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A framework for representing microbial decomposition in coupled climate models

Katherine E. O. Todd-Brown · Francesca M. Hopkins · Stephanie N. Kivlin · Jennifer M. Talbot · Steven D. Allison

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Abstract Accurate prediction of future atmospheric CO_2 concentrations is essential for evaluating climate change impacts on ecosystems and human societies. One major source of uncertainty in model predictions is the extent to which global warming will increase atmospheric CO_2 concentrations through enhanced microbial decomposition of soil organic carbon. Recent advances in microbial ecology could help reduce this uncertainty, but current global models do not represent direct microbial control over decomposition. Instead, all of the coupled climate models reviewed in the most recent Intergovernmental Panel on Climate Change (IPCC) report assume that decomposition is a first-order decay process, proportional to the size of the soil carbon pool. Here we argue for the development of a new generation of models that link decomposition directly to the size and activity of microbial communities in coupled global models. This process begins with the formulation and validation of fine-scale models that capture fundamental microbial mechanisms without excessive mathematical complexity. These mechanistic models must then be scaled up through an aggregation process and validated at ecosystem to global scales prior to incorporation into global climate models (GCMs). Parameterizing microbial models at the global scale is challenging because some microbial properties such as in situ extracellular enzyme activities are very difficult to measure directly. New parameter fitting procedures may therefore be needed to infer the values of important microbial variables. Validating decomposition models at the global scale is also a challenge, and has not yet been accomplished with the land carbon models embedded in current GCMs. Fortunately new global datasets on soil carbon stocks and fluxes offer promising opportunities to validate both existing land carbon models and new microbial models. If challenges in scaling, parameterization, and validation can be overcome, a new generation of microbially-based decomposition models could substantially improve predictions of carbon–climate feedbacks in the Earth system. Development of new models structures would also reduce any bias due to the assumption of first-order decomposition across all of the models currently referenced in reports of the IPCC.

K. E. O. Todd-Brown · F. M. Hopkins · S. D. Allison
Department of Earth System Science, University of California, Irvine, Irvine, CA 92697, USA

S. N. Kivlin · J. M. Talbot · S. D. Allison (✉)
Department of Ecology and Evolutionary Biology, University of California, Irvine, 321 Steinhaus, Irvine, CA 92697, USA
e-mail: allisons@uci.edu

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Introduction

Citizens and policymakers depend on mathematical models to predict the impact of greenhouse gas emissions on climate and human societies. Global-scale models that generate these predictions have advanced tremendously, and now simulate the coupling between biophysical processes and climate (Friedlingstein et al. 2006; Cox et al. 2000), enabling us to examine potential feedbacks between the biosphere and the climate system. Nonetheless, the magnitude and direction of these feedbacks remain unclear (Knutti et al. 2008). The expected amount of CO_2 in the atmosphere at the end of the twenty-first century varies by up to 200 ppm due to uncertainties in the land carbon (C) cycle (Friedlingstein et al. 2006). This difference translates into a global temperature uncertainty of $\sim$1.5°C (Meir et al. 2006).

Reducing uncertainty in carbon–climate model projections can be accomplished by modeling fundamental biophysical processes and using relevant data for model parameterization and validation. In coupled global climate models (GCMs), the land C cycle component must accurately represent sinks and sources of CO_2, which are primarily driven by plants and microorganisms. While the vegetation component of land C models has developed rapidly over the past several decades (e.g. Foley et al. 1996; Sitch et al. 2008), there has been very little change in the representation of decomposition processes. Models of the global C cycle have not kept pace with rapid advances in the ecology of microbial communities that primarily drive decomposition (Chapin et al. 2009). This knowledge gap is potentially problematic because decomposition releases ten times more CO_2 to the atmosphere than human-caused emissions (Schlesinger 1997). Furthermore, soils store >2,300 Pg C, nearly four times the amount of C in plant biomass (Jobbágy and Jackson 2000). Therefore, even small changes in soil C turnover could have large consequences for atmospheric CO_2 concentrations and the stability of the global climate system.

Microbial communities of bacteria, fungi, and archaea control the rates of C and nutrient flux in nearly all terrestrial ecosystems (Sinsabaugh 1994; Schlesinger 2004; Schimel 1995). As a result, microbes are expected to mediate decomposition responses to global changes, such as climate warming (Bardgett et al. 2008). Changing climatic conditions will affect the physiology of microbial communities, which may lead to changes in the rates of biogeochemical processes under microbial control (Bradford et al. 2008; Malcolm et al. 2008). It is therefore essential to account for the response of microbial communities to environmental parameters in order to predict feedbacks between global change and decomposition processes.

Because microbes affect biogeochemical feedbacks to climate change, and because the predictions of coupled GCMs are critical for climate policy, there have been many calls to integrate microbial communities into broad-scale models (Schimel 2001; McGuire and Treseder 2010; Strickland et al. 2009; Allison and Martiny 2008). Such an integration would involve direct control of biogeochemical rates by microbial populations, and ultimately allow changes in microbial community size and composition to affect these rates (Allison and Martiny 2008). This integration has already begun at small scales (Treseder et al. 2011a), but has not yet influenced the structure of coupled climate models at the global scale (Ostle et al. 2009). Therefore, our objective is to provide a rationale for directly representing microbes in coupled GCMs, and to describe a framework for scaling, parameterization, and validation of microbial models.

Carbon cycling in current coupled GCMs

Current models of global climate contain land, ocean, and atmospheric submodels that are mathematically coupled (Friedlingstein et al. 2006). Energy and mass exchange between the submodels, and climate change in the atmosphere can affect the net flux of C from the land surface and the ocean. Conversely, the biophysical properties of the land and ocean affect the absorption of radiation and the emission of greenhouse gases, thereby influencing atmospheric temperature and moisture. When submodels are coupled, hundreds of parameters and processes can interact to generate ecosystem feedbacks to climate. This complexity means that modelers must often distill fundamental biophysical processes down to a relatively small set of parameters. Furthermore, it is desirable if these parameters are readily available from empirical studies.

Although a number of model components are responsible for uncertainty in climate predictions, recent model comparisons suggest that a substantial fraction of this uncertainty arises from land submodels (Friedlingstein et al. 2006; Cadule et al. 2010). Specifically, it is unclear how much CO_2 will be emitted from the land surface as the climate warms, and therefore unclear how strong the climate–carbon cycle feedback will become globally. Some of this uncertainty may be attributed to the vegetation component of the land models, which influences atmospheric CO_2 directly through photosynthesis and autotrophic respiration (Friedlingstein and Prentice 2010; Friedlingstein et al. 2006; Matthews et al. 2007). However, the soil component of land models is equally or more likely to contribute to this uncertainty given the large stocks of C sequestered in soil (Jobbágy and Jackson 2000), and the relatively poor understanding of soil heterotrophic processes relative to plant photosynthesis.

The soil biogeochemical models embedded in GCMs differ in structure, but all share some important commonalities (Table 1). We focus here on models that were used in the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report, or will be used in the Fifth Assessment Report. These models vary widely in the number of soil C pools they represent, ranging from one to nine. Soil C is often separated into different pools based on recalcitrance, which is an estimate of resistance to microbial degradation. The pools may distinguish litter from soil organic matter fractions, and at least one model (Biome-BGC) includes a coarse woody debris pool. In all of the models, the production of CO_2 from the organic pools depends on soil moisture and temperature, although the exact form of the temperature relationship varies somewhat. Most models use a constant Q_{10} value (the factor by which a biological process increases in rate for every 10°C change in temperature), but IBIS and Sim-CYCLE use an Arrhenius relationship, and VEGAS uses lower Q_{10} values for soil C pools with longer turnover times.

A key similarity across all of the models is the representation of organic matter decomposition as a first-order process, meaning that C loss and CO_2 production from each pool are directly proportional to the pool size (Fig. 1a). As an example of a

Table 1 Land models and soil carbon representations used in coupled climate models (Friedlingstein et al. 2006)

Land carbon model	Coupled model	Soil carbon model structure	References
TRIFFID	HadCM3LC, UVic-2.7	Single C pool with moisture and Q_{10} temperature responses	Cox (2001)
SLAVE	IPSL-CM2C	Two litter pools, fast and slow soil C pools based on CENTURY model with moisture and Q_{10} temperature responses	Friedlingstein et al. (1995)
ORCHIDEE-STOMATE	IPSL-CM4-LOOP	Four litter pools; fast, slow, passive soil C pools with moisture and Q_{10} temperature responses	Krinner et al. (2005)
LSM-CASA	CSM-1	Nine soil C pools with soil moisture and transpiration control and Q_{10}/climate temperature responses	Potter et al. (1993)
JSBACH-BETHY	MPI	Two soil C pools with moisture and Q_{10} temperature responses	Knorr (2000)
IBIS	LNLL	Litter and soil C pools with soil water-filled pore space controls and Arrhenius temperature responses	Foley et al. (1996)
Sim-CYCLE	FRCGC	Two soil C pools with soil moisture and Arrhenius temperature responses	Ito and Oikawa (2002)
VEGAS	UMD	Three soil C pools with different Q_{10} temperature responses	Zeng et al. (2005)
LPJ	CLIMBER2-LPJ, BERN-CC	Above and belowground litter pools; 2 soil C pools with moisture and modified Q_{10} temperature responses	Sitch et al. (2003)
CLM-CN-Biome-BGC	CESM	Coarse woody debris, 3 litter, and 3 soil C pools that cascade with moisture and Q_{10} temperature responses	Thornton and Rosenbloom (2005)

relatively simple model with this structure, the JSBACH-BETHY land C model (Knorr 2000) represents soil heterotrophic respiration (R) as:

$$R = f_a k_f C_f + k_s C_s \quad (1)$$

where C_f and C_s are the sizes of fast and slow turnover pools of soil C, f_a is a partition coefficient, and k_f and k_s are the decay rate parameters for each of the pools. The decay rates are a function of moisture and temperature:

$$k_f = \alpha^{\kappa} Q_{10}^{T/10} / \tau_f \quad (2)$$

and

$$k_s = \alpha^{\kappa} Q_{10}^{T/10} / \tau_s \quad (3)$$

where α and κ are moisture sensitivity parameters, T is temperature, and τ is the turnover time of each C pool. This representation of decay as a first-order process is typical of current GCMs and contrasts with the second-order structure of many small-scale models (e.g. Schimel and Weintraub 2003), whereby decay rates depend on both substrate C and microbial biomass (or enzyme) pools.

Challenges with current models

The complete absence of second-order processes in popular models of soil organic matter turnover is potentially problematic because it is inconsistent with current understanding of decomposition mechanisms. In particular, soil C decomposition depends on the activity of biological communities dominated by microbes (Schimel and Weintraub 2003). Since most plant litter and soil organic matter contains a large fraction of polymeric substances (Kögel-Knabner 2002), some microbes produce extracellular enzymes to degrade complex organic matter prior to uptake and conversion to microbial biomass and CO_2 (Sinsabaugh et al. 1991; Burns 1978). Other microbes may specialize on metabolism of simple organic molecules that do not require enzymatic degradation (Hanson et al. 2008). Furthermore, we know that microbial communities responsible for decomposition contain vast levels of genetic and metabolic diversity (Tringe et al. 2005). Thus, current knowledge dictates that decomposition rates depend on the size and composition of the decomposer microbe pool, in addition to the size of the soil C pool. Although some landscape-level models include a microbial pool or analogous labile soil fraction (Parton et al. 1988), these pools are effectively C substrates and do not influence the rate constants of other pools.

Assuming first-order dynamics for soil C turnover means that changes in microbial community composition due to evolutionary or ecological mechanisms, or adaptation of microbial physiology to new conditions, cannot be easily represented in current models. Recent evidence from empirical studies suggests that microbial abundance and community composition are highly sensitive to environmental changes, such as warming, N addition, and altered precipitation (Allison and Martiny 2008; Hawkes et al. 2011). Furthermore, microbial communities may shift in composition, adapt physiologically, or evolve in response to new conditions, such as warmer temperatures, thereby limiting the decomposition response to climate change (Bradford et al. 2008; Malcolm et al. 2008; Andrews et al. 2000; Lipson and Schmidt 2004). Although the importance of these biological responses may vary across systems, current biogeochemical models do not account for them at all.

First-order models assume that the activity of decomposers only depends on the built-in relationships with temperature and moisture. This assumption implies that the biomass and composition of the decomposer community can be ignored in favor of directly specifying the outcome of temperature and moisture effects on the rate of decomposition. If photosynthesis were analogous to decomposition in current models, then gross primary productivity would be proportional to total plant biomass with a rate constant dependent on variables like surface temperature and soil moisture. Such a coarse representation would ignore vegetation community dynamics, variation in leaf traits, and the leaf-level biochemical mechanisms known to govern photosynthetic rates. GCMs now include dynamic vegetation models that account for fine-scale controls over photosynthesis and plant respiration (Friedlingstein et al. 2006; Sitch et al. 2008). In contrast, microbial community structure, physiology, and enzymatic mechanisms are omitted from these models.

Another issue with first-order models is that they cannot account for priming effects, whereby the addition of fresh, microbially-accessible C leads to

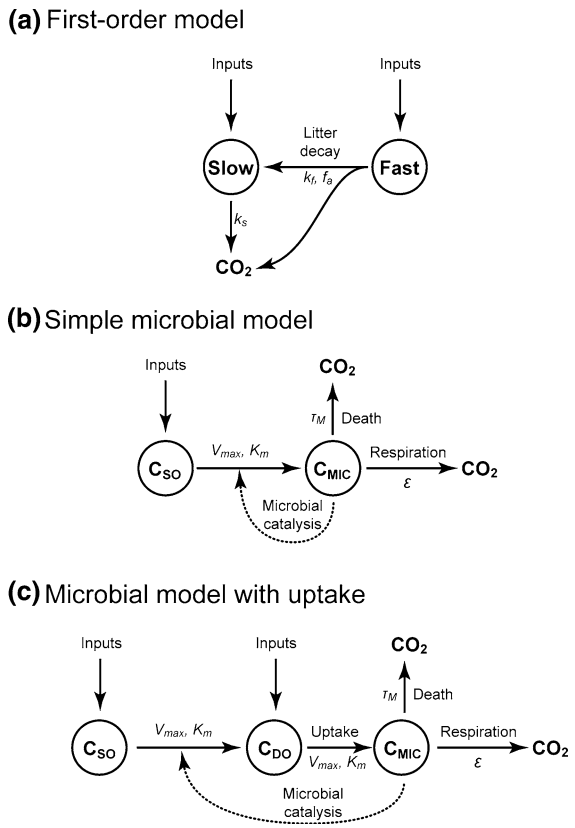

Fig. 1 Structures for models based on **a** first-order decay with slow and fast soil carbon pools from Knorr (2000), **b** microbially-catalyzed decay with soil organic carbon (C_{SO}) and microbial (C_{MIC}) pools, and **c** microbially-catalyzed decay with direct uptake from a dissolved organic carbon (C_{DO}) pool. Parameters are shown in *italicized text*

the loss of native soil C (Kuzyakov et al. 2000). This effect is important for modeling C dynamics because climate warming may alter C substrate inputs to soil through increased decomposition rates and changes in plant community composition, productivity, and belowground allocation (Saleska et al. 2002; Raich et al. 2006). Changing substrate availability is only coarsely represented in current models, which are not able to account for the priming effect (Wutzler and Reichstein 2008; Fontaine and Barot 2005).

There are several reasons why influential models of soil C cycling do not include microbial controls on decomposition rates. Many of these models were developed in the 1980s and 1990s, prior to the widespread use of molecular approaches to characterize the diversity and function of microbial communities. Furthermore, assuming that decomposition is a first-order process may be reasonable if microbial communities are relatively stable in biomass and functional composition in the face of environmental change. Indeed, this assumption may have been appropriate for models that were validated against empirical data (Smith et al. 1997; Parton et al. 1988). However, these empirical tests were often conducted in specific geographical regions over relatively short time intervals, conditions which may have limited applicability at global scales. Furthermore, the structure and physiology of microbial communities may vary with climate, even on seasonal timescales (Dumbrell et al. 2011; Bradford et al. 2008). Thus, simplifying assumptions that were reasonable during model development and testing may need to be reconsidered in models of global environmental change.

The potential drawbacks of modeling decomposition as a first-order process are particularly pressing given that all of the models used in the most recent IPCC assessment use this approach. One way the IPCC estimates uncertainty in model predictions is to compare the variation in outputs from independent models (IPCC 2007). Including at least some models with second-order dynamics representing microbial control would increase the diversity of model structures and predictions. Such an effort would help prevent biases that could arise from averaging the predictions of an ensemble of models that all make the same first-order assumptions (Knutti et al. 2008).

Models with microbial control over decomposition

At the microbial scale, a number of models have been developed to capture the biological mechanisms underlying decomposition (e.g. Fontaine and Barot 2005; Schimel and Weintraub 2003; Allison 2005; Vetter et al. 1998; Lawrence et al. 2009; Moorhead and Sinsabaugh 2006). Like the land C models in GCMs, these microbial models have diverse structures, and it is not yet clear which (if any) are most appropriate for scaling up to the global level. Therefore our approach here is to describe generic microbial models that illustrate some of the parameters and processes that may be important in a mechanistic model of soil C dynamics. For example, one simple model of microbial control over decomposition with

second-order dynamics can be constructed by multiplying a proportionality constant (V) by the microbial biomass (C_{MIC}) and a single, homogenous pool of soil organic C substrate (C_{SO}). The units for V could be $m^2\ s^{-1}\ g^{-1}$ microbial biomass, and pools such as C_{MIC} and C_{SO} could be in units of g m^{-2}:

$$\frac{dC_{SO}}{dt} = V \cdot C_{MIC} \cdot C_{SO} \quad (4)$$

However, Schimel and Weintraub (2003) found that this system was unstable because the microbial biomass either crashes or rapidly consumes all of the soil C substrate. To make the system reach equilibrium, they formulated the decomposition rate as a saturating function of microbial enzyme concentration. Allison et al. (2010) found that the decomposition rate would also stabilize if it was a saturating function of substrate concentration, according to the Michaelis–Menten equation. Whether rate equations include microbial biomass or enzyme levels is probably not critical, since enzyme production is tightly coupled to microbial biomass in both models.

A model with stable equilibria that captures microbial mechanisms is shown in Fig. 1b and requires four parameters (Table 2). In this model, CO_2 is respired (R) directly from microbial biomass rather than from the soil C pools:

$$R = \frac{V_{max} \cdot C_{MIC} \cdot C_{SO} \cdot (1-\varepsilon)}{K_m + C_{SO}} + C_{MIC} \cdot \tau_M \quad (5)$$

This model is still a simplification of microbial decomposition because there is only one microbial biomass pool and one soil organic C pool. Although there is no explicit pool for microbial extracellular enzymes, decomposition of C_{SO} is assumed to be an enzymatic process that follows Michaelis–Menten kinetics, where V_{max} is the maximum potential decomposition rate (in units such as g substrate $s^{-1}\ g^{-1}$ microbial biomass) and K_m is the half-saturation constant (in units of g m^{-2}). This assumption implies that enzymes are physically attached to microbial cell walls or turn over rapidly relative to microbial biomass. Enzyme pools would then be closely linked to microbial biomass, as observed in some field studies (Waldrop et al. 2000).

The model in Eq. 5 also assumes that microbes are adapted for efficient uptake, so they assimilate all products of enzymatic degradation and convert them to biomass or CO_2. Assimilation is partitioned according to a C use efficiency parameter ε. Biomass turnover is first-order with rate τ_M, and all dead biomass is converted into CO_2. This formulation assumes that dead microbial biomass is relatively labile (Jenkinson 1976); however, microbial biomass

Table 2 Comparison of model structures adapted from Knorr (2000) and Allison et al. (2010)

	First-order	Microbial	Microbial + uptake
Pools	2	2	3
Base parameters	(1) k_f: fast pool decay constant (2) k_s: slow pool decay constant (3) f_a: partitioning of fast pool decay	(1) V_{max}: max decay per unit microbial biomass (2) K_m: half saturation constant for microbial decay (3) ε: carbon use efficiency for assimilation (4) τ_M: Microbial death rate	(1–4) Same as microbial model (5) V_{max} for uptake (6) K_m for uptake
Additional temperature response parameters	(1) Q_{10} (same for both pools)	(1) E_a: activation energy (2) m_{Km}: slope parameter for K_m (3) m_ε: slope parameter for ε	(1–3) Same as microbial model (4) $E_{a\text{up}}$ for uptake (5) $m_{Km\text{up}}$: slope parameter for uptake $K_{m\text{up}}$
Additional moisture response parameters[a]	(1) α: water stress factor (2) κ: exponent for α	(1) α: moisture limitation parameter for V_{max}	(1) α: moisture limitation factor for V_{max} (2) α_{up}: moisture limitation factor for uptake V_{maxup}

[a] Not included in original microbial models

is increasingly recognized as a source of stabilized C in soils (Sutton and Sposito 2005; von Lützow et al. 2006). This stabilization process could be represented by multiplying microbial turnover by the fraction of dead biomass that re-enters the soil organic C pool, but accurate estimates of this fraction will require additional empirical studies (Liang et al. 2011).

Including explicit microbial parameters provides the opportunity to mechanistically represent the effect of abiotic variables on decomposition. The key advance here is that abiotic variables may independently affect microbial biomass and microbial activity. In current models, temperature and moisture are assumed to affect only activity (Fig. 1a). Microbial respiration is assumed to increase exponentially with temperature, an assumption that is supported by numerous laboratory studies (Lloyd and Taylor 1994; Davidson et al. 2006). However, temperature could also have direct and independent effects on microbial biomass. Therefore, biomass-specific respiration would increase, but community-level respiration could be mediated by increases or decreases in microbial biomass with temperature (Allison et al. 2010).

Our simple model can incorporate functions describing the environmental dependence of key biochemical parameters. For instance, representing climate effects through $V_{\max}$ and K_m makes it unnecessary to specify decay constants (k-values) in the decomposition model because climate responses become an emergent property of enzyme–substrate interactions (Davidson and Janssens 2006). The $V_{\max}$ parameter represents the proportionality constant between enzyme concentration and process rate (hydrolysis, uptake, respiration, etc.). This parameter has a well-established dependence on temperature as defined by the Arrhenius equation, which has an exponential form:

$$V_{\max} = V_{\max 0} \cdot \alpha \cdot e^{-\frac{E_a}{rT}} \tag{6}$$

where $V_{\max 0}$ is a pre-exponential coefficient, E_a is the activation energy for the reaction, and r is the ideal gas constant. The activation energy represents the temperature sensitivity and biochemical resistance of the substrate to catalysis. $V_{\max}$ can also respond to soil moisture through a parameter α, which would decline at lower soil water potentials (Davidson et al. 1998).

The temperature responses of K_m and ε are uncertain, and almost nothing is known of their moisture responses. There is some evidence from animal physiology literature that enzyme K_m values tend to increase with temperature, thereby reducing affinity for substrate and slowing catalysis (Hochachka and Somero 2002). K_m has also been hypothesized to increase with temperature in soil, and modeling studies suggest that this effect could offset the positive temperature dependence of $V_{\max}$, yielding no net effect of warming on decomposition rates (Davidson and Janssens 2006; Davidson et al. 2006). The offset is only important at low substrate concentrations, but concentrations of individual substrates may be relatively low due to the large diversity of chemical compounds present in soil (German et al. 2011). Declines in K_m with increasing temperature could be exacerbated by concurrent reductions in soil moisture and productivity that reduce effective substrate availability for enzymes (Davidson and Janssens 2006). Therefore, we suggest representing K_m for extracellular enzymes as a linear function of temperature with slope m_{Km} and intercept K_{m0}:

$$K_m = K_{m0} + m_{Km} \cdot \mathrm{T} \tag{7}$$

This formulation allows substrate availability to modulate the effect of temperature on microbial respiration: when substrate concentration is high, the temperature effect on $V_{\max}$ will predominate, whereas under low substrate concentrations, the temperature effect on K_m will partly cancel the increase in $V_{\max}$. Indeed, this effect has been confirmed experimentally, and may partly explain the large variation in observations of Q_{10} (Gershenson et al. 2009).

Although data are limited, there is some evidence that ε declines with temperature increase (Devêvre and Horwath 2000; Steinweg et al. 2008; van Ginkel et al. 2000; Wetterstedt and Ågren 2011). The simplest way to represent this relationship would be a linear equation with ε dependent on a slope parameter m_ε and an intercept ε_0:

$$\varepsilon = \varepsilon_0 - m_\varepsilon \cdot \mathrm{T} \tag{8}$$

A similar approach could be used to represent the effects of nutrients or other environmental variables on microbial decomposition. Biochemical and physiological parameters of the microbial community can be functions of these variables, as we have suggested with temperature and moisture. For example, the role of

nitrogen (N) in regulating ecosystem-climate feedbacks has recently been recognized (Sokolov et al. 2008; Thornton et al. 2007), and N responses could also be represented for microbial parameters. When N is more available, microbes might produce C-degrading enzymes that target more recalcitrant compounds (Treseder et al. 2011b) or have lower K_m values (M. Stone and S. D. Allison, unpublished data). In addition, microbes decomposing organic matter pools with C:N ratios above a critical threshold (Manzoni et al. 2010) would be expected to increase their C use efficiencies as N availability increases (Schimel and Weintraub 2003; Ågren et al. 2001). These efficiencies could be calculated for microbes degrading any organic matter pool with a known C:N ratio in GCMs that account for N dynamics. Although we are discussing N here as an illustrative example, the microbial responses to other environmental drivers could be included in our framework as more empirical data become available. For instance, microbial parameters could respond to P availability in addition to N if P dynamics are included in GCMs.

We have described a simple model of microbial decomposition as a function of environmental parameters, but additional complexity could improve model realism and flexibility. Litter and soil C pools could be added to represent chemical heterogeneity in soil organic matter, and the number of microbial biomass or enzyme pools could be increased to represent functional diversity in decomposer communities. For example, a more realistic model could include extracellular production of a dissolved organic C (C_{DO}) pool that microbes take up with membrane transport proteins (Fig. 1c; Table 2). This model requires additional V_{maxup} and K_{mup} parameters to describe uptake rate as a saturating function of C_{DO} concentration:

$$\frac{dC_{DO}}{dt} = \frac{V_{max} \cdot C_{MIC} \cdot C_{SO}}{K_m + C_{SO}} - \frac{V_{maxup} \cdot C_{MIC} \cdot C_{DO}}{K_{mup} + C_{DO}} + C_{in} \quad (9)$$

where C_{in} represents the input of C to the C_{DO} pool. Respiration is then a function of microbial uptake and turnover:

$$R = \frac{V_{maxup} \cdot C_{MIC} \cdot C_{DO} \cdot (1 - \varepsilon)}{K_{mup} + C_{DO}} + C_{MIC} \cdot \tau_M \quad (10)$$

The tradeoff is that this model requires at least five more parameters than our simple model when the temperature responses of the uptake parameters are represented. Adding a second soil organic C pool would add two additional kinetic parameters if we were to assume constant temperature and moisture sensitivity for both pools.

Microbial diversity could be introduced by adding a second pool of microbial biomass to degrade one or more soil C pools. This approach was pioneered by Moorhead and Sinsabaugh (2006), who proposed a model of litter decomposition based on the succession of three functional groups of microbes with different enzymatic capabilities. The model was able to replicate qualitative trends in litter decomposition and response to N addition, but required at least 15 parameters to describe C metabolism without climate controls. Even in our simple model, adding a second functional group of microbes would further increase the number of parameters by at least three if uptake and C use efficiency differed across microbial groups.

Choosing an appropriate level of model complexity to represent the heterogeneity of soil C is clearly a challenge for microbial model development. Representing all soil C as one homogenous pool is probably too simplistic because soil C fractions differ in chemical composition and temperature sensitivity for decomposition (Craine et al. 2010; Fierer et al. 2005; Karhu et al. 2010; Trumbore 2000). Our more complex model (Eqs. 9, 10) represents two soil C pools which would allow the temperature sensitivity of soil respiration to vary temporally and across ecosystems according to the availability of C_{SO} versus C_{DO}. Separating these pools could be important because soil respiration represents the combined activity of microbial enzymes responsible for intracellular respiration, uptake, and extracellular hydrolysis (Ågren and Wetterstedt 2007). Over longer time scales, extracellular catalysis probably becomes the rate-limiting step as more readily available C pools become exhausted. Therefore models may need to distinguish the temperature dependence of extracellular enzymes from that of microbial uptake and metabolism.

Other pool structures should also be considered in microbial decomposition models, keeping in mind that computational and statistical costs limit the number of additional pools that can be included. One alternative approach that avoids these costs is to represent soil C heterogeneity using a continuous C quality parameter that declines as a function of soil C

quantity (Ågren and Bosatta 1996b). As microbes consume soil C, they are expected to leave behind more recalcitrant fractions with lower quality. The temperature sensitivity of V_{max} could then be represented to increase as C quality declines, consistent with biochemical theory and experiments (Davidson and Janssens 2006; Fierer et al. 2005). We might also expect microbial C use efficiency to decline with decreasing quality as C substrates become more energetically difficult to degrade (Ågren and Bosatta 1996a).

Hybrid approaches for representing soil C heterogeneity may also be worth exploring. The continuous quality approach accounts for heterogeneity, but assumes that decomposition of all soil C is under microbial control. In reality, some forms of soil C may be high in chemical quality but inaccessible to microbes due to abiotic factors such as mineral association (Kleber et al. 2011). These stabilized substrates may differ in their fundamental response to environmental drivers and may therefore need to be represented as a separate pool. Overall, it will be essential to employ rigorous comparison and validation approaches to optimize the structure and number of pools in potential soil C models.

Scaling up microbial models

We have described only a subset of microbial models, and more effort will be required to determine which microbial mechanisms should be scaled up to the global level. This scaling process is one of the major hurdles to the inclusion of microbes in global models. Many coupled GCMs operate with a spatial resolution of $\sim 1^\circ \times 1^\circ$, an area which will certainly include high levels of microbial diversity and heterogeneity. It is also unclear if short-term responses (1–10 years) measured at the plot scale will apply to global simulations spanning decades during which microbial communities may adapt and evolve. However, these scaling issues are not unique to microbial processes, and successful approaches have been developed for other ecosystem processes. For example, Williams et al. (1997) developed a protocol for scaling up models of gross primary productivity. A fine-scale mechanistic model was used to predict productivity across a wide range of conditions, and these predictions were then aggregated across time and space. A broad-scale model with simplified equations was then developed to replicate the aggregated output from the fine-scale model. The broad-scale model successfully predicted gross primary productivity across disparate ecosystems using broad environmental drivers, such as daily irradiance and leaf area index.

This scaling approach could be applied to microbial decomposition by validating our proposed models with plot or microcosm data, and then modifying the mechanistic equations for use in a broad-scale model. As with the Williams et al. (1997) analysis, some fine-scale microbial parameters and mechanisms could be ignored when scaling up because they have little effect on the aggregated model predictions. In addition to climate drivers, vegetation and soil physiochemical variables that are well-characterized at regional to global scales are excellent candidates for inclusion in scalable microbial models. For example, soil texture and pH data have been shown to be effective at scaling microbial respiration rates across landscapes (Pansu et al. 2010). In moving to the global scale, microbial modelers could also build on the approaches used in dynamic global vegetation models to account for microbial dynamics over space and time (Sitch et al. 2008). Given that plant communities provide C and nutrient inputs to belowground communities, microbial parameters could be driven by vegetation composition and productivity, providing a convenient and realistic mechanism for representing microbial responses to global change.

Model parameterization

Traditionally, soil C models have been parameterized using plot-level soil C and respiration data sets (e.g. Parton et al. 1993). Models like CENTURY (Parton et al. 1988) and ROTH-C (Jenkinson and Rayner 1977) were parameterized based on best-fit assessments by the model developers, and these parameters are still used today in many GCMs (Randerson et al. 1996). Although parameterization has historically been the result of expert tuning, new optimization techniques are now available to impartially optimize model fit (Wang et al. 2009). For example, nested sampling (Skilling 2006) and Monte Carlo Markov Chain (MCMC) optimizations (Metropolis et al. 1953;

Vrugt et al. 2009; Ricciuto et al. 2008) explore a parameter space defined by a priori probabilities to find the parameter set most likely to fit the observational data. This procedure generates a posterior distribution of likely parameters for which the model best describes the data. Such an approach provides not only an unbiased parameter set but also an estimate of variability that can be used in further model evaluations.

Emerging microbial datasets (e.g. Sinsabaugh et al. 2008; Cleveland and Liptzen 2007) represent an opportunity to provide physiological parameters that improve GCM predictions. On the other hand, modelers must overcome limitations that prevent these datasets from being used directly for model parameterization at broad scales. For example, measurements of enzyme V_{max} and K_m in field soils represent apparent potentials rather than actual in situ activities, which are extremely difficult to assay directly (Wallenstein and Weintraub 2008; Burns 1982). Furthermore, even if we could measure in situ enzyme kinetics, the resulting values would each apply to a single class of enzyme with a single chemical substrate, rather than the community of enzymes and substrates that are represented in broad models. Models incorporating N dynamics will require additional parameterization of the enzymatic processes that convert organic N to mineral forms (Schimel and Bennett 2004).

These parameterization challenges could be overcome by developing models at fine scales and then simplifying and re-parameterizing the models at broad scales. At the fine scale, parameterization could be based on data from laboratory or microcosm studies that show a direct link between enzyme kinetics and decomposition rates. Once these models are validated, they could be simplified and scaled up while retaining essential microbial mechanisms (Williams et al. 1997). The broad-scale models representing enzymatic mechanisms could then be fit to field decomposition and CO_2 respiration data with MCMC or nested sampling approaches to obtain aggregated enzyme parameters at the broad scale. Sensitivity analyses would be essential for estimating the impact of uncertainty in these parameter estimates. Although the parameters are obtained indirectly with this approach, the underlying model structure would be well supported by the fine-scale mechanistic model. Indirect approaches have also been used to parameterize current land C models, for which pool sizes, turnover rates, and transfer coefficients are difficult or impossible to obtain directly from empirical data (Parton et al. 1988).

Model validation

As microbial models are developed and parameterized across scales, model validation and inter-comparison approaches (Randerson et al. 2009; Treseder et al. 2011a; Morales et al. 2005) should be used to test whether the predictive ability of microbe-based models is better than current models. One simple technique is to calculate the fit between model outputs and empirical datasets using an R^2 value. This approach has been used to assess the fit of soil C models to data at the regional scale (Smith et al. 1997). Models can be ranked more quantitatively by taking a Bayesian approach that also considers measurement uncertainty and the likelihood of the data (Wang et al. 2009). Akaike's Information Criterion (Akaike 1974) is one possible metric that tests model fit to data but also penalizes models with more parameters. Bayesian model selection is another technique that provides a rigorous test of model skill and fit, but can be computationally difficult for models with many parameters (Sivia and Skilling 2006; Ricciuto et al. 2008).

Validation of microbial models will require likely require data comparisons across a range of scales. At the ecosystem to regional level, the infrastructure implemented through Long-Term Ecological Research sites and the National Ecological Observatory Network should allow researchers to create datasets useful for model validation. Many of the land submodels from current GCMs are tested at continental scales, and a similar approach could be employed with microbial models. For example, CO_2 flux data from networks such as the North American Carbon Program and CarboEurope could be used to validate continental-scale model predictions (Schwalm et al. 2010; Suzuki and Ichii 2010).

The ultimate test of microbial models is whether they improve predictions of global C stocks and fluxes in coupled GCMs. There is probably room for improvement, given that current GCM predictions of atmospheric CO_2 diverge by up to 200 ppm across the twenty-first century (Friedlingstein et al. 2006).

However, model-data comparisons at the scale of the global C cycle have been scarce, making it difficult to know how much the current models need to be improved, and what their weaknesses are. Any global-scale analysis of microbially-based models will therefore have to begin with a rigorous benchmarking of the existing models. Fortunately, datasets are becoming available at the global scale that could be used to validate these models. For example, the Harmonized World Soil Database synthesizes soil properties, including soil organic C, at a spatial resolution comparable to GCM outputs (Fischer et al. 2008). There are also several global datasets on litter decomposition rates and soil CO_2 effluxes (Bond-Lamberty and Thomson 2010; Cornwell et al. 2008), although they would need to be interpolated and globally gridded for comparison to GCM outputs. Moreover, data on soil CO_2 effluxes would have to be partitioned into autotrophic versus heterotrophic components to validate microbial effects on ecosystem C dynamics.

Model-data integration

Successful model development clearly depends on empirical research for calibration and testing, but empiricists can also benefit from modeling efforts that identify relevant research areas. One motivation for changing model structures is to align them with emerging data streams on microbial community structure and function. A strength of mechanistic models is that as theoretical and empirical knowledge of fundamental processes improves, so can the models. However, the models can also highlight gaps and areas of uncertainty where additional data collection would improve model performance (Luo 2007). For example the turnover times of microbial biomass and enzymes are poorly characterized (Allison 2006), yet essential for all the models presented here. Similarly, the temperature and moisture sensitivities of microbial C use efficiency and enzyme kinetic parameters have rarely been quantified (but see Steinweg et al. 2008; Trasar-Cepeda et al. 2007). The development of enzyme-based models could be advanced through improved methods to estimate in situ enzyme activities so that modelers need not rely on laboratory potentials (Wallenstein and Weintraub 2008). To improve models, microbial ecologists should strive to quantify physiological traits and processes in microbial communities in addition to assessing composition with high-throughput sequencing (Wallenstein and Hall 2011). These fundamental aspects of microbial biogeochemistry represent exciting areas of new empirical research that will also assist in building models to predict climate feedbacks in the Earth system.

Conclusions

The soil C component of coupled climate models has lagged behind recent advances in mechanistic understanding of microbial decomposition. Empirical work in microbial ecology and theoretical studies at microbial scales have revealed important controls over decomposition that are not reflected in current models. Furthermore, current global models all represent decomposition with first-order dynamics that not only miss relevant mechanisms, but may also limit the range of predictions that would be generated from a more diverse set of model structures. Therefore, second-order models with direct microbial control over decomposition are worth exploring at multiple scales, including the entire globe. Although these efforts will be challenging due to limited data for parameterization, such data gaps could be overcome through additional empirical studies, scaling approaches, and model fitting techniques. Progress in reducing model uncertainty could be rapid once models switch to more biologically realistic structures based on established theory and microbial parameters.

Overall, the framework we recommend for representing microbes in coupled GCMs includes the following steps: (1) build models at multiple scales that include second-order dynamics dependent on microbial biomass; (2) parameterize these new models using emerging microbial data from laboratory and plot-level studies; (3) validate models at larger spatial scales using ecosystem, continental, and global data on C cycling processes; (4) conduct rigorous statistical comparisons across models and with empirical data to quantify the benefit of including microbial properties; (5) periodically update models to reflect advances in understanding of microbial function, diversity, and evolution. Although challenging, this new generation of model development and data integration is necessary to advance our ability to

predict Earth system responses and feedbacks to global change.

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