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Modeling ecosystem-scale carbon dynamics in soil: The microbial dimension

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ABSTRACT

In predicting how soil C fluxes and stocks will change with the environment, models are a critical tool for integrating datasets with theory. Models developed in the 1980's were based on 1st order kinetics of C-pools defined by turnover time. However, new models generally include microbes as decomposers although they vary in the number and nature of microbial pools. They don't, however, integrate modern omics-based datasets because models have coarse resolution and need to function even in the absence of community data—geographically or into the future. There are several issues new models must address to be valuable for large-scale synthesis. First, how to incorporate microbes and their activities—how many pools of organisms? How should they be defined? How should they drive C-cycling? Should their synthesis of degradative enzymes be treated implicitly or explicitly? Second, carbon use efficiency (CUE)—the partitioning of processed C between respiration and re-synthesis into biomass. This term is critical because the size of the biomass influences its rate of organic matter processing. A focus has been on CUE's temperature sensitivity—most studies suggest it declines as temperature rises, which would limit decomposition and organic matter loss. The final novel modeling element I discuss is "priming"—the effect of fresh inputs on decomposition of native organic matter (OM). Priming can either repress or accelerate the breakdown of native OM. But whether, and how, to capture priming effects in soil organic matter models remains an area of exploration.

Soil microbial ecology has struggled for many years to integrate with ecosystem scale biogeochemistry. To understand how microbial systems regulate whole ecosystem processes, we must bridge the scales between what organisms do and what ecosystems do. A critical tool in this venture is models. While "modeling" usually implies a mathematical framework, a model is first and foremost a conceptual framework about how components of a system relate to each other. After the concept is developed, one may write equations that capture the behavior, providing output that can be tested and calibrated against data. When the theory, equations, and data all mesh together, they form a stable intellectual "triangle" that can become a paradigm (Blankinship et al., 2018, Fig. 1). Modeling microbial systems in soil has developed substantially over the decades, yet there remains a large gap between what we can measure as microbial ecologists, and what we can model as biogeochemists. We still struggle to develop models of soil biogeochemistry that adequately capture microbial dynamics while explaining the behavior of ecosystems and which can be widely validated against field data.

Within microbial ecology, models have evolved from simple descriptions of microbial growth (Monod 1949; Chapman and Gray, 1986) to more elaborated models of community dynamics and resource use (Chakrawal et al., 2021). In contrast, ecosystem models have emphasized the pools of resources, focusing on simple equations (Parton et al., 1987), and only adding biological detail where it substantially enhances the prediction of pools or fluxes (e.g. Wieder et al., 2013; Sulman et al., 2014). Ecosystem models can be seen as simplistic or even unrealistic in how they treat microbial systems. Blankinship et al. (2018) argue that we still rely on such models because they continue to work at the ecosystem to regional scales, and monthly to annual time scales, for which they were designed, whereas modern microbial models struggle to develop a "stable triangle" that weaves together the model with its underlying theory and with a measurement suite that would be necessary to parameterize and run it (Fig. 1). In this paper I will focus on ways in which the theory has been developing and has been integrated into model formulations. A full discussion of data assimilation approaches is beyond the scope of this review. We still struggle to establish the most appropriate conceptual framing to capture complex dynamics (e.g. Shi et al., 2018). What processes need to be incorporated into a new

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generation of models to more reliably and robustly capture future carbon and ecosystem dynamics? How do we at least merge the theory with the models?

1. CENTURY and Roth-C: the foundational soil C models

The seminal biogeochemical models, which remain central in how global systems are modeled, remain CENTURY (Parton et al., 1987) and Roth-C (Jenkinson, 1990). These were developed at a similar time and reflected the state of theory in both biogeochemistry and soil science, as well as the state of computational power in the 1980's when they were developed. They are similar in their conceptualization, and both have evolved over the years (e.g. Parton et al., 1998; Farina et al., 2013). CENTURY assumes that soil organic matter is composed of three pools whose dynamics are captured in first-order turnover equations driven by the size of the source pools (Fig. 2). There is an active pool that turns over rapidly, a pool that turns over slowly, and a passive pool that has a very long turnover time; RothC considers this last pool to be "inert" (Jenkinson, 1990).

In CENTURY, the active pool is conceptualized as being primarily "live microbes and microbial products along with soil organic matter with a short turnover time" (Parton et al., 1987). The passive pool was originally thought to include chemically recalcitrant material, but is now thought to be primarily mineral associated organic material (MAOM) that is protected by absorption on, or entrapment within, the mineral phase. The intermediate, slow, pool is the least defined: "physically protected and/or in chemical forms with more biological resistance to decomposition" (Parton et al., 1987). However, these assignments are not fundamental to the formulation of these models—the active and slow fractions were estimated by fitting respiration curves from laboratory incubations while the passive pool was estimated from ^{14}C dating methods (Parton et al., 1987). Thus these models are based on more of a phenomenological, or empirical, approach, recognizing that organic matter has a range of turnover times and may be apportioned into pools that reflect the range of behaviors. In these models, pool sizes and their turnover times are a function of climatic conditions and soil texture. Notably, the reaction kinetics are first-order—there is no active microbial role in regulating turnover although in Parton et al. (1987) they state that "all C decomposition flows are a result of microbial activity." Microbial activity, however, is implicit, embedded within the rate constants, rather than an explicit function of microbial biomass. This reflects an inherent assumption that the size of the active biomass will remain in equilibrium with resource availability and hence does not need to be explicitly represented as a driver of pool turnover. Models that work like CENTURY and Roth-C remain core tools in global scale modeling (Todd-Brown et al., 2011; Wieder et al., 2014). Not only are they simple and straightforward, but they capture essential truths, and have done a remarkable job of capturing of SOM dynamics across the globe. These models set a standard that any global model must match.

However, there has been increasing pressure and movement to develop a new generation of more mechanistically realistic models, models that will better describe existing datasets about fluxes, pool sizes, and organic matter chemistry. The majority of models that have been developed during the last decade have incorporated more complex microbial dynamics and behavior.

Yet, new models still struggle with "triangle" issues—particularly on the data side. We can develop theory that matches new models; in fact, it is by framing a model that we lay out what the theory actually is. But data sets remain complex; there may well be multiple mechanisms operating at a fine scale, yet we are challenged to identify these to explain behaviors that we observe at scales from the soil core to the whole globe. Multiple suites of processes might be invoked to explain a particular pattern. Relatively few models have been validated against independent data sets involving multiple elements (e.g. CO_2 fluxes and pool sizes of SOM components; Abramoff et al., 2022). This raises concerns over "equifinality" in the model systems—that is that multiple model structures might produce patterns that fit the data equally well (Marschmann et al., 2019). This is a serious concern as datasets are often messy; it can be difficult to determine the best performing model formulations (Wieder et al., 2014).

A particular challenge in validating new generations of models is that in the short-term, the fate of fresh plant inputs is largely the same—they will be decomposed and most of the C will be released as CO_2. Hence in fitting a time series of CO_2 emissions, it doesn't require sophisticated

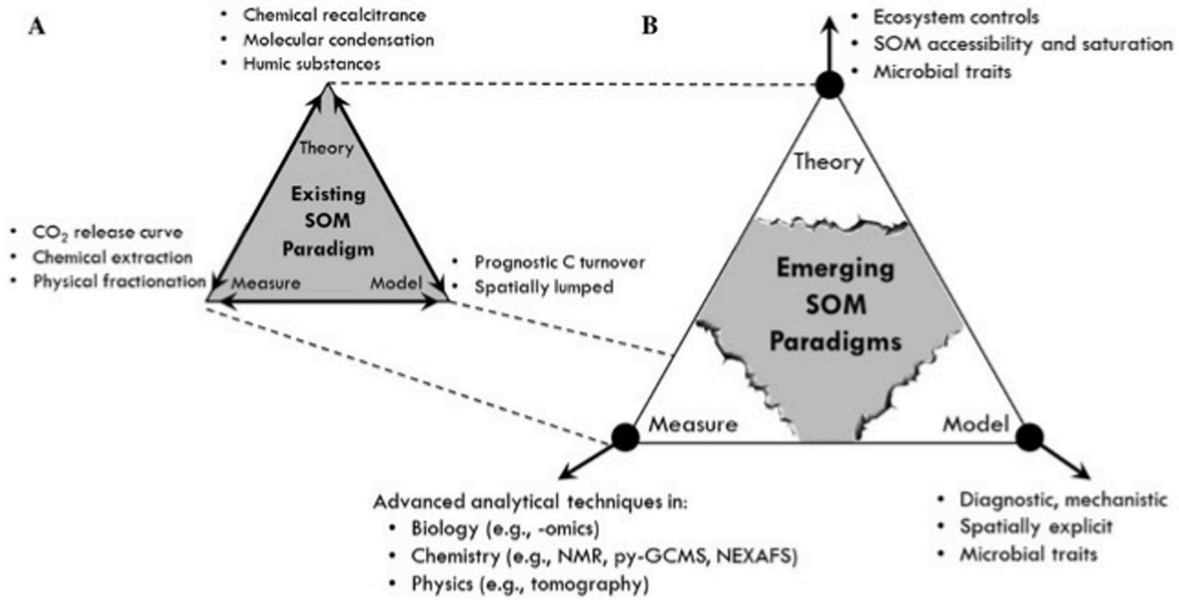

Fig. 1. A representation of existing and emerging approaches to evaluating soil organic matter (SOM) dynamics. The existing approach is robust because all three nodes—theory, measurement, and modeling—form strong bidirectional linkages and are well balanced (a). Recent and ongoing innovation at each node expands the SOM paradigm triangle as understanding of the controls on SOM dynamics grows. However, if expansion at a node outpaces integration of linkages within the triangle, then cracks form causing a lack of applicability and adaptability to changing environmental conditions (b). Reprinted with permission from Blankinship et al. (2018).

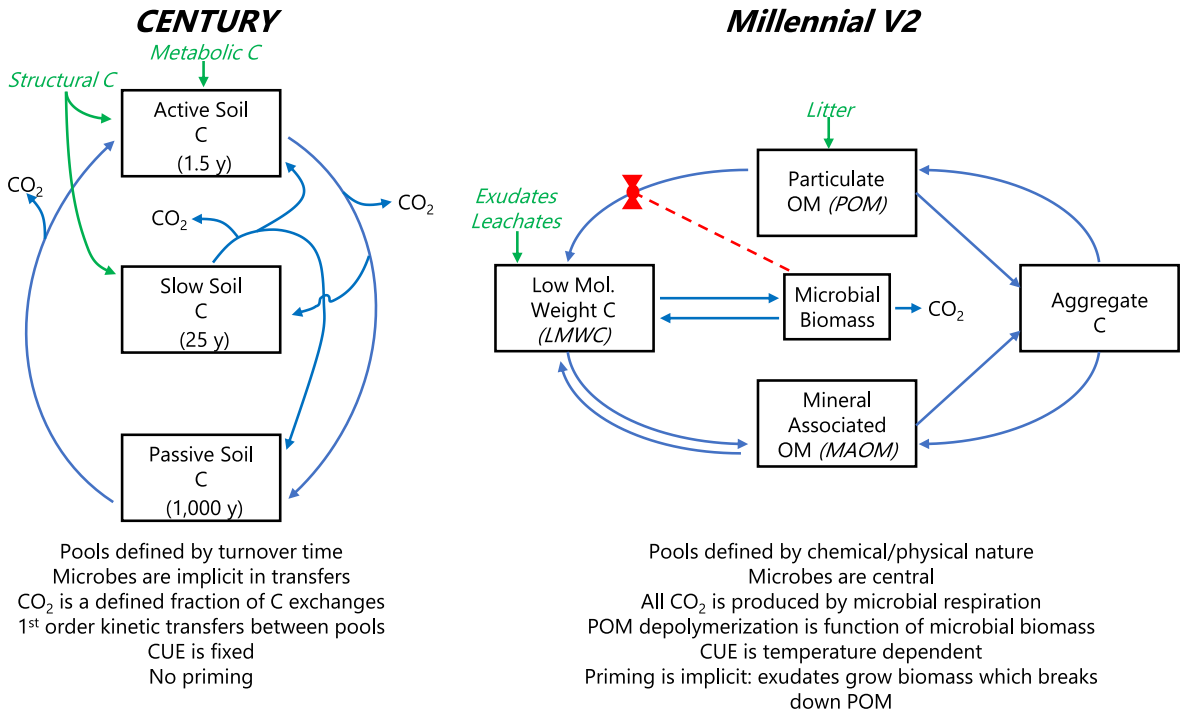

Fig. 2. A comparison of a representative 1st order kinetic model (CENTURY; Parton et al., 1987) and a recent microbial model (Millennial V2; Abramoff et al., 2022). CENTURY defines soil C pools based on their turnover times, and pool exchanges are based on 1st order kinetics, with transfers a function of soil texture. Microbial activity is embedded implicitly within pool transfers. In contrast Millennial V2 defines chemically/physically measurable pools. Depolymerization of particulate OM to low molecular weight C (LMWC) is catalyzed by the microbial biomass and is dependent on the size of the biomass. All respiration is carried out explicitly by the microbial biomass after LMWC has been taken up. In CENTURY, carbon use efficiency (CUE) is built into the transfer functions while in Millennial it is a function of microbial C use and respiration. CENTURY has no priming, whereas it is implicit in Millennial V2—if exudates increase biomass, that will accelerate breakdown of POM.

model structures to get the overall patterning correct. Rather, where differences are likely to appear and to become important are in the longer-term trajectories of SOM and microbial dynamics. Small short-term differences can amass to large long-term differences when they are able to accumulate over decades. Models that are more explicit about the fate of carbon and that identify specific chemical forms that materials move into should be ultimately easier to test and validate because they would have more points to compare and so would be less likely to suffer from equifinality.

2. Issues to consider in new generations of models

2.1. Microbial agents

It has become clear that new generations of SOM models must do better than linear 1st order models such as CENTURY—newer models are more responsive and more dynamic than a pool-driven 1st order model is capable of (e.g. Wieder et al., 2013). A primary assumption in a CENTURY-type model is that microbial activity is resource limited and so resource supply regulates the rate of overall processing. Newer models recognize that pure substrate control is limited in its ability to explain the dynamics of SOM processing; the actual decomposers should be a component of the model structure to capture the dynamics, but how best to include the activity of the decomposer community remains less clear (Wieder et al., 2013). For example, Millenial Version 2 (Abramoff et al., 2022) assumes a single microbial biomass pool that is involved in depolymerizing particulate organic matter (POM) to release low molecular weight carbon (LMWC) that microbes then take up and metabolize. In contrast, the MIMICS model has two groups of microorganisms, one active on metabolic components of plant litter, while the other acts on structural litter; both can also metabolize soil organic C (Wieder et al., 2014). Sulman et al.'s CORPSE model (2014) also has two biomass pools, but they are considered to be spatially separated, one acting in the rhizosphere and the other in the bulk soil. The complex BAMS1 model assumes that fungi depolymerize plant polymers to monomers that are then taken up by aerobic bacteria, which reprocess some of those compounds into cell materials and respire the rest (Riley et al., 2014). To model tundra organic soils, SCAMPS has only a single microbial biomass pool, but this can shift in its stoichiometry and resource allocation towards producing different classes of extracellular enzymes, each of which targets a particular class of substrates: phenolics, cellulose, or N-rich materials (Sistla et al., 2014); functionally the biomass can become more "bacterial" (lower C/N, less exoenzyme production) or more "fungal" (higher C/N, and more exoenzyme production). MEND is somewhat analogous but is designed to work in mineral soils (Wang et al., 2015); it has separate categories of decomposing enzymes but it has both active and dormant microbes; adding dormancy matched microbial biomass levels in a long-term lab incubation better than other model structures. Moorhead and Sinsabaugh (2006), in contrast, divide the soil community into three guilds: opportunists, decomposers, and miners that compete with each other for available resources. But they define this as a "theoretical model" that they compared to litter decomposition rather than to whole-soil SOM dynamics. They also acknowledge "A number of patterns of behavior in our microbial based model will be very difficult to directly verify."

Other, more elaborate, model structures have offered similar qualifications—for example Tang and Riley (2017) involves an elaborate model of redox reactions—to solve enzyme catalyzed multi-reactant processes, they use double Monod kinetics (both substrate and enzyme can show saturation). They analyze this with sophisticated SUPECA kinetics, which marries synthesizing unit (SU) kinetics with an equilibrium chemistry assumption (ECA) approach to solving the equations. But they state that "we are not suggesting that SUPECA kinetics should replace existing soil biogeochemical (BGC) models, but rather that

mechanistic analysis using a SUPECA-based model can inform process understanding and thereby improve such models." Such complex models are appropriate in limited circumstances and to develop new insights that can be simplified into more generally applicable equation structures and parameterizations.

Notably, none of these models assign taxonomic identity to the biomass pools, although Moorhead and Sinsabaugh (2006) come closest. Partly that is because if there is only one microbial group there is no need for identity. With CORPSE, if the assumption is that the microbial groups are separated spatially, bulk soil community analyses would be inappropriate. But it is equally worth noting that it remains challenging to link from DNA-based taxonomy to the broad functional classes required in a large-scale model (Guo et al., 2020).

It is important to note that simply adding a decomposer to a model doesn't necessarily make it "better." For example, Fujita et al. (2014) found that a linear model did a better job of capturing respiration patterns across a range of soils that varied in SOM levels. A multiplicative model (in which decomposition is a function of both the size of the SOM pool and of the biomass) produced too little respiration at low SOM levels, but too much at high levels. Making the function a Michaelis-Menten saturation curve solved the overestimation at high levels but not the underestimation at low SOM. Calibrating their models to capture the average conditions meant that when SOM levels and the associated biomass were low, the respiration rate was necessarily low. They concluded that "including the non-linear kinetics of microbial substrate consumption does not seem necessary to improve the model performance, unless capturing temporal fluctuation of fluxes is of main concern." Of course, capturing such temporal fluctuation of fluxes *is* a concern for many biogeochemical models!

In adding levels of microbial sophistication to a model, however, it is equally important to capture other mechanisms that constrain soil processes—the physical and chemical processes that regulate SOM dynamics. Which pools and which mechanisms are the right ones to include is always the question. As Manzoni et al. (2016) notes "most ecosystem-scale biogeochemical models lack this level of detail in their pool structure and thus require kinetic laws that account for detailed processes and yet only depend on a few modeled pools." For such reasons, Riley et al. (2014) argued that "the next generation of land BGC models to be used for climate prediction should include, explicitly or implicitly, representation of vertical carbon transport, microbial activity, mineral surface interactions, temperature and moisture controls on independent processes, and nutrient dynamics." However, it is worth noting that the models that target litter decomposition (e.g. Moorhead and Sinsabaugh, 2006) or organic soils (Sistla et al., 2014), where the substrate chemistry is better defined and protection mechanisms less dominant, are generally more microbially explicit.

It is possible to build a model that matches patterns in the data but that relies on the wrong mechanism. For example, to model the microbial responses to repeated dry-wet cycles, Lawrence et al. (2009), found that of four models of increasing complexity, the most elaborate best fit the data; in this model, exoenzymes acted even while soils were dry, causing bioavailable material to accumulate for microbial use during the next rewetting event. This mechanism enabled the model to be sensitive to the length of time the soil remained dry, with larger pulses following longer dry periods. However, when Homyak et al. (2018) tested this hypothesis by incubating dry plant roots under chloroform (to allow enzyme activity but prevent microbial uptake of the products) enzymes remained viable but there was no accumulation of the reducing sugars that should be there, were enzymes active. They concluded that physical mechanisms were likely responsible for mobilizing mineral associated OM into a water extractable phase as soils dried. Hence it appears that the Lawrence model was getting the "right" answer, but possibly for the wrong reasons.

When we are considering mineral associated organic matter (MAOM), which can comprise much of the slow and passive pools, the rate-limiting step in overall SOM turnover will almost certainly be the mobilization step—the reaction that releases OM from protection. This step is likely regulated by abiotic chemistry, and so can perhaps be reasonably modeled with 1st order kinetic equations based on substrate-concentration—the rate is equal to the size of the pool times a rate constant that reflects the nature of the chemistry ($dC/dt = -kC$; where k is a rate constant and C is the size of the carbon pool). This is what Abramoff et al. (2022) do in Millennial V2, where processing MAOM is driven by desorption.

2.2. POM vs. MAOM

A key area where the role of different mechanisms may be important is in processing plant detritus vs. mineral associated organic matter (Fig. 2). Detritus constitutes the main input of OM into soil, and the microbial role in fragmenting, hydrolyzing, and metabolizing particulate organic matter (POM) is undeniable. Since this flux represents the largest flow of C into the soil system, models that emphasize respiration will necessarily emphasize the decomposition pathways. However, when we consider C-sequestration and fates of C other than being respired to CO_2, we need to emphasize the processes that regulate the dynamics of MAOM, which often comprises the larger pool of C in the soil (Abramoff et al., 2017). In this case, models must likely emphasize the physical and chemical processes that influence inputs and outputs to MAOM: production of microbial necromass, sorption/desorption, etc. These are smaller flows than respiration but are the processes that control the long-term dynamics of SOM and of ecosystem C storage. Microbial models are commonly fit to time series of CO_2 efflux because efflux is important, but also because it is easy to measure (Lawrence et al., 2009; Brangarí et al., 2020). Estimating necromass production, stabilization of microbial products etc. is technically much more difficult, not only in defining what to measure (and how to measure it), but in detecting changes over time. Yet, as models emphasize how ecosystems, and carbon stocks, will respond to climate change and land management, capturing the dynamics of the stabilized pools has become more important; it is no longer good enough to get the bulk CO_2 fluxes close enough to "right" and allow the flows into slow or stable pools as just a small "error" term.

Which are the most important fluxes to capture in a model are sensitive to time scale—in the short-term (annual or shorter) capturing CO_2 flux dynamics is critical. How does microbial activity respond to seasonal cycles with weather events, drying/rewetting cycles, and changes in plant inputs? However, when the time scale shifts from days or weeks to years or decades, it is safe to assume that fresh plant litter will be processed, so a model that is a little off about *when* litter is metabolized probably won't matter much. Rather, a model's long-term accuracy will be determined by whether it ultimately gets the fate of litter C correct—can the model accurately predict changes in soil C stocks? Increasing the amount of litter C that ultimately becomes MAOM from 1% to 2% would be undetectable within the perspective of annual C-flows, but would still be a doubling of an important flux for long-term soil C dynamics; over decades, such a difference could lead to large differences in sequestered C pools. Thus, models need to pay more attention to the mechanisms that regulate the long-term stabilization of soil C (Georgiou et al., 2021).

2.3. Enzyme based models

The 1st order assumption increasingly is seen as inadequate, particularly for plant litter decomposition (Wider et al. 2013; Abramoff et al., 2022). For the labile fraction of plant material, the size of the active population of microbial biomass is likely a driver on the overall decomposition rate, producing kinetics that are 2nd order, sensitive to the size of both the carbon pool and the microbial biomass ($dC/dt = -kCB$; where B is the size of the biomass). Particulate detritus is regulated a little differently, as it is composed of polymers that require extracellular enzymes to fragment polymers into monomers or oligomers that

can be taken up and then metabolized. That gives a rate equation, which at its simplest, would be $dC/dt = -kCE$; where E is the pool size of the relevant extracellular enzymes. In each of these models, however, this pure second order formulation leads to a situation where, if decomposition fuels sufficient growth, the B or E terms grow, accelerating decomposition and microbial growth further, fueling a runaway explosion until all substrate is consumed. Thus, a simple second-order model inherently becomes unstable. Something *must* constrain the maximum rate or the system blows up and crashes. One way to stabilize these equations is to make the B or E term a saturation function in which, as enzyme levels increase, activity per unit enzyme decreases, reaching some maximum possible reaction velocity:

$$dC/dt = -V_{max}\ E\ /\ (E + K_m)$$

where V_{max} is the maximum possible rate and K_m is the "half-saturation constant"—the substrate concentration at which the rate is ½ of V_{max}. This is "reverse Michaelis-Menten kinetics" where enzymes compete for substrate binding (Schimel and Weintraub, 2003), rather than the classic Michaelis-Menten equation where mobile substrates compete to bind at an enzyme active site.

There are several families of issues related to soil enzymes that influence how we incorporate them into ecosystem models. First is the diversity of enzymes and how we should measure their activities to predict decomposition. Second is how to measure their occurrence and activity; modern enzyme assays measure the amount of enzyme present rather than its true activity. Third, are the specific kinetic parameters that one associates with the enzyme activities.

The first challenge in using exoenzymes to drive decomposition models is that microorganisms produce a wide array of enzymes that are involved in breaking down organic material. Models can't capture all of them individually and so they generally abstract them into functional groups of enzymes. Schimel and Weintraub (2003), one of the earliest models to explicitly consider enzyme behavior, aggregated exoenzymes into a single pool. Allison et al. (2010) in a model designed to explore global patterns did likewise, having one enzyme pool that scaled with microbial biomass. However, Allison (2012) took a different approach to modeling litter decomposition in the trait-based DEMENT model which explored litter decomposition through an individual-based model that allowed a wider array of theoretical organisms with different enzyme arrays to interact in a spatial grid to predict decomposition dynamics. In this model different organisms can produce an array of degradative enzymes. Kaiser et al. (2015) built an analogous (spatial/individual) model that distinguished between exoenzyme producers and non-producers ("cheaters") to explore litter decomposition. Both models could reasonably predict litter decomposition but involve substantial computational overhead that would be inappropriate for a coarser-scale, 3-dimensional, whole-soil model.

Numerous studies now measure a suite of enzyme activities to capture resource limitations to the microbial community—typically "model" enzymes that target C-, N-, and P-acquisition; commonly β-glucosidase, N-acetyl glucosaminidase, leucine aminopeptidase, and acid phosphatase (German et al., 2011). These can be used to model microbial activity and even to develop patterns of resource limitation and of carbon use efficiency (e.g. Sinsabaugh et al., 2016, but see Schimel et al., 2022). But, to choose a single model C-acquiring enzyme to represent the entire guild of enzymes lumps multiple groups of soil microorganisms and their degradative systems. Perhaps most importantly, it assumes that the hydrolytic and oxidative enzyme systems work and respond in parallel. This, however, is not true, at least when it comes to detritus decomposers—white rot fungi synthesize extensive oxidative enzymes, while other fungi rely more extensively on hydrolytic enzyme systems and as a result leave behind complex polyphenol-rich material that is resistant to further decay (Fukasawa, 2021). Whether the same patterns of alternative, rather than parallel, enzyme decay pathways occurs in SOM processing remains unclear. Regardless, we are left with a challenge in matching modeled and measurable pools of active enzymes. We must use some suite of bio-indicator enzymes to reflect the processes they are responsible for, but which do we choose? The decision is a function of the theory we use in developing any specific model.

A new approach to exploring the role of depolymerizing enzymes is the C-STABILITY model (Sainte-Marie et al., 2021), which treats depolymerization as a continuous process in which polymers are fragmented over time into components that become small enough to be assimilated. They are able to explore the relative roles of enzymes which cleave small pieces from the end of a polymer (exo-cleaving) vs. those that chop up a polymer randomly (endo-cleaving). They also combine compartmental and continuous approaches to characterizing SOM.

Having decided which enzymes to capture, we are still left with the limitations of our enzyme measurement approaches. Modern enzyme assays are potential measurements, in which substrate supply is maximized by adding an artificial substrate that is cleaved to release products that can be readily analyzed (German et al., 2011). For C-degrading enzymes, a common assay uses a MUB-crosslinked substrate, which upon hydrolysis, fluoresces and is straightforward to measure (German et al., 2011). However, these are assays of the size of the pool of the target enzymes, rather than an estimate of the rate at which a native enzyme is capable of reacting a particular substate at its ambient concentration. We generally assume that the potential activity is related to the actual activity; an assay that estimates the enzyme pool should provide an index of the actual in situ activity, but this is more of an assumption than a conclusion (Homyak et al., 2018).

Were enzymes short-lived in the environment, the assumption that the pool size is related to activity would probably be reasonable. In fact, models that drive litter decay based on the size of the active microbial community (e.g. Moorhead and Sinsabaugh, 2006; Sulman et al., 2014) must assume that the size of the enzyme pool is directly correlated with the size of the producing community (Fatichi et al., 2019). There is sometimes an implicit assumption that the size of the active enzyme pool is related to the size of the gene pool that codes for the enzymes, allowing correlation between the size of microbial populations and the rate of enzymatic activity (e.g. Treseder et al., 2018; Diamond et al., 2019).

However, important exoenzymes are relatively stable in the soil environment. Schimel et al. (2017) found that when soils were incubated under chloroform (to prevent microbial production and consumption of exoenzymes and their products), most hydrolytic enzymes in mineral soils lost activity exponentially, but slowly; retaining >½ of their activity even after 3 months. The exception was alpha-glucosidase which lost activity more quickly. The one soil in which activities were lost rapidly was an organic tundra soil, in which enzymes lost half their activity within 2–4 weeks. In a live soil, decay and loss might be more rapid, but enzymes are readily stabilized by mineral association (Schimel et al., 2017). Over annual or longer time scales it seems likely that enzyme pools would reflect the average status of the populations that produce the enzymes, but it should not be safe to assume that the standing enzyme pools will reflect changes in the status of the enzyme-producing community over shorter time periods, such as are commonly used in incubation experiments. There should be a lag between changes in the producing community and measured enzyme activities, and there should be a substantial background level of enzyme activities. Even in the face of catastrophic disturbance to the soil community, the background pool of enzymes should maintain a level of activity that would buffer the functioning of the community.

Finally, there is the challenge of estimating the parameter values for the actual enzyme-meditated reaction rate equation. The Michaelis-Menten equation assumes that mobile substrates compete for binding at the enzyme active site; the "reverse Michaelis-Menten equation" assumes mobile enzymes must compete for binding at a reaction site on an insoluble polymer molecule (Schimel and Weintraub, 2003; Tang, 2015). Both have analogous mathematical structures that require two

parameters—a V_{max} term and a half-saturation (K_m) term. We have no good ways of directly estimating what these specific terms should be—in part because the model enzymes are theoretical or mathematical constructs to which we fit models, and in doing so, estimate parameter values to generate a "best fit" model that includes the needed parameters (Schimel and Weintraub, 2003). Hence the values we estimate through a model might bear little actual resemblance to the true kinetic fits for actual enzyme molecules (e.g. Allison, 2012).

These challenges in modeling exoenzyme behavior directly are a major reason that most models have assumed that enzyme pools will be in equilibrium with the size of the biomass that produces them. Thus, instead of including enzymes in a model, they instead just model the populations of the organisms. This approach, either implicitly or explicitly, is common. For example, the MIMICS model (Wieder et al., 2014) has two groups of microorganisms, one active on metabolic and the other on structural litter. Millenial V2 operates similarly, with microbes active in decomposing POM, but relying on desorption reactions to mobilize MAOM into an accessible pool (Abramoff et al., 2022). Exoenzymes are not a component in these models, yet the organisms metabolizing structural/particulate litter rely on exoenzymes to fragment litter molecules; exoenzymes are thus implicit within the model structure.

Such challenges are inherent in developing models within the Blankinship et al. (2018) "triangle" structure—having used theory to develop the structure of the model equations, we rely on empiricism to determine the best values for they key terms in the equations. Experiments must be designed that will provide the data needed to fit to the theories and models; this should include identifying key pools and processes that are measurable and that would distinguish between different model formulations. Undoubtedly this will involve isotope tracer studies and more sophisticated chemical analyses of SOM chemistry.

2.4. Microbial community driven models

"However, one grand challenge in climate change biology is to integrate microbial community information, particularly omics information, into ecosystem models to improve their predictive ability for projecting future climate and environmental changes." (Guo et al., 2020).

How much detail about microbial community composition it will be desirable to include in ecosystem-scale soil organic matter models remains unclear, and this represents a major gap between ecosystem- and microbial-scale studies. It is notable how microbial ecology has increasingly emphasized 'omics-based perspectives to evaluate the composition of microbial communities, and there has been growing focus on using these tools both to evaluate microbial function and to associate community composition with function. Tools such as network analysis are increasingly applied to evaluate the functional structure of communities and to collapse complex communities into a more manageable collection of clusters and to identify particular keystone organisms (Goberna and Verdú 2022; Guseva et al., 2022).

As some models have become more physiologically detailed, the potential to use omics-based data to parameterize them has grown. For example, the MEND model (Wang et al., 2015) includes specific enzyme systems; Guo et al. (2020) showed that including Geochip-based abundances for a number of functional genes improved the model fit and reduced parameter uncertainties, particularly under warming. The model also demonstrated persistent microbial acclimation to elevated temperatures and as a result, lower soil C losses.

This work raises the question of how to effectively integrate omics-based data with ecosystem-scale modeling. That, however, begs the question of whether it is practical to do so—or even desirable to try. On the practicality side, it is notable that the simplest community data sets contain many more "pools" than biogeochemical models, where two microbial pools are a lot to handle. Microbial community composition data are inherently high resolution, while models are low resolution, aiming for broad applicability. Higher resolution brings complexity that constrains applicability. Guo et al. (2020) showed that it is possible to enhance a sophisticated model's performance by calibrating it with omics information, but they equally demonstrated the complexities of doing so.

Even where we can gene-enable a biogeochemical model, it remains dependent on having the genetic data to parameterize the data. Without having that key dataset, you would have to predict the community composition; that could be done by coupling the biogeochemical model to a community assembly model that incorporates mechanisms at a fine level of resolution. But doing so would likely create a model that is dependent on the specific community assembly and so would be highly site specific—a model for exploring microbial ecology rather than ecosystem dynamics. On top of that, a model that incorporates microbial communities has a parameterization problem: to run the model you have to collect those data. As noted by Treseder et al. (2012): "The integration of microbial details into ecosystem models often requires parameterization of new variables that can be difficult to assess … or the invocation of mechanisms that are relatively unexamined in situ …"

And of course, we don't have a time machine, so our ability to model past conditions with a community-enabled model would depend on having community data from past times, nor could we compare a model to future conditions because it would be impossible to have future community data. Most validation of mechanistic microbial models relies on either relatively short experimental time series (e.g. Lawrence et al., 2009; Guo et al., 2020), or analyzing spatial patterns (Wieder et al., 2014), including space-for-time substitutions, such as relying on temperature gradients to predict the effects of future warming (e.g. Jensen et al., 2014; Yang et al., 2022). To project future conditions, a community-based mechanistic model would have to predict the values of different populations. But if we understand the drivers on community composition well enough to model those dynamics, and we understand how community composition drives biogeochemistry, then we should be able to "model past" the microbes by building kinetic models that link directly from environmental drivers to biogeochemical processes. This is essentially what a model such as CENTURY does. There are no microbes visible in CENTURY, but the model doesn't assume a sterile world! Rather, such models assume that microbial communities are in equilibrium with their environment, allowing microbial processes and interactions to be embedded within the model's rate constants (Todd-Brown et al., 2011).

The approach of modeling past the microbes, however, struggles when one can't assume that microbial communities are in equilibrium with the environmental drivers—when temporal dynamics are rapid enough that community composition might be out of balance with the environment. This is likely when either the focal time scale of the model is short—trying to capture rapid temporal dynamics (e.g. drying/rewetting, Lawrence et al., 2009; Brangarí et al., 2020), or when the longer-term behavior of the overall system is sensitive to such high-frequency events and the potential for disconnection between respiration and microbial growth that can arise (Brangarí et al., 2020, 2021).

One area where community analysis will likely enrich modeling is in developing a better picture of biomass and community turnover—in a microbial model, turnover of microbial populations is critical in regulating the overall size of the microbial biomass and so of its role in decomposition. But is turnover just replacing carbon within existing cells or does this represent actual death and regrowth? If the latter, that has implications for the production of stabilized necromass that would be important to capture (Sokol et al., 2022). Actual cell death and regrowth are measurable using genetic techniques (Buckeridge et al., 2022); a model could parameterize the flow of C into necromass or MAOM based on estimates of death rate.

I suspect that we will continue to see increasingly elaborated, fine-scale, microbial models that, in their core, are community dynamics

models and incorporate the ecological consequences of community shifts, but which have limited power at the larger scales of ecosystems or regions and years to decades. For example, Fu et al. (2022) showed that different community compositions in litter decomposition (ground maize straw) were associated with either positive or negative priming behavior. Early r-selected taxa were associated with negative priming, while later K-selected "decomposers" were associated with positive priming of SOM. Insights from such fine-scale approaches may then be used to enrich ecosystem models; for example, as we learn what selects for the different decomposer communities, we may be better able to predict and model priming behavior. Or in the case of Guo et al. (2020), where adding genetic information to the MEND model offered insights into temperature adaptation of communities to warming—an insight that could be captured in a less omics-explicit model formulations.

2.5. Carbon use efficiency (CUE): growing the microbes

A critical parameter in all SOM models is the partitioning of metabolized C between loss via respiration and assimilation into new organic forms—typically microbial biomass. This is most commonly referred to as "carbon use efficiency" (CUE) although other terms are sometimes used (e.g. microbial growth efficiency, Wieder et al., 2013; Schimel et al., 2022). The importance of efficiency in regulating ecosystem behavior is well illustrated by the MEMS (Microbial Efficiency Matrix Stabilization) model (Cotrufo et al., 2013). MEMS posits that in the conversion of plant litter into SOM, labile litter may initially decompose faster than recalcitrant litter, but because microbes are able to assimilate the carbon from labile litter more efficiently, it has a higher CUE. This higher CUE leads to the formation of more microbial biomass and more necromass, leading to higher ultimate stabilization into SOM—fast decomposition but effective stabilization. Recalcitrant litter, in contrast, is processed with a low CUE; it decomposes slowly, but ultimately produces less SOM.

Wieder et al. (2013) highlight the importance of Microbial Growth Efficiency (which is essentially equivalent to CUE) in a different way—in their CLM microbial model, warming reduces MGE, which reduces microbial biomass and the population of decomposers, which reduces decomposition and so allows SOM to accumulate. Without this temperature adjustment of MGE, warming activates soil microbes; globally soils lost almost 300 Pg C by the year 2100 whereas if MGE declined with temperature, soils gained ~10 Pg. Even in first order models CUE/MGE is important in regulating long-term pool sizes, but in a microbial model, regulating the size of the microbial biomass gains importance and so CUE becomes an even more critical parameter. Allison et al. (2010), in their enzyme-based model predicted similar patterns—that if CUE decreased with temperature and the kinetic parameters of the enzyme pool could acclimate to temperature, SOC could actually increase. And CUE does appear to decrease with increasing temperature (Qiao et al., 2019; Fanin et al., 2022), although not all studies have found this decrease (Pold et al., 2019).

CUE is regulated at two fundamental levels. The first is the inherent biochemistry of processing particular substrates, while the second is the larger-scale cellular dynamics that ultimately influence C-partitioning (Schimel et al., 2022). The first level is tied into substrate chemistry and established biochemical pathways. For example, as pyruvate enters the TCA cycle, it necessarily loses a C as CO_2 in being converted to acetyl-coA. This will be true for most specific molecules—there is little flexibility in the chemistry of particular reactions. This is largely why Cotrufo et al.'s (2013) MEMS model predicts higher ultimate stabilization of labile litter—labile components such as protein, cellulose, and hemi-cellulose are inherently easier for microbes to assimilate and stabilize than lignin, suberin, or tannin.

The flexibility is in which reactions a cell "chooses" based on external conditions. For example, if a cell has energy reserves available, it might carboxylate pyruvate to produce oxaloacetate as a building block for biosynthesis rather than decarboxylating it to generate ATP within the TCA cycle. Many factors regulate which biochemical pathways a specific molecule goes into, because microorganisms are adept at regulating their biochemistry to optimize fitness. Hence with any given substrate, biochemistry sets an upper limit on CUE, but cellular needs will regulate the actual CUE. For example, glucose can have a short-term CUE as high as 75% (Sugai and Schimel, 1993) but overall CUE is rarely greater than 40% (Hagerty et al., 2018; Geyer et al., 2019; Zheng et al., 2019; Hu et al., 2022).

Within a modeling context there are two primary issues that have been discussed as important regulators on overall CUE; these are maintenance and stoichiometry. Maintenance represents the energy an organism must spend simply to maintain cell viability and function—maintaining membrane integrity and adenylate energy charge, repairing cell damage etc. (Joergensen and Wichern, 2018; Hunt et al., 2022). This is why Wieder et al. (2013) assumed that microbial growth efficiency should decline as temperature increased—maintenance should have to continue as long as microbes remain viable and non-dormant. Chemical reactions increase in rate with temperature, so as temperature increases, maintenance rates should increase. Growth pathways, on the other hand, don't change with temperature—the TCA cycle remains the TCA cycle. Hence in a growing cell, the resources needed to create a daughter cell should remain fixed, even if reproduction might occur more rapidly at higher temperature, but maintenance rates should increase independently of growth. Thus, at higher temperatures, microbial communities would likely invest more of their total energy in maintenance. Since CUE reflects the balance between growth and maintenance, it should decline as temperatures increase. However, experimental work has shown more complex patterns—some studies show the expected decline in CUE with temperature, but not all (Zhang et al., 2022).

Stress, more generally, should decrease CUE, as stress of any sort should increase maintenance costs. Temperature is one obvious such stress that has been considered in global models (e.g. Wieder et al. (2013). Drought and rewetting are also common stressors that should increase maintenance costs and so decrease CUE. For example, under drought stress, soil microbes synthesize trehalose to protect their membranes (Thammahong et al., 2017). In a dry soil trehalose comprised almost 50% of the total chloroform-extractable C flush, and was rapidly hydrolyzed to glucose upon rewetting (Slessarev and Schimel, 2020); the glucose would then be rapidly metabolized. Most work on moisture stress effects on microbes has emphasized such short-term respiratory activity, rather than on longer-term energetic efficiencies. The short-term response of soil respiration to moisture stress in mineral soils appears to be dominated by diffusive substrate supply despite great variation in organisms' moisture sensitivities (Manzoni et al., 2012). In contrast, the effect of moisture on CUE has been poorly explored (Moyano et al., 2013; Domeignoz-Horta et al., 2020). A particular challenge to exploring how moisture influences CUE is that most of the available methods add water to apply substrates (labeled organic compounds or ^{18}O water). To avoid this, Heron et al. (2009) applied ^{13}C acetate and $^{15}NH_3$ in the vapor-phase so that they could explicitly evaluate the effects of soil moisture on CUE, but they saw no significant effect until soil moisture dropped to 0.05 g H_2O/g soil, when the C-based value of CUE actually increased! They postulated that the water potential had not declined to a level that would constitute a real stress to soil microbes. Other stressors (e.g. heavy metals) also impose biochemical costs on microbes that appear as increases in respiration and decreases in growth (Xu et al., 2018)—i.e. increased maintenance and reduced CUE.

As essentially all soil models drive microbial processes with temperature and moisture, capturing the changes in CUE would seem important, especially for microbial models, which drive growth and respiration with the size of the biomass pool, and are being used to explore long-term SOM dynamics. Thus, the effect of drying and rewet cycles on overall CUE is an important area for future global change research. Is trehalose accumulation a standard response to drought?

When soils are rewet, can that C be recaptured and used to fuel cell growth, or does it just fuel the Birch Effect respiration pulse (Schimel, 2018)?

Somewhat similarly to physical or chemical stresses, nutrient imbalance can reduce CUE (Sinsabaugh et al., 2016; Schimel et al., 2022). When microbes metabolize substrates that have high C:N or C:P ratios, they cannot assimilate all the available C into cell biomass. Rather, their CUE becomes constrained by nutrient availability and cells may "burn off" excess C in the process of overflow metabolism (Schimel and Weintraub, 2003). By assuming that microbial communities are ultimately regulated by their ability to process plant detritus, which requires exoenzyme processing of both C and N, it is possible to model an estimate of overall community CUE *after* accounting for possible overflow metabolism (Sinsabaugh et al., 2016). This model uses the ratio of C-assimilating enzymes to N-assimilating enzymes to assess whether microbes are C- vs. N-limited and calculates what CUE would have to be to enable microbes to produce biomass with the appropriate C:N ratio. Thus the Sinsabaugh et al. (2016) model predicts lower CUE when processing substrates that have a high C:N ratio. In contrast, the CUE on nutrient-rich substrates is driven by the inherent ability to process the substrate molecules. This modeling approach gives a broad-brush perspective on CUE—more appropriate for cross-study comparison than to estimate a "real" partitioning within a specific study.

Overall, the effects of environmental variation on CUE is an area that calls for substantially greater attention. In microbial models, the amount of C that becomes cell biomass is a critical variable as it can fuel a positive feedback, with increasing biomass accelerating C loss. Yet, shifts in CUE are difficult to measure. The "traditional" approach of using ^{13}C or ^{14}C labeled tracer molecules to estimate partitioning is powerful but limited because it only gives a short-term value for the specific compound added (Sugai and Schimel, 1993; Geyer et al., 2019; Hagerty et al., 2022). There are, however, methods of estimating microbial growth that are less sensitive to the specific assimilation pathway of a particular organic substrate (Geyer et al., 2019). Notable among these is using ^{18}O assimilation into DNA to measure cell growth (Blazewicz and Schwartz, 2011) but this method is still sensitive to assumptions about whether the ^{18}O in DNA is from the added ^{18}O-labeled water vs. internal metabolic water, as well as fungal/bacterial ratios, and other factors that connect cell replication and DNA synthesis to overall C use and assimilation (Pold et al., 2020). The calorespirometric ratio—the total heat produced by metabolism relative to CO_2 release—is another pathway-insensitive route to estimating CUE. But, it too is sensitive to the assumptions that underly the scaling from heat generation to actual carbon usage (Geyer et al., 2019). Still, these approaches provide important data to facilitate exploring how environmental conditions influence CUE, and while each method has limitations, if applied in a comparative approach, any relative shifts in estimated CUE should provide information that will be valuable for parameterizing models.

2.6. Priming: fueling the microbes

In modeling soil microbial dynamics, one phenomenon that has gained attention is "priming"—that is an alteration in the decomposition of native SOM as a result of adding fresh organic matter (FOM; Bingeman et al., 1953; Kuzyakov et al., 2000; Bernard et al., 2022). Usually it is assumed that priming accelerates the breakdown of native SOM. However, "negative priming," in which native SOM breakdown is *slowed* by fresh additions can also occur (Bernard et al., 2022). The specific mechanisms involved in priming are complex, potentially including both abiotic processes, in which fresh compounds may destabilize MAOM and make it more accessible to attack, and biological processes, in which the fresh materials can fuel production of degradative enzymes that might target particulate OM from plant detritus (Bernard et al., 2022). Priming is thus sensitive to many factors including the nature of the added compounds, the available substrates, and the organisms present.

In the context of modeling natural ecosystems, the aspect of priming that is probably of greatest interest is root, or rhizosphere, priming, where root exudates can fuel microbes that then accelerate their attack on native SOM constituents (Kuzyakov, 2002). Rhizosphere priming is potentially important in regulating how roots and soil microbes interact with each other. Both positive and negative priming mechanisms are possible. If microbes gain enough available C from roots, they might not attack native SOM (Kuzyakov, 2002), but positive priming seems more common, where either microbes gain extra energy to synthesize new enzymes or via "nutrient mining" (Bernard et al., 2022). In this process, C-rich exudates can lead microbes to become N limited and so they invest resources to synthesize enzymes to break down N-containing molecules.

How to incorporate priming into microbial models of SOM turnover is, however, unclear—whether to even try is a question. At the largest scale, if a model has been calibrated against field data (e.g. CENTURY), one might assume that any priming that might have occurred has been accounted for in the model's core parameterization—the model wouldn't match the data if that were not the case. However first-order pool-based models have no mechanism for directly including priming into their formulations (Huang et al., 2018). For more mechanistic modeling, where we care about getting the dynamics right, and not just the right overall outcome, capturing substrate interactions could prove important.

Bernard et al. (2022) separate efforts at modeling priming into two broad (but overlapping) spatio-temporal scales. They note that "Most of the models aim at understanding priming at small scales and over short time periods, whereas models aimed at quantifying the importance of priming on the SOM balance are developed at larger scales and over longer time periods." One approach to incorporating priming in a model is that taken by ORCHIMIC (Huang et al., 2018), which uses a pool structure similar to CENTURY (active, slow, and passive soil C), but it makes the breakdown of the C pools a function of the size of the active pool.

In some formulations, priming may be implicit within a model—if fresh OM stimulates microbial growth, and microbial biomass regulates SOM breakdown, then adding FOM in the model will accelerate native SOM breakdown. This should be the case with models such as Millenial V2 (Abramoff et al., 2022), where the breakdown in POM is a function of the size of the microbial biomass. Hence, adding low molecular weight carbon (LMWC) will increase biomass and the rate of attack on the POM pool, effectively priming the process. However, in this model, there is no inherent priming of MAOM as the mobilization of MAOM is dependent on desorption, which releases MAOM into the LMWC pool. The most sophisticated modeling of priming is probably that in the CORPSE model (Sulman et al., 2014), which has a separate rhizosphere compartment in which root exudates fuel microbial growth with a high carbon use efficiency, and where microbial biomass in turn drives decomposition. Thus, in CORPSE, fresh root-derived carbon inputs directly drive accelerated decomposition of native SOM.

It seems likely that in microbial models, priming will be best addressed implicitly—if microbes can grow effectively on labile constituents, and their attack on native SOM is at least partially a function of the size of the biomass, then priming becomes an emergent property of the system—if plants that produce more fresh roots and root exudates invade a site, there will be more labile material to fuel growth and attack. Then resource stoichiometry might regulate whether those labile inputs satisfy microbial needs and so drive negative priming, or whether C-rich inputs fuel nutrient mining and positive priming (Na et al., 2022). If such mechanisms are built into a model, then priming would also be built in, without requiring approaches such as having the size of the labile C pool directly influence the decomposition of the particulate or slow SOM pools.

3. Conclusions

"The ultimate test of microbial models is whether they improve predictions of global C stocks and fluxes in coupled GCMs." (Todd--Brown et al., 2011). That quote is from a paper titled "A framework for representing microbial decomposition in coupled climate models" and hence it is unsurprising that it emphasizes climate models. Rather it could be translated to "The ultimate test of microbial models is whether they improve predictions of C-stocks and fluxes at the scale of space and time a model was crafted for." But to know whether a new model *improves* predictions, it is vital to compare it to conventional, or at least different, models (Treseder et al., 2012). Does adding novel formulations, requiring new processes and new parameterizations, give a more accurate prediction of how the soil system behaves? It seems clear that any major new generation model will be more microbially explicit than CENTURY and its ilk, as argued by (Schmidt et al., 2011): "The way forward for global land models is to change their organizing principle from carbon pools with intrinsic decomposition rates (based on correlations with texture or litter quality, and modified by climate and land-use type) to more mechanistic representations of the stabilization processes that actually govern carbon dynamics and therefore the strength of climate feedbacks."

Additionally, in developing next generation models, we need to consider efficiency—does the new model offer predictions that are enough superior to existing models to justify adding complexity? As Brangarí et al. (2020) comment on their model of drying/rewetting: "It can be argued that a model of this complexity is likely to fit any data set thanks to the large number of parameters, but it could also capture the observed patterns for wrong reasons." Avoiding such equifinality issues (Marschmann et al., 2019) with a more complex model calls for testing it against an appropriate range of variables; not just output variables such as respiration and total microbial biomass but also internal pools and fluxes such as soil C pools and microbial growth. It's important to keep in mind that "biogeochemical models always require some process simplification, and those simplifications may not represent all relevant interactions … the level to which mechanistic detail needs to, or can, be included in land models remains unclear." (Riley et al., 2014). Riley et al. (2014) further argue that "Performing more sophisticated sensitivity analyses, parameter inversions, and perhaps developing reduced order models should allow a determination of the trade offs between increasing model complexity, parameter uncertainty, and model structural uncertainty."

In this paper I've identified several areas where new microbial models have been struggling over the last decade: notably the mechanisms of microbial action, carbon use efficiency, and priming. It seems likely that a new paradigm-forming soil C model would consider each of these phenomena carefully. Getting the role of the soil microbial biomass as an agent of decomposition "right" will likely be critical as it creates a multiplicative effect and thus, a model that is sensitive to parameters that regulate biomass. It seems likely that next generation models will emulate CORPSE or Millenial V2 in making some components of the SOM system sensitive to the size of the active microbial biomass, while other components may be less sensitive. Some such approach to limit the ability of the microbial biomass to drive a runaway positive feedback cycle is likely necessary. Reverse Michaelis-Menten kinetics can represent this effect phenomenologically but these other modeling approaches capture the pattern by capturing likely mechanisms. Particularly important is to recognize that abiotic reactions may be critical in regulating microbial access to SOM (Georgiou et al., 2021).

In parallel with these issues will be concerns over CUE. This is a vital parameter in microbial models because it regulates the size of the microbial biomass under different circumstances and so the size of the decomposer pool. The environmental variables that CUE is sensitive to will regulate how the entire decomposer system responds to environmental drivers—temperature influences over CUE appear to be particularly important (Pold et al., 2019). Finally, there is priming—the interactions among different substrates that may regulate the overall decomposition system; particularly important is exploring how fresh root carbon may influence the decomposition of intact, native SOM. Priming has been less considered than the previous issues, but may well be important to consider, particularly to get long-term SOM dynamics correct when vegetation is changing.

The last decade has seen great expansion in the development of microbial models to explain the dynamics of soil organic matter. This reflects the growth of a new generation of modelers who recognized that first-order models such as CENTURY and Roth-C had reached their limits, and that new models need to capture more complex spatial and temporal dynamics in soil systems; warming and changing water regimes call for models that can capture the more complex dynamics. It also reflects an integration between microbial ecology and whole-system biogeochemistry, although how much microbial ecology will be appropriate to include in whole-system biogeochemical models remains an open question. I hypothesize that we will develop alternate families of models—coarser models that have only a few microbial pools will dominate for large-scale application and for integrating into global biogeochemical models (e.g. MIMICS, Millennial, CORPSE), while models that elaborate the microbiology more extensively, such as DEMENT (Allison, 2012) or BAMS1 (Riley et al., 2014) will find application at the finer scales and for more targeted and short-term analyses. For each scale of model, we will develop a separate intellectual "Triangle" (Blankinship et al., 2018) that locks together the theory and measurements with the actual model. Having recognized that future biogeochemical models will be microbial, it becomes clear that the factors that regulate CUE and thus, the size of the microbial biomass, are critical in regulating the overall activity of microbial communities. More important than the speed of microbial action will be the fate of the products—are they respired or reprocessed into new microbial biomass. Finally, the mechanisms that regulate microbial access to substrates becomes vital. To what extent is access regulated by abiotic sorption/-desorption reactions on clay minerals or entrapment within soil aggregates? An important aspect of this is priming—do microbes have the energy they need to metabolize native SOM? Can they be fueled by fresh plant inputs? Or alternatively do fresh inputs repress attack on native SOM? Priming, thus, remains an active area of research, and one that has been poorly addressed by prior modeling efforts. New models are addressing various aspects of each of these phenomena, although unsurprisingly, there remains a lot of speculation about how best to capture the phenomena in ways that will have broad applicability. Developing new microbial models will thus be essential to integrating microbial ecology and biogeochemistry and to predicting how ecosystems will respond to ongoing environmental change.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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References

Abramoff, R., Xu, X., Hartman, M., Brien, S.O., Feng, W., Davidson, E., Finzi, A., Moorhead, D., Schimel, J., Torn, M., Mayes, M.A., 2017. The Millennial model : in

search of measurable pools and transformations for modeling soil carbon in the new century. Biogeochemistry 137, 51–71.
Abramoff, R.Z., Guenet, B., Zhang, H., Georgiou, K., Xu, X., Viscarra Rossel, R.A., Yuan, W., Ciais, P., 2022. Improved global-scale predictions of soil carbon stocks with Millennial Version 2. Soil Biology and Biochemistry 164, 108466. https://doi.org/10.1016/j.soilbio.2021.108466.
Allison, S.D., 2012. A trait-based approach for modelling microbial litter decomposition. Ecology Letters 15, 1058–1070.
Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience 3, 336–340.
Bernard, L., Basile-Doelsch, I., Derrien, D., Fanin, N., Fontaine, S., Guenet, B., Karimi, B., Marsden, C., Maron, P.A., 2022. Advancing the mechanistic understanding of the priming effect on soil organic matter mineralisation. Functional Ecology 36, 1355–1377.
Bingeman, C.W., Varner, J.E., Martin, W.P., 1953. The effect of the addition of organic materials on the decomposition of an organic soil. Soil Science Society of America Proceedings 17, 34–38.
Blankinship, J.C., Berhe, A.A., Crow, S.E., Druhan, J.L., Heckman, K.A., Keiluweit, M., Lawrence, C.R., Marín-Spiotta, E., Plante, A.F., Rasmussen, C., Schädel, C., Schimel, J.P., Sierra, C.A., Thompson, A., Wagai, R., Wieder, W.R., 2018. Improving understanding of soil organic matter dynamics by triangulating theories, measurements, and models. Biogeochemistry 140, 1–13.
Blazewicz, S.J., Schwartz, E., 2011. Dynamics of ^{18}O incorporation from $H_2^{18}O$ into soil microbial DNA. Microbial Ecology 61, 911–916.
Brangarí, A.C., Manzoni, S., Rousk, J., 2020. A soil microbial model to analyze decoupled microbial growth and respiration during soil drying and rewetting. Soil Biology and Biochemistry 148, 107871.
Brangarí, A.C., Manzoni, S., Rousk, J., 2021. The mechanisms underpinning microbial resilience to drying and rewetting – a model analysis. Soil Biology and Biochemistry 162, 108400.
Buckeridge, K.M., Creamer, C., Whitaker, J., 2022. Deconstructing the microbial necromass continuum to inform soil carbon sequestration. Functional Ecology 36, 1396–1410.
Chakrawal, A., Herrmann, A.M., Manzoni, S., 2021. Leveraging energy flows to quantify microbial traits in soils. Soil Biology and Biochemistry 155, 108169.
Chapman, S.J., Gray, T.R.G., 1986. Importance of cryptic growth, yield factors and maintenance energy in models of microbial growth in soil. Soil Biology and Biochemistry 18, 1–4.
Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Global Change Biology 19, 988–995.
Diamond, S., Andeer, P.F., Li, Z., Crits-Christoph, A., Burstein, D., Anantharaman, K., Lane, K.R., Thomas, B.C., Pan, C., Northen, T.R., Banfield, J.F., 2019. Mediterranean grassland soil C–N compound turnover is dependent on rainfall and depth, and is mediated by genomically divergent microorganisms. Nature Microbiology 4, 1356–1367.
Domeignoz-Horta, L.A., Pold, G., Liu, X.J.A., Frey, S.D., Melillo, J.M., DeAngelis, K.M., 2020. Microbial diversity drives carbon use efficiency in a model soil. Nature Communications 11, 1–10.
Fanin, N., Mooshammer, M., Sauvadet, M., Meng, C., Alvarez, G., Bernard, L., Bertrand, I., Blagodatskaya, E., Bon, L., Fontaine, S., Niu, S., Lashermes, G., Maxwell, T.L., Weintraub, M.N., Wingate, L., Moorhead, D., Nottingham, A.T., 2022. Soil enzymes in response to climate warming: mechanisms and feedbacks. Functional Ecology 36, 1378–1395.
Farina, R., Coleman, K., Whitmore, A.P., 2013. Modification of the RothC model for simulations of soil organic C dynamics in dryland regions. Geoderma 200–201, 18–30.
Fatichi, S., Manzoni, S., Or, D., Paschalis, A., 2019. A mechanistic model of microbially mediated soil biogeochemical processes: a reality check. Global Biogeochemical Cycles 33, 620–648.
Fu, X., Song, Q., Li, S., Shen, Y., Yue, S., 2022. Dynamic changes in bacterial community structure are associated with distinct priming effect patterns. Soil Biology and Biochemistry 169, 108671.
Fujita, Y., Witte, J.-P.M., van Bodegom, P.M., 2014. Incorporatingmicrobial ecology concepts intoglobal soil mineralization models to improve predictions of carbon and nitrogen fluxe. Global Biogeochemical Cycles 28, 223–238.
Fukasawa, Y., 2021. Ecological impacts of fungal wood decay types: a review of current knowledge and future research directions. Ecological Research 36, 910–931.
Georgiou, K., Malhotra, A., Wieder, W.R., Ennis, J.H., Hartman, M.D., Sulman, B.N., Berhe, A.A., Grandy, A.S., Kyker-Snowman, E., Lajtha, K., Moore, J.A.M., Pierson, D., Jackson, R.B., 2021. Divergent controls of soil organic carbon between observations and process-based models. Biogeochemistry 156, 5–17.
German, D.P., Weintraub, M.N., Grandy, A.S., Lauber, C.L., Rinkes, Z.L., Allison, S.D., 2011. Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. Soil Biology and Biochemistry 43, 1387–1397.
Geyer, K.M., Dijkstra, P., Sinsabaugh, R., Frey, S.D., 2019. Clarifying the interpretation of carbon use efficiency in soil through methods comparison. Soil Biology and Biochemistry 128, 79–88.
Goberna, M., Verdú, M., 2022. Cautionary notes on the use of co-occurrence networks in soil ecology. Soil Biology and Biochemistry 166, 108534.
Guo, X., Gao, Q., Yuan, M., Wang, G., Zhou, X., Feng, J., Shi, Z., Hale, L., Wu, Linwei, Zhou, A., Tian, R., Liu, F., Wu, B., Chen, L., Jung, C.G., Niu, S., Li, D., Xu, X., Jiang, L., Escalas, A., Wu, Liyou, He, Z., Van Nostrand, J.D., Ning, D., Liu, X., Yang, Y., Schuur, E.A.G., Konstantinidis, K.T., Cole, J.R., Penton, C.R., Luo, Y., Tiedje, J.M., Zhou, J., 2020. Gene-informed decomposition model predicts lower soil carbon loss due to persistent microbial adaptation to warming. Nature Communications 11, 4897.
Guseva, K., Darcy, S., Simon, E., Alteio, L.V., Montesinos-Navarro, A., Kaiser, C., 2022. From diversity to complexity: microbial networks in soils. Soil Biology and Biochemistry 169, 108604.
Hagerty, S.B., Allison, S.D., Schimel, J.P., 2022. Testing microbial models with data from a C glucose tracer experiment. Soil Biology and Biochemistry 172, 108781.
Hagerty, S.B., Allison, S.D., Schimel, J.P., 2018. Evaluating soil microbial carbon use efficiency explicitly as a function of cellular processes: implications for measurements and models. Biogeochemistry 140, 1–15.
Herron, P.M., Stark, J.M., Holt, C., Hooker, T., Cardon, Z.G., 2009. Microbial growth efficiencies across a soil moisture gradient assessed using 13C-acetic acid vapor and 15N-ammonia gas. Soil Biology and Biochemistry 41, 1262–1269.
Homyak, P.M., Blankinship, J.C., Slessarev, E.W., Schaeffer, S.M., Manzoni, S., Schimel, J.P., 2018. Effects of altered dry season length and plant inputs on soluble soil carbon. Ecology 99, 2348–2362.
Hu, J., Huang, C., Zhou, S., Kuzyakov, Y., 2022. Nitrogen addition to soil affects microbial carbon use efficiency: meta-analysis of similarities and differences in 13C and 18O approaches. Global Change Biology 28, 4977–4988.
Huang, Ye, Guenet, B., Ciais, P., Janssens, I.A., Soong, J.L., Wang, Y., Goll, D., Blagodatskaya, E., Huang, Yuanyuan, 2018. ORCHIMIC (v1.0), a microbe-mediated model for soil organic matter decomposition. Geoscientific Model Development 11, 2111–2138.
Hunt, K.A., von Netzer, F., Gorman-Lewis, D., Stahl, D.A., 2022. Microbial maintenance energy quantified and modeled with microcalorimetry. Biotechnology and Bioengineering 119, 2413–2422.
Jenkinson, D.S., 1990. The turnover of organic carbon and nitrogen in soil. Philosophical Transactions of the Royal Society of London - B 329, 361–368.
Jensen, A.E., Lohse, K.A., Crosby, B.T., Mora, C.I., 2014. Variations in soil carbon dioxide efflux across a thaw slump chronosequence in northwestern Alaska. Environmental Research Letters 9, 025001.
Joergensen, R.G., Wichern, F., 2018. Alive and kicking: why dormant soil microorganisms matter. Soil Biology and Biochemistry 116, 419–430.
Kaiser, C., Franklin, O., Richter, A., Dieckmann, U., Kaiser, C., 2015. Social dynamics within decomposer communities lead to nitrogen retention and organic matter build-up in soils. Nature Communications 6, 8960.
Kuzyakov, Y., 2002. Factors affecting rhizosphere priming effects. Journal of Plant Nutrition and Soil Science 165, 382–396.
Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry 32, 1485–1498.
Lawrence, C.R., Neff, J.C., Schimel, J.P., 2009. Does adding microbial mechanisms of decomposition improve soil organic matter models ? A comparison of four models using data from a pulsed rewetting experiment. Soil Biology & Biochemistry Biochemistry 41, 1923–1934.
Manzoni, S., Moyano, F., Kätterer, T., Schimel, J., 2016. Modeling coupled enzymatic and solute transport controls on decomposition in drying soils. Soil Biology and Biochemistry 95, 275–287.
Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93, 930–938.
Marschmann, G.L., Pagel, H., Kügler, P., Streck, T., 2019. Equifinality, sloppiness, and emergent structures of mechanistic soil biogeochemical models. Environmental Modelling & Software 122, 104518.
Monod, J., 1949. The growth of bacterial cultures. Annual Review of Microbiology 3, 371–394.
Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. Ecological Monographs 76, 151–174.
Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biology and Biochemistry 59, 72–85.
Na, M., Hicks, L.C., Zhang, Y., Shahbaz, M., Sun, H., Rousk, J., 2022. Semi-continuous C supply reveals that priming due to N-mining is driven by microbial growth demands in temperate forest plantations. Soil Biology and Biochemistry 173, 108802.
Parton, W., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51, 1173–1179.
Parton, W.J., Hartman, M., Ojima, D., Schimel, D., 1998. DAYCENT and its land surface submodel: description and testing. Global and Planetary Change 19, 35–48.
Pold, G., Domeignoz-Horta, L.A., DeAngelis, K.M., 2020. Heavy and wet: the consequences of violating assumptions of measuring soil microbial growth efficiency using the 18O water method. Elementa 8, 20.
Pold, G., Sistla, S.A., Deangelis, K.M., 2019. Metabolic tradeoffs and heterogeneity in microbial responses to temperature determine the fate of litter carbon in simulations of a warmer world. Biogeosciences 16, 4875–4888.
Qiao, Y., Wang, J., Liang, G., Du, Z., Zhou, J., Zhu, C., Huang, K., Zhou, X., Luo, Y., Yan, L., Xia, J., 2019. Global variation of soil microbial carbon-use efficiency in relation to growth temperature and substrate supply. Scientific Reports 9, 1–8.
Riley, W.J., Maggi, F., Kleber, M., Torn, M.S., Tang, J.Y., Dwivedi, D., Guerry, N., 2014. Long residence times of rapidly decomposable soil organic matter: application of a multi-phase, multi-component, and vertically resolved model (BAMS1) to soil carbon dynamics. Geoscientific Model Development 7, 1335–1355.
Schimel, J., Becerra, C.A., Blankinship, J., 2017. Estimating decay dynamics for enzyme activities in soils from different ecosystems. Soil Biology and Biochemistry 114, 5–11.
Schimel, J., Weintraub, M.N., Moorhead, D., 2022. Estimating microbial carbon use efficiency in soil: isotope-based and enzyme-based methods measure fundamentally

different aspects of microbial resource use. Soil Biology and Biochemistry 169, 108677.
Schimel, J.P., 2018. Life in dry soils: effects of drought on soil microbial communities and processes. Annual Review of Ecology, Evolution, and Systematics 49, 409–432.
Schimel, J.P., Weintraub, M.N., 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry 35, 549–563.
Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.
Shi, Z., Crowell, S., Luo, Y., Moore III., B., 2018. Model structures amplify uncertainty i predicted soil carbon responses to climate change. Nature Communications 9, 2171.
Sinsabaugh, R.L., Turner, J.M., Talbot, J., Waring, B.G., Powers, J.S., Kuske, C.R., Moorhead, D.L., Follstad Shah, J.J., 2016. Stoichiometry of microbial carbon use efficiency in soils. Ecological Monographs 86, 172–189.
Sistla, S.A., Rastetter, E.B., Schimel, J.P., 2014. Responses of a tundra system to warming using SCAMPS: a stoichiometrically coupled, acclimating microbeplantsoil model. Ecological Monographs 84, 151–170.
Slessarev, E.W., Schimel, J.P., 2020. Partitioning sources of CO_2 emission after soil wetting using high-resolution observations and minimal models. Soil Biology and Biochemistry 143, 107753.
Sokol, N.W., Slessarev, E., Marschmann, G.L., Nicolas, A., Blazewicz, S.J., Brodie, E.L., Firestone, M.K., Foley, M.M., Hestrin, R., Hungate, B.A., Koch, B.J., Stone, B.W., Sullivan, M.B., Zablocki, O., Trubl, G., McFarlane, K., Stuart, R., Nuccio, E., Weber, P., Jiao, Y., Zavarin, M., Kimbrel, J., Morrison, K., Adhikari, D., Bhattacharaya, A., Nico, P., Tang, J., Didonato, N., Paša-Tolić, L., Greenlon, A., Sieradzki, E.T., Dijkstra, P., Schwartz, E., Sachdeva, R., Banfield, J., Pett-Ridge, J., 2022. Life and death in the soil microbiome: how ecological processes influence biogeochemistry. Nature Reviews Microbiology 20, 415–430.
Sainte-Marie, J., Barrandon, M., Saint-André, L., Gelhaye, E., Martin, F., Derrien, D., 2021. C-STABILITY an innovative modeling framework to leverage the continuous representation of organic matter. Nature Communications 12, 1–13.
Sugai, S.F., Schimel, J.P., 1993. Decomposition and biomass incorporation of ^{14}C-labeled glucose and phenolics in taiga forest floor: effect of substrate quality, successional state, and season. Soil Biology and Biochemistry 25, 1379–1389.
Sulman, B.N., Phillips, R.P., Oishi, A.C., Shevliakova, E., Pacala, S.W., 2014. Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO_2. Nature Climate Change 4, 1099–1102.
Tang, J.Y., 2015. On the relationships between the Michaelis-Menten kinetics, reverse Michaelis-Menten kinetics, equilibrium chemistry approximation kinetics, and quadratic kinetics. Geoscientific Model Development 8, 3823–3835. https://doi.org/10.5194/gmd-8-3823-2015.
Tang, J.-Y., Riley, W.J., 2017. SUPECA kinetics for scaling redox reactions in networks of mixed substrates and consumers and an example application to aerobic soil respiration. Geoscientific Model Development 10, 3277–3295.
Thammahong, A., Puttikamonkul, S., Perfect, J.R., Brennan, R.G., Cramer, R.A., 2017. Central role of the trehalose biosynthesis pathway in the pathogenesis of human fungal infections: opportunities and challenges for therapeutic development. Microbiology and Molecular Biology Reviews 81, e00053-16.
Todd-Brown, K., Hopkins, F., Kivlin, S., Talbot, J.M., Allison, S.D., 2011. A framework for representing microbial decomposition in coupled climate models. Biogeochemistry 109, 19–33.
Treseder, K.K., Balser, T.C., Bradford, M.A., Brodie, E.L., Dubinsky, E.A., Eviner, V.T., Hofmockel, K.S., Lennon, J.T., Levine, U.Y., MacGregor, B.J., Pett-Ridge, J., Waldrop, M.P., 2012. Integrating microbial ecology into ecosystem models: challenges and priorities. Biogeochemistry 109, 7–18.
Treseder, K.K., Berlemont, R., Allison, S.D., Martiny, A.C., 2018. Nitrogen enrichment shifts functional genes related to nitrogen and carbon acquisition in the fungal community. Soil Biology and Biochemistry 123, 87–96.
Wang, G., Jagadamma, S., Mayes, M.A., Schadt, C.W., Steinweg, M.J., Gu, L., Post, W.M., 2015. Microbial dormancy improves development and experimental validation of ecosystem model. The ISME Journal 9, 226–237.
Wieder, W., Boehnert, J., Bonan, G., 2014a. Evaluating soil biogeochemistry parameterizations in Earth system models with observations. Global Biogeochemical Cycles 28, 211–222.
Wieder, W.R., Bonan, G.B., Allison, S.D., 2013. Global soil carbon projections are improved by modelling microbial processes. Nature Climate Change 3, 1–4.
Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Bonan, G.B., 2014b. Integrating microbial physiology and physio-chemical principles in soils with the MIcrobial-MIneral Carbon Stabilization (MIMICS) model. Biogeosciences 11, 3899–3917.
Xu, Y., Seshadri, B., Sarkar, B., Wang, H., Rumpel, C., Sparks, D., Farrell, M., Hall, T., Yang, X., Bolan, N., 2018. Biochar modulates heavy metal toxicity and improves microbial carbon use efficiency in soil. Science of the Total Environment 621, 148–159.
Yang, R.M., Zhu, C.M., Zhang, X., Huang, L.M., 2022. A preliminary assessment of the space-for-time substitution method in soil carbon change prediction. Soil Science Society of America Journal 86, 423–434.
Zhang, Q., Qin, W., Feng, J., Zhu, B., 2022. Responses of soil microbial carbon use efficiency to warming: review and prospects. Soil Ecology Letters. https://doi.org/10.1007/s42832-022-0137-3.
Zheng, Q., Hu, Y., Zhang, S., Noll, L., Böckle, T., Richter, A., Wanek, W., 2019. Growth explains microbial carbon use efficiency across soils differing in land use and geology. Soil Biology and Biochemistry 128, 45–55.