



# Quantifying microbial control of soil organic matter dynamics at macrosystem scales

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**Abstract** Soil organic matter (SOM) stocks, decomposition and persistence are largely the product of controls that act locally. Yet the controls are shaped and interact at multiple spatiotemporal scales, from which macrosystem patterns in SOM emerge. Theory on SOM turnover recognizes the resulting spatial and temporal conditionality in the effect sizes of controls that play out across macrosystems, and couples them through evolutionary and community assembly processes. For example, climate history shapes plant functional traits, which in turn interact with contemporary climate to influence SOM dynamics. Selection and assembly also shape the functional traits of soil decomposer communities, but it is less clear how in turn these traits influence temporal macrosystem patterns in SOM turnover. Here, we review evidence

that establishes the expectation that selection and assembly should generate decomposer communities across macrosystems that have distinct functional effects on SOM dynamics. Representation of this knowledge in soil biogeochemical models affects the magnitude and direction of projected SOM responses under global change. Yet there is high uncertainty and low confidence in these projections. To address these issues, we make the case that a coordinated set of empirical practices are required which necessitate (1) greater use of statistical approaches in biogeochemistry that are suited to causative inference; (2) long-term, macrosystem-scale, observational and experimental networks to reveal conditionality in effect sizes, and embedded correlation, in controls on SOM turnover; and (3) use of multiple measurement grains to capture local- and macroscale variation in controls and outcomes, to avoid obscuring causative

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understanding through data aggregation. When employed together, along with process-based models to synthesize knowledge and guide further empirical work, we believe these practices will rapidly advance understanding of microbial controls on SOM and improve carbon cycle projections that guide policies on climate adaptation and mitigation.

**Keywords** Forecasting · Functional redundancy · Jensen's Inequality · Logical inference fallacies · Multilevel models · Soil carbon

## Introduction

The response of soil organic matter (SOM) to environmental change has high societal significance, given the importance of SOM for soil fertility and as a global reservoir of carbon (Jobbágy and Jackson 2000; Tarnocai et al. 2009; Bünemann et al. 2018; Oldfield et al. 2019). For example, elevated atmospheric CO<sub>2</sub> and climate warming will be accentuated if they cause net losses in global SOM stocks. Process-based, land-carbon models are commonly used to evaluate the plausibility of such scenarios and model projections range from large SOM losses to gains across the current century (Friedlingstein et al. 2006; Arora et al. 2013; Wieder et al. 2013). Yet all the models are built on the understanding that the emergent pattern of SOM response across broad spatial scales (i.e. macrosystems) is the product of multiple, interdependent controls operating on SOM at local scales (Doetterl et al. 2015; Cotrufo et al. 2019; Wiesmeier et al. 2019; Abramoff et al. 2019). This local scale of action on SOM means that changes in SOM stocks, decomposition and persistence may not themselves be considered macrosystem phenomena. However, the temporal pattern in SOM response across a macrosystem that emerges as controls change arises, in part, from cross-scale interactions among the controls (Delgado-Baquerizo et al. 2017), making the emergent pattern an outcome of macrosystem processes (see Box 1).

We use *cross-scale interactions* to describe how the identity and influence of controls on SOM are interdependent on processes operating at different temporal and/or spatial scales (e.g. Cash et al. 2006; Vervoort et al. 2012). For example, SOM persistence

is controlled by soil variables such as texture and mineralogy, which in turn are influenced by factors such as geology, climate and erosion which vary and operate at multiple different scales (Rasmussen et al. 2018; Berhe et al. 2018; Vaughan et al. 2019; von Fromm et al. 2020). Equally, the relative abundance of plant traits is associated with climate and soil fertility (Shiklomanov et al. 2020; Kuppler et al. 2020; Lancaster and Humphreys 2020), with for example colder and drier environments selecting for species with lower litter qualities (e.g. lower nitrogen content, thicker leaves). The recalcitrant litters of these species interact with climate controls, slowing SOM decomposition rates to a greater extent than would be projected from temperature and moisture conditions alone (Aerts 1997). Spatial and temporal patterns in SOM turnover across macrosystems under changing conditions therefore emerge from biotic and abiotic controls which vary, and also influence one another, at multiple scales (Bonan et al. 2002; Sierra et al. 2011; Pavlick et al. 2013; Poulter et al. 2015; Jian et al. 2018; Ye et al. 2019).

These cross-scale interactions are represented in land carbon models, for example through associations of plant growth forms and strategies with climate (Moorcroft et al. 2001; Reich 2014; Fisher et al. 2015, 2018). The resulting associations between temperature, moisture and the nature of plant inputs (e.g. nitrogen content) reliably estimate spatial macrosystem patterns in SOM processes such as litter decomposition (Parton et al. 1987; Bonan et al. 2013). A challenge now is to translate the understanding of spatial controls on SOM turnover into robust projections of future macrosystem SOM patterns (Bradford et al. 2016b; Lehmann et al. 2020). In addressing this challenge, microorganisms have re-emerged as potential, broad-scale controls on the rates of SOM decomposition, formation and persistence (Tenney and Waksman 1929; Blankinship et al. 2018). Empirical insights into microbial controls have stimulated biogeochemical modeling efforts that query how representation of microbial processes influence projections of global and regional SOM stocks (Wieder et al. 2015, 2018; Lehmann et al. 2020). Model results show that the magnitude and direction of projected carbon cycle feedbacks to atmospheric and climatic change are strongly dependent on how microbes are represented (Tang and Riley 2015; Sulman et al. 2018; Wieder et al. 2019). These results highlight the need to

fill microbial knowledge gaps to build confidence in temporal projections of emergent macrosystem patterns in SOM turnover.

Here, we present perspectives on how empirical research might be designed to productively and efficiently develop knowledge that can be applied to process-based, biogeochemical models, to investigate the role microbes might play in shaping future SOM dynamics across macrosystems. Three general recommendations emerge: (1) the need for much greater uptake of statistical approaches in biogeochemistry that are suited to causative inference focused on quantifying the functional forms and effect sizes of controls; (2) the necessity for multiple empirical approaches to tease out controls from multi-causal, conditional and correlated data (i.e. use of triangulation as an approach), in particular macrosystem-scale, experimental and long-term observational networks; and (3) a shift in thinking within the field from what we consider the ‘mean approach’ to one focused on ‘variance biogeochemistry’. Before discussing these recommended practices, we first present the case as to why we might expect microbes to shape temporal macrosystem patterns in SOM turnover. We then discuss why process-based models might be particularly amenable as a synthesis approach for what we envisage to be an increasing flow of empirical information from implementation of our three recommendations. We anticipate that convergence of the empirical practices, with synthesis via process-based models, will facilitate substantial progress toward an improved understanding of SOM turnover and more confident projection of future macrosystem SOM stocks, distributions and sensitivities under ongoing environmental change.

### Box 1. Terminology

As a relatively new area of enquiry, macrosystem biology includes many terms that are not singularly defined. For example, macrosystems can be considered greater in lateral extent than 1000 km, whereas other definitions refer to them as continental or global scale but not regional. Questions about the meaning of terms are further compounded because macrosystem work draws together many fields and sub-fields, each replete with its own definitions. We recognize the futility of trying to propose a standard set of definitions (i.e. getting scientists to consensus!) and that limiting

plurality of ideas could be counterproductive by constraining how we approach questions. However, for clarity in this paper we use the following definitions for terms.

#### *Biogeochemical understanding*

*Biogeochemical process* A process within elemental cycles whereby there is an enzyme-catalyzed transformation of an element from one molecular form to another, which results in the flow (i.e. flux) of the element between two pools (i.e. stocks). For example, heterotrophic soil respiration, photosynthesis and nitrification are all biogeochemical processes.

*Causation* Knowledge of the identity of a control and, ideally, the magnitude of its conditional effect on the outcome (i.e. response variable; in this paper, outcomes are biogeochemical stocks, forms and process rates). Note that the process of using observational and experimental studies, together with models, to identify and quantify controls falls under the general umbrella of *causative inference*.

*Causative statistical inference* The use of statistical approaches that are suited to robustly identifying the conditional functional form and effect sizes of controlling variables. The approaches are tailored to reveal the effects of controls (as opposed to defining what the cause of an effect is), relative to other controls, and in particular to tease out causation from correlation.

*Conditional* When the effect size of one control is dependent on the value of at least one other control, or if the identity of controls changes in space and/or time, then outcomes and their relationships with controls can be conditional on the spatiotemporal grain and extent of inquiry.

*Effect size* The quantitative influence of a defined change in the value of a control on the size or rate of the response variable. The effect size is most likely conditional on the values of other controls.

#### *Models*

*Confidence* Expert opinion concerning the extent to which well-supported, and often competing, causative understanding is represented within and among process-based models. Confidence in model projections grows with fuller representation of causative

understanding among models, and as poorly-understood causation is refined and then represented.

*Process-based biogeochemical model* Mathematical formalization of causative (i.e. mechanistic) knowledge whereby  $x$  controls  $y$  under condition  $z$ , as opposed to the relationship being correlative (i.e. associational). These models are typically used to evaluate how changes in the values of controls influence the size and turnover rate of elemental stocks and flow rates.

*Projection* Process-based model estimates of future (> 5- and < 100-year) biogeochemical stocks and flux rates, typically based on scenarios of control values that are outside the conditions under which the model was constructed (i.e. extrapolation), such as might be experienced through altered management or global environmental change.

*Structural and parameter assumptions* The manner in which causative understanding of controls and their effect sizes, respectively, are represented within and among models. Exclusion or inclusion of a control is a structural assumption. However, so is the decision to represent the same control (e.g. microbial growth efficiency) in different structural forms (e.g. first- or second-order).

*Structural and parameter uncertainties* The certainty with which understanding of controls and their effect sizes (i.e. parameter estimates), respectively, are known. Parameter uncertainty is reduced with more observations, especially when collected at multiple grains and extents to reveal conditionality in effect size. Structural uncertainty is also reduced through empirical work, but in this instance through work designed to resolve competing or ambiguous causative pathways. Reductions in both parameter and structural uncertainties builds confidence in model projections.

## Scale

*Broad and fine scale* Broad refers to scales of time and space that are of greater extent and grain size. For example, broad scale might refer to an extent of 1000 km<sup>2</sup> measured over 10 years, versus a finer scale extent being an area of 1 m<sup>2</sup> measured for 6 months.

*Cross-scale* Temporal shifts in the values of controls that emerge from interactions between controls and/or biogeochemical outcomes operating at different temporal and/or spatial scales. For example, wetter climates may select for plant traits that are

associated with greater productivity. These traits may be associated with higher evapotranspiration rates (feeding back to climate) and also higher foliar litter leaf quality, which stimulates nutrient cycling, and in turn selects for traits linked to even greater productivity.

*Emergence* A pattern is emergent if the controls and their effect sizes are not identifiable from single-grain observations. Given that temporal macrosystem patterns may be underlain by coupling or uncoupling of abiotic and biotic controls (e.g. functional traits unable to track or adapt to climate change), the future macrosystem might be considered a new entity and hence emergent behavior would be considered 'strong'. The possibility of strong emergent behavior demands that macrosystems be considered as complex adaptive systems, where complexity and adaptability mean that confidence in process-based projection of emergent patterns will only be gleaned through cross-scale consideration of controls.

*Extent and grain* Extent is the temporal or spatial size of the study (e.g. 1000 km<sup>2</sup> or 1 m<sup>2</sup>), whereas grain refers to the resolution of a single observation within that study (e.g. hourly CO<sub>2</sub> concentrations measured in the headspace of a 20-cm dia. soil collar would have a grain of 1 h and 314 cm<sup>2</sup>).

*External validity* How well data reflect what is occurring in the absence of investigator intervention. Observational data typically have high external validity, albeit the process of measurement (e.g. inserting a collar into the soil to measure CO<sub>2</sub> efflux) could decrease external validity by altering the value of the measured process or control. The ability to detect causation from observational data is challenging given correlations and interactions among controls, meaning such data typically have low internal validity.

*Internal validity* How amenable data are for identifying causation. Highly-controlled experiments typically have high internal validity, in that the outcome is known to be a product of the investigator's manipulation of a control. However, given the design of controlled interventions (e.g. step-change experiments for elevated CO<sub>2</sub>) and conditionality in controls, the effect size in controlled experiments generally has low external validity.

*Macrosystem* A system with a spatial extent whereby emergent patterns in properties of the system are controlled by interacting variables operating at scales equal to or beyond, as well as within, the

macrosystem extent. For example, temperate mixed forest on the east coast of the U.S. might be considered a macrosystem from the perspective of the emergent pattern of SOM stocks across the system. Specifically, the emergent pattern in SOM is a product of interacting controls that vary in magnitude across the system, which are influenced by processes operating at scales beyond and within the macrosystem (e.g. mean annual climate and functional traits, respectively). Note that in contrast to the modern definition of ecosystem, the definition of macrosystem is not size independent. Macrosystem definitions offered to date do not appear to unambiguously specify a temporal extent, but given our focus on projection of future SOM dynamics, we consider temporal patterns that emerge at time scales > 5 years beyond the present.

*Multi-scale* We use multi-scale to discuss the need for multiple grains of observation. Different grains of observation can lead to different conclusions about causation. For example, coarser grains average variation within the grain of observation of the control under study, which can markedly influence the estimated effect size of that control (i.e. Jensen's inequality). A similar phenomenon can occur when the effect of the control under study is conditional on the value of another control (i.e. Simpson's Paradox), and here the sign of the effect may even switch.

## Microbial control of macrosystem SOM dynamics

### Scale dependence in microbial controls

Historical environmental regimes (e.g. climate, substrate chemistry, predators) can shape the functional traits represented within decomposer communities, introducing scale dependence in how community metabolism responds to variation in contemporary conditions (Maynard et al. 2019; Lustenhouwer et al. 2020; Geisen et al. 2020). Perhaps best known is that different histories of leaf litter inputs can create functional differences among decomposer communities (Hättenschwiler and Gasser 2005; Ayres et al. 2009; Schimel and Schaeffer 2012; Pioli et al. 2020). Functional differences appear underlain by community differences in traits, including expression of exoenzymes that catalyze SOM decomposition (German et al. 2011). These differences can translate to differences in SOM turnover where, for example,

decomposition rates of contemporary litter inputs are dependent on whether the microbial community has a history of exposure to the litter species (Gholz et al. 2000; Keiser et al. 2014; Veen et al. 2019).

How climate history shapes microbial community effects on SOM dynamics under contemporary climate variation is less well known. Certainly, decomposer communities adapt to long-term changes in climatic regimes (Bárcenas-Moreno et al. 2009; Rinnan et al. 2009; Lennon et al. 2012; Evans and Wallenstein 2014). For example, dominant heterotrophic microbes and extracellular enzymes show local adaptation to temperature history (German et al. 2012; Rousk et al. 2012; Bradford et al. 2019; Dacal et al. 2019). Additionally, microbial communities show compositional shifts due to niche partitioning under changing moisture regimes (Evans et al. 2014), and fungal and bacterial isolates vary markedly in the range of moisture limitation over which they remain active (Lennon et al. 2012). These responses do not simply track short-term changes in moisture but also exhibit a historical legacy with regards to moisture and temperature regimes (Evans and Wallenstein 2012, 2014; Maynard et al. 2019).

Broad differences in how plants respond to contemporary climate arise through past climate as a selective force where, for example, cold and dry regimes select for more stress-tolerant and hence constitutive (i.e. less plastic) phenotypes (Sprugel 1989; Bond 1989). Similarly, these climates select for decomposer fungi that express traits constitutively, constraining their ability to up-regulate activity when compared to decomposers selected under favorable climate conditions (Crowther et al. 2014). The prevailing climate regime is then expected to select for the dominance of organisms that express more constitutive versus inducible (i.e. more plastic) traits, differentiating community physiology (Malik et al. 2020) and hence community response to contemporary climate (Crowther et al. 2019).

Collectively then, both evolutionary theory and empirical data suggest that microbial communities adapt to historical climate and plant-litter regimes, which may influence emergent macrosystem patterns in SOM (Buzzard et al. 2019; Malik et al. 2020; Anthony et al. 2020). However, macrosystem-scale observations of SOM dynamics, such as multi-site litter decomposition experiments, tend to find that variation in outcomes is adequately explained by

climate and litter trait controls (Aerts 1997; Cornwell et al. 2008; Currie et al. 2010; Bradford et al. 2016a). One possible explanation for these findings is that microbial community effects are obscured by among-site relationships between SOM dynamics and climate and litter controls (Bradford et al. 2017; Wilson and Gerber 2020). Such embedded causation can lead to conclusions that there are common local and macrosystem relationships between microbes and SOM processes (Fig. 1). Indeed, for plants there is evidence that functional community differences can be obscured by correlations with variation in abiotic controls (Rudgers et al. 2018). For example, Lauenroth and Sala (1992) found that regional-spatial patterns between precipitation and plant productivity did not match with long-term (50-year), temporal patterns. They found that productivity responses to high rainfall years were muted at their dry site when compared to productivity at the wetter end of the climate gradient. The inability of the spatial relationship observed among sites, to explain the temporal pattern observed within a site, was attributed to the constitutive phenotypes of the dry-adapted plants. If functional differences in microbial communities are similarly embedded within climate gradients, emergent macrosystem patterns under a changing climate may differ for those projected under assumptions of scale-invariant versus -dependent microbial community functioning (Fig. 1).

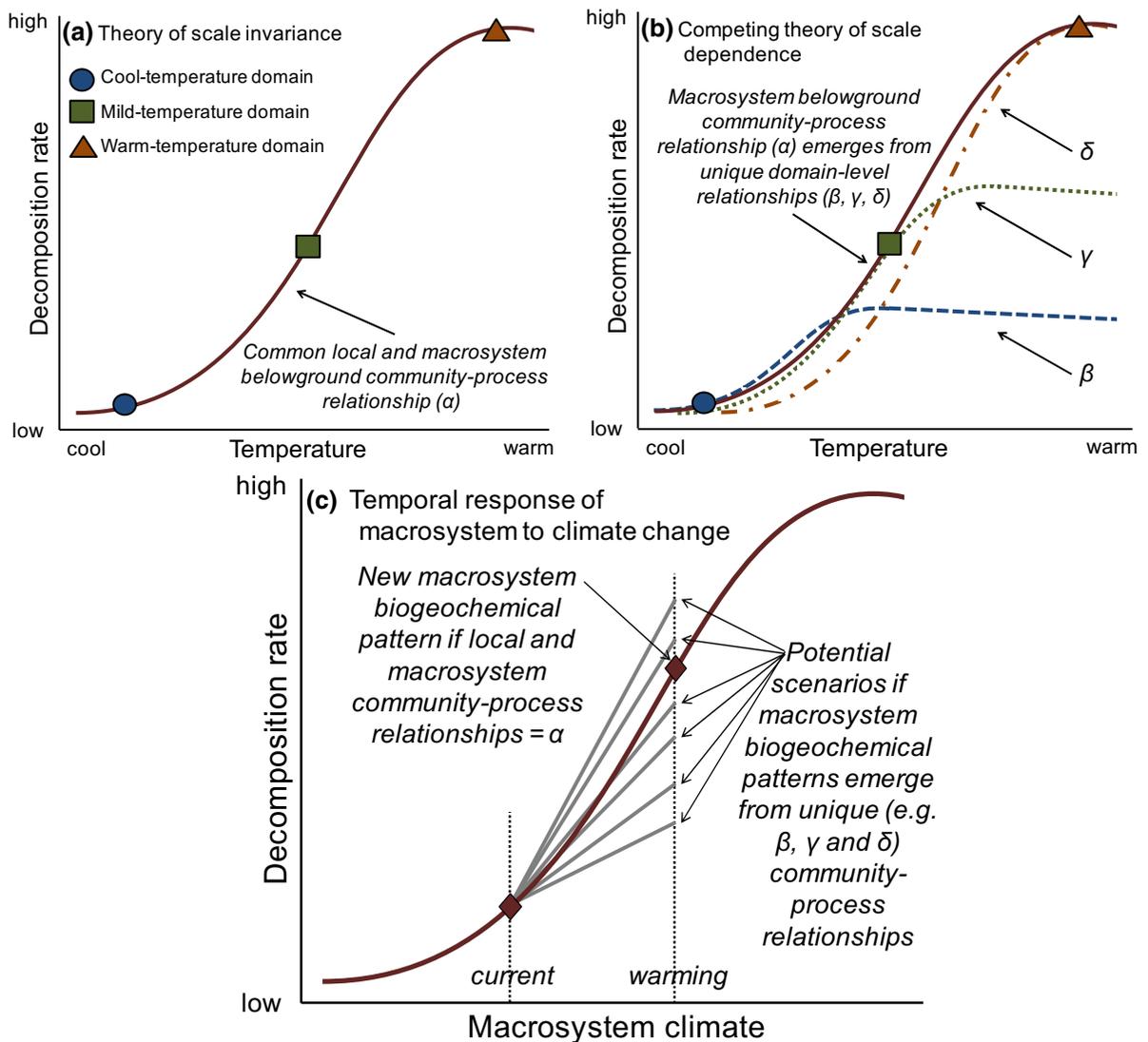
In support of the idea that climate history differentiates microbial community function with respect to SOM dynamics, Averill et al. (2016) reported that the prevailing climate shaped the moisture response of soil extracellular enzyme potentials across a precipitation gradient in Texas, USA. Contrary to expectations of drier sites having more constitutive traits, drier sites had higher maximum potential rates. Nevertheless, these data highlight that climate history can generate spatially-dependent patterns in the functional abilities of microbial communities. Strickland et al. (2015) examined how such histories influenced the abilities of soil communities, from boreal, temperate and tropical sites, to mineralize a standard litter substrate. Using a factorial lab experiment with four incubation temperatures (15 to 30 °C) and five moisture levels (ranging from drier to optimum to wetter), they found that the tropical community had the highest rates of carbon mineralization under moist and warm conditions but those rates also declined the

most when the imposed conditions were sub-optimal. As a result, the constitutive functioning of the boreal community led to the greatest mineralization rates under cold and dry conditions, with functioning of the temperate community intermediate. The spatially-dependent functional differences among the microbial communities were consistent with expected trade-offs in microbial growth strategies under different climate regimes.

Selection therefore appears to generate conditionality in how microbial decomposer communities interact with climate and litter substrate controls on SOM dynamics (Evans and Wallenstein 2012; Glassman et al. 2018; Lustenhouwer et al. 2020). We note that we define ‘selection’ following Hochachka and Somero (2002) to include extant variation in traits that are acted upon by contemporary abiotic and biotic variables to influence community assembly (sensu Kraft et al. 2015). When conditionality is pronounced, temporal macrosystem patterns will likely be influenced by how microbial communities track shifts in plant traits and climate. The extent to which communities track climate and thereby modify direct effects of climate is a pressing unanswered question in biogeochemistry (Koven 2013). Yet limited dispersal and niche conservatism in at least some microbial communities (Peay et al. 2012) raises the possibility that disturbances, such as climate change, may decouple contemporary controls and result in novel macrosystem patterns (Fig. 1c). There is theoretical and empirical support for macrosystem patterns emerging from such interactions between broad-scale drivers and fine-scale processes (Peters et al. 2007; Heffernan et al. 2014). To validate this expectation for microbes and SOM turnover, in Fig. 2 we present a hypothetical scenario whereby microbial and climate controls are uncoupled. The scenario shows the potential dependency of emergent temporal patterns in SOM dynamics to assumptions of scale-invariant versus -dependent microbial community functioning.

#### Microbial representation in models

Process-level understanding in widely-applied, soil models (e.g. DAYCENT, RothC) reflects dominant theory about controls on the activities of decomposer communities and their influence on SOM dynamics. The theory conforms to ideas of scale invariance in microbial effects. It is assumed that SOM



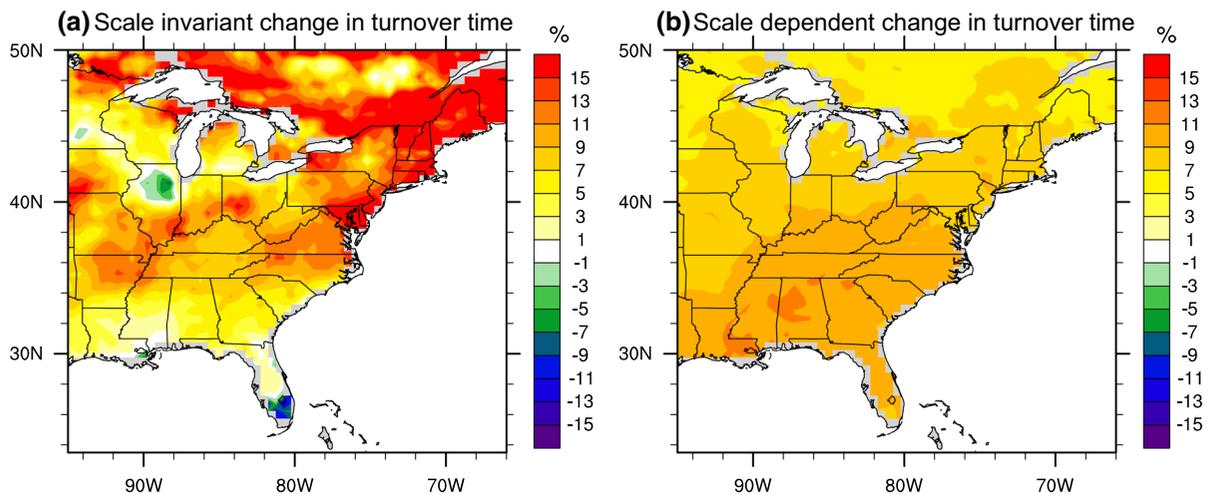
**Fig. 1** Ecosystem theory holds that macro-system-scale controls on many soil organic matter processes, such as litter decomposition, operate in the context of common decomposer community functional relationships across space. This assumption of scale invariance means that broad-scale patterns in control-process relationships are representative of how controls operate at local scales (a). Among-site relationships in decomposer community function (a) should then be able to estimate temporal

responses of the macro-system (c). If the pattern instead emerges from finer-scale relationships (b), illustrated here as unique domain (or sub-macro-system) level relationships, then macro-system behavior will be emergent and only understood by examining how natural selection influences the functional traits represented in a community. Differences in functional traits across communities can then introduce scale-dependence in community effects

decomposition, formation and heterotrophic respiration are primarily mediated—but not regulated—by microbes (Jenkinson and Rayner 1977; Parton et al. 1987; Bradford et al. 2016b; Blankinship et al. 2018). Reflecting this theory, microbes are implicitly represented through first-order decay dynamics (Todd-Brown et al. 2012). For projecting macro-system SOM

patterns, the prevailing assumption is then that microbial community effects are non-conditional in space and time, with microbial activity dictated by climate and other proximate controls similarly at local and macro-system scales (Bonan et al. 2013).

The assumption of a common microbial influence across the macro-system is based on empirical



**Fig. 2** Macrosystem implications of scale invariance **a** versus scale dependence **b** on the change in a representative soil organic matter process, litter turnover time (% change). Under a business-as-usual scenario, temperatures across the eastern U.S. are projected to increase 3–5 °C by the end of the century, but these regional-scale projections in changes to the physical climate show sub-regional variation that acts locally. Thus, macrosystem-scale biogeochemical projections that use a scale-invariant approach in the biotic response **a** result in spatially heterogeneous changes in litter turnover time (for a fixed litter quality), that are solely driven by spatial variation in the physical climate system. If, however, one applies a scale-dependent approach **b** variability in the decomposer community response will change (and in this case dampen) the magnitude of

macrosystem variation in projected turnover times. Note that these plots are a spatial extension of the hypotheses presented in Fig. 1, where in **a** we model the assumption of scale invariance through a linear response to changes in local climate conditions. As such, the largest changes in litter turnover occur in regions where warming alleviates—to a certain extent—cold conditions that are less favorable for decomposition (e.g. NE United States and SE Canada). By contrast, in **b** we can constrain the response for the same regions to represent scale dependence arising from historical climate legacies that limit the phenotypic plasticity of local microbial communities. Consequently, the largest changes in litter turnover occur in regions with historically more favorable climate conditions (e.g. SE United States)

evidence of functional equivalence (or redundancy) among soil decomposer communities (Allison and Martiny 2008). Equivalence is reasoned to occur because of high phylogenetic diversity in these communities, rapid population turnover, functional convergence, and/or global dispersal kernels (Martiny et al. 2006; Talbot et al. 2014). There is now abundant data suggesting instead that decomposer microorganisms can be dispersal limited, show niche conservatism and adaptation to local conditions (Cline and Zak 2014; Talbot et al. 2014; Morrissey et al. 2019). Furthermore, examples of functionally distinct decomposer communities, arising through differences in traits and organismal interactions, are accumulating in the literature (Crowther et al. 2015; Albright et al. 2020; Fitch et al. 2020; Domeignoz-Horta et al. 2020). Given conditionality in the identity and effect sizes of controls on SOM dynamics across macrosystems, it should perhaps be unsurprising that there are empirical data consistent with functional equivalence under some conditions and with functional differences in

others. Notably, SOM dynamics emerge from the specific ecosystem context (Schmidt et al. 2011; Neal et al. 2020), necessitating that we accept conditionality as true. Consequently, questions as to whether or not to represent microbes as functionally equivalent or distinct become obsolete. Instead, we should ask where, when and how functional microbial differences must be represented if we are to build confidence in the accuracy of our projections of future macrosystem patterns.

Accurate model projections are not dependent on representation of all controls within a system (Xie et al. 2020). Models of intermediate complexity often yield the most accurate projections of system behavior under disturbance (Clark et al. 2020). Hence accurate projections are achievable with incomplete understanding and/or omission of some known mechanisms. Yet for temporal macrosystem projections relevant to how carbon cycle-climate feedbacks will play out under a novel set of conditions over the next 30 years, model accuracy can only be evaluated against

empirical data after the change has taken place. With the future unknown, confidence in projections of process-based models is premised instead on a number of criteria, with one of the most influential being representation of the breadth of well-supported, causative understanding (i.e. structural uncertainties, Knutti and Sedláček 2013; Baumberger et al. 2017).

To be inclusive of structural uncertainties, a model-ensemble approach is needed where microbes must be represented in competing models, or different versions of the same model, as functionally equivalent versus distinct. Such modeling work is underway. For example, comparisons of microbial-implicit and -explicit representations of microbial-SOM relationships reveal the sensitivity of projected macrosystem SOM patterns to structural assumptions about microbial control (Buchkowski et al. 2017; Sulman et al. 2018; Zhang et al. 2020). Wieder et al. (2019) showed that a microbial-implicit model based on assumptions of microbial density-independence and functional equivalence projected slight increases in arctic SOM under simulated global change, whereas two microbial-explicit models projected modest to substantive losses of arctic SOM. Both microbial-explicit models represented SOM outcomes as microbial density-dependent, yet they still led to divergent projections, highlighting the need to better understand microbial controls to decrease projection uncertainty.

#### Synthesis through process-based models

We suggest that a focus on building confidence in macrosystem projections, by investigating the sensitivity of emergent patterns to scale dependency in microbial community functioning, identifies process-based models as an important approach for synthesis to advance causative understanding. Model comparisons help to clarify assumptions and, thus, can be used to examine how differing hypotheses about microbial controls influence macrosystem SOM dynamics. Even when considering only a single physiological variable, such work reveals that model projections are sensitive to how microbes are represented (Rousk et al. 2012; Ye et al. 2019). By focusing on the structural and parameter assumptions to which ensemble-model projections are most sensitive, we suggest that synthesis using process-based models will be an efficient approach to identifying uncertainties that can be addressed through empirical research to

advance causal understanding that builds confidence in model projections. Put another way, when poorly-constrained or -understood microbial information minimally affects SOM projections (Buchkowski et al. 2017), models can be simplified and empirical research directed toward improved estimation of other parameters (Transtrum et al. 2015).

Process-based, soil biogeochemical models are therefore a powerful synthesis approach because they can be used to represent our best and competing understanding of microbial influences on SOM dynamics, and to guide empirical research toward addressing microbial-knowledge gaps that generate the most projection uncertainty. Yet there appears to have been little consideration for how to optimize empirical research to generate this microbial information. In the next section we discuss three general practices that, when employed together, we expect to expediently advance knowledge of microbial controls on temporal SOM dynamics at macrosystem scales.

### Empirical needs to advance microbial knowledge

#### Causative statistical inference

To inform process-based models for projection of macrosystem SOM patterns, statistical approaches for analyzing observational and experimental data must be tailored to quantify conditional functional forms and effect sizes of controlling variables. Note that we distinguish ‘causal inference’ from ‘causative statistical inference’, where the latter is focused on teasing out from datasets correlation versus causation, and specifically on quantifying the effects of causes relative to other causes (*sensu* Holland 1986, see Box 1). Yet much of the analysis in biogeochemistry is grounded in approaches that emphasize statistical significance and minimizing unexplained variation (e.g. maximizing  $r^2$  values). This philosophy of approach has been advanced recently through development of machine-learning and automated model-selection approaches based on metrics such as AIC, that identify the so-called best model(s). Yet ‘best’ does not relate to causative inference, but rather to reproducing the outcome (Burnham and Anderson 2004). These approaches, in their purist form, are anathema to causative statistical inference (Wadoux et al. 2020; Tredennick et al. 2021). Their focus is on

predicting the outcome most accurately under current conditions (i.e. statistical interpolation), rather than on elucidating the true form and effects sizes of controls (e.g. Clark et al. 2020). The latter information is needed to inform assumptions of process-based models that focus on extrapolation of knowledge to project outcomes under novel future conditions.

Causative statistical inferential approaches focus on identifying relative and absolute effect sizes, and forms of relationships (e.g. parabolic or sigmoidal), between a causative predictor (i.e. control) and the outcome variable (Holland 1986; Manski 2008). The approaches might entail comparing multiple statistical model structures to test how robust the coefficient estimate is for a control (e.g. temperature), when different assumptions are made about which other controls and their potential interactions to include (e.g. soil moisture availability). For example, if the coefficient size is robust across structures as  $r^2$  deviates, then there is greater credibility that the conditional effect size of the control has been accurately quantified (Oster 2019). Notably, with this approach concerns about whether statistical significance and/or a high  $r^2$  has been achieved because of such things as overfitting are minimized. Instead, the focus is on the robustness of the form and size of the estimated coefficient for the control of interest, and much less so on the values of metrics such as AIC,  $P$  values and  $r^2$ .

Causative statistical inference, however, is not a panacea. Numerous challenges are inherent with analyzing field data in this way, such as whether important controls have been omitted, and whether the estimated coefficient for one control is independent of correlated controls (Laubmeier et al. 2020). An overarching challenge is that model results are dependent on the assumptions made by the investigator about how the included variables relate to each other. This fact requires the investigator to explore the sensitivity of the model results to the assumptions made (as described in the previous paragraph). Nevertheless, the risks of model misspecification are magnified as models become more complex and contain more parameters, as we might expect when attempting to understand microbial effects on macrosystem SOM patterns. Prior knowledge of the system is then essential for informing measurements, analysis and interpretation (e.g. Ferraro et al. 2019). Further, because our knowledge is incomplete, ‘big data’ in macrosystem science will be valuable for

filling data gaps related to how the influence of microbial controls are conditional on the values of other controls that vary across space and time. When used judiciously (Shiffrin 2016), machine-learning can aid with the screening of hundreds of predictors to help identify controls hitherto not considered or quantified because of incomplete information on the myriad controls on SOM turnover, which likely change with the scale of analysis (Keiser et al. 2016; Waring et al. 2016).

Moving forward, we should employ a suite of statistical approaches to elucidate the mechanisms underlying macrosystem patterns, by leveraging the benefits of one approach to help address the challenges of another (Laubmeier et al. 2020). For example, the use of spatial cross-validation and out-of-fit verification (rather than in-fit  $r^2$ ), which are commonplace in machine learning to assess model fit and improve predictive power, could likewise be generally adopted in causal statistical inference. Nevertheless, we suggest that there should be greater awareness of the mismatch between common, increasingly-used approaches such as machine-learning and model selection, and the development of causative understanding (see Ferraro et al. 2019; Tredennick et al. 2021). There is a plethora of papers published in biogeochemistry and related fields each year within which identification of causation from observational and experimental data is falsely equated with significant  $P$ , high in-fit  $r^2$ , and low AIC values (Mac Nally et al. 2018). The results of many of these studies are contextualized in terms of informing process-based models without recognition that the basis of the statistical approaches used is incongruent with this aim. Without greater awareness, reasonable criticisms of approaches such as hierarchical mixed models, which are suited to causative statistical inference with multi-scale data (Soranno et al. 2014; Wagner et al. 2016; Dixon Hamil et al. 2016), result in naïve recommendations that they be replaced with ANOVA designs given ease of specification and hence likelihood of determining accurate  $P$  values (e.g. as in Arnqvist 2020). Instead, when the goal is to generate knowledge to improve the ability to project temporal changes in emergent macrosystem patterns, the biogeochemistries need to move wholesale into the ‘post  $P < 0.05$  era’ deemed essential for good practice in causative statistical inference (Wasserstein et al. 2019).

## Triangulation of study approaches

An increase in the use of causative statistical inferential approaches will be effective only when partnered with study designs tailored to identify controls *and* their conditional effect sizes. This combined approach can then meet both structural and parameterization needs of process-based models. That is, there is a requirement to identify controls and the size of their effects under different conditions. Meeting these twin objectives to advance macrosystem biogeochemical knowledge will require multiple empirical approaches, where the advantages of different approaches can be used to compensate, to a certain extent, for the caveats of another approach. This assertion runs counter to recent calls in microbial ecology (e.g. Prosser 2020) for a renewed focus on the ‘basic scientific method’. We suggest that narrow adoption of only the deductive approach is poorly suited to advancing knowledge of how microbes influence emergent patterns in SOM. Instead, we see the need for ‘triangulation’ (Munafò and Davey Smith 2018), a philosophy of practice that argues for the necessity of multiple approaches to tease out causation from complex, environmental data where there is a plethora of correlated, putative controls.

The challenge of identifying causation is further complicated in macrosystem biogeochemistry by the conditionality in space and time of the effect sizes of any one control. Long-term, observational networks that span variation within the macrosystem, and which take common measurements for multiple variables, can help to quantify how effect sizes change as context changes (Soranno et al. 2019). These needs are being met, for example, through the continental spatial scale and 30-year extent of the National Ecological Observatory Network (NEON). Those data being generated capture spatial and temporal macrosystem patterns in biogeochemical processes, stocks and their controls. The temporal extent required to generate a robust understanding of controls is, however, an open question. Time-series analyses suggest multiple decades of data as a potential minimum for explaining population transitions to new states (Bestelmeyer et al. 2011). If similar timescales apply for understanding SOM turnover, the fact the first data were available across the 47 NEON terrestrial sites between 2016 and 2018 means the utility of these data for evaluating temporal macrosystem projections may not be fully

realized for > 20 years. Whether true or not, long-term, observational networked data have high external validity, in that they document ‘true’ emergent macrosystem patterns (Naeem 2001; Bradford and Reynolds 2006). Hence, they provide those data required to evaluate how model structural and parameter assumptions, as well as projections, match with observations.

The correlated and conditional nature of such observational data mean that they have low internal validity. That is, the investigator has low confidence that the controls and their effect sizes can be identified unambiguously (Naeem 2001; Bradford and Reynolds 2006). Experiments across the same networks are therefore essential for teasing out causation and can generate information in the nearer-term, across multiple contexts, that can be used to develop and refine biogeochemical models ahead of the availability of longer-term data (Bestelmeyer et al. 2011; Jian et al. 2020). ‘Context-awareness’ has been employed in applied ecosystem science for many decades (Ziliak 2019) and continues today with experimental networks (e.g. Keuskamp et al. 2013; Hodapp et al. 2018). The need for networked experiments is amplified for understanding how microbes influence macrosystem biogeochemical patterns given the embeddedness of microbial functional effects within known controls. For example, as in Fig. 1, spatial effects of climate on decomposition may conflate direct effects on organism metabolic rates with indirect effects that operate via selection for microbial traits. Controlled lab and field experiments can identify such embedded causation (e.g. Glassman et al. 2018; Hawkes et al. 2020).

Controlled experiments have been effective for revealing functional differences among microbial communities, yet relatively little attention has been paid to quantifying conditional sizes of microbial effects. These parameter estimates are required for use in process-based models to query the magnitude of microbial influence on emergent macrosystem patterns. To robustly quantify effect sizes, we need experiments that vary multiple controls, even if we are interested in a singular control. For example, Milcu et al. (2018) in a multi-lab comparison of microcosms across Europe found that the effect of the control of interest was more reproducible across labs when variation was introduced in non-target controls. The investigators concluded that deliberate introduction of controlled variation in non-target controls decreased

the likelihood that responses to the control of interest were influenced by unaccounted lab-specific factors. Introducing controlled variation ‘swamped out’ effects of uncontrolled variation, making the effect of the control of interest more similar among labs. We see the need to build on this approach, which relied on significance tests and commonality in the grand mean of the control of interest across labs. Instead, given conditionality in the identity and effect sizes of controls, we see regression designs as more relevant where the conditional effect size of the control of interest (e.g. microbial community composition) is determined at multiple, experimentally-imposed levels of other controls (e.g. moisture and mineralogy). These designs are more labor-intensive but will yield more robust microbial effect sizes.

Networked experiments can avail of these insights by varying non-target controls in a manner that reflects their observed variability in each sub-macrosystem context (Smith and Peay 2020). In designing such networks, a challenge will be to identify the scales at which controls change across space and time (Mouquet et al. 2015). For example, Keiser et al. (2016) showed that controls on soil nitrification rates across multiple sub-watersheds depended on forest disturbance history. When plots across all sub-watersheds were considered, two controls emerged as important. However, their effect sizes changed and additional controls emerged when only disturbed or only undisturbed watersheds were considered. Historical contingencies may therefore generate pronounced conditionality in controls on soil biogeochemical processes even at spatial scales of a few kilometers. Such results highlight the need for multi-scale research, where study extent is systematically varied, to test the robustness of structural and parameter assumptions to the scale of inquiry. When the generated information is strongly scale sensitive, as in the Keiser et al. (2016) example, the results further highlight the need to consider how the scale of inference relates to the desired scale of projection.

With process-based models as a synthesis tool, structural and parameter knowledge from controlled experiments can be represented and tested against networked, multi-scale, measurements. Potentially, longer-term data may reveal an uncoupling of embedded microbial effects from other controls (Fig. 1), but such possibilities will depend on how closely microbial community function tracks correlated controls

such as climate. Nevertheless, by representing microbes as controls within models, we can evaluate potential consequences of such uncoupling on SOM turnover at macrosystem scales. Relatively recent computational advances mean that integration of these multiple data streams with models can be direct. For example, instead of using parameter estimates informed by data, parameters can be directly estimated for differential-equation models in a manner that permits comparison of models with different structures (Hoffman and Gelman 2014; Betancourt 2018). Hence, it is feasible to directly compare model structures and resulting parameter estimates that represent assumptions of scale-invariant versus -dependent microbial control, as well as the possibility that both assumptions hold true within different sub-macrosystem contexts. To avail of these computational advances, models need to be developed that have stocks and processes that empiricists can directly measure (but see Waring et al. 2020). This development has begun (Abramoff et al. 2018) and demands from empiricists multi-scale, data streams from networked observations and experiments to both inform model assumptions and evaluate projections.

#### Variance biogeochemistry

Although we have been using multi-scale to refer to the need to evaluate how spatial and temporal extent influences conclusions about controls and their effect sizes, there is also a need to consider how the grain (i.e. the spatial or temporal resolution of a single observation) of measurement or analysis affects our understanding of macrosystem biogeochemical patterns. Firstly, microbes respond to their local environment and evidence is accumulating that there is high, local-scale variation (e.g. sub-meter to tens of meters) in the identity and magnitude of controls on soil biogeochemical processes (Waring et al. 2016; Bradford et al. 2017; Faber et al. 2018; Nunan et al. 2020). Further, temporal changes in macroclimate can be uncoupled from changes in microclimate (Lembrechts and Lenoir 2020; Zellweger et al. 2020), meaning that our understanding of changing controls can be strongly dependent on the grain at which they are measured. Secondly, structural and parameter assumptions can depend on the spatial and temporal grain at which SOM stocks, fluxes and their controls are measured (Ruel and Ayres 1999; Bradford et al. 2014; Adhikari

et al. 2020). Thirdly, although issues with use of aggregated data have been appreciated in ecosystem ecology for years (Rastetter et al. 1992; Luo et al. 2013), much of biogeochemical understanding is still derived from the analysis of site-mean data (Tomczyk et al. 2020; Wilson and Gerber 2020). For example, regression analyses of climatic and litter controls on SOM process rates from continental networks typically use site-mean data for both controls and response variables (Aerts 1997; Cornwell et al. 2008; Currie et al. 2010). The use of means collapses variation and increases  $r^2$  values (Bradford et al. 2016a; Adhikari et al. 2020), which leads to false confidence in the inferred causative relationships. More importantly, measurements of variables at a single, aggregated grain can lead to false inferences about the identity and effects sizes of controls (e.g. Schmitz 2010; Meyer et al. 2010).

We see the need for a shift in the field from a focus on the mean toward a practice that we refer to as ‘variance biogeochemistry’. Such a shift would be consistent with shifts in related fields, such as community ecology, where false inferences have driven research that eschews species-level means for local-level, individual data (Clark 2010; Bolnick et al. 2011; Urban et al. 2012). That structural and parameter inferences about the drivers of system change can be dependent on the grain of observation and analysis is not surprising. There are numerous mathematical explanations for why relationships between mean values (i.e. group averages) of two variables may obscure or misrepresent true relationships. These explanations are often referred to as the ‘ecological inference fallacy’. Some of the best-known underlying instances of this fallacy are Jensen’s Inequality and Simpson’s Paradox, which show respectively that environmental variance and interacting factors can shape patterns and processes in nature that are independent of average conditions (Ruel and Ayres 1999; Denny 2017).

For example, Jensen’s Inequality shows that variance in the X variable for an accelerating or decelerating function, can lead to average results of the function that differ from the results inferred from the underlying X–Y relationship. That is, the average of a function is not necessarily the same as the function of the average. We can then expect that moisture control on SOM decomposition rates, for instance, may not be accurately captured by correlations of site means

given that moisture tends to have high within-site variability. Work to inform soil sensor designs at the NEON sites across the U.S. showed that variation in soil moisture within a site was high, with  $\sim 100$  spatial points required at most sites to provide a reasonable estimate of the site mean (Loescher et al. 2014). At any one point within a site, then, moisture is likely to differ markedly from the site mean.

To test whether such high within-site variation in well-established controls on SOM dynamics might change inferences from among-site means, Bradford et al. (2017) ran a climate gradient study looking at early-stage decomposition of two grass litters at six sites. Litterbags were arrayed across transects to capture within-site heterogeneity in microenvironmental conditions, which were measured for each litterbag. They analyzed decomposition rates using site-mean versus plot-level data on putative controls. Consistent with the NEON results, moisture varied markedly within each site and hence site means were a poor surrogate for plot-level moisture conditions. In turn, the moisture–decomposition relationship was strongly scale-dependent: there was a pronounced moisture–decomposition relationship for the plot-level data but a weak group-level relationship estimated from the site-means. Such observations show that patterns emerging from among-site comparisons of controls, when expressed as site means, can fail to represent the true control-SOM relationship. Similarly, Ruel and Ayres (1999) showed how conclusions about the response of respiration to temperature can deviate increasingly from the true value as variation in temperature around the mean value increases. The grain of observation (or analysis) therefore has the potential to strongly influence conclusions about the causative relationships operating between microbes and other controls on SOM dynamics.

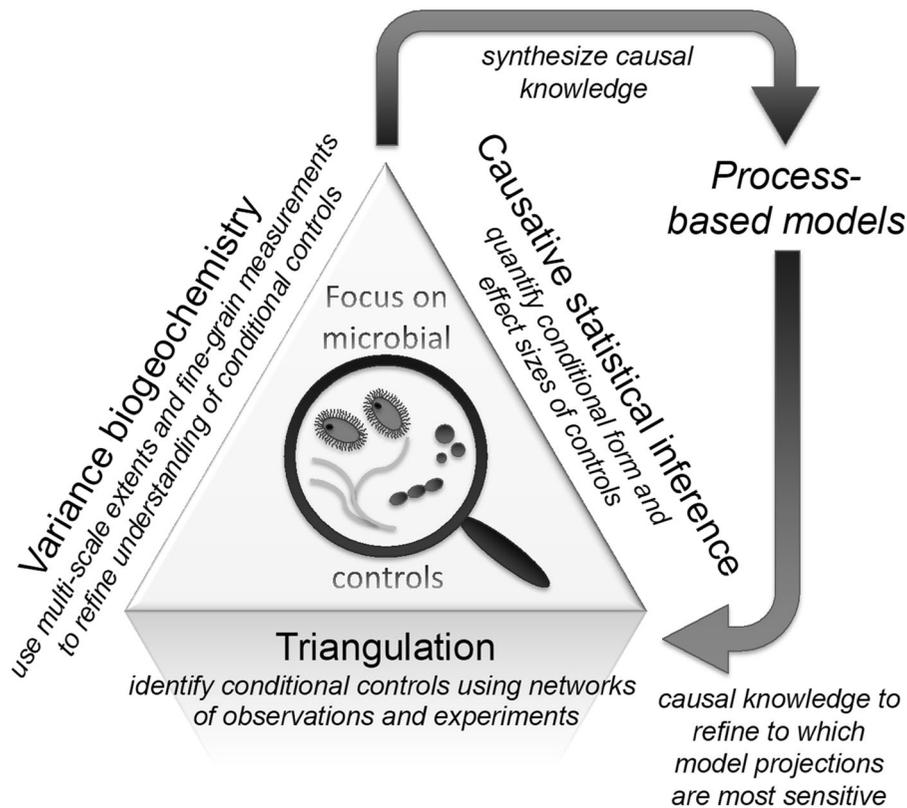
In particular, if the traits of soil microbial communities are shaped by the environmental regime, then collecting fine-scale data to accurately capture variation in environmental conditions is necessary to expand interpretation beyond emergent, coarser-scale relationships that can obscure or alter mechanistic interpretations (Robinson 1950; Levin 1992; Gelman et al. 2007; Firn et al. 2019; but see McGill 2019). Similar challenges related to grain of observation equally apply to the analysis of microbial communities themselves (Naylor et al. 2020). For example, future macrosystem SOM dynamics are likely to emerge

from shifting trait abundances and interactions within microbial communities (Fukami 2015; Maynard et al. 2017; Smith and Peay 2020), so traits alone are unlikely to capture all the necessary attributes of communities that influence ecosystem stocks and processes (van der Plas et al. 2020). Further, the extent to which niche breadth, trait variation and dispersal influence the persistence of functional legacies within microbial communities is largely unknown (Baym et al. 2016; Maynard et al. 2019; Sorensen and Shade 2020). Yet evidence is accumulating that the legacies persist under altered climate regimes for at least several years (Hawkes et al. 2020). Collectively, it seems reasonable to conclude that use of community-mean trait values is likely to obscure our ability to explain spatial patterns in the functional capabilities of microbial communities and how they will shift temporally (Dickie et al. 2012; Wright and Sutton-Grier 2012; Funk et al. 2017).

Reconsideration of how observational grain shapes our causative understanding of SOM dynamics also has implications for how we synthesize those data arising from biogeochemical studies. In this paper we suggest synthesis via process-based, biogeochemical models. We do this in part because of the pitfalls inherent to the ever-increasing adoption of formal meta-analyses for synthesis. Formal meta-analyses in biogeochemistry (and most fields) analyze the mean effect sizes of controls, making their causative interpretation vulnerable to inference fallacies arising from phenomena such as Jensen's Inequality and Simpson's Paradox. Even the emerging use of meta-regression does nothing to circumvent these data aggregation issues (Deeks et al. 2020; Spake et al. 2020). Meta-analysis is therefore a questionable choice for causative statistical inference aimed at developing structural and parameter knowledge that can then be used to inform process-based models used for temporal macrosystem projections. Worryingly, then, there has been a move toward adoption of standards (e.g. PRISMA by the PLoS family of journals, Moher 2009), intended for meta-analysis of randomized, controlled-trial, mean data, as the required reporting guidelines for all meta-analyses. We suggest that the definition of meta-analysis should be broader, as a synthesis of individual observations from multiple studies, with means used for supplemental analyses to investigate scale-dependent outcomes (see Spake et al. 2020). An expanded definition is feasible given the

trend to deposit individual data in open-access repositories when work is published. Far too many authors are still failing to deposit their data, and one consequence of this failure is the continued reliance on synthesis of aggregated data and the potentially fallacious understanding its analysis yields.

Regardless of the historical reasons as to why 'mean biogeochemistry' is so pervasive in SOM science, theory on inference and mathematical proofs rigorously support the expectation that data aggregation can change the identity, effect size and even the sign of controls. The establishment of macroscale ecological networks will help redress data limitations for macrosystem science (e.g. Soranno et al. 2014; Fei et al. 2016). When coupled with advances in micro-instrumentation, -omic technologies, integration of remote sensing with field samples, and data science (e.g. Isaac et al. 2020; Kearney et al. 2020; Naylor et al. 2020; Chadwick et al. 2020), they present an opportunity to examine the influence of 'data-grain' on our understanding of microbial effects on emergent macrosystem patterns. There will not be a single, correct grain (Rose et al. 2017; Wutzler et al. 2020). At the same time, we recognize that the simple action of taking a soil core aggregates many microenvironments, meaning that from a practical perspective we commonly start with aggregated data. We are not therefore suggesting that every microenvironment be isolated, but instead simply that more attention be paid to asking when, for example, consolidating soil cores might alter our interpretation of causative variables. Further, we recognize that reductionist, fine-grained measurements may fail to adequately explain emergent macroscale patterns (Blankinship et al. 2018; McGill 2019), highlighting the need for a combination of approaches to unravel the complexity by which microbial processes affect SOM dynamics at this scale. Relatedly, if reliable projection is the end goal, we need to ascertain the extent to which data can be aggregated, while retaining the same causative interpretation, if heterogeneity and complexity are to be represented in process-based models (Fisher and Koven 2020). Yet we believe that increasing scale-awareness in biogeochemistry will pave the way for variance biogeochemistry as an effective practice that will help to quantify microbial controls on emergent patterns of SOM dynamics at macrosystem scales.



**Fig. 3** A suggested set of four overarching research practices necessary to advance and refine causal understanding of how microbial controls influence macrosystem patterns in soil organic matter dynamics. Integration of the practices is argued to be necessary to robustly identify and quantify microbial community controls. Each side of the triangle represents one broad empirical practice, with the arrow emerging from the triangle illustrating how process-based models can be used to synthesize knowledge gained from the three empirical practices. The use of process-based models for synthesis is intended to

formalize causative understanding generated by the empirical work and to identify knowledge gaps (by generating competing hypotheses) to which macrosystem projections are most sensitive, thereby guiding further empirical research (depicted by the arrow returning from models to the empirical triangle). We suggest that such a coordinated set of practices is required to rapidly and effectively build confidence in future macrosystem projections of SOM dynamics relevant to adapting to and mitigating major environmental issues, such as carbon cycle-climate feedbacks and soil degradation

## Conclusions

Ecosystem biogeochemical models that operate at only one scale of integration are unlikely to incorporate mechanisms properly (Agren et al. 1991). Yet structural and parameter assumptions in models are commonly based on empirical work conducted and/or analyzed at a single, aggregated scale. We present evidence that the predominance of ‘mean biogeochemistry’ obfuscates causative understanding. For microbial controls on emergent SOM dynamics, it likely falsely reinforces the assumption of spatial invariance and hence of functional equivalence among soil microbial communities (Fig. 1). To build

confidence in projections of macrosystem SOM dynamics will then take more than representation of microbes as controls in soil biogeochemical models. Empiricists will need to adopt a suite of practices (Fig. 3), to resolve how microbes shape emergent macrosystem SOM patterns, that are suited to identifying and quantifying correlated controls that exert their influence conditionally in space and time.

We suggest that one of the practices should be much greater adoption of statistical approaches tailored primarily for identifying the conditional functional form and effect sizes of controls. A shift toward causative statistical inference will be impeded by the current overreliance on a limited number of metrics,

such as  $P$  and  $r^2$  values. However, the beginnings of a move in STEM more generally toward presentation and analysis of individual observations, given issues of interpreting causation from aggregated data (e.g. Weissgerber et al. 2015), suggests the statistical-significance barrier is far from impenetrable.

Triangulation will also need to be widely practiced given what is termed the ‘partial observability’ problem by philosophers of ecology (Sarkar 2016). The problem specifies that it is difficult to estimate parameters accurately in complex systems. One of the main reasons for the difficulty is the embedded correlation typical of controls on SOM dynamics, such as climate or litter quality and functional differences among microbial communities (Fig. 1). Correlation can be uncoupled—at least partially—through longer-term, networked, observational and controlled experimental work. We also see potential for microbial trait and community composition research to reveal when controls are likely operating directly on microbial metabolism and indirectly through selection for different phenotypes and organismal interactions. Overall, however, we assert that for complex systems causality will only be identified by systematically revealing cause-and-effect relationships using evidence gleaned from different approaches to design, execution, and analysis of research (Munafò and Davey Smith 2018).

For the third practice, we suggest the need for greater consideration of variance, where the focus is on individual observations, or disaggregated data, and when and where aggregation is justified. This need addresses a range of challenges in macrosystem biogeochemical science, which fall under the ‘complexity’ and ‘uniqueness’ problems that describe, respectively, the conditional nature of controls on emergent system behaviors and their historical contingencies (Sarkar 2016). These problems highlight the need for multi-scale research to investigate how context, study extent, and measurement and analysis grain influence causative understanding. In particular, variance biogeochemistry as a practice recognizes that quantification of fine-scale variation is likely necessary to identify controls, and their true effect sizes, on microbially-mediated biogeochemical processes.

The philosophical problem of ‘structural uncertainty’ in ecology, where differences in theoretical assumptions make enormous predictive differences (Sarkar 2016), helps to explain why we suggest that

research integrating the three empirical practices should be synthesized and informed through a focus on building confidence in projections from process-based models. As such, we build on previous recommendations for macrosystem research to start with a conceptual model (Soranno et al. 2014), by suggesting that the concepts be formalized through process-based models (Fig. 3). Our recommendation will permit multiple, competing hypotheses to be formalized at the outset of the research. Model pipelines and ensembles can collectively represent the conditional, contingent and only partially-observed controls and parameter estimates to identify those assumptions to which model projections are most sensitive. Those assumptions can then be examined through empirical work following the three overarching practices we identify and then refined in model representations. We suggest that doing so will advance causative understanding of microbial controls on emergent macrosystem patterns in SOM, while building confidence in projections of phenomena such as carbon cycle-climate feedbacks. As such, we foresee that a local-scale lens focused on microscale organisms has strong potential to yield macroscale understanding of SOM dynamics relevant to addressing global-scale, societal problems.

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**Ethical approval** The authors declare that they have no conflicting or competing interests with respect to the viewpoints presented in this manuscript.

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