is 1.58. In contrast, for the local-scale analysis the slope coefficient for temperature is 2.05 (Supplementary Table 2), suggesting that the effect of temperature and hence carbon cycle–climate feedbacks is 1.3-times stronger if analysed as disaggregated versus mean data. These different temperature sensitivities suggest a need to revisit how ecosystem models are conventionally structured to determine whether they are robust when analysed using local-scale data.

To explore further the potential for data-rich observations collected over environmental gradients to provide useful validation tools for Earth-system models[13], and to help generate parameter estimates that account for multiple controlling factors, we applied a simple exponential decay model modified by a Q_{10} temperature function (Supplementary Methods). Such models are typically applied to decomposition data[3]. The low within-site replication for a common litter and time period of decomposition in most multi-site studies means that only a single rate constant (that is, k value) can be generated for a common litter type for each stage of decomposition[3]. This approach assumes that the decomposer community can be modelled as a single entity. Our well-replicated data set, in contrast, permitted estimates of multiple rate constants and hence, conceptually, multiple decomposer communities under different local-scale controls. We find that
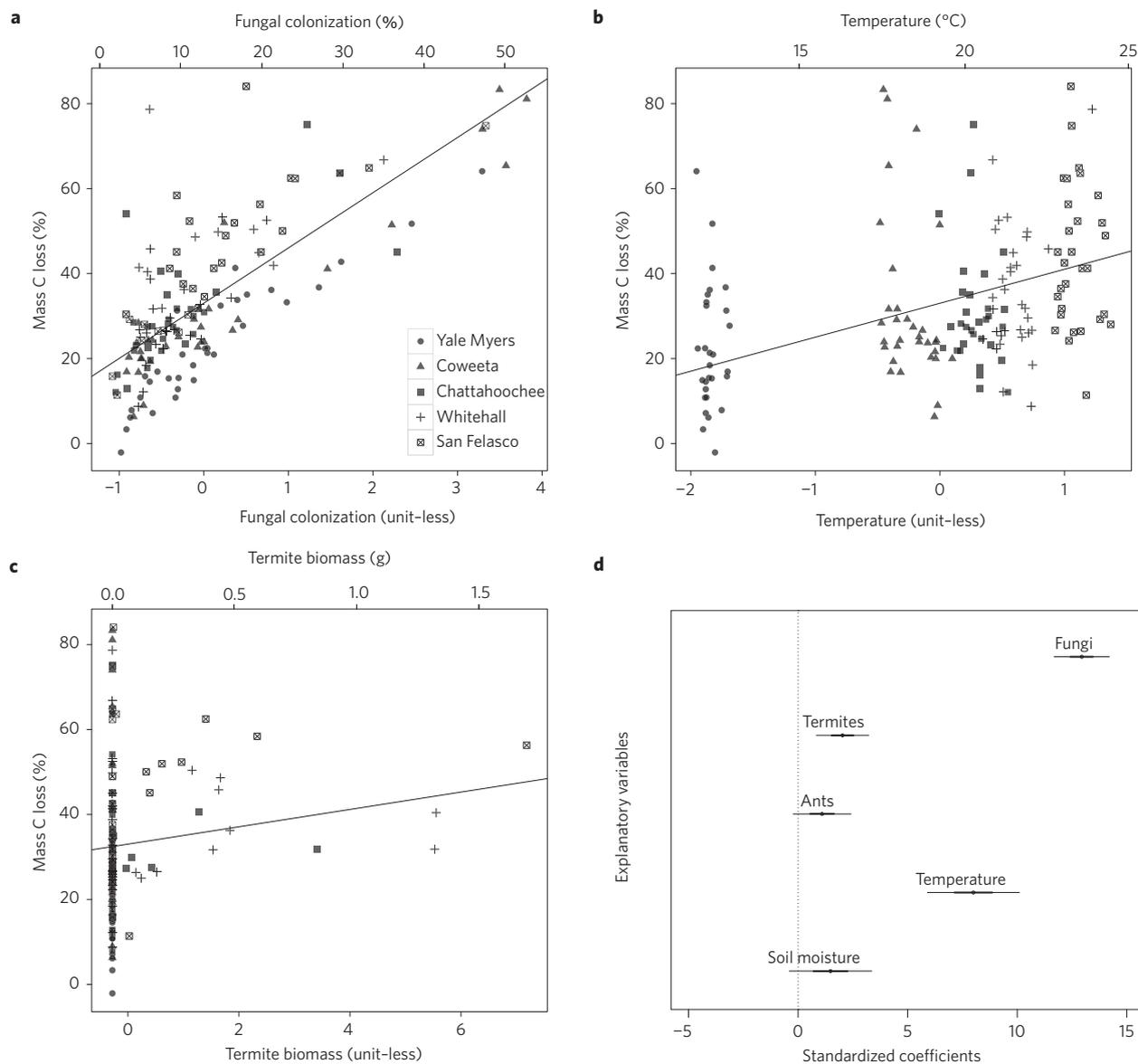
Figure 3 | Decomposition of wood blocks is greater with higher temperatures, fungal colonization and termite biomass across a regional gradient in eastern US temperate forest. a–c, Relationships between decomposition and the significant explanatory variables. **d**, Relative influence on decomposition of the explanatory variables retained in the best-fit model. Decomposition is expressed as the proportion of wood carbon lost from the initial carbon mass of a common wood substrate. Data points (**a–c**) represent observations for individual wood blocks ($n = 158$), and are plotted against the top x axis for fungal colonization (**a**; %), temperature (**b**; °C), and termites (**c**; g wood-block^{-1}) for comparison with Supplementary Table 1. Regression lines (**a–c**) are shown for significant explanatory variables and are standardized (bottom x axis, unit-less) for the influence of the other variables in the full linear mixed model, which retained soil temperature, moisture, fungi, termites and ants (**d**). The errors for significant ($p < 0.05$) model variables do not cross zero (**d**). Plotting the standardized variables (**a–c**) and coefficients (**d**) permits us to make a relative comparison of the influence of each variable and model term on mass loss despite the different scales on which the variables are measured. The standardized coefficients reveal that fungi had the most influence on mass loss, and termites the least (**d**).

the two-decomposer model, in comparison with the conventional single-decomposer model, markedly reduces uncertainty in Q_{10} estimates (Supplementary Table 3) and better predicts observed rates of wood decomposition across all samples ($r^2 = 0.47$ compared with 0.19 for the single-decomposer model; Supplementary results and discussion). Further, using a simple steady-state model we found that stock estimates for dead wood, using the two-decomposer model, differed from the single-decomposer model by as much as a factor of two (Supplementary Table 4). These analyses illustrate that models parameterized with local-scale versus mean observations can lead to carbon stock projections that substantively differ. Our analyses do not address, however, the validity of

using cross-site relationships (whether based on disaggregated or mean data) to inform models that make temporal projections of climate change effects[33] (Supplementary Results and Discussion and Supplementary Fig. 1). Hence, it remains an open question as to how local adaptation in decomposer communities will moderate carbon-cycle responses to changing climate[15].

Understanding of controls on wood decomposition is much sparser than our understanding for leaf litter decomposition, which has been the focus of most broad-scale decomposition studies[2,3,5,12,17]. Dead wood, however, represents a global carbon store estimated to be in the range of 73 ± 6 Pg (ref. 8) and so understanding its fate under global change is important for

projecting the strength of carbon cycle–climate feedbacks. Our work highlights the importance of local-scale controls on microbial decomposer dynamics in influencing wood decomposition rates. Future work, if it is to be useful for ecosystem models, should prioritize identifying the local-scale factors that determine fungal colonization and hence wood decomposition rates. For example, it may be that downed wood inputs decompose faster if located adjacent (within a few metres) to older woody debris where the fungi from those logs can use the wood energy and nutrients to forage and rapidly colonize new resources[25]. If such factors do explain some of the within-site variation we observed, estimates of woody debris stocks would provide information that could be readily assimilated into ecosystem models. Similar work on local-scale factors is probably necessary to refine understanding of controls on other plant inputs to the decomposer sub-system. That is, aggregating our wood data created the same strong relationship between decomposition and regional climate (Fig. 2) observed in leaf litter decomposition studies, suggesting that artefacts introduced by aggregation might apply generally to the decomposition dynamics of organic matter in terrestrial systems.

Local-scale controls and not climate most strongly influenced microbial activity and consequently the decomposition of dead wood, highlighting the importance of local factors as the primary control on the carbon dynamics of decomposing wood at regional scales. We emphasize that the manner in which local-scale observations are scaled to regional gradients dictates inferences about which variables regulate process rates at broad scales, how much variation each factor explains, and the magnitude (for example Q_{10}) of the relationships. Population and community ecologists increasingly recognize that local-scale variation dictates regional-scale responses[6]. Our data show that similar accounting for local-scale controls on ecosystem processes will probably be necessary for Earth-system models to predict reliably how carbon cycling will respond to environmental disturbance.

Methods

Full details are given in the Supplementary Methods. Briefly, our research was conducted at five locations spanning ~12° latitude in eastern US temperate, second-growth forest. At four sites in each location (20 sites total), 70-m transects were established and wooden blocks placed on the forest floor at 10-m intervals. Our design captured both local- and broad-scale spatial variation in climate by varying slope aspect (north- or south-facing), slope position (wetter downslope to drier upslope), and location (northern to southern sites). Although Coweeta is ~6° latitude from the most northern (Yale Myers) and southern (San Felasco) locations, the mountainous elevation makes it ecologically similar to Yale Myers. Wooden blocks (15 × 12 × 2 cm) were placed in the field for 13 months and consisted of untreated white pine. They were large enough to detect termite colonization and were modified to permit ant nesting by creating nesting chambers. Blocks were placed in contact with the surface soil and flush with the litter layer. Soil temperature and moisture were measured at each wood block on six occasions. Wood blocks were also checked for termite and ant colonization. Wooden blocks were retrieved, the fauna counted and weighed after drying at 65 °C, and then drilled to create sawdust for fungal biomass and total carbon determinations. Drilled wood blocks were re-weighed, dried at 65 °C to constant mass, and weighed again. We accounted for differences in initial masses across wood blocks by expressing mass loss as percentage carbon loss. Potential controls on decomposition were analysed with linear mixed models, permitting transect to be treated as a random effect and hence account for the spatial clustering of the experimental design (Supplementary Methods).

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Additional information

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Competing financial interests

The authors declare no competing financial interests.