

Ignoring temperature variation leads to underestimation of the temperature sensitivity of plant litter decomposition

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Abstract. The majority of terrestrial net primary production decomposes, fueling detrital food webs and converting dead plant carbon to atmospheric CO₂. There is considerable interest in determining the sensitivity of this process to climate warming. A common approach has been to use spatial gradients in temperature (i.e., latitude or elevation) to estimate temperature sensitivity. However, these studies typically relate decomposition rates to average temperatures at each site along such gradients, ignoring within-site temperature variation. To evaluate the potential effects of temperature variation on estimates of temperature sensitivity, we simulated plant litter decomposition using both randomly generated and real time series of temperature. This simulation approach illustrated how temperature variation leads to higher decomposition rates at a given mean temperature than is predicted from simulations in which temperature is held constant. Increases in decomposition rate were most evident at cooler sites, where temporal variation in temperature tends to be greater than at warmer sites. This unbalanced effect of temperature variation shifted the slope of the relationships between average temperature and decomposition rate, resulting in lower estimated temperature sensitivities than were used to simulate decomposition. For example, estimates of activation energy (E_a) were as much as 0.15 eV lower than the true E_a when decomposition was simulated with the true E_a set to the canonical respiration value of 0.65 eV. We found that the estimated E_a was lower than the true E_a for surface, soil, and air temperatures, but not for stream temperatures, for which there was only a weak relationship between temperature variation and mean temperature. Our results suggest that commonly used methods may underestimate the temperature dependence of litter decomposition, particularly in terrestrial environments. We encourage publication of temperature data that include variation estimates and suggest an alternative method for calculating temperature sensitivity that accounts for variation in temperature.

Key words: apparent activation energy; breakdown; climate variability; decay; detritus; inherent activation energy; metabolic theory; temperature dependence.

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INTRODUCTION

The temperature sensitivity of organic carbon processing is a key control on the global carbon cycle (Kirschbaum 2006, Yvon-Durocher et al. 2012). About 120 billion tonnes of organic carbon

is fixed annually by terrestrial plants (Beer et al. 2010), and the decomposition of this material is both a critical part of the carbon cycle (Brown and Lugo 1982) and the basis of many terrestrial and aquatic food webs (Moore et al. 2004). Higher temperatures are expected to increase

rates of biological reactions exponentially (within the range of 0°–40°C; Brown et al. 2004), including that of heterotrophic respiration—a key process underlying the decomposition of terrestrially derived litter and wood in both aquatic and terrestrial systems (Webster et al. 1999, Bradford et al. 2016). However, it is unclear whether the temperature sensitivity of cellular respiration (i.e., activation energy, E_a , of 0.60–0.70 eV or 57.89–67.54 kJ/mol) accurately describes the complex process of detrital decomposition (Follstad Shah et al. 2017). A common approach to determine the temperature sensitivity of decomposition is to take advantage of spatial temperature gradients (e.g., latitudinal; Boyero et al. 2011, Bradford et al. 2016, Follstad Shah et al. 2017, Tiegs et al. 2019). However, such studies generally relate decomposition only to mean temperatures and ignore temperature variation, which can also vary across spatial gradients.

Studies that model soil decomposition have noted that temperature sensitivity estimates made using mean temperature can be biased (Agren and Axelsson 1980, Kirschbaum 2010). This occurs because higher temperatures increase heterotrophic respiration rates exponentially (Enquist et al. 2003, Brown et al. 2004, Allen et al. 2005); thus, deviations above a mean temperature will increase decomposition to a greater degree than deviations below will reduce it (Fig. 1). Accordingly, increases in variation without increases in mean temperature can increase decomposition rates (Dang et al. 2009, Sierra et al. 2011). This effect of variation can be problematic because intra-annual variation in air temperatures tends to increase as mean annual air temperatures decline across global gradients (Kirschbaum 2010, Wang and Dillon 2014). For example, tropical regions typically experience warmer, more stable climates, while temperate regions experience cooler, more variable climates. Consequently, we expect the degree to which variation increases observed rates of decomposition to increase with distance from the equator (Savage 2004). This deviation biases relationships between decomposition and average temperatures and leads to lower estimated temperature sensitivities of decomposition when decomposition is considered over longer (e.g., multi-season) periods and temperature variation

is ignored (Kirschbaum 2010). While the basis of this phenomenon has been well described theoretically (Agren and Axelsson 1980, Savage 2004) and demonstrated empirically in the context of soil decomposition (Kirschbaum 2010), studies estimating the temperature sensitivity of plant litter decomposition have generally ignored the influence of temperature variation (Boyero et al. 2011, Follstad Shah et al. 2017, Tiegs et al. 2019).

Litter decomposition studies may be particularly susceptible to bias in estimates of temperature sensitivity caused by temperature variation because of their relatively long duration. Measurements of litter decomposition use sampling units (typically coarse-mesh bags containing senescent plant litter, hereafter litterbags) that are deployed for periods of time ranging from weeks to years (Karberg et al. 2008, Benfield et al. 2017) and that typically experience a wide

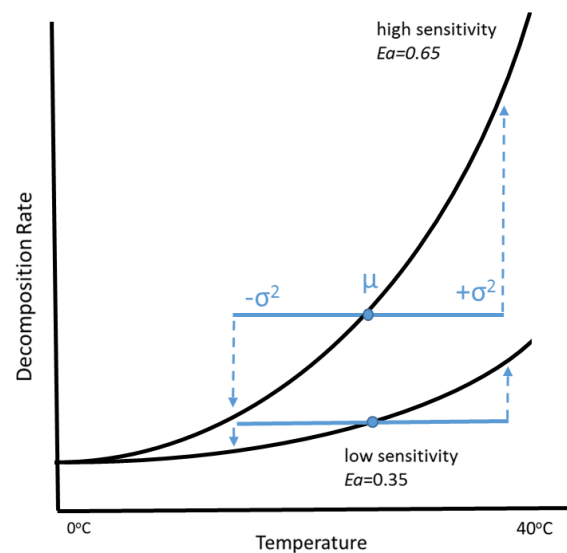


Fig. 1. Illustration of how increased variation around a decomposition rate may lead to higher average decomposition rates over time. The shape of an exponential curve implies that a process rate increases more when a temperature is one standard deviation above its mean than it decreases when temperature is one standard deviation below its mean. This should lead to higher observed average rates over time. The difference between the rates one standard deviation above and below the mean should be greater when a process is more sensitive to temperature, for example, higher temperature sensitivity or E_a .

range of temperatures over the duration of each study. Thus, we expect the resulting estimates of temperature sensitivity of litter decomposition to be somewhat lower than the true temperature sensitivity driving the process (Agren and Axelsson 1980, Kirschbaum 2010). Furthermore, we expect these estimates of temperature sensitivity to be contingent on the length of time that the litter has been incubated and the specific relationship between mean temperatures and variation present in the study. As such, published estimates of temperature sensitivity may not accurately estimate litter decomposition under different experimental or future climatic conditions.

While it is known that there is a relationship between intra-annual variability and mean temperatures in air, it is unclear whether this trend is as strong in the environments in which plant litter actually decomposes. Most terrestrial plant litter decomposes in soil, on the soil surface, or in streams. Temperatures in these environments generally display a dampened response to changes in ambient air temperature (Zheng et al. 1993, Caissie et al. 2001), and water temperatures rarely fall below 0°C. Additionally, respiration increases across the 0°–40°C temperature range, but tends to drop to very low levels outside of this range (Brown et al. 2004), which may modulate responses of decomposition rates to temperature variability in very cold or warm environments.

Our overall goal was to explore potential bias introduced into large-gradient estimates of the temperature sensitivity of plant litter decomposition and provide guidance for interpretation of their results. However, true temperature sensitivities are always unknown when estimates are made using empirical measurements of decomposition, making it impossible to evaluate whether an estimate is biased. Our approach, therefore, is to use simulations in which true temperature is known. We first characterize empirical relationships between temperature means and standard deviations across gradients within decomposition environments (soil, soil surface, and streams). To do this, we use publicly available datasets of temperature to assess the degree to which mean annual temperatures and the standard deviations of daily temperature are related. We next quantify the influence of

temperature variation on observed decomposition rates. We do this using randomly generated time series of temperature to simulate decomposition across a range of mean temperatures and standard deviations of temperature. Third, we estimate the degree to which global relationships between mean temperatures and variation in temperature could result in biased estimates of E_a . To do this, we return to the global temperature data and simulate decomposition using a range of true (i.e., known) E_a values to simulate decomposition. We use standard methods to calculate an estimated E_a from these data, which we then compare with the true E_a used to generate them. Finally, we highlight an alternative approach to calculating the activation energy of decomposition that is not biased by temperature variation and that has been used in similar contexts (Yvon-Durocher et al. 2012), but which has yet to be adopted in estimating the temperature dependence of plant litter decomposition.

METHODS

Our general approach to simulating decomposition assumes that instantaneous decomposition rates are a function of temperature only. Under natural conditions, rates of decomposition are not just a function of temperature, as moisture and substrate quality are also dominant controls (Tuomi et al. 2009, Bradford et al. 2016). Further, macroconsumers and other processes such as photodegradation can be important in some instances (Austin 2011, Bush et al. 2017). While these factors may confound estimates of temperature effects if they are correlated with the temperature gradient, we argue that we must first understand their effects individually before we can consider them in combination (Tuomi et al. 2009). Here, our focus is on temperature.

Relationships between mean temperature and temperature variation

To quantify how relationships between mean temperature and variation in temperature differ among the environments in which plant litter decomposes (streams, on the soil surface, and in the upper layers of soil), we used regional-level temperature data from several environments and a dataset of global air temperatures. We combined two regional databases of stream temperature for

the western and eastern United States (NorWeST and SHEDS), both of which report daily mean stream temperatures (Isaak et al. 2017, SHEDS Development Team 2018). We also used data from the U.S. Climate Reference Network (USCRN), which contains paired measurements of air, land surface, and soil temperature measurements at 5 cm below the surface taken daily at sites throughout the United States (Bell et al. 2013, Diamon et al. 2013). Because we could not locate soil, soil surface, or stream temperature data collected at the global scale, we used air temperature data to explore global trends in temperature using the National Oceanic and Atmospheric Administration product Global Summary of the Day (GSOD), which provides daily air temperature measurements across the globe (Menne et al. 2012). We only included sites in our analysis that had measurements for at least 360 days a year, though we did not require these days to be consecutive and simply omitted missing values (Table 1; Appendix S1: Figs. S1 and S2). As these are all published datasets that already had undergone quality checks, we performed no additional processing or error checking assuming that any residual errors were random and served to add noise but not bias to our results. To address our first question and understand how relationships between mean temperature and variation in temperature differ across these datasets, we used mixed-effects models. We regressed mean annual temperature against the standard deviation of daily temperatures over a year for each dataset and included a random effect for site to account for repeated measurements. Mixed-effects models were run using the lme4 package in R (Bates et al. 2014).

Influence of temperature variation on decomposition

To address our second goal and estimate the impact that temperature variability can have on decomposition rates, we generated 200,000 time series of temperature. Each simulation comprised one year of daily temperature values, which were normally distributed without seasonal structure, with a randomly selected mean (between 0° and 25°C) and standard deviation (between 0° and 15°C). By randomly generating these time series, we ensured that temperature means and standard deviations were orthogonal.

We simulated decomposition using a daily time step, allowing the instantaneous rate of decomposition (r_{inst}) to be set by temperature. At each time step (i.e., one day), we used the Boltzmann-Arrhenius equation,

$$r_{\text{inst}} = r_{\text{ref}} \times e^{\frac{-E_a}{k_B} \times \left(\frac{1}{T} - \frac{1}{T_{\text{ref}}} \right)}, \quad (1)$$

to calculate the instantaneous decomposition rate (r_{inst}) at the respective temperature and a known true E_a . In this equation, k_B is the Boltzmann constant (8.617×10^{-5} eV/K), and the reference decomposition rate (r_{ref}) and reference temperature in degree K (T_{ref}) are set to arbitrary realistic values (0.0204 d^{-1} and 15°C, or 288°K, throughout; Manning et al. 2015). We constrained this model to estimate r_{inst} only when temperatures were >0°C and <40°C. Outside of this range, we set r_{inst} to 0. We ran simulations for our random datasets at three plausible values of true E_a (i.e., 0.45, 0.65, and 0.85 eV; Kirschbaum 2010). We then used the modeled instantaneous decomposition rates (r_{inst} in Eq. 1) to calculate the mass (M) remaining after the time step as a function of

Table 1. Sources and attributes of the datasets that were used in our analysis of relationships between mean temperature and temperature variation in different habitats.

Database abbreviation	Environment	Geographical extent	Number of sites	Range of years	Resolution of temperature data	Citation
NorWeST	Streams	NW United States	3504	1993–2015	Daily means	Isaak et al. (2017)
SHEDS	Streams	NE United States	397	1999–2017	Daily means	SHEDS Development Team (2018)
USCRN	Air, soil surface, 5cm below soil surface	United States	115 soil, 137 surface, 226 air	2000–2017	Daily means, and hourly means	Diamon et al. (2013)
GSOD	Air	Global	9541	1973–2017	Daily means	Menne et al. (2012)

the mass remaining at the beginning of the time step (M_0) and the length of the time step (t , which was always 1 d):

$$M = M_0 e^{-r_{\text{inst}} t} \quad (2)$$

In order to treat our simulations like a litterbag experiment, we only used a subset of this time series of mass remaining data by extracting the values at 0, 60, 120, 180, 240, 300, and 350 d. Finally, we estimated the decomposition rate by linearizing the exponential decay model, in which the slope between sampling day and the natural log-transformed percent mass remaining data is the estimated decomposition rate, or $r_{\text{estimated}}$.

To determine the influence of temperature variation on $r_{\text{estimated}}$, we used linear models to estimate the relative influence of temperature variability (i.e., standard deviation of temperature) and mean temperature on $r_{\text{estimated}}$ generated from the randomly distributed datasets. Estimated decomposition rates were first \log_{10} -transformed so that regression coefficients could be interpreted as percent changes in $r_{\text{estimated}}$.

Estimating E_a from temperature gradients

To address our third goal, we estimated the activation energy based on $r_{\text{estimated}}$ from the simulated data and the site mean temperatures. For each of the publicly available temperature datasets described above, we simulated decomposition using a daily time step as we did with the randomly generated data. Then, we determined the temperature sensitivity, as it has been interpreted elsewhere, as the slope between natural log-transformed values of $r_{\text{estimated}}$ and the inverse of the Boltzmann constant times the mean temperature in degrees Kelvin (Boyero et al. 2011, Follstad Shah et al. 2017, Tiegs et al. 2019). Due to the sampling effort involved in measuring plant litter decomposition, most experiments have a relatively small number of sites across a wide spatial gradient (e.g., Boyero et al. 2011, Tiegs et al. 2019). We attempted to mimic this constraint in experimental design by conducting a bootstrapped sampling of our $r_{\text{estimated}}$ data and using subsets of the data to estimate E_a . First, we binned our data by absolute latitude; the global data were grouped into ten 5° bins ranging from 0° to 45° absolute

latitude, while the U.S. data (i.e., USCRN and stream data) were grouped into ten 2° bins ranging from 30° to 50° latitude. We then selected random subsets, with one site from each bin, 10,000 times for each dataset (e.g., stream data, or global air temperatures). When multiple years of data existed at a given site, one year of data was picked at random. Then, for each of these randomly selected subsets of data and true E_a , the E_a was estimated as the slope of the regression between the natural log-transformed $r_{\text{estimated}}$ and $1/k_B T$, where T is the average temperature during the year and k_B is the Boltzmann constant. We present mean estimates of E_a and confidence intervals from these 10,000 simulations for each dataset, as well as the value of the true E_a .

Estimating E_a while accounting for temperature variation

We also used a second approach to estimate E_a based on methods used to address similar problems with temperature variation in models of annual ecosystem respiration (Yvon-Durocher et al. 2012). We estimated both E_a and r_{ref} by fitting the equations we used to generate the data to the mass remaining data and all of the temperature data. While E_a and r_{ref} are both constants in our initial simulations, neither would be known parameters when collecting data from the field so we must estimate both from the simulated data. A key difference between this approach and the one described above is that this approach uses the complete time series of temperature and values of mass remaining, whereas the first approach collapses temperature down to a single mean value and mass remaining measurements down to a single $r_{\text{estimated}}$ value. As described above, we fit these models to subsets (i.e., ten sites at a time) of the whole datasets to mimic the constraints of real studies (Table 2). To fit these alternative models, we simulated decomposition for each site in each subset of data in the same way that we did when generating the data (Eqs. 1 and 2). Initial estimates of E_a and r_{ref} were made based on values from the literature (i.e., 0.65 eV and 0.001 d⁻¹; Boyero et al. 2011), and decomposition was simulated at each site, allowing daily temperature, estimated E_a , and r_{ref} to determine r_{inst} . Then, the estimated mass remaining values from days 0, 60, 120, 180, 240, 300,

and 350 were extracted. We then calculated the log-likelihood of the differences between these newly modeled values and the true simulated values, assuming a normal probability density distribution with a mean of zero. We then optimized the estimated E_a and r_{ref} to maximize the log-likelihood of the model using the `mle2` function in the `bbmle` package (Bolker 2017; method described more fully in Appendix S1). Due to the high amount of computational time involved, we only performed 100 estimations for each dataset and only made estimates for the data in the three USCRN datasets. All analyses were performed in R version 3.4.0 (R Core Team 2016).

RESULTS

Relationships between mean temperature and temperature variation

We generally found mean temperature and the standard deviation of temperature to be negatively related. The global air temperatures had an average decline in variation of $0.35 (\pm 0.001 \text{ SE})$ standard deviations per one-degree increase in mean temperature. The USCRN data had declines of $0.32 (\pm 0.13 \text{ SE})$, $0.29 (\pm 0.21 \text{ SE})$, and

$0.16 (\pm 0.02 \text{ SE})$ standard deviations per one-degree increase in mean temperature in the air, soil, and surface temperature datasets, respectively (Fig. 2). However, stream temperature variation showed only a weak relationship with mean temperature ($R^2 = 0.04$) and variation actually increased with temperature by $0.09 (\pm 0.007 \text{ SE})$ standard deviations per one-degree increase in mean temperature (Fig. 2; full regression equations in Appendix S1: Table S1).

Impacts of temperature variation on decomposition rates

Manipulating variation in temperature resulted in a wide range of $r_{\text{estimated}}$ at a given mean temperature, with increases in variation tending to increase $r_{\text{estimated}}$ (Fig. 3). Increasing temperature variation by one standard deviation led to increases in $r_{\text{estimated}}$ that were equivalent to an increase in temperature ranging from 0.17° to 0.57°C depending on the true E_a (Fig. 3; Appendix S1: Table S2). Decomposition rates increased with increased temperature variation (SD) in all true E_a scenarios, with variation effects greatest in the highest true E_a scenario (Fig. 3; Appendix S1: Table S2). At low temperatures,

Table 2. Summary of difference between methods 1 and 2 of estimating the temperature sensitivity of decomposition, or the activation energy E_a .

Method	Data requirements	General approach	Number of estimates	Observations of decomposition per estimate	Examples of use
1	One estimate of decomposition rate, measurement of mean temperature	Decomposition rates are natural log-transformed, and E_a is estimated as the slope of the line between natural log-transformed rates and the inverse of the mean temperature in degrees Kelvin times the Boltzmann constant	10,000	9 for the U.S. data, 10 for the global data	Boyero et al. (2011), Follstad Shah et al. (2017), Tiegs et al. (2019)
2	Model is fit to raw mass remaining data from decomposition experiment and requires continuous temperature data (daily means)	To estimate E_a , decomposition is simulated (using Eq. 2) where on each day the instantaneous breakdown rate is determined by the Boltzmann-Arrhenius equation. The mass remaining data are extracted on each day that "measured" mass remaining data exist and the estimates of E_a and r_{ref} are subsequently optimized to minimize the difference between the "measured" and estimated mass remaining data	100	9 for the U.S. data, 10 for the global data	Yvon-Durocher et al. (2012)

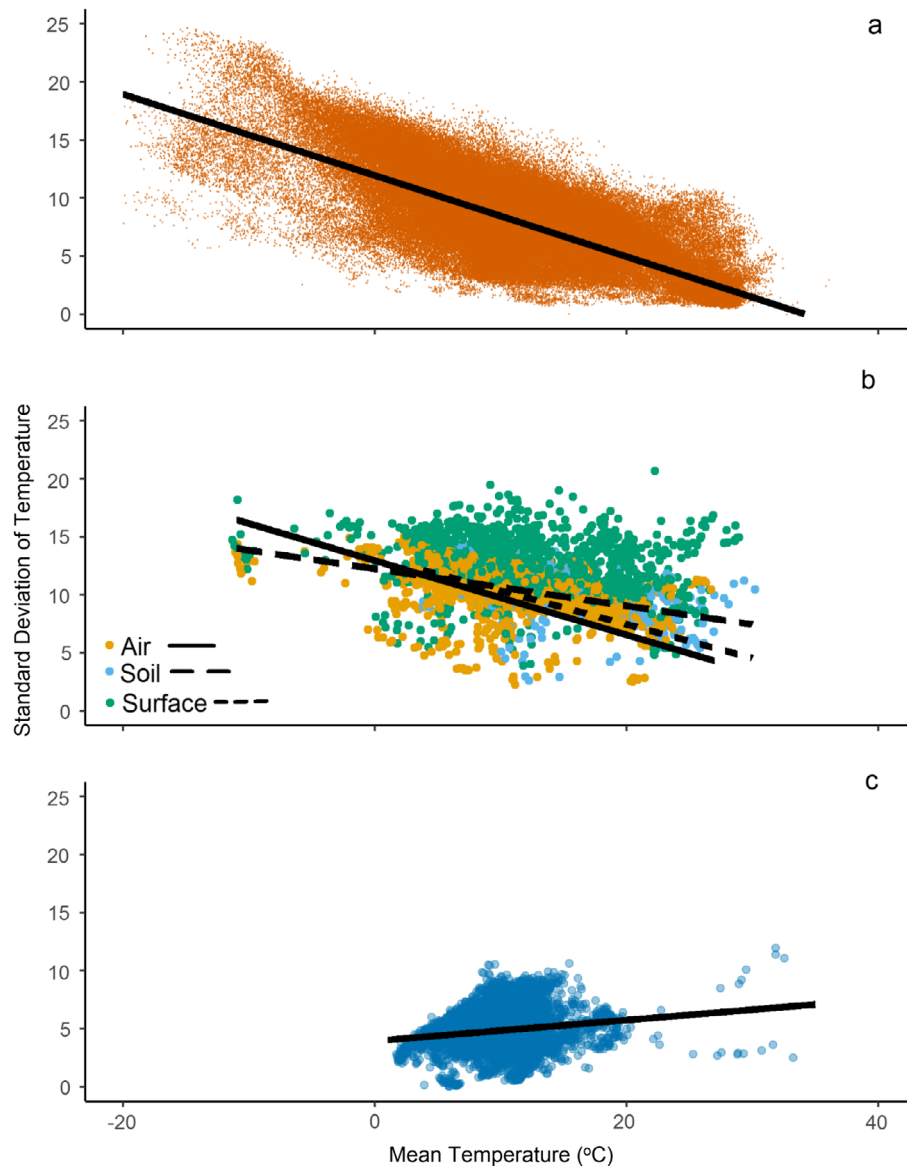


Fig. 2. Relationships between annual mean temperatures and the standard deviation of temperature for global air temperature sites (a), U.S. Climate Reference Network (USCRN) sites (b), and stream temperature throughout the United States (c). The USCRN data contain sites with temperature measurements in air, soil, and the soil surface.

increased variation tended to increase $r_{\text{estimated}}$; however, at higher temperatures, increased variation tended to increase $r_{\text{estimated}}$ only up to an intermediate level of variation, after which $r_{\text{estimated}}$ plateaued or declined (Fig. 3; Appendix S1: Table S2). This plateau effect was likely due to greater variation in warmer simulations that led to more days of decomposition

over 40°C, at which r_{inst} was set to zero. To confirm that our handling of temperatures over 40°C was the cause of this effect, we ran simulations that set r_{inst} at temperatures above 40°C to the rate of decomposition at 40°C, which showed that variation increased $r_{\text{estimated}}$ at all temperatures (Appendix S1: Fig. S2). Thus, whether decomposition ceases at extremely high

temperatures such as 40°C will dictate how this function is actually affected in high-temperature/high-variation conditions. However, our analysis indicates these conditions are not commonly observed in meteorological databases (Fig. 2).

Comparing estimates of E_a and true E_a

Estimates of E_a made by relating $r_{\text{estimated}}$ to mean temperatures were generally lower than the true E_a values used to simulate the decomposition data, with the exception of the stream dataset (Figs. 4, 5; Appendix S1: Table S3). When the true E_a was 0.65 eV, the estimated E_a ranged from 0.50 eV for the USCRN surface temperature data to 0.65 eV for the stream temperature data (Figs. 4, 5). These differences between true E_a and estimated E_a were due to different levels of

temperature variation in the warm and cool sites. In the warm terrestrial sites, where there was less variation in temperature, $r_{\text{estimated}}$ was similar to the simulations with a constant mean temperature (i.e., black line in Fig. 4). Conversely, $r_{\text{estimated}}$ values in cool sites were often much greater than expected at their mean temperature (Fig. 4a, b). This unbalanced distribution of temperature variation, and the subsequent increases in $r_{\text{estimated}}$, led to E_a estimates lower than the true E_a . The magnitude of the difference between true and estimated E_a generally increased at higher true E_a (Fig. 5). Unlike the other datasets, the stream temperature dataset produced estimates of E_a that were similar to the true E_a (Fig. 5). This appeared to be due to a lower amount of variation in temperature

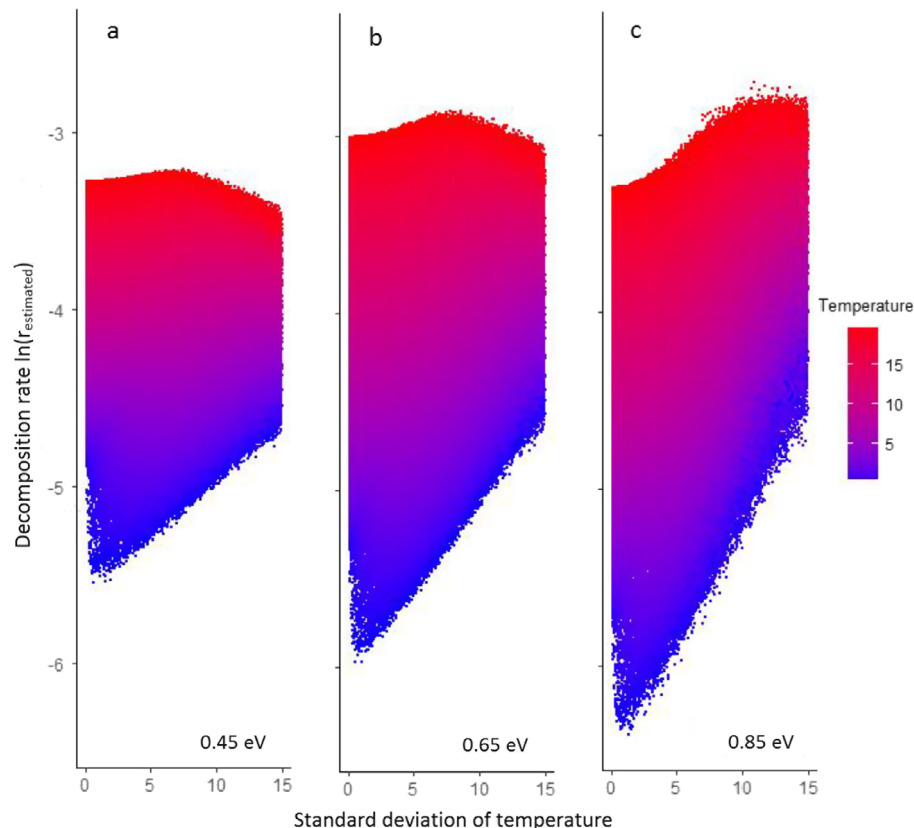


Fig. 3. Relationship between variation in temperature and decomposition rates ($r_{\text{estimated}}$) across a range of mean temperature. Decomposition was simulated across a range of mean temperatures and levels of variation at three different activation energies (0.45, 0.65, and 0.85 eV; panels a, b, and c, respectively). The first-order decomposition rate ($r_{\text{estimated}}$) was calculated from the simulated mass remaining data. Regression equations that compare the effect of mean temperatures and temperature variation on decomposition are presented in Appendix S1.

at the lower-temperature stream sites, compared to the lower-temperature terrestrial sites (Figs. 2, 4).

The second method of estimating E_a was able to reproduce the values of true E_a we used to simulate the data. In each case, with only 100 bootstrapped simulations, this alternative approach was able to closely estimate the values of true E_a (Appendix S1: Table S4). This represents a considerable improvement over the results obtained by the first method with the USCRN data (Figs. 4b, 5) but has some caveats that we discuss below.

DISCUSSION

Plant litter decomposition studies may be underestimating temperature sensitivity by ignoring the influence of temperature variation

on decomposition. Previous estimates of the temperature sensitivity of decomposition are likely biased low because spatial relationships between mean temperature and temperature variation can shift the slope of the relationship between temperature and decomposition rates. It is important to consider these effects of temperature variation explicitly because climate change is altering both mean temperatures and temperature variability (Wang and Dillon 2014). Furthermore, we observed that the deviation between the true E_a and the estimated E_a tends to be greater at higher true E_a because temperature variation tends to have greater positive effects on decomposition when the true E_a is higher. Similarly, when there is only a weak relationship between mean temperature and variation, as in our stream data, we do not observe the same bias in estimates of E_a .

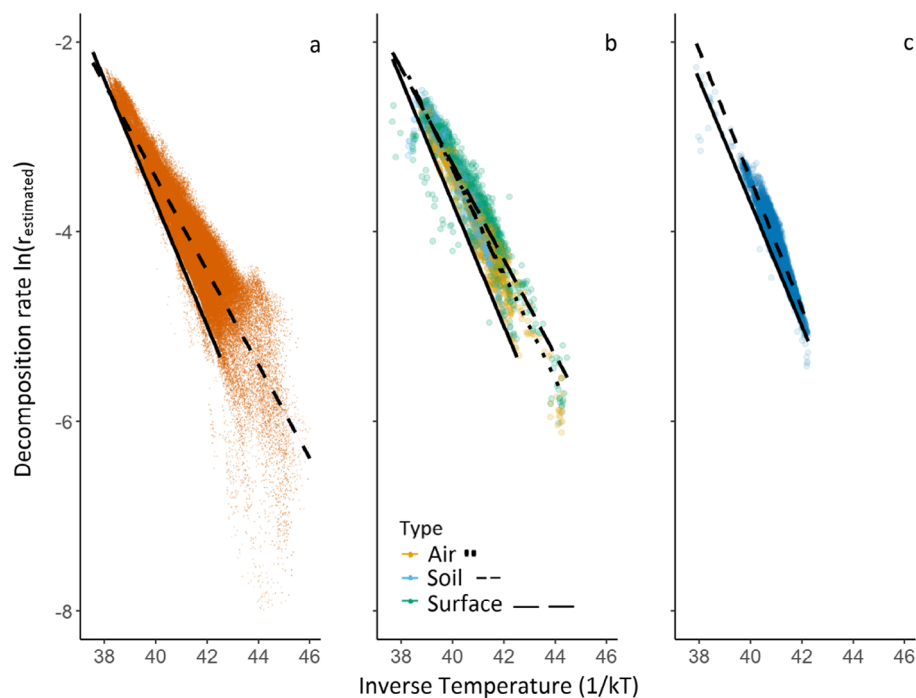


Fig. 4. Inverse temperature compared to the natural log-transformed estimated decomposition rates ($r_{\text{estimated}}$). The panels represent the different datasets: global air temperatures (a), U.S. Climate Reference Network (USCRN) data for air, soil, and soil surface (b), and stream temperatures throughout the United States (c). All simulations were run with a true E_a of 0.65 eV. The solid black line represents simulations which occurred at a constant mean temperature, and the slope equal to 0.65 eV. The dashed lines are the slopes of the simulated data and represent the estimated E_a which were 0.50, 0.51, 0.59, 0.51, and 0.65 eV, respectively, in the global, U.S. air, U.S. soil, U.S. surface, and stream datasets.

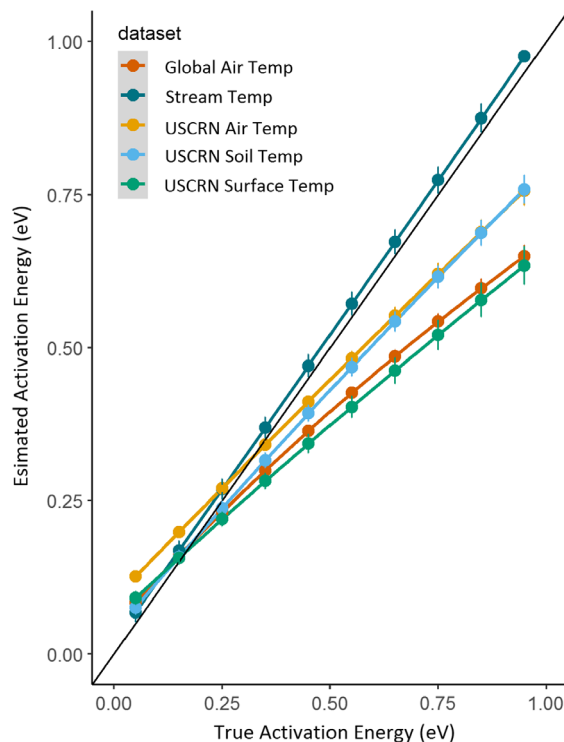


Fig. 5. Estimated activation energies (E_a) estimated from simulated data compared to true E_a used to simulate the data. The black line indicates a 1:1 relationship between true and estimated activation energies, and the other lines represent the different datasets: global air temperature data (orange), stream temperature data (dark blue), air temperature data in the U.S. Climate Reference Network (USCRN, yellow), soil temperatures in the USCRN (light blue), and surface temperatures in the USCRN (green). Regression equations are given in Appendix S1: Table S3.

Current approaches to measuring temperature effects on decomposition of litter in terrestrial environments likely underestimate the true temperature sensitivity of the process. Our simulations resulted in estimates of E_a that were generally lower than the true E_a for the global air temperature dataset and for all the USCRN data, and that were much lower at high true E_a . Quantifying temperature sensitivity using mean temperatures tends to lead to flatter response to temperature and adds noise around the regression line, even in our simulated system in which all variation in decomposition is attributed to temperature. Thus, by simultaneously lowering

the value of a temperature coefficient and adding variability, ignoring temperature variation may lead to underestimates of the relative influence of temperature in studies comparing the effect of multiple factors on plant litter decomposition (e.g., Silver and Miya 2001, Bradford et al. 2016). However, the greater risk is in using estimates of temperature sensitivity derived from large-scale comparisons of decomposition rates and average temperatures. Because variation in temperature can significantly impact decomposition rates at a mean temperature, the usefulness of an estimate of E_a will depend on the underlying relationship between mean temperatures and variation in temperature remaining unchanged. Thus, because an estimate of E_a is conditional on the underlying temperature-variation relationship, it will likely not be transferable. We observed this in our data, when using air temperature data from different spatial scales (i.e., regional vs. global) led to somewhat different estimates of E_a (e.g., estimated E_a of 0.53 and 0.49 at a true E_a of 0.65, respectively; Fig. 5), and we found even larger differences in E_a estimates between different decomposition environments at the regional level (Fig. 4b). Furthermore, there is evidence that intra-annual temperature variability has been changing, with larger shifts in polar regions than in temperate or tropical latitudes (Wang and Dillon 2014). This raises concerns about whether current spatial relationships between mean temperatures and variability in temperatures will persist over ecologically relevant time periods and whether empirical estimates of temperature sensitivity will be robust to these changes.

Some recent studies of the temperature sensitivity of decomposition in stream ecosystems have estimated E_a values that are lower than the canonical value for cellular respiration (0.65 eV; Brown et al. 2004, Enquist et al. 2003). Boyero et al. (2011) conducted a global litterbag experiment and estimated an apparent E_a of 0.41 eV, while a meta-analysis by Follstad Shah et al. (2017) estimated an apparent E_a of 0.34 eV; both values are considerably lower than the E_a of cellular respiration. However, a global experiment using cellulose fabric as an analog for plant detritus found an apparent E_a similar to the canonical value in streams (0.68 eV) and an E_a of 0.40 eV in riparian zones (Tiegs et al. 2019). We observed

lower and less variable decomposition rates at low temperatures in the stream dataset than in the other datasets. While atmospheric conditions are a dominant influence on stream temperature, hydrology can also significantly influence the thermal regime of streams as groundwater, melting snow, and glaciers can stabilize temperatures (Caissie 2006, Ficklin et al. 2013). While our results suggest that temperature variation causes less of a problem in estimating E_a in stream environments, there may still be situations in streams where relationships between temperature means and variation are important to consider. Our stream temperature datasets were limited in size and scope, and relationships between temperature means and variations in streams should be examined over larger spatial scales and different time periods.

While this study focused solely on the influence of temperature on decomposition, temperature is not the only factor that influences decomposition rates, and other factors may be more important in some situations (Bradford et al. 2014, Djukic et al. 2018). Temperature may not limit decomposition in all areas (e.g., very dry areas), but because global temperatures are changing, it is important to have accurate estimates of the temperature sensitivity of decomposition to predict future rates (Davidson et al. 2006). Factors such as moisture may also covary with temperature across landscapes and so influence estimates of temperature sensitivities (Tiegs et al. 2019). Ideally, to predict future rates of decomposition researchers should make unbiased estimates of each effect (e.g., temperature and moisture) and model the influences of each effect and interaction (Tuomi et al. 2009). Furthermore, while we elected to simulate decomposition over 360 d, decisions about when and how long to incubate plant litter are often made with consideration of logistics, litter lability, and plant phenology and can range from a few weeks to multiple years (Spänhoff and Meyer 2004, Imberger et al. 2008). These differences in study duration can influence the underlying relationship between temperature means and variation, altering the bias introduced (Appendix S1: Fig. S6). Accordingly, our results do not offer a direct path for revision of any estimates of temperature sensitivity made elsewhere, but they do serve to illustrate that

temperature variation can affect these estimates of temperature sensitivity.

The improved method for calculating the temperature sensitivity of decomposition we present offers a promising solution to the problems we highlight in this paper. This approach accurately estimated the true E_a used to simulate the data in all cases (Appendix S1: Table S4). However, it requires some assumptions that must be considered carefully before being implemented with real data. Both in simulating our decomposition data and in estimating E_a , we assume that E_a is constant throughout decomposition and across sites. These assumptions are commonly made elsewhere (Boyer et al. 2011, Follstad Shah et al. 2017), but recent work suggests that the temperature sensitivity of respiration may vary substantially from site to site (Song et al. 2018), and it is possible that changes in chemical composition during decomposition also alter temperature sensitivity (Davidson et al. 2006, Adair et al. 2008). We also assumed that no decomposition occurs outside of the 0°–40°C window, based on the limits described by the MTE (Brown et al. 2004). We found that the response of decomposition at high temperatures to increased temperature variation changed substantially when we altered this assumption (Fig. 3; Appendix S1). How to handle these high temperatures is an important consideration, and our two scenarios are maximally simple bookends on the idea of a thermal window (Portner 2010). Finally, we assume that instantaneous rates respond to mean daily temperatures. We made this assumption in part because decomposition rates are typically presented on a day⁻¹ basis (Benfield et al. 2017; note that hourly temperature data are considered in Appendix S1). Because all of these assumptions were the same when we simulated the data and estimated E_a , we were able to reproduce the true E_a values used to simulate the data. Thus, this demonstration is only meant to illustrate that this method has the potential to alleviate the issues with temperature variation that we have identified. Further testing with real decomposition data is needed to evaluate the sensitivity of E_a estimates to these assumptions—and ideally to test them directly.

The difference in timescale at which the underlying processes driving organic matter decomposition (e.g., respiration) respond to temperature

and the timescale at which we measure decomposition rates represents the fundamental source of bias in estimates of temperature sensitivity. While we have elected to use the framework of activation energies to describe and model temperature sensitivity, these phenomena should be common to any exponential relationship of a rate with temperature (Kirschbaum 1995, Tuomi et al. 2009). While other ecological processes (e.g., growth of poikilotherms, population-level processes; Hung et al. 1993) are measured over similarly long timescales, most biogeochemical processes are quantified over much shorter time periods, ranging from hours to days (e.g., primary production, respiration, and nitrogen fixation), suggesting that the issues highlighted here are not common to all processes. There is now an understanding that using mean observations of controlling factors (e.g., climate) across replicates within a site can give misleading results in regional litterbag decomposition studies (Bradford et al. 2016), and our studies have highlighted that there are similar issues with analyzing mean values of controlling factors over long periods of time (as have previous studies, e.g., Savage 2004, Yvon-Durocher et al. 2012).

We have several suggestions for future best practices and new lines of research. We encourage studies of the effect of temperature on decomposition to report not only mean temperatures but also temperature variation, and preferably to include raw temperature data in online supplements. We also suggest further exploration of the improved approach to estimating temperature sensitivities that we present here. This approach to estimating temperature sensitivity includes some assumptions that should be tested empirically: Temperature sensitivity does not vary by site or through time; instantaneous decomposition rates respond to temperature at some fixed timescale (i.e., daily or hourly temperature); and microbial decomposition ceases at temperatures over 40°C. Incorporating these recommendations will improve estimates of the temperature sensitivity of decomposition, allowing better prediction of rates under future temperature regimes.

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