Title

Building Predictive Models for Diverse Microbial Communities in Soil

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Introduction

The key role of microbes in soil processes has been appreciated for decades. In his book *Principles of Soil Microbiology*, Selman Waksman [1927] noted that soil organic matter "depends upon the activities of the soil microorganisms, which are in their turn influenced by environmental soil conditions including moisture, aeration, soil reaction, and presence of available nitrogen and mineral nutrients" (p. 669). This statement foreshadowed a current, 21st century, explosion of interest in linking microbial communities with soil functioning and global change [Bardgett *et al.*, 2008]. Despite this renewed interest, our ability to make reliable, quantitative predictions of microbial functioning has advanced relatively little since the 1920s. The aim of this chapter is to provide relevant background and a vision to overcome this challenge.

As key players in all of the planet's biogeochemical cycles, microbes influence ecosystem process rates and their responses to human-caused perturbation [Singh *et al.*, 2010]. For example, microbes control soil carbon sequestration through decomposition of organic matter (a loss pathway) and formation of stable organic residues (an input pathway). Bacteria, fungi, and archaea mineralise nutrients that support plant growth in unmanaged and agricultural ecosystems. Soil methanogens produce methane, a potent greenhouse gas, while methanotrophs consume methane [Gulledge and Schimel, 2000; McCalley *et al.*, 2014]. Nitrifiers and denitrifiers produce nitric and nitrous oxide gases that contribute to air pollution and greenhouse warming, respectively [Firestone *et al.*, 1980; Firestone and Davidson, 1989].

Now is an opportune time to make progress on predictive models of microbial processes in soil. That microbes influence biogeochemical processes has long been known, but there is increased urgency to predict how these processes and their associated ecosystem services will respond to human-caused environmental change. Harking back to Waksman, environmental conditions such as temperature, moisture, nutrient availability, and organic matter inputs are being altered at a global scale through changes in land use, climate, and nutrient inputs.

Reliable predictions require more than just recognition that microbes are important for a process. Fundamental, mechanistic understanding must be established from empirical studies. The mechanisms must be unified into a theoretical framework that provides a basis for quantitative mathematical models. The models must then be scaled, analysed, and validated against independent observations. Often, the models fail to predict patterns in the data and must be refined over and over again. Perhaps not surprisingly, this challenging series of steps has not yet been accomplished at a large scale with soil microbes [Wieder *et al.*, 2015].

Still, several recent scientific developments make a focus on prediction tractable and worthwhile. The molecular revolution (genomics, metabolomics, proteomics, etc.) and the microbiome concept have increased the potential for rapid advances in fundamental understanding of diverse microbial communities [Tringe *et al.*, 2005; Sharon *et al.*, 2013]. Although more work must be done to fully interpret the datasets emerging from these advances, it is now feasible to quantify the genetic content and distribution of soil microbes at high spatial, temporal, and taxonomic resolution. Well-conceived models are essential for translating genetic data into predictions with relevance for critical environmental issues.

Another key discovery is that biological processes interact dynamically with the physical environment to influence ecosystem processes. Soils are complex adaptive systems [Levin, 2002] in which biological interactions may be quantitatively important relative to abiotic factors in determining function. Rather than just responding to the environment, as Waksman suggested, soil microbes alter the environment through a range of eco-evolutionary mechanisms that were not well understood a century ago. For example, social evolution theory (related to game theory) has informed our understanding of mutualistic and antagonistic interactions that play out among microbes [Allison, 2005; West *et al.*, 2006; Folse and Allison, 2012; Foster and Bell, 2012].

In the short term, microbes can acclimate to environmental changes through physiological mechanisms. Changes in gene expression may result in acclimation to temperature, substrate availability, and time of day [Hurley *et al.*, 2014]. Yeasts can acclimate their physiology in anticipation of future environmental changes [Mitchell *et al.*, 2009]. Acclimated microbes should respond differently to environmental changes than non-acclimated microbes, meaning that predictive models need to account for physiological mechanisms [Crowther and Bradford, 2013].

Likewise, numerous studies have shown that the genetic content of microbial communities also changes with the environment [Shade *et al.*, 2012]. Both evolutionary and ecological mechanisms contribute to such responses. Genetic variants with higher fitness in a given environment will increase in frequency due to natural selection. Experimental evolution studies have shown for example that bacterial genes associated with stress tolerance and protein stability increase rapidly in frequency under selection by high temperatures [Tenaillon *et al.*, 2012]. Shifts in the environment often alter the competitive interactions in soil microbial communities, leading to changes in composition and functioning through ecological mechanisms [Allison and Martiny, 2008].

Advances in our understanding of physiological, evolutionary, and ecological mechanisms in microbial communities are relevant for building predictive models. Such models must be able to predict phenomena such as hysteresis and historical contingencies. Hysteresis occurs when a the relationship between a process rate, such as soil respiration, and an environmental driver, such as temperature, differs based on the previous state of the system (i.e., whether the system was recently warm or cold) [Updegraff *et al.*, 1998]. Historical contingencies, or legacies, arise when a current process rate depends on the history of the system in addition to current environmental conditions [Evans and Wallenstein, 2012]. Both hysteresis and historical contingencies are likely driven by physiological, evolutionary, and ecological responses of microbial communities.

History of microbial biomass models

Models of microbial processes in soil have evolved considerably over time. The first large-scale biogeochemical models such as RothC and CENTURY included microbial biomass, but it played no direct role in organic matter decomposition [Jenkinson and Rayner, 1977; Parton *et al.*, 1988]. Instead the models assumed that microbial activity was a linear function of the substrate pool size. Factors like substrate chemistry, temperature, moisture, and soil texture were included as coefficients in the linear function. Schimel [2001] defines this approach as *implicit* with the dynamics and influence of the microbial community implied indirectly by the environmental conditions. An implicit approach is convenient because linear models are easy to analyse mathematically [Xia *et al.*, 2013], and they make predictions that are consistent with empirical data from laboratory and field experiments [Powlson *et al.*, 2011].

On the other hand, models with explicit microbes represent a direct role of microbial biomass in soil processes [Schimel, 2001]. The defining feature of microbial-explicit models is the mathematical coupling of dynamic microbial biomass with substrate pools [Todd-Brown *et al.*, 2012]. Substrate decomposition rates depend on the quantity of microbial biomass, and microbial biomass depends on the quantity of substrate. In some microbial-explicit models, decomposition rates depend on enzymes produced by microbes rather than the quantity of microbial biomass per se [Allison *et al.*, 2010]. Organic matter loss rates in all microbial-explicit models are non-linear with respect to substrate concentration because of the coupling to microbial biomass.

The concept of explicit microbes dates back at least to Waksman [1927], but microbial-explicit mathematical models did not appear until almost 50 years later. In 1979, O. L. Smith described and

validated an analytical model of soil organic matter decomposition [Smith, 1979a, 1979b]. The model represented enzymatic degradation of multiple substrate pools with Michaelis-Menten kinetics and included carbon, nitrogen, and phosphorus submodels along with a plant component. Yet Smith's model failed to gain a major foothold in the biogeochemical literature, possibly because it was viewed as too complex [Andrén and Paustian, 1987] or contained too many equations [Fawcett and Higginson, 2012]. Not until almost 25 years later did the idea begin to take hold with models by Schimel and Weintraub [2003] and Fontaine and Barot [2005].

Over the last 10 years, there has been an explosion of interest in microbial-explicit models. They have begun to include aspects of microbial functional diversity [Allison, 2005; Moorhead and Sinsabaugh, 2006] and explore responses to changing environmental conditions [Allison *et al.*, 2010; Davidson *et al.*, 2012; Sistla *et al.*, 2014]. Newer models consider important microbial interactions with soil mineralogy [Wang *et al.*, 2013; Wieder *et al.*, 2014]. Several models have been scaled up to simulate soil carbon pools and dynamics in the Earth system [Wieder *et al.*, 2013; Sulman *et al.*, 2014]. Enough conceptual diversity has developed to allow model intercomparisons and data assimilation at the local to global scale [Lawrence *et al.*, 2009; Li *et al.*, 2014; Wang *et al.*, 2014; Hararuk *et al.*, 2015], and readers may consult recent review articles dedicated to microbial-explicit models [Todd-Brown *et al.*, 2012; Wieder *et al.*, 2015].

All of this attention has stimulated calls to incorporate microbial-explicit models into Earth system models as an alternative to conventional first-order models [Todd-Brown *et al.*, 2012; Treseder *et al.*, 2012; Wieder *et al.*, 2015]. Recent analyses have revealed major shortcomings with the conventional approach for modelling soil organic matter dynamics [Todd-Brown *et al.*, 2013, 2014]. Still, scaling of microbial-explicit models should be done with caution. The modelling community has a responsibility to analyse the variation, advantages, and shortcomings inherent in the conceptual and mathematical diversity of current microbial models. Such an effort will help instil confidence in global predictions that arise from microbial-explicit models and ultimately appear in climate assessment reports that influence societal decisions. To that end, the following sections lay out key approaches at the heart of microbial modelling.

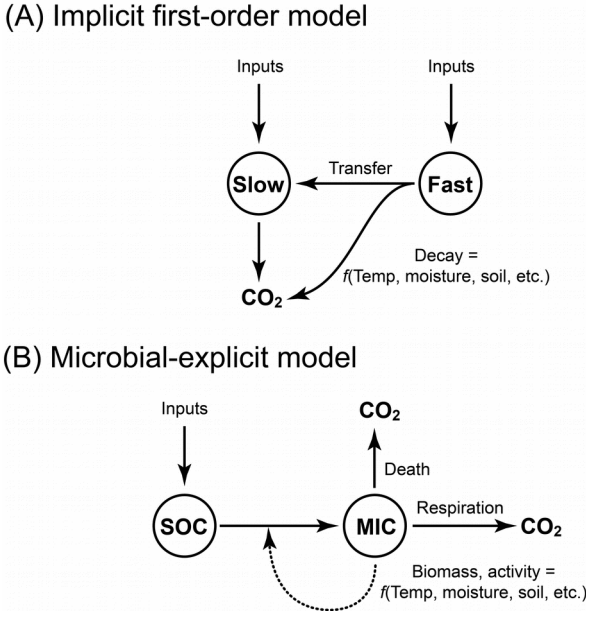

Figure 1. Distinction between the implicit approach to modelling microbial processes (A) and the microbial-explicit approach (B). SOC = soil organic carbon; MIC = microbial biomass carbon.

Microbial modelling approaches

Under the implicit approach of conventional biogeochemical models, microbial communities are represented through environmental response functions (Fig. 1). For instance, a Q_{10} function is commonly used to describe how decay coefficients and soil respiration (*k*-values) increase with increasing temperature [Davidson *et al.*, 2006]. This approach assumes that the rate of enzyme-driven microbial metabolism increases exponentially with increasing temperature. Most models also assume that the rate is the same for metabolism of different soil substrates and microbial communities. Response functions for other environmental variables such as soil moisture and texture have different forms, but are also assumed to apply across substrates and ecosystems.

The simplest explicit approach for representing microbial communities is to include a single biomass pool that is mathematically linked to substrate inputs and outputs [German *et al.*, 2012]. In this case the model fluxes are a function of the biomass pool size which is in turn dependent on substrate availability and environmental variables. For instance, the biochemical response to temperature is captured by modifying the kinetic parameters for enzyme catalysis. The form of this function is often very similar to the Q_{10} function employed by conventional models. However with the microbial-explicit model, the kinetic parameters are biomass-specific, so changes in microbial biomass also influence the total rate of substrate decay by enzymes.

On one hand, this change in model approach is relatively subtle. There are no new pools; most conventional models already include pools for microbial biomass. The environmental response functions are nearly identical and involve the same parameters. Both model types include kinetic parameters—*k*-values in the implicit models and Vmax values in the explicit models. Thus microbial-explicit models with a single biomass pool are not inherently more complex than implicit models.

On the other hand, differences in the mathematical structure of microbial-explicit models—how the pools interact—have a big impact on the model behaviours. In particular, the explicit models are less sensitive to changing inputs [Allison *et al.*, 2010; Wieder *et al.*, 2013]. As substrate pool sizes increase, so does microbial biomass. Because the two pools are mathematically coupled, the increase in biomass increases substrate turnover and reduces substrate pool size. Microbial-explicit models reflect Waksman's (paraphrased) observation—microbes eat soil carbon.

In general, microbial-explicit models differ from implicit models in their response to perturbations. The up-and-down dynamics of coupled substrate and microbial pools manifest as oscillations in response to changes in pool sizes [Wang *et al.*, 2014]. For example, if microbial biomass declines due to temperature effects on growth efficiency, substrate pool sizes increase. The increase then supports more biomass and the system exhibits oscillations that dampen over time.

It remains unclear whether the behaviours of simple microbial-explicit models are realistic. There is little empirical evidence that soil substrate and microbial biomass pools oscillate in response to disturbance. However, few studies have looked for such behavior, and there is some evidence from soil warming experiments, such as Harvard Forest, that the transient dynamics of microbial-explicit models are consistent with observational data [Allison *et al.*, 2010]. The insensitivity of microbial-explicit models to substrate inputs is also debatable, as inputs are clearly required to generate soil organic matter in the first place. Still, the global-scale relationship between net primary production and soil carbon stocks is weak [Todd-Brown *et al.*, 2013], making it difficult to reject the microbial model predictions.

Another key question for microbial models is whether diverse communities should be represented as a single biomass pool. This simplifying assumption reduces the potential to incorporate many of the biological processes known to be important in microbial communities. To address this issue, a number of

microbial-explicit models include aspects of functional diversity in the microbial biomass pool by defining distinct functional groups or allowing for variation in functional traits [Moorhead and Sinsabaugh, 2006; Wieder *et al.*, 2014].

Functional group approaches, common in vegetation models, separate biomass into classes with different functional parameters. For example, in vegetation models, functional groups are assigned based on leaf morphology (broadleaf or needleleaf), growth form (grass, shrub, tree), leaf longevity (deciduous versus evergreen), and other characteristics. The parameters are static within a functional group, so grasses cannot become trees, for instance. Moorhead and Sinsabaugh [2006] used an analogous approach with litter-decomposing microbes. They defined opportunist, decomposer, and miner guilds that target early, middle, and late stages of litter decay, respectively. As each functional guild consumes substrate, it alters the chemical environment and shifts the competitive landscape such that guilds bloom and die off in succession as litter decays. As with plant functional groups, the functional parameters of the microbial guilds do not change—succession is driven by the environment.

The functional group approach is one example of trait-based approaches that are now being applied to model functional diversity in microbial communities. A trait can be defined as a parameter associated with the microbial biomass. For example, Moorhead and Sinsabaugh specified guilds based on traits like enzyme maximum catalytic rate (Vmax), enzyme half-saturation constant (Km), maximum substrate uptake rate, basal respiration rate, and C:N ratio. Other trait-based models use a continuous approach rather than specifying guilds a priori. Sistla *et al*. [2014] allowed the C:N ratio of the microbial biomass to vary based on carbon substrate and soil nitrogen availability. Lower C:N ratios corresponded to bacterially-dominated communities whereas higher ratios corresponded to fungal-dominated communities.

A major challenge with trait-based approaches is that trait parameters are often uncertain, especially when specifying many functional groups. To circumvent this issue, some models use a stochastic approach to assign trait parameters and allow environmental conditions to select, or filter, the resulting functional groups. This idea was pioneered by Follows *et al*. [2007] who randomly assigned trait parameters to 78 hypothetical functional groups of phytoplankton and then observed the abundance and geographic distribution of each group after years of simulated competition in the global ocean. At the end of the simulation, the distributions of the dominant hypothetical groups matched the distributions of several known lineages of phytoplankton. There was also correspondence between the randomly-assigned trait parameters of the hypothetical groups and the measured traits of the known lineages—real patterns emerged from the model dynamics.

Allison [2012] applied a similar approach to litter-decomposing microbial communities. The model was able to replicate patterns in litter decomposition and enzyme activity from a Hawaiian rainforest, but the abundance distribution of hypothetical functional groups was more difficult to validate. Unlike with phytoplankton, the geographic distributions and functional trait parameters for most litter- and soil-associated microbes are unknown.

Key microbial traits for modelling

The increasing interest in trait-based modelling approaches justifies a closer look at the key trait parameters involved in microbial functioning (Table 1). Community ecologists have developed a useful conceptual framework that distinguishes *response* and *effect* traits [Lavorel and Garnier, 2002; Webb *et al.*, 2010]. Response traits govern the response of organismal physiology or abundance to environmental conditions, whereas effect traits describe how the organism affects biogeochemical processes. The categories are not mutually exclusive, as traits underlying growth, stoichiometry, and turnover influence both ecosystem processes and microbial responses to resource availability.

Growth-related traits are fundamental for microbial-explicit modelling and fall into both response and effect categories. Typically the instantaneous growth rate of microbial biomass in these models is an emergent property determined by trait interactions with environmental conditions. The key underlying traits are related to resource acquisition and metabolic losses such as respiration. For heterotrophic microbes, resource acquisition is determined by kinetic parameters for uptake such as biomass-specific Vmax and Km. Biomass-specific Vmax can be specified directly or result from multiplying enzyme-specific Vmax by the cellular investment in uptake enzymes, which allows for cellular regulation of uptake investment.

In many microbial-explicit soil models, resource acquisition by microbes also depends on extracellular enzyme traits [Allison, 2005; Wang *et al.*, 2013; Kaiser *et al.*, 2014]. Analogous to uptake, there are enzyme-specific kinetic parameters for Vmax and Km. Other trait parameters may determine investment in enzyme production expressed as a fraction of microbial biomass or microbial uptake. Therefore instantaneous resource acquisition rates for heterotrophic microbes may depend on a suite of kinetic traits that interact with the availability of high and low molecular weight substrates.

Table 1. Microbial trait parameters.

Parameter	Description	Values	Units	Citations
Enzyme-specific Vmax	Quantity of product formed per unit time per unit enzyme	24-60	$g\ g^{-1}\ day^{-1}$	[Allison *et al.*, 2010; Wang *et al.*, 2013]
Biomass-specific Vmax	Quantity of product formed per unit time per unit microbial biomass	0.24	$g\ g^{-1}\ day^{-1}$	[German *et al.*, 2012; Li *et al.*, 2014]
Enzyme Km	Michaelis-Menten half-saturation constant for enzymes	0.050-0.600	$g\ cm^{-3}$	[Allison *et al.*, 2010; German *et al.*, 2012; Wang *et al.*, 2013]
Substrate Km	Reverse Michaelis-Menten half-saturation constant for substrate	0.0003	$g\ C\ g^{-1}$ soil	[Schimel and Weintraub, 2003]
Biomass-specific enzyme production	Quantity of enzyme produced per unit time per unit microbial biomass	0-0.00028	$g\ C\ g^{-1}\ C\ day^{-1}$	[Allison, 2005, 2012, 2014]
Uptake-specific enzyme production	Quantity of enzyme produced per unit resource uptake	0-0.12	$g\ C\ g^{-1}\ C$	[Allison, 2005, 2012, 2014; Kaiser *et al.*, 2014]
Enzyme-specific uptake Vmax	Rate of resource uptake per unit enzyme	14400	$g\ g^{-1}\ day^{-1}$	[Allison, 2005]
Biomass-specific uptake Vmax	Rate of resource uptake per unit microbial biomass	0.012-0.24	$g\ g^{-1}\ day^{-1}$	[Wang *et al.*, 2013; Li *et al.*, 2014]
Uptake Km	Michaelis-Menten half-saturation constant for uptake proteins	1×10^{-6}-3×10^{-4}	$g\ cm^{-3}$	[Allison, 2005; Allison *et al.*, 2010]
Enzyme specificity	Inverse of the number of substrates targeted by a given enzyme	1/3-1		[Allison, 2012]
Growth efficiency	Fraction of resource uptake allocated to biomass growth	0.14-0.77	$g\ g^{-1}$	[Six *et al.*, 2006; Sinsabaugh *et al.*, 2013]
Basal respiration rate	Rate of respiration per unit microbial biomass for cellular maintenance	0.064-0.216	$g\ g^{-1}\ day^{-1}$	[Allison, 2005; Kaiser *et al.*, 2014]

Enzyme respiration rate	Rate of respiration per unit enzyme produced	0.1-1	g C g^{-1} C	[Allison, 2005, 2012]
Bacterial cell size	Mass of individual bacterial cells	30-300	fg C	[Allison, 2005; Kaiser *et al.*, 2014]
Fungal cell size	Mass of individual bacterial cells	750-7500	fg C	[Allison, 2014; Kaiser *et al.*, 2014]
Cellular N quota	Minimum fraction of cellular biomass as nitrogen	0.1	g g^{-1}	[Allison, 2012]
Cellular P quota	Minimum fraction of cellular biomass as phosphorus	0.015	g g^{-1}	[Allison, 2012]
Biomass turnover rate	Fraction of microbial biomass loss per unit time	0.01-0.04	day^{-1}	[Allison, 2005, 2012]
Enzyme turnover rate	Fraction of enzyme loss per unit time	0.020-0.024	day^{-1}	[Allison, 2012; Wang *et al.*, 2013]
Osmolyte content	Fraction of microbial biomass allocated to osmolytes	0.10	g C g^{-1} C	[Schimel *et al.*, 2007]
Residue content	Fraction of microbial biomass allocated to resistant compounds	0.5-0.94	g g^{-1}	[Allison *et al.*, 2010; Kaiser *et al.*, 2014]
Vmax temperature sensitivity	Activation energy for Vmax	34-53	kJ mol^{-1}	[Allison *et al.*, 2010; Allison, 2012; Wang *et al.*, 2013]
Km temperature sensitivity	Activation energy for Km	20-30	kJ mol^{-1}	[Wang *et al.*, 2013; Allison, 2014]
Growth efficiency temperature sensitivity	Change in growth efficiency per change in temperature	-0.016-0	g g^{-1} $^oC^{-1}$	[Allison *et al.*, 2010]
Turnover temperature sensitivity	Change in turnover rate per change in temperature	0.003-0.004	day^{-1} $^oC^{-1}$	[Hagerty *et al.*, 2014]

At a minimum, microbial-explicit models must include trait parameters for a convex (e.g. saturating) function that relates resource acquisition rate to resource pool size [Wutzler and Reichstein, 2008]. There must be a parameter that determines the maximum rate of resource acquisition, and the function must level off, otherwise microbial biomass grows indefinitely and consumes all substrate. Functions that level off with increasing substrate concentration (e.g. Michaelis-Menten kinetics), or increasing enzyme concentration [e.g. reverse Michaelis-Menten; Schimel and Weintraub, 2003] both serve this purpose.

A number of other trait parameters specify metabolic losses from microbial biomass. Most models include a growth efficiency parameter corresponding to the fraction of substrate uptake converted into microbial biomass, with the remainder being respired [Allison *et al.*, 2010; Allison, 2014]. Some models also include a basal respiration parameter that specifies respiration rate as a fraction of microbial biomass [Allison, 2005; Kaiser *et al.*, 2014]. If there are pathways for enzyme or other metabolite production, these may be associated with respiratory fluxes as well [Allison, 2005; Kaiser *et al.*, 2014]. Together, respiratory losses, metabolite production, and substrate uptake combine to determine the emergent growth rate of microbial biomass.

Cell size is also an important trait for growth [Yoshiyama and Klausmeier, 2008]. Given a similar biomass-specific growth rate, larger cells divide less frequently and have lower population growth rates. Larger cells also have a lower surface area to volume ratio, which can reduce cell-specific resource uptake

rates. In models, specifying larger minimum cell sizes or larger cell sizes required for duplication results in lower microbial population sizes and potentially lower resource acquisition rates. Smaller populations reduce the spatial extent of microbial biomass and may be at higher risk for stochastic extinction.

Aside from cell size, trait parameters may specify growth form. Some microbes, such as fungi and actinomycetes, display filamentous growth whereas many bacteria and archaea grow as colonies on surfaces. Still others are free-living in aqueous phases. Filamentous growth may be specified in cellular automaton models with probabilities of movement differing for each growth direction [Boswell, 2008]. Instead of new biomass spreading out from a central point at random, the growth becomes directional. Directionality rules may be combined with physiological differences associated with filamentous growth, particularly the ability to translocate carbon and nutrients along the filaments. In this way, fungal growth strategies can be represented in microbial models as large cells that grow directionally with connectivity of nutrient pools [Allison, 2014].

For models including nutrient dynamics, cellular stoichiometry is a key trait. Stoichiometry may be specified as a fixed parameter [Kaiser *et al.*, 2014] or vary within maximum and minimum limits [Allison, 2012; Sistla *et al.*, 2014]. When metabolic processes result in biomass stoichiometry that deviates from the fixed value or exceeds the limits, the elements in excess are lost. For example, cells respire excess carbon as CO_2 or mineralise excess nitrogen. In some models, cellular stoichiometry may also affect resource uptake rates through a nutrient demand function [Allison, 2005]. When microbes with different life history traits and stoichiometric ratios are represented in microbial models, feedbacks in the microbial community can alleviate nutrient limitation [Kaiser *et al.*, 2014].

To prevent microbial biomass from growing indefinitely, models must specify parameters for biomass turnover. Processes such as predation, starvation, and environmental stress may trigger microbial turnover, although the mechanism is usually not defined explicitly in models. Turnover rate parameters may reflect traits of the microbial biomass as well as external drivers, such as predation pressure. Many modelling studies have specified turnover rates as constants [Schimel and Weintraub, 2003; Moorhead and Sinsabaugh, 2006; Allison *et al.*, 2010], but microbial traits such as cell wall thickness, investment in osmolytes, and antibiotic production could cause variation in turnover rates. In their MIMICS model, Wieder *et al*. [2014] assign different turnover parameters to microbial functional groups with fast versus slow growth strategies.

Related to turnover are traits that affect the fate of dead microbial biomass. Microbial residues are thought to be important contributors to soil organic matter formation [Grandy and Neff, 2008]. Most conventional and microbial-explicit models include transfer coefficients that specify the fraction of turnover entering one or more soil carbon pools, which may include dissolved or polymeric forms [Schimel and Weintraub, 2003; Allison *et al.*, 2010; German *et al.*, 2012; Kaiser *et al.*, 2014]. Many studies use a constant transfer coefficient, although the MIMICS model specifies a higher transfer of residues to soil organic pools from the slow-growing microbial functional group [Wieder *et al.*, 2014], and Kaiser *et al*.'s [2014] model represents variation in the stoichiometry of residues. MIMICS assumes that microbial traits such as cell wall chemistry differ across functional groups and alter the fraction of dead biomass that is stabilized as SOC versus being respired quickly as CO_2 or transferred to fast-turnover pools like DOC.

Microbial modelling studies have started to explore the consequences of response traits related to temperature and moisture. Response trait parameters are used as coefficients in functions that specify how resource acquisition, growth, and turnover traits vary with environmental conditions. For example, enzyme Vmax can be specified as a constant [Schimel and Weintraub, 2003], or a function of temperature. Several microbial-enzyme models use the Arrhenius function to describe the temperature relationship, effectively defining the activation energy as a response trait parameter [Allison *et al.*, 2010; Wang *et al.*, 2013; Wieder *et al.*, 2013].

This response function approach has been implemented in a number of microbial-explicit models with a range of trait parameters. Equilibrium soil carbon pools are very sensitive to varying the slope parameter in a linear function describing the dependence of microbial growth efficiency on temperature [Allison *et al.*, 2010; Li *et al.*, 2014]. An analogous sensitivity is apparent when microbial turnover rates increase as a function of increasing temperature [Hagerty *et al.*, 2014]. Moisture responses are not yet well studied, but there are efforts underway to define moisture response functions for enzyme kinetic parameters and microbial turnover rates (Allison unpublished).

Due to physiological and evolutionary constraints, traits are often correlated. For example, high rates of resource acquisition correlate with low growth yields [Pfeiffer *et al.*, 2001], and this rate-yield tradeoff is well-established in microbial physiology [Frank, 2010]. Allocating energy to resource uptake increases the rate of acquisition but reduces the fraction of acquired resources available for growth. There is also a positive correlation between extracellular enzyme Vmax and Km, meaning that enzymes with higher catalytic rates also require higher substrate concentrations to achieve the maximum rate [Sinsabaugh *et al.*, 2014].

Life history strategies, or syndromes, may arise from correlations among multiple traits with different strategies residing in different regions of trait space. Among plants, the ruderal (weedy) strategy is characterized by high leaf nitrogen, high rates of photosynthesis, high specific leaf area, and high vulnerability to herbivory. For microbes, Fierer *et al*. [2007] have proposed a copiotroph-oligotroph life history continuum, whereby copiotrophs have higher resource acquisition rates, higher nutrient demands, and potentially lower growth yields than oligotrophs. Different trait-based strategies represent a key organizing principle for communities of microscopic phytoplankton [Litchman *et al.*, 2015].

Modelling efforts can exploit trait correlations and life history continua to represent microbial processes. When assigning trait parameters in models, such correlations reduce the dimensionality of the parameter space because some trait parameter combinations do not occur. This approach has been used in both marine and terrestrial systems with complex microbial communities [Follows *et al.*, 2007; Allison, 2012]. Members of the community may possess any strategy along the life history continuum but cannot break the rules and fall into an unoccupied area of trait space. Such trade-offs may constrain processes such as decomposition at the ecosystem scale [Allison, 2014].

Defining strategies *a priori* is impossible if the trait correlations are unknown, but there is an alternative inverse approach. Initial trait parameters can be assigned to cover a large volume of trait space with environmental selection ruling out unfavourable trait combinations [Allison, 2012]. Although computationally more intensive, this approach allows viable strategies to emerge from the model dynamics. Both approaches can be applied simultaneously with known trade-offs parameterized *a priori* and additional refinement of strategies occurring through environmental selection.

Scaling up microbial models

Microbes interact at the micron scale, whereas biogeochemical models aim to predict microbial processes at the ecosystem to global scale. Bridging these scales is an important challenge because accurate predictive models rely on integration of key mechanisms across scales. Whereas most current models operate on a single scale, a hierarchical approach is necessary to address the challenge of scaling microbial models.

Several models capture key mechanisms of microbial interaction at the micron scale. These agent-based models reveal how social interactions and spatial structure in microbial communities influence biogeochemical processes [Allison, 2005, 2012; Folse and Allison, 2012; Kaiser *et al.*, 2014]. The upshot

is that micron-scale interactions must be considered in macro-scale processes. Although they represent less than one square millimetre of physical space, these models are too complex conceptually and computationally to run at larger scales where different sources of environmental variation contribute to biogeochemical processes.

Moving up from the micron scale, other important mechanisms operate at the scale of soil aggregates and the rhizosphere. Aggregates couple the physical influence of soil minerals with biological processes of organic matter formation and turnover [Jastrow, 1996; Sollins *et al.*, 1996; Kleber *et al.*, 2007]. In the rhizosphere, root exudation and turnover affect substrate availability to the microbial biomass, leading to processes such as nutrient mineralization and priming of soil organic matter decomposition [Talbot *et al.*, 2008; Cheng *et al.*, 2014]. The importance of these processes means that microbial-explicit models should represent the spatial scale of aggregates and the rhizosphere. The CORPSE model [Sulman *et al.*, 2014] is an excellent example of how physical stabilization and rhizosphere processes can be represented to predict microbial effects on soil carbon storage under elevated CO_2.

At the plot scale and beyond, established tools in ecosystem ecology can be applied to scale up microbial models. The soil state factor approach [Jenny, 1980] defines climate, parent material, topography, vegetation type, and time as the key drivers of soil formation. Landscape variation in state factors can be used to specify the local environment for microbial processes. For example, by overlaying maps of temperature, precipitation, elevation, plant chemistry, and soil type, it becomes possible to specify the environment for microbial interactions at any point on Earth.

A hierarchical approach involves a set of nested microbial models, each capturing key mechanisms at an appropriate spatial scale. Rather than running micron-scale, agent-based models at every grid point in a global model, a hierarchical approach distils emergent patterns from small scales and applies them at larger scales. Micron-scale models can be run across environmental gradients, such as temperature and moisture, to construct response functions for macro-scale processes like enzymatic decomposition and heterotrophic respiration. The parameters from these response functions can then be used in larger-scale models with greater confidence because they emerge from micro-scale processes. Likewise, aggregate or rhizosphere models incorporating the emergent micro-scale functions can be run across state factor gradients to scale up processes to the ecosystem or global level.

There are statistical and computational techniques available to reduce model complexity in a mechanistically informed way. Although not yet applied to soil microbial biomass models, emulation approaches have been used in other fields to distil the complexity of numerical models [Castruccio *et al.*, 2014]. Emulation fits complex model output to a statistical model. Parameters from the statistical model are then used to emulate the behavior of the more complex model. Castruccio *et al*. [2014] used a statistical emulator to represent the relationship between radiative forcing and temperature in climate model outputs. A similar approach could be used to construct functions for the response of microbial processes, such as heterotrophic respiration, to environmental variables based on outputs from micro-scale agent-based models. The functional parameters could then be used in larger scale models.

An alternative but less mechanistic approach to scaling involves the application of community-averaged trait values. Rather than capturing mechanisms operating at the micron or aggregate scale that shape community composition and the associated distribution of traits, empirical approaches can provide information about trait values averaged across the community. These values can then be applied in ecosystem- to global-scale models. In particular, metagenomic techniques allow quantification of gene frequencies in a sampled community [Berlemont *et al.*, 2014]. If these frequencies are assumed to correspond to traits, they can be summed or averaged to estimate community-wide trait values [Fierer *et al.*, 2014]. Alternatively, community-averaged traits may be measured directly; for example, most

empirical assays of extracellular enzyme potential and microbial growth efficiency represent community averages, and these have been applied in ecosystem models [German *et al.*, 2012; Hagerty *et al.*, 2014].

Challenges and future directions

Ideally, recent advances in microbial ecology could inform revised global models that make more accurate predictions of soil biogeochemistry. This objective is within reach, but there are important challenges to overcome, including model parameterization, validation, and scaling approaches. A recent review by Wieder *et al*. [2015] described specific recommendations to address these challenges.

One of Wieder *et al*.'s [2015] major recommendations focused on coordination between modellers and empiricists regarding microbial parameters. Some parameters such as growth efficiencies and temperature response coefficients are represented in many microbial-explicit models, yet relatively few studies measure them. Conversely, few microbial-explicit models have considered moisture responses whereas many empirical studies have focused on this topic [Lennon *et al.*, 2012; Placella *et al.*, 2012; Meisner *et al.*, 2013].

In light of the recent focus on microbial trait-based models, there should also be greater attention to assembling model-relevant trait data [Litchman and Klausmeier, 2008]. Numerous datasets exist, but they are often dispersed across the literature, and new efforts to synthesize trait information in databases would benefit modelling efforts. Trait databases are available for plants [Kattge *et al.*, 2011] and are being assembled for phytoplankton [Litchman *et al.*, 2015], bacteria [Martiny *et al.*, 2013], and fungi [Treseder and Lennon, 2015]. Still, these databases should be expanded and leveraged to engage modellers who aim to represent microbial traits.

Microbial-explicit models should be thoroughly tested against empirical data and compared amongst themselves to identify strengths and weaknesses. Adequate testing is essential to ensure confidence in larger-scale predictions based on microbial-explicit models. Bayesian inference is particularly useful for model-data integration because empirical data can be assimilated to both test models and estimate parameters along with uncertainties [Hararuk *et al.*, 2015]. These approaches are most useful when multiple independent empirical datasets are available. If validation datasets are limited, it becomes impossible to identify unique parameter values in microbial-explicit models [Sierra *et al.*, 2015].

In addition to trait parameter information, future microbial model development would benefit from databases of empirically-measured output variables. For example, datasets on soil carbon and nutrient stocks, microbial biomass pools, litter decay rates, and rates of soil respiration over time are essential for model validation and data assimilation [Wieder *et al.*, 2015]. Measurements of these variables in response to disturbances such as temperature change, resource pulses, moisture pulses, and nutrient addition can provide additional constraints on model predictions.

New scaling approaches are needed to assemble the hierarchy of models that will allow better global-scale predictions. Model emulators represent one promising approach but have not yet been applied to microbial systems. Monte Carlo simulation approaches are also promising for analysing emergent behaviours of micro-scale models. One issue with microbial-explicit models is that they assume homogeneity of biomass and soil carbon pools. When these homogeneous pools are mathematically coupled, they oscillate in response to perturbations [Li *et al.*, 2014; Hararuk *et al.*, 2015], a behaviour for which there is little empirical support, especially at large scales.

Still, we know that microbes and soil organic matter interact at the micron scale where there is high variation in biomass density and substrate availability [Sierra and Müller, 2015]. When this heterogeneity is represented through repeated random sampling of microbial trait parameters and substrate input rates,

pool size oscillations occur at different frequencies. If the pool dynamics of many random simulations are aggregated, the oscillatory behaviour dampens and disappears (Fig. 2). These results suggest that microbial mechanisms operating in heterogeneous microsites are consistent with empirical data when aggregated at larger scales. By coupling Monte Carlo-type simulations with statistical emulation, we may be able to incorporate microbial mechanisms into models while accurately representing emergent behaviours at large scales.

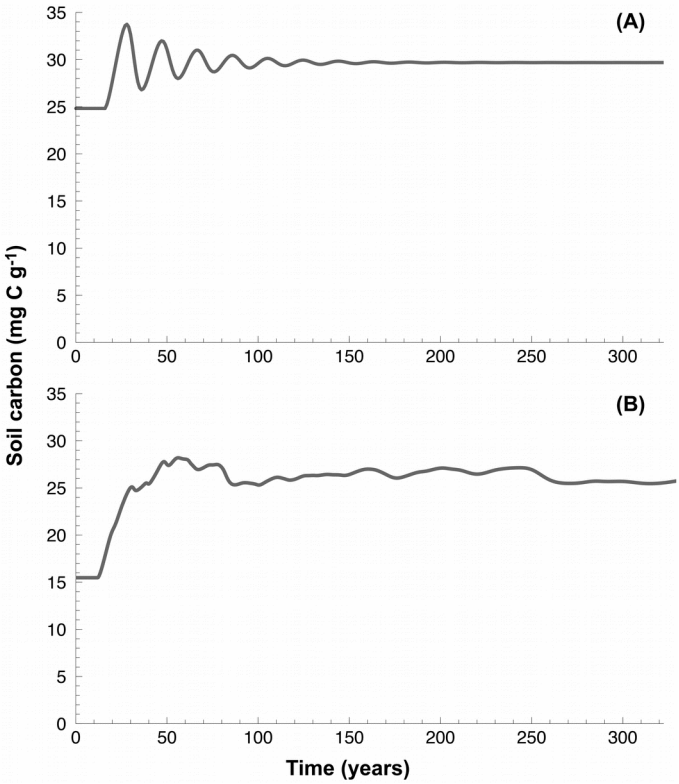

Figure 2. Aggregation of micro-scale processes to generate macro-scale emergent properties. (A) When a two-pool microbial-explicit model [German *et al.*, 2012] is perturbed by a 5ºC temperature increase, the soil carbon pool oscillates asymptotically to a higher equilibrium value based on parameters from Li *et al*. [2014]. (B) When heterogeneous microsites are averaged, the oscillatory pattern diminishes (W. Sherman, *unpublished*). The line represents the average of 68 microsites, each defined by unique parameter values for Vmax, Km, biomass turnover, and substrate input drawn at random from plausible distributions.

An additional need for scaling microbial models centres on state factor relationships. It is not yet clear how emergent microbial properties and responses vary with state factor gradients. There have been some studies of microbial trait parameters across environmental gradients [German *et al.*, 2012; Whitaker *et al.*, 2014], but more studies with additional environmental drivers are needed to scale up to the global level. Additional gridded data products on state factor variables at the global scale represent another key need for scaling up these models.

Conclusions

Now is an opportune time to make progress on modelling and scaling microbial processes to improve biogeochemical predictions. New empirical tools, particularly sequencing technology, are making unprecedented volumes of data available with the potential to inform microbial models. Realizing this potential will require new theory to translate sequences into ecologically relevant traits. Coupled with increased efforts to assemble data on microbial traits and processes, these advances will provide a basis

for parameterizing new trait-based models. Increases in computational power to support Monte-Carlo approaches and richer data sources from remote sensing and ecological experiments will facilitate the upscaling of microbial models.

The recent blossoming of microbial modelling approaches presents both an opportunity and a challenge. There is great potential for improving Earth system models by representing microbial processes with greater fidelity and elegance. The diversity of modelling perspectives is stimulating healthy debate about the best way to account for microbes in the Earth system. At the same time, all microbial-explicit models are relatively unproven. More rigorous validation is necessary to avoid scaling up theoretical approaches with fundamental flaws. Still, this challenge can be overcome with sufficient intellectual investment to yield Earth system predictions with much greater certainty and confidence than is currently possible.

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