FUTURE DIRECTIONS

Understanding the dominant controls on litter decomposition

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Summary

1. Litter decomposition is a biogeochemical process fundamental to element cycling within ecosystems, influencing plant productivity, species composition and carbon storage.

2. Climate has long been considered the primary broad-scale control on litter decomposition rates, yet recent work suggests that plant litter traits may predominate. Both decomposition paradigms, however, rely on inferences from cross-biome litter decomposition studies that analyse site-level means.

3. We re-analyse data from a classical cross-biome study to demonstrate that previous research may falsely inflate the regulatory role of climate on decomposition and mask the influence of unmeasured local-scale factors.

4. Using the re-analysis as a platform, we advocate experimental designs of litter decomposition studies that involve high within-site replication, measurements of regulatory factors and processes at the same local spatial grain, analysis of individual observations and biome-scale gradients.

5. *Synthesis*. We question the assumption that climate is the predominant regulator of decomposition rates at broad spatial scales. We propose a framework for a new generation of studies focused on factoring local-scale variation into the measurement and analysis of soil processes across broad scales. Such efforts may suggest a revised decomposition paradigm and ultimately improve confidence in the structure, parameter estimates and hence projections of biogeochemical models.

Key-words: biogeochemical models, ecological fallacy, ecosystem processes, experimental design, litter decomposition, nutrient cycling, plant–soil (below-ground) interactions, scale, soil carbon, variability

Introduction

Decomposition is a biogeochemical process fundamental to nutrient, carbon and energy cycling within and among ecosystems, and also between the biosphere and atmosphere (Wardle 2002; Schlesinger & Bernhardt 2013; Wieder, Bonan & Allison 2013). Decomposition in most ecosystems largely results from the activities of microorganisms and animals which breakdown non-living organic matter into simpler forms, to gain energy and matter to build and maintain their own biomass (Swift, Heal & Anderson 1979; Bradford *et al.* 2002a; Handa *et al.* 2014). Controls on the activities of these organisms thus influence the rate at which energy and matter flow through decomposer food webs, and regulate the supply rate of nutrients into available forms for plant uptake and growth (Swift, Heal & Anderson 1979; Hunt & Wall 2002; Drake *et al.* 2011). Indeed, for many decades decomposition studies have been motivated, at least in part, by understanding the rate at which plant available nutrients are liberated from decomposing organic matter (Tenney & Waksman 1929; Swift, Heal & Anderson 1979; Parton *et al.* 2007). Much of our understanding of the factors that regulate the rate at which organic matter decomposes arises from assessing the breakdown and transformation of leaf litter (Prescott 2010).

More than 85 years ago Tenney & Waksman (1929) hypothesized that the rate of decomposition is in part a factor of temperature, moisture availability and the chemical composition (or quality) of the plant litter. Over the next few decades a foundational paradigm in ecology developed, where climate (e.g. temperature and moisture) was viewed as the predominant factor regulating litter decomposition rates

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at global and regional scales (Meentemeyer 1978; Parton, Stewart & Cole 1988; Wall *et al.* 2008). Litter quality was then presumed to take precedence as a dominant regulator only where climate became less constraining to decomposer activity (Swift, Heal & Anderson 1979). However, interactions between climate and litter quality effects on decomposition were also appreciated (Olson 1963; Meentemeyer 1978). For example, dominant plant functional types shift with climate, meaning that litter quality and climate together become less favourable for decomposition (Aerts 1997). Resulting theoretical developments relating litter traits to decomposition call for revision of the climate-centric foundational paradigm (Cornwell *et al.* 2008; Zhang *et al.* 2008), suggesting instead that variables other than climate explain most variation in decomposition rates at regional and global scales (Fig. 1).

Conceptions of the dominant factors regulating the rate of leaf litter decomposition extend beyond the academic realm to influence prescriptions of ecosystem management and even global environmental policy. For example, knowledge of controls on leaf litter decomposition rates often inform models used to project how ecosystem organic matter stocks will respond to disturbances such as climate warming, and hence affect the magnitude of feedbacks between the biosphere and atmosphere that might drive further climate change (Bonan *et al.* 2013; Ciais *et al.* 2013; Todd-Brown *et al.* 2014). To inform policy on global climate change, there is therefore a need to ensure that the dominant factors regulating decomposition are identified with a high degree of confidence.
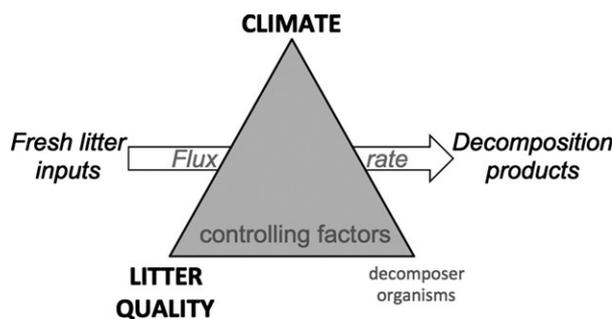

Fig. 1. The decomposition triangle is the classical conceptualization of the dominant factors regulating litter decomposition rates (see Swift, Heal & Anderson 1979) and is modified here to represent the contemporary paradigms. The original model posits that the physico-chemical environment, litter traits and decomposer organisms, are fundamental controls on decomposition rates. Swift, Heal & Anderson (1979) separated physico-chemical controls into climatic and edaphic factors, emphasizing the primacy of climate (shown). The assumed importance of climate grew disproportionately as regional-scale decomposition studies were conducted in the 1980s through 2000s. A recent idea is that litter quality is instead the dominant control at broad spatial scales. Both of these contemporary paradigms assume that the activities of decomposer organisms are regulated by climate and litter quality, and so do not exert independent control on decomposition rates. As such, the decomposer organisms are shown in small grey font to emphasize that under contemporary paradigms climate and litter quality are considered the dominant factors regulating the rate at which organic matter decomposes.

In this paper, we lay out a framework for a next generation of litter decomposition studies designed to help (i) assess our confidence in the 'climate-decomposition' paradigm (Fig. 1) and, if necessary, (ii) advance the conceptualization of a revised paradigm. To demonstrate the need for this framework we re-analyse a classical regional-scale decomposition experiment (Berg *et al.* 1993) previously used to demonstrate the predominance of climate as a regulator of litter decomposition rates. We use these data to illustrate that inference about climate, as a dominant regulator of decomposition rates, can be a product of both experimental design and analysis. We propose that a next generation of multi-site studies require experimental designs that include individual (vs. mean) observations and analyses, a within-biome spatial scale and high within-site replication. We suggest that these recommendations will help discern the true extent to which climate regulates decomposition, and potentially lead to the identification of other important factors that act to influence rates across broad spatial scales.

The data set

To demonstrate how conclusions about factors regulating litter decomposition rates might be influenced by experimental design and analysis, we searched for data sets (i) covering broad spatial scales, (ii) with high within-site replication and (iii) with measurements of both control and response variables at the scale of individual observations. Our search was unsuccessful. However, the data set of Berg *et al.* (1993) met the first two of the three criteria, enabling some insights into how experimental design might influence understanding of those factors regulating litter decomposition rates.

Berg *et al.* (1993) followed conventional practice by presenting and analysing mean decomposition rate values for multiple sites, but the mean site values they presented were calculated from a high number (20–25) of replicates. In total they had 39 sites spanning subarctic to subtropical habitats where needles of Scots pine (*Pinus sylvestris* L.) from a common source were decomposed in a field litterbag experiment for a year. Decomposition rate data for each litterbag for 20 of these 39 sites were available for the re-analysis presented here. These 20 sites were from a subset of 22 sites that Berg *et al.* (1993) found had similar patterns of decomposition because of a maritime (as opposed to continental) influence on the timing and distribution of precipitation. All of the 20 sites were pine monocultures, with Scots pine being the most common tree species. The 20 sites ranged in latitude from ~69° to ~43° north, across a 16.9 °C range in mean annual temperature (MAT: −1.7 to 15.2 °C), a 1080-mm range in mean annual precipitation (MAP: 420–1500 mm), and a 350-mm range in actual evapotranspiration (AET: 326–644 mm). We analyse MAT as the climate variable in this re-analysis but the same conclusions are drawn from analysis of AET; whereas MAP is comparatively weakly related to the observed decomposition rates and much more weakly correlated to MAT and AET than they are to one another ($r = 0.92$). Full experimental details are given in Berg *et al.* (1993).

Not documented in Berg *et al.* (1993) was the care taken to minimize 'noise' in the among-site climate signal. Specifically, bags were placed on level ground, in low fertility stands (sediment soils with granitic bedrock) with similar canopy cover, and away from rocks and on top of an intact litter layer. Litterbags were also constructed and later deconstructed in the same laboratory. The experimental design therefore potentially biases towards finding a stronger effect of climate, because it minimizes within-site variation that might be suggestive of unmeasured controls. In addition, the single litter source does not permit determination of the role litter quality plays in regulating decomposition rates.

Perhaps most importantly, the Berg *et al.* (1993) data set does not include measurements of response (decomposition rate) and regulating (e.g. temperature or moisture) variables at the same spatial grain (i.e. the litterbag). Specifically, climate is measured at the site level and therefore our re-analysis cannot generate robust parameter estimates of climate regulation of decomposition rates (*sensu* Bradford *et al.* 2014a). There is also the possibility that the within-site variation in decomposition rates we report could be the product of caveats with the litterbag approach (e.g. macrofauna enter some bags as juveniles and then grow and remain there) and/or microclimatic differences within a site. Given the care to minimize within-site variation, in addition to the broad climate gradient among sites, this latter possibility seems unlikely. However, such possibilities can only be evaluated when multi-site studies measure climate variables at the same spatial resolution as decomposition variables (e.g. at the litterbag scale, as we recommend in this paper). Our intention here is simply to use the Berg *et al.* (1993) data set to illustrate how the design and analysis of regional- to global-scale decomposition studies could inflate the perceived importance of climate as a regulatory factor, thus unintentionally reinforcing the current climate-decomposition paradigm.

Re-analysis

There are three common characteristics in the design and analysis of most broad-scale litter decomposition experiments: (i) assessment of relationships between regulatory and decomposition variables that are grouped to site-level means; (ii) broad gradients in the putative regulatory variables and (iii) low-replication for any one litter quality per incubation time at a site (Moore *et al.* 1999; Gholz *et al.* 2000; Wall *et al.* 2008; Currie *et al.* 2010). We discuss each characteristic in turn to demonstrate how they shape inferences about factors regulating decomposition rates.

GROUPED VS. INDIVIDUAL DATA

Analysis of grouped vs. individual data can lead to flawed conclusions because it can alter the estimated strength and even direction of a measured factor on a process (Gelman *et al.* 2007; Oakes 2009; Clark 2010; Schmitz 2010; Bradford *et al.* 2014a,b; Wood & Mendelsohn 2015). When data are grouped the variance among individual observations is collapsed into a single mean value (Gelman *et al.* 2007; Schmitz 2010). Hence, we should expect to ascribe more variation to climate when site-level means across a climate gradient are analysed (Bradford *et al.* 2014a). Indeed, MAT explains 86% of the variance in the mean data for the 20 sites. The explanatory power of MAT is reduced to 71% when the individual data are instead plotted (Fig. 2). Analysis of grouped vs. individual data might therefore exaggerate the variation explained by climate – and therefore the predominance of climate as a regulatory factor – by masking true underlying variability in the data.

SPATIAL SCALE

The statistically significant ($P < 0.001$), negative, quadratic terms in both models shown in Fig. 2 highlight that the effect of climate on mean decomposition rate decreases, at least in the Berg data set, as temperature increases. At the cold end of the climate gradient, climate may well be the predominant factor regulating decomposition rates and hence overwhelms the influence of other factors (emphasized by the low within-site variation at the coldest site). Conversely, towards the warmer end of the gradient, mean decomposition rates are relatively constant across sites whereas within-site variability remains high, suggesting that other factors regulating decomposition rate take precedence over climate (Prescott 2010).
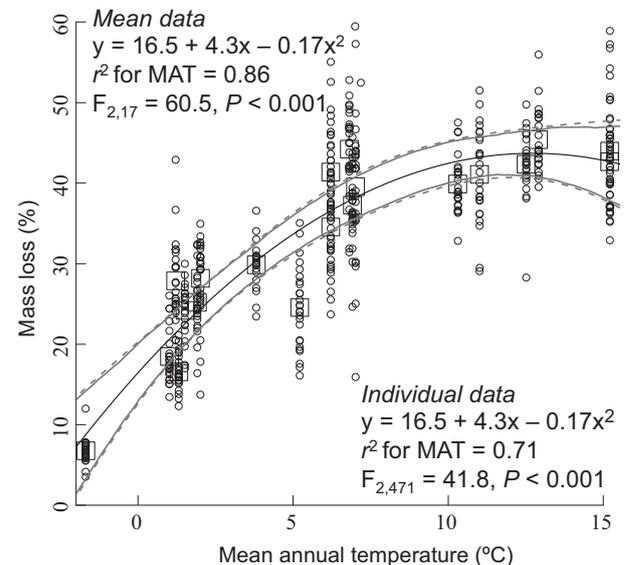

Mean data
$y = 16.5 + 4.3x - 0.17x^2$
r^2 for MAT = 0.86
$F_{2,17} = 60.5$, $P < 0.001$

Individual data
$y = 16.5 + 4.3x - 0.17x^2$
r^2 for MAT = 0.71
$F_{2,471} = 41.8$, $P < 0.001$

Fig. 2. Decomposition of Scots pine (*Pinus sylvestris* L.) needle litter from a common source after 1 year, at 20 sites spanning a climate gradient stretching from Fennoscandian through European Atlantic coastal locations. Site mean decomposition rates (large open squares) and replicate litterbag data per site (small open circles; $n = 25$ for most sites, total n is 494) are shown against mean annual temperature (MAT). Data are analysed with linear regression (mean) or a linear mixed model (individual replicate data), with the total variation partitioned into within-site (random) and between-site (fixed) components (Nakagawa & Schielzeth 2013). Grey lines represent the 95% confidence intervals for the mean (hatched) and replicate (solid) data. Disaggregating these data reduces the variance explained by climate by 15% (from an adjusted r^2 value of 0.86–0.71).

Such insights emphasize that multiple factors act to regulate litter decomposition rates and that they change in predominance as the values of regulatory factors also change.

The potential role of non-climate factors in regulating decomposition rate (Fig. 2) is strongly apparent if we divide our 20 sites into two groups based on whether they are warmer or colder than the median MAT value (6.75 °C). Doing so reveals that climate explains 56% vs. 5% of the variation in decomposition rates at the cold vs. warm end of the gradient, respectively (Fig. 3). Note that we expect r^2 values for a
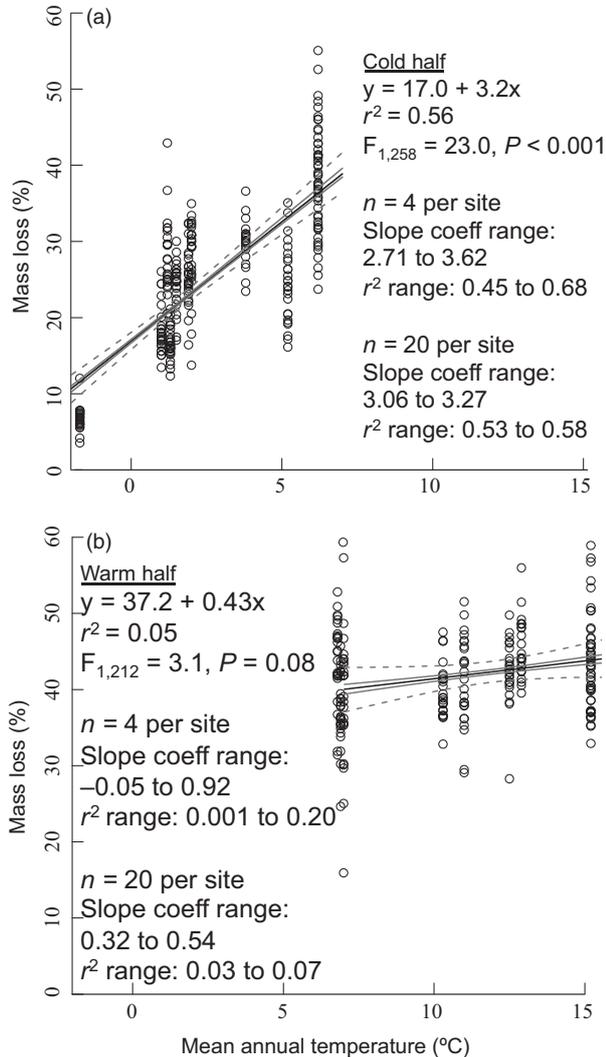
factor to change as we alter the scale of a study and we do not mean to suggest that ill-considered comparisons of r^2 values across studies of differing spatial and temporal extents is a useful way forward. Instead we maintain the same scale of difference in climate: there is the same absolute variation (~8.5 °C) in MAT across each half of the gradient. Hence, the changing explanatory power of MAT is not an artefact of condensing spatial scale and instead suggests that, across the same absolute gradient in climate, MAT can switch from a dominant regulatory factor to a minor one.

REPLICATION

Most broad-scale litterbag studies have few (two to four) replicate litterbags per incubation time at a site (Moore *et al.* 1999; Gholz *et al.* 2000; Wall *et al.* 2008). Obviously there are practical trade-offs in multi-site studies: few replicates ensure there is time and money to incorporate more sites, more time points and other treatments in the design (Adair *et al.* 2008; Wall *et al.* 2008; Makkonen *et al.* 2012). As a result, climate-gradient decomposition studies have dramatically extended our understanding of how litter decomposition proceeds across time in different environments and in relation to markedly varying litter qualities (Parton *et al.* 2007; Harmon *et al.* 2009; Powers *et al.* 2009; Makkonen *et al.* 2012). Use of low replication in these studies is generally understood to reduce precision in the resulting parameter estimates. Often overlooked, however, is that low within-site replication can obscure underlying variability and hence hinder the ability to identify additional factors regulating decomposition rates. The focus on analysing site-level means in these studies then masks major limitations to low replication in terms of understanding the extent and magnitude of climate (vs. other regulatory factor) effects on decomposition. To illustrate this point, we use a bootstrapping technique to simulate the conclusions that might be drawn about climate as a control if Berg *et al.* (1993) had used four instead of at least 20 replicates per site.

In the cold half of the gradient, a single study with four replicates would be likely to conclude that climate explains anywhere from 45% to 68% of the variance in decomposition rates (Fig. 3). The r^2 estimate is much better constrained with 20 replicates (53–58%), as is the slope coefficient (it only varies ~2% from the mean within the 95% confidence intervals, vs. ~13% with $n = 4$). We observe greater uncertainty around the r^2 and slope estimates in the warm side of the gradient, where climate effects are weaker (Fig. 3). Here, climate might explain between 3% and 7% of the variance in a study with 20 replicates but 0.1–20% in a study with four replicates. Most importantly, from the context of extrapolating understanding to predictive models, the slope coefficient for climate, derived with four replicates, varies from negative to positive! The influence of a change in climate on decomposition rates is then constrained much better with higher replication (Fig. 3).

The fact that lower replication reduces precision in the resulting estimates is, of course, no surprise given that basic

Fig. 3. Decomposition rates of Scots pine for the replicate data shown in Fig. 2, but with the sites divided into colder (a: 11 sites) and warmer (b: 9 sites) ends of the gradient. Data are analysed with LMMs, treating site as a random effect. Climate explains more than half of the variation among cold sites, but has little explanatory power among warm sites. The slope coefficients and their adjusted r^2 values (for the fixed effects) are based on boot-strapping (10 000 iterations) using $n = 4$ or 20, where the small open circles show the observations from which the data-points were pulled for each iteration. Black lines are the mean slope estimate and grey boundary lines the 95% bootstrap confidence intervals for $n = 4$ (hatched) and 20 (solid). The overall regression relationships and their statistical significance are shown, along with the ranges in slope coefficients and fixed-effect r^2 values to demonstrate implications of low replication and spatial gradient (see text).

statistics suggests this trade-off, but the expectation is that low-precision estimates remain unbiased. Yet our re-analysis shows that low replication can reduce precision and promote *inferential* bias. Specifically, when there is high within-site variability relative to among-site variability, as in the warm half of the gradient, lack of precision is so great with four replicates per site that inferences about the extent to which decomposition rates respond to a change in temperature are almost certainly incorrect. That is, in any one study with four replicates we could find the slope coefficient to be more than double, or as much as six times smaller, the 'true' value (Fig. 3). Large-scale decomposition studies are rarely repeated in an identical manner, so the fact that estimates obtained with $n = 4$ are asymptotically unbiased is of little use; instead, decomposition studies must be designed in such a way as to have minimal bias in a single implementation.

A way forward

Given the issues of previous experimental design and analysis revealed by the Berg *et al.* (1993) data set, we propose seven essential characteristics of next-generation litter decomposition experiments that should enable a robust evaluation of the

climate-decomposition paradigm. These characteristics are summarized in Table 1.

REVISED EXPERIMENTAL DESIGNS AND MEASUREMENTS

Our first recommendation is to collect regulatory variables at the same spatial and temporal grain as the process of interest. For example, measure microclimate, not site-level climate, to understand how temperature and moisture affect decomposition rates. Key to the adoption of this recommendation is the recognition that the inferred influence of a regulatory factor, when data are aggregated, can be misleading or entirely incorrect (Gelman *et al.* 2007; Clark 2010; Bradford *et al.* 2014a). That is, the full data might suggest different conclusions to summary statistics such as the mean (Weissgerber *et al.* 2015).

Our second recommendation is for high within-site replication (Table 1), so that factors regulating within- vs. among-site variation in decomposition rates can be compared using observations collected at the same spatial grain (Bradford *et al.* 2014a). Such approaches will help remove artificial delineations between microclimate and site climate as

Table 1. A prescription for the experimental design and analysis of broad-scale studies required to test and advance understanding of the dominant factors regulating litter decomposition rates

Approach	Details
1. Individual measurements	Measurements of regulatory variables must be taken at the spatial and temporal grain of the individual unit being assessed (e.g. a litterbag). For example, site-level climate data must be superseded by temperature and moisture data collected for each unit
2. High within-site replication	Experimental designs that capture the environmental variation in potential regulatory factors within a site will ensure that the influences of among site variation in factors on decomposition rates are not over-inflated relative to within-site variation
3. Regional spatial scales	Many broad-scale decomposition studies are motivated by using spatial gradients in regulatory factors (e.g. climate) to make inferences about how change over time in those factors at a location will influence decomposition rates. There is really no solution to the inferential caveats involved in this approach, where between-group spatial observations are extrapolated to project within-group temporal responses. Inferences from this approach can be strengthened through other approaches (e.g. experimental warming at a location) and – for space-for-time designs – an explicit consideration of the appropriate extent of the spatial gradient to ensure that the range in climatic conditions is representative of projected temporal changes in climate (see text)
4. Measure alternate factors	To determine the factors causing the unexplained local-scale spatial variation in decomposition rates, plausible but typically unmeasured variables must be investigated. For example, soil nitrogen availability in the vicinity of the litter, biotic interactions such as top–down control and fungal–fungal interference competition (Crowther *et al.* 2014, 2015)
5. Individual analyses	At some level analyses must be grouped (e.g. placing multiple leaves in a single litterbag and measuring the aggregate mass loss) but care should be taken to avoid aggregating data to an extent that masks substantive unexplained variation, indicating the existence of unidentified controls
6. Non-independence	Data collected at a single site, within a multi-site comparison, are statistically non-independent. Various statistical approaches (e.g. linear mixed models or specification of the variance–covariance matrix) can handle this data structure and so generate robust inferences about the variance explained and form of the relationship between a regulatory factor and decomposition rates (Engqvist 2005; Dormann *et al.* 2007; Baayen, Davidson & Bates 2008; Bolker *et al.* 2009; Zuur *et al.* 2009)
7. Standardized effect strengths	Regulatory factors are usually measured on different scales and have different units (e.g. temperature in °C and moisture in %). The relative influence of different factors within a multiple regression model can then only be compared once the observed data have been standardized, which has the additional advantage that statistical interactions can be compared against the main factors comprising the interaction (Gelman 2008; Schielzeth 2010; Nakagawa & Schielzeth 2013). Other standardizations can be used but the overall objective remains the same: to discern the relative and absolute effect size of multiple regulatory factors, across changing spatial and temporal contexts

regulatory factors; instead recognizing that direct regulatory effects of climate on decomposition rates manifest at the local (i.e. micro) scale at which decomposer organisms perceive climate. Microclimate measurements would then better match with assumptions in soil biogeochemical models that temperature and moisture directly regulate organism physiological rates (Manzoni *et al.* 2012). Site climate, in contrast, is a proxy for temperature and moisture but also numerous other variables (e.g. plant community composition, soil weathering) that influence decomposer communities. Notable is that the responses of these other variables will likely be asynchronous with changing climate, potentially hindering the use of site-level mean climate as a temporal proxy for regulatory effects of temperature and moisture on decomposition rates.

Our third recommendation is that the 'breadth' of the spatial scale investigated in a multi-site decomposition experiment needs to be carefully chosen (Table 1). For example, analysis of those data collected across a huge gradient in climate might lead to the erroneous conclusion that climate is a dominant factor explaining variation in decomposition rates over the entire gradient, when in actual fact this is only true for part of the gradient (Figs 2 and 3). Inferences about the role a factor plays in explaining variation in decomposition therefore depends on the magnitude of the range over which it is evaluated. This dependence is commonly appreciated; yet it might also depend on what part of the range is investigated, with the explanatory power changing even when the same absolute variation in the regulatory factor is compared across different parts of a gradient (Fig. 3, see also Prescott 2010). Future studies might then use climate gradients more representative of within-biome climate change scenarios for the end of the century (e.g. 4–9 °C shifts in MAT), matching more closely their spatial scale of enquiry to the anticipated temporal change in climate (IPCC 2013) and hence helping in regional downscaling efforts.

Use of climate gradients to inform models that project temporal responses of decomposition to climate change will still need to be interpreted in light of the caveats of 'space-for-time substitutions' (e.g. Lauenroth & Sala 1992; Fukami & Wardle 2005). For example, traits of decomposer organisms and leaf litter change as climate does, generating co-linearity in regulatory factors (Aerts 1997; Crowther *et al.* 2014). This co-linearity will be exacerbated when making projections across broader regional extents, thus further hindering the usefulness of climate-gradient litter decomposition studies that do not explore non-climate controls. Furthermore, there are caveats associated with the use of litterbags because they can, for example, constrain access to the litter by decomposer organisms and affect the litter microclimate (Bradford *et al.* 2002b). Mass loss is also a proxy for decomposition, and does not account for the transformations that occur as part of this process that lead to, for example, the formation of microbial biomass and other compounds that remain as mass but no longer represent the plant input (Bradford *et al.* 2014a). Nevertheless, we expect multi-site litterbag decomposition studies to remain an important tool for informing projected effects of climate change on ecosystem processes, provided the spatial and temporal scales of interest are aligned.

The fourth recommendation is to measure putative regulatory factors, both abiotic (e.g. soil nutrient availability) and biotic (e.g. competition among decomposers), to identify whether such factors can explain some of the local variation currently unaccounted for in decomposition studies (e.g. Bradford *et al.* 2014a). Some of this variation may arise from differences in litter chemical and physical properties, including for inputs from the same species, but such effects may not be apparent with the use of common litter types across sites (e.g. Parton *et al.* 2007). Without taking such local-scale measurements the dominance of climate on decomposition becomes an unintentional artefact of the study design; it is fundamentally impossible to identify additional controls if they are never measured.

REVISED STATISTICAL ANALYSES

The latter three characteristics that we recommend for next-generation decomposition studies relate to the analysis of decomposition data (Table 1). Our fifth recommendation is that for continuous data – which includes the majority of both regulatory and response variables in decomposition research – individual data points are displayed and also used in those statistical models applied to explain the observations. Such a recommendation echoes recent calls made broadly in science (Leek & Peng 2015; Weissgerber *et al.* 2015), as well in related ecological fields (Clark 2010), given the potential for data aggregation to lead to incorrect mechanistic inferences and hence inaccurate projections.

Our sixth recommendation is that future multi-site decomposition studies employ advances in statistical modelling that explicitly account for phenomena such as auto-correlation. Indeed, a rationale for the previous focus on site-level means in broad-scale decomposition studies might have been concerns about pseudo-replication. These are ameliorated somewhat if measurements of controls are measured at the same grain as decomposition rates (e.g. at the scale of an individual litterbag), because replicates can then be considered independent. Nevertheless observations within a site will likely remain autocorrelated at least to some extent and, in any one study, this autocorrelation might be attributable to unmeasured controls. This autocorrelation can be handled by a whole variety of common statistical methods (Table 1).

Our seventh and final recommendation is the use of standardized coefficients (Table 1). Most decomposition models involve multiple regression frameworks (e.g. climate and litter quality as controls, Adair *et al.* 2008) but most controls are measured using different unit scales (e.g. °C vs. %N). The relative difference in the magnitude (e.g. slope coefficient) of the effect of one factor vs. another on decomposition can then only be usefully compared once the coefficients have been standardized (e.g. through the calculation of *z*-scores). That is, the relative importance of a factor in regulating decomposition rates is revealed (within a data set) by the standardization. The added advantage is that the influence of interactions between regulatory factors (e.g. litter quality effects might be

stronger under more favourable climate) can also be compared with the influence of the single factors involved in the interaction (Table 1). A much richer understanding of the absolute, relative and interactive effects of different factors regulating decomposition can be obtained using now widely available statistical approaches.

We only describe a subset of statistical approaches and advocate that analytical methodologies go beyond these. For example, comparing summary statistics such as r^2 or standardized coefficients among studies may lead to unproductive debate about which factors most strongly regulate litter decomposition rates. This is because the relative and absolute importance of regulatory variables will be specific to the study, given their dependence on when and where data observations are collected. That is, we expect the regulatory strength of any one factor to change in space and time as its value changes and so also do those of other factors (Prescott 2010). Sensitivity analyses (Frey & Patil 2002; Saltelli & Annoni 2010), for example, offer one option to explore the relative strength of regulatory factors under different contexts. The aim should be exactly this: to understand the influence of a change in a regulatory factor on decomposition rates in light of changing spatial and temporal contexts. Such analyses should move us beyond discussions about variance explained – which our re-analyses highlight can be misleading – to help form conceptual models of regulatory factors on litter decomposition rates that are based on the strength of effects across changing conditions. From a more applied perspective, such models can play an important role in shaping the structure of biogeochemical models and hence projections of how carbon and nutrients flow through decomposer subsystems as the environment changes.

Implications for biogeochemical and Earth system models

Perhaps the most important message of our paper is that aggregating data removes local variation in regulatory and response variables, enhancing the perceived influence of the factor of interest and potentially obscuring the influence of unmeasured factors (Gelman *et al.* 2007; Schmitz 2010; Bradford *et al.* 2014a). Given that in multi-site decomposition studies replicate variation is usually averaged away by mean site-level climate, it then seems unsurprising that the structure of most biogeochemical models is built around temperature and moisture as predominant controls on litter pool turnover rates (Meentemeyer 1978; Tuomi *et al.* 2009; Todd-Brown *et al.* 2014). This commonality of structure then leads to a focus on reducing inter-model differences in decomposition projections by refining existing model parameter estimates (e.g. Arora *et al.* 2013; Exbrayat, Pitman & Abramowitz 2014); instead of asking the broader questions about the necessity to evaluate alternative structures, parameter estimates and regulatory factors (Wieder, Bonan & Allison 2013). Therefore, all modelling exercises rely on the conceptual, as well as mathematical, 'quality' of the data with which they are formulated. A next generation of multi-site litter

decomposition studies that include, at a minimum, the characteristics we suggest (Table 1) would help inform both the parameterization and structuring of biogeochemical models.

Further, analyses of data-rich observations can facilitate robust evaluation of models (Ogle & Barber 2008; Luo *et al.* 2011). For example, the sheer number of environmental scalars that are used to modify decomposition rates among models (Conant *et al.* 2011; Sierra, Müller & Trumbore 2012) illustrates the process-level uncertainty in basic climate-decomposition relationships (Davidson & Janssens 2006). Certainly, there are numerous attempts using empirical data to evaluate the parameterization of individual models (e.g. Ise & Moorcroft 2006; Tuomi *et al.* 2009; Ahrens *et al.* 2014) and competing model structures (Adair *et al.* 2008; Manzoni *et al.* 2012; Moyano, Manzoni & Chenu 2013). However, analyses of well-replicated data sets taken across eco-climatological gradients that capture both within- and among-site variation in carefully selected variables could be used to generate with much more certainty both parameter values and their associated errors (e.g. Keenan *et al.* 2013). More broadly, such an approach – combined with the study designs we propose – should provide a rigorous basis for translating theoretical understanding of environmental regulators of litter decomposition rates to biogeochemical and Earth system models.

A new decomposition paradigm

The classical decomposition triangle (Fig. 1) is based on the idea that climate, litter quality and decomposer organisms are all important regulators of decomposition rate (Swift, Heal & Anderson 1979). The consideration of spatial scale has developed this idea to emphasize climate and secondarily litter quality as predominant broad-scale controls, although the relative dominance of these two factors is under debate. Under both conceptualizations, decomposer organisms are assumed to directly influence decomposition rates only at very local scales (but see Wall *et al.* 2008; Gracia-Palacios *et al.* 2013). Studies testing whether these organisms should be included in biogeochemical models generally seek to explain the residual variation (often ~30%) not captured by climate and litter quality at broad spatial scales (Wall *et al.* 2008). Our re-analysis, however, suggests that this focus on looking for additional regulatory factors that explain the residual variation from mean-level analyses is misguided. That is, these unmeasured factors may account for the *majority* of the variability in decomposition, rather than a small, residual amount. For example, across temperate sites, the variation attributed to unmeasured regulatory factors may account for > 70% of the total variation in decomposition rates when disaggregated data are instead considered (Fig. 3, Bradford *et al.* 2014a). Indeed, there is growing evidence that for soil processes the majority of process-level variation occurs at finer and not broader spatial scales (Keiser, Knoepp & Bradford 2015; Waring *et al.* 2015). There therefore appears to be strong potential to 'discover' overlooked factors that strongly regulate litter decomposition rates by resolving fine-scale variation within the context of broad spatial gradients.

We hypothesize that the approaches we propose will confirm climate and litter quality as important regulators of litter decomposition rates through their influence on decomposer organisms. However, we also suggest that they will identify equally important regulatory factors that remain unrecognized and that the influence of any one factor, even at regional spatial scales, will be strongly context-dependent. We already know that photo-degradation dominates litter decomposition in arid environments (Austin & Vivanco 2006) and, under some regional contexts, climate appears a relatively minor control on biotically mediated decomposition (Bradford *et al.* 2014a). Furthermore, there appears to exist thresholds where the dominant regulator switches from one factor to another (Prescott 2010). The only way to characterize such possibilities, to generate a revised conceptual model of litter decomposition, is to use study designs and analyses (Table 1) that enable a robust evaluation of climate and other factors as dominant controls on decomposition rates.

We can only speculate as to what the additional factors regulating decomposition rates will be but do suggest that arguments about the relative control exerted by climate vs. litter quality on litter decomposition may be pre-mature (Zhang *et al.* 2008; Conant *et al.* 2011). Perhaps instead Tenney & Waksman (1929) were correct, where the appropriate decomposition model also includes soil nitrogen availability. In reality, however, the number and types of regulatory factors may be surprising (e.g. Keiluweit *et al.* 2015) and it is feasible that decomposer microorganisms exert control independent of climate and litter quality (Strickland *et al.* 2009; McGuire & Treseder 2010; Keiser *et al.* 2011; Allison 2012; Allison *et al.* 2013). Accepting that climate and litter quality may not necessarily be the predominant controls at regional scales – and instead are only considered as such because of previous experimental approaches – is the first step towards identifying all of the dominant controls on decomposition rates across space. Once these regulatory factors are known, a new paradigm can be formulated to explain the rates of carbon and nutrient flows through the decomposer sub-system.

Acknowledgements

Data accessibility

Data and associated R code are available from the Dryad Digital Repository (Bradford *et al.* 2015).

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