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Discussions

Integrating microbial physiology and physiochemical principles in soils with the MIcrobial-MIneral Carbon Stabilization (MIMICS) model

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Abstract

Previous modeling efforts document divergent responses of microbial explicit soil bio-geochemistry models when compared to traditional models that implicitly simulate microbial activity, particularly following environmental perturbations. However, microbial models are needed that capture current soil biogeochemical theories emphasizing the relationships between litter quality, functional differences in microbial physiology, and the physical protection of microbial byproducts in forming stable soil organic matter (SOM). To address these limitations we introduce the MIcrobial-MIneral Carbon Stabilization (MIMICS) model. In MIMICS, the turnover of litter and SOM pools are governed by temperature sensitive Michaelis–Menten kinetics and the activity of two physiologically distinct microbial functional types. The production of microbial residues through microbial turnover provides inputs to SOM pools that are considered physically or chemically protected. Soil clay content determines the physical protection of SOM in different soil environments. MIMICS adequately simulates the mean rate of leaf litter decomposition observed at a temperate and boreal forest sites, and captures observed effects of litter quality on decomposition rates. Initial results from MIMICS suggest that soil C storage can be maximized in sandy soils with low-quality litter inputs, whereas high-quality litter inputs may maximize SOM accumulation in finely textured soils that physically stabilize microbial products. Assumptions in MIMICS about the degree to which microbial functional types differ in the production, turnover, and stabilization of microbial residues provides a mechanism by which microbial communities may influence SOM dynamics in mineral soils. Although further analyses are needed to validate model results, MIMICS allows us to begin exploring theoretical interactions between substrate quality, microbial community abundance, and the formation of stable SOM.

1 Introduction

The response of the terrestrial carbon (C) cycle to projected environmental change remains highly uncertain in Earth system models (Arora et al., 2013; Friedlingstein et al., 2006). Some of this uncertainty results from challenges in representing biological processes that drive exchanges of water, energy and C between the land surface and atmosphere. Aboveground, Earth system models rely on empirical differences in plant physiology and life history strategies to represent the biogeochemical and biogeophysical effects of vegetation dynamics in global simulations (Bonan, 2008; Roy et al., 1993). Although imperfect, these and other data (e.g. Kattge et al., 2011) are improving and refining the autotrophic, or "green", representations of the terrestrial C cycle (Bonan et al., 2012). Comparatively less attention has been given to revising biologically driven representations of the soil heterotrophic, or "brown", C cycle. Accordingly, Earth system models display wide variation in their soil C projections (Todd-Brown et al., 2013). Given the size of global soil C pools (Hugelius et al., 2013; FAO et al., 2012; Jobbágy and Jackson, 2000) and potential magnitude of soil C–climate feedbacks (Jones et al., 2003, 2005; Jenkinson et al., 1991) greater attention should be directed towards critically evaluating and improving the theoretical and numerical representation of soil biogeochemistry models that are used at multiple scales.

A growing body of literature calls for significant revisions to the theoretical basis for modeling soil C dynamics (Cotrufo et al., 2013; Dungait et al., 2012; Conant et al., 2011; Schmidt et al., 2011). Traditional soil C stabilization concepts do not explicitly simulate microbial activity or soil microbial communities but, instead, strongly emphasize the relationship between litter chemical recalcitrance and soil C storage. In contrast, new theoretical and experimental research show that soil microbes strongly mediate the formation of soil organic matter (SOM) through the production of microbial products that appear to form mineral-stabilized SOM (Wallenstein et al., 2013; Miltner et al., 2012; Wickings et al., 2012; Kleber et al., 2011; Grandy and Neff, 2008; Six et al., 2006). These insights suggest that basic physiological traits such as microbial

growth efficiency (MGE) and growth kinetics have direct influences on litter decomposition rates and net microbial biomass production, while the subsequent turnover of microbial biomass strongly influences input rates to SOM. Further, the ultimate fate of SOM inputs also depends upon the mineral-stabilization of these microbial-derived products. However, despite wide recognition that microbial physiology and soil mineral interactions facilitate the formation of stable SOM, this theoretical insight has not been adequately represented in process-based models.

These emerging concepts highlight the need to explicitly simulate the microbial processes responsible for decomposition and stabilization of organic matter (Todd-Brown et al., 2012; Treseder et al., 2012; Allison et al., 2010; Lawrence et al., 2009; Bardgett et al., 2008; Schimel and Weintraub, 2003), even if the magnitude of microbial control over soil C dynamics in mineral soils remains poorly defined (Schimel and Schaeffer, 2012). Microbial explicit approaches in recent models range in complexity from simple fungal to bacterial ratios (Waring et al., 2013), microbial guilds specializing in different litter C substrates (Miki et al., 2010; Moorhead and Sinsabaugh, 2006) and complex community dynamics (Allison, 2012; Wallenstein and Hall, 2012; Loreau, 2001). These models incorporate the complexity of microbial physiology and competitive interactions on litter decomposition dynamics and provide valuable insight to our understanding of "upstream" soil C inputs, but focus less attention on the stabilization of microbial residues in mineral soils. Other recent work demonstrates that simple non-linear microbial models are feasible at the global scale, and result in divergent responses compared with traditional soil biogeochemistry models (Wieder et al., 2013b). But again, this microbial modeling framework does not adequately capture how microbial physiology and activity may facilitate the stabilization of SOM.

Microbial attributes that regulate microbial residue inputs to SOM and their interactions with the soil matrix are effectively absent in traditional soil biogeochemical models, and poorly accounted for in current microbial-based models. Thus, our chief motivation is to develop a process-based modeling framework to explore the potential role of microbial physiology and the stabilization of microbial biomass at the soil–mineral inter-

face as key drivers in the formation of SOM (Miltner et al., 2012; Liang et al., 2011; Bol et al., 2009; Grandy et al., 2009). In this model litter and SOM turnover are governed by microbial biomass pools, which correspond to different microbial functional types. Inherent physiological differences between microbial functional types provide a basis to begin simulating belowground biological and metabolic diversity and explore how the relative abundance of different microbial functional groups regulates biogeochemical processes (Miki et al., 2010). Microbial growth rates, growth efficiency and turnover are subject to intrinsic physiological constraints (Beardmore et al., 2011; Molenaar et al., 2009; Dethlefsen and Schmidt, 2007) but are also sensitive to external forces, such as resource chemistry (Manzoni et al., 2012; Keiblinger et al., 2010; Steinweg et al., 2008; Rousk and Bååth, 2007; Thiet et al., 2006), such that both community composition and the soil environment should determine the optimization of physiological traits and their downstream influence on SOM dynamics.

We use recent experimental insights to guide our incorporation of microbial physiological processes into predicting SOM stabilization. Physiological differences across species have been linked to life-history strategies optimized for different resource environments (Resat et al., 2012; Beardmore et al., 2011; Russell and Cook, 1995). For instance, in resource rich environments fast-growing r-strategists (copiotrophs) are typically characterized by a lower MGE but higher growth rates, relative to slower-growing K-strategists (oligotrophs; Fierer et al., 2007, 2012a; Ramirez et al., 2012; Klappenbach et al., 2000; Pianka, 1970). This physiology gives copiotrophs a competitive advantage under resource-rich conditions such that they tend to dominate in these environments. At an individual species-level, MGE, growth rates, and turnover are expected to increase as resource quality increases. However selection for a copiotroph-dominated community may drive up community-level growth rates and turnover at the expense of a lower MGE. The effect of this trade-off on total biomass production and microbial-derived inputs to physically protected SOM is uncertain, and remains a challenging, often missing, aspect of microbial-based soil C models.

In order to more rigorously evaluate dynamics between microbial physiology, soil environmental conditions and SOM formation we introduce the MIMICS (MIcrobial-MIneral Carbon Stabilization) model, which is building on initial efforts by Wieder and others (2013b) to represent microbial processes in global soil C predictions made by the Community Land Model (Lawrence et al., 2011). MIMICS incorporates the relationships between microbial physiology, substrate chemical quality, and physical stabilization of SOM (Wang et al., 2013; Goldfarb et al., 2011; Fontaine and Barot, 2005). Here it is specifically used to explore how microbial physiological traits can be applied to a process-based soil biogeochemistry model that emphasizes the fate of microbially derived inputs to SOM and their stabilization.

2 Methods

2.1 Model configuration

To develop MIMCS, we modified the CLM microbial model, a soil biogeochemistry model that explicitly represents microbial activity and microbial physiology (Wieder et al., 2013b), to simulate two plant litter, microbial biomass, and SOM pools (LIT, MIC and SOM in Fig. 1, respectively); this structure blends aspects of traditional and microbial explicit models. In particular, MIMICS simulates physically and biochemically protected SOM pools that are also represented in the MEND model (Wang et al., 2013), and multiple substrate pools are represented in the EEZY model (Moorhead et al., 2012), while simplifying the overall model structure by eliminating explicit enzyme pools (Wieder et al., 2013b). A vertical dimension could be added to this basic six-pool model structure (Koven et al., 2013), but here we focus on the dynamics simulated within a single soil layer (0–30 cm).

The representation of plant litter pools in MIMICS is based on well-established paradigms of litter chemistry and decomposition dynamics (Melillo et al., 1982). We partition fresh litter inputs into high and low quality pools (LIT$_m$ and LIT$_s$, receptively)

that correspond to the metabolic and structural pools used in in CENTURY and DAY-CENT (Parton et al., 1987, 1994). As in DAYCENT, partitioning into these pools is based on a linear function of litter nitrogen to lignin ratios (f_{met}; Table 1). A fraction of inputs (f_i) bypasses litter and microbial biomass pools, and is directly transferred to corresponding SOM pools. For metabolic litter inputs, this fraction is analogous to dissolved organic matter fluxes that leach out of leaf litter or root exudates that quickly become sorbed onto mineral surfaces. For structural litter inputs, this is analogous to a relatively small proportion of the structurally complex compounds that could be incorporated into SOM before microbial oxidation. Thus, f_i for structural litter inputs is inversely related to litter quality (Table 1).

Decomposition of litter and SOM pools is based on temperature sensitive Michaelis–Menten kinetics (Allison et al., 2010; Schimel and Weintraub, 2003) through the basic equation:

$$\frac{dC_s}{dt} = \text{MIC} \times \frac{V_{max} \times C_s}{K_m + C_s} \tag{1}$$

where C_s is an individual C substrate pool (LIT or SOM) and MIC corresponds to the size of the microbial biomass pool, both in $mg\,C\,cm^{-3}$. Thus, rates of C decomposition depend on donor C (either LIT or SOM) and receiver (MIC) pool sizes as well as kinetic parameters V_{max} and K_m. The maximum reaction velocity (V_{max}; $mg\,C_s\,(mg\,MIC)^{-1}\,h^{-1}$) and half saturation constant (K_m; $mg\,C\,cm^{-3}$) are respectively calculated as:

$$V_{max} = e^{V_{slope} \cdot T + V_{int}} \cdot av \cdot V_{mod} \tag{2}$$
$$K_m = e^{K_{slope} \cdot T + K_{int}} \cdot ak \cdot K_{mod} \tag{3}$$

where T represents soil temperature, which we assumed to be 15 °C unless otherwise noted. The temperature sensitivity of kinetics parameters (described in Table 1) are derived from observational data (German et al., 2012), with modifications based on assumptions regarding microbial functional types, litter chemical quality and soil texture

effects (V_{mod} and K_{mod}; Table 1). See Appendix A for a more detailed description of equations governing C fluxes in MIMICS.

Two microbial functional types are represented in MIMICS that roughly correspond to copiotrophic and oligotrophic growth strategies (MIC_r and MIC_K, respectively; Lipson et al., 2009; Dethlefsen and Schmidt, 2007; Fierer et al., 2007). We have intentionally classified our microbial functional types based on these broad ecological life-history traits because they explicitly parameterize the growth physiologies we are exploring in MIMICS and avoid the exclusivity of fungal: bacteria ratios (Strickland and Rousk, 2010). We assume that the copiotrophic community (MIC_r) has a higher growth rate when consuming metabolic litter and physically protected soil C because of the relatively low C : N ratio and chemical complexity of these pools (LIT_m and SOM_p, respectively); whereas the kinetics of the oligotrophic community (MIC_K) are comparatively more favorable when consuming structural litter and chemically protected soil C (LIT_s and SOM_c, respectively; Fig. 1, Table 1) relative to MIC_r. We recognize the uncertainties in these classifications, but argue they provide a tractable starting point to begin representing microbial metabolic diversity in regional to global scale models. We consider the SOM_p pool to be largely derived of low C : N, labile materials that are either microbial products or highly processed litter (Grandy and Neff, 2008), whereas the low quality SOM_c pool consists of litter that is higher in structural C compounds such as lignin.

We implement physical protection of SOM through environmental scalars that increase the K_m of SOM pools with increasing soil clay content. This environmental scalar is more dramatic for the physically protected SOM pool (SOM_p) than it is for the chemically protected pool (SOM_c), and strongly reduces microbial access to substrates in mineral soils (Schimel and Schaeffer, 2012). Other aspects of soil mineralogy certainly regulate SOM stabilization (Heckman et al., 2013; Kramer et al., 2012; Kaiser et al., 2011; von Lützow et al., 2008; Jastrow et al., 2007), but in order to represent microbial driven soil biogeochemical processes at global scales we constrain the com-

plexity of our parameterization to clay content, shown to be a primary factor in physical stabilization mechanisms (Kleber et al., 2011; Mikutta et al., 2006; Sollins et al., 1996).

Microbial growth efficiency determines the fraction of assimilated C that builds microbial biomass (del Giorgio and Cole, 1998). We have incorporated new experimental insights into the model's MGE dynamics by first accounting for substrate quality, which is positively related to MGE (Frey et al., 2013; Keiblinger et al., 2010; Steinweg et al., 2008; Table 1). Second, we explore the theoretical evidence that there is differential MGE for each microbial functional type whereby, for a given substrate, fast growing copiotrophic communities should have lower growth efficiency than slower growing oligotrophic communities (Sinsabaugh et al., 2013; Lipson et al., 2009; Fierer et al., 2007; Pfeiffer et al., 2001; Russell and Cook, 1995). We recognize the importance of considering MGE sensitivity to changes in temperature and nutrient availability in refining our understanding of microbial physiological response to perturbations (Lee and Schmidt 2014; Tucker et al., 2014; Wieder et al., 2013b; Manzoni et al., 2012; Bradford et al., 2008; Frey et al., 2008; Steinweg et al., 2008), although these theoretical considerations are not addressed in this manuscript.

A fixed fraction of the microbial biomass pools turns over at every time step (τ), with partitioning into physically and chemically protected SOM pools dependent on the chemical quality of litter inputs (f_c, Table 1). We assume the turnover rates of copiotrophic microbial communities will be greater than their oligotrophic counterparts (Fierer et al., 2007), and that the turnover of MIC_r will increase with higher quality litter inputs. We also assume the majority of τ will be partitioned into the physically protected SOM pool, especially from MIC_r, and that partitioning from MIC_K to chemically protected pools be inversely related to litter quality.

2.2 Initial model evaluation: litter decomposition study

Validating assumptions and parameterization in MIMICS presents unique challenges. Given the difficulty in obtaining empirical data on MGE and microbial turnover, and the methodological limitations to resolving the flow of microbial C into SOM (Six et al.,

2006), our model evaluation is restricted to the litter fluxes and decomposition dynamics that are represented in the left portion of our model (Fig. 1). Leaf litter decomposition studies provide process-level evaluation of soil C dynamics across biomes and with multiple litter types (Bonan et al., 2013; Yang et al., 2009). We take a similar ap-
5 proach in evaluating MIMICS, using data from the LIDET study. LIDET was a decade long multisite study designed to investigate climate – litter quality dynamics in decaying litter (Currie et al., 2010; Harmon et al., 2009; Adair et al., 2008; Parton et al., 2007; Gholz et al., 2000). Here we used a subset of LIDET data (from Parton et al., 2007) that have been previously used to evaluate litter decomposition dynamics in Earth sys-
10 tem models (Bonan et al., 2013). Although similar exhaustive evaluations of leaf litter decomposition dynamics are outside the scope of this paper, we used data from six leaf litters of various chemical quality decomposed at two LIDET sites (Harvard Forest and Bonanza Creek) to begin evaluating process-level simulations provided by our non-linear microbial model.
15 Litterbag studies are relatively simple to replicate using traditional soil biogeochemistry models based on first-order kinetics (Bonan et al., 2013). In these donor control models pool size has no bearing on rates of litter decay, so decomposition dynamics can be simulated by adding a fixed amount of litter to appropriate pools subject to environmental scalars (e.g., soil temperature and soil moisture) that modulate base
20 rates of decomposition over time. However, in MIMICS, decomposition does not follow simple first-order kinetics because the size of both donor and receiver pools modulate decay rates via environmentally sensitive microbial kinetics parameters (Eq. 1). Since the size of the microbial biomass pools exerts strong influence over rates of litter decay, MIMICS had to be equilibrated at steady-state before adding a cohort of litter to track
25 over the experimental period. Second, augmenting litter pools initially increased rates of decomposition and enlarged microbial biomass pools, which further accelerated decomposition rates (see Eq. 1). To overcome these complications we took several steps to facilitate evaluation of leaf litter decomposition studies using non-linear microbial models.

We applied a Newton–Raphson approach to analytically calculate steady-state C pools using the stode function in the rootSolve package in R (R Development Core Team, 2011; Soetaert, 2009). We calculated steady-state pools and site productivity estimates at the Harvard Forest and Bonanza Creek Long-Term Ecological Research sites (Knapp and Smith, 2001). Mean annual soil temperatures were estimated as 10.7 and 3.9 °C at Harvard Forests (May 2001–October 2010) and Bonanza Creek (June 1984–December 2004), respectively (data from the Climate and Hydrology Database Projects – a partnership between the Long-Term Ecological Research program and the US Forest Service Pacific Northwest Research Station, Corvallis, Oregon; http://climhy.lternet.edu/, accessed August 2013). Productivity estimates provided litter inputs that were distributed at hourly intervals evenly throughout the year. We created a daily climatology from a decade or more of soil temperature records at each site and calculated steady-state pools with hourly litter inputs and mean annual soil temperature. We assumed soils at both sites had 10 % clay content and metabolic litter inputs were 30 % of total litter inputs. From their steady-states, models for each site were run for an additional thirty years with hourly litter inputs and daily soil temperature climatologies, allowing all C pools to equilibrate to seasonally fluctuating temperatures. Data for control simulations continued beyond this equilibration period for an additional decade. In experimental simulations we added $100\,\mathrm{g\,C\,m}^{-2}$ to litter pools on October first, with partitioning between $\mathrm{LIT_m}$ and $\mathrm{LIT_s}$ dependent on litter quality (f_{met}, Table 1). To avoid changing results by augmenting microbial biomass pools through this litter addition (Eq. 1), we forced the experimental simulation to maintain the same microbial biomass pool as the control simulation. We calculated the percent mass remaining as the difference in litter pools from experimental and control simulations. Model parameterizations were modified to provide the best fit for Harvard Forest data, and independently evaluated using results from Bonanza Creek.

2.3 Steady-state soil C pools and sensitivity analysis

Initial parameter values were evaluated with data from LIDET sites to explore how steady-state litter, microbial biomass and soil C pools vary with soil texture and litter chemical quality. We calculated steady-state conditions for all MIMICS pools using the stode function. Soil texture effects on turnover of SOM pools (P_{scalar} and C_{scalar}; Table 1) provide strong influence on steady-state SOM pools. We chose values for these parameters assuming that low clay soils would provide low physical protection of soil C (i.e, low K_m), that increases exponentially with increasing soil clay content (Table 1). We further constrained initial parameterizations to keep the ratio of total soil microbial biomass to SOM roughly within observational constraints (Serna-Chavez et al., 2013; Xia et al., 2012). This provides useful bounds because much larger SOM pools can be simulated with this model by adjusting soil texture effects on the half-saturation constant for C fluxes from SOM to microbial biomass pools (using the P_{scalar} and C_{scalar}, Table 1). From these initial conditions (Table 1) we modified individual parameters 10 % to illustrate important model assumptions, characteristics, and uncertainties.

3 Results

3.1 Model evaluation: litter decomposition

In Fig. 2 we show the mean percent mass remaining (±1 SD) of six different leaf litter types decomposed at Harvard Forest and Bonanza Creek for LIDET observations (points and error bars) and MIMICS simulations (lines and shaded area). After calibrating model parameters to fit LIDET observations from Harvard Forest (Table 1), MIMICS can replicate litter decomposition dynamics well at both sites. Beyond capturing the mean state that reflects broad climatic influences on leaf litter decomposition, observed litter quality effects on litter decomposition rates (error bars) are well simulated in the model (shaded area).

Final litter mass remaining was lower than LIDET observations at the warmer Harvard Forest site (Fig. 2a), suggesting a third litter C pool corresponding to leaf litter lignin may be necessary to capture the long tail of leaf litter decomposition dynamics (Adair et al., 2008). Some of the assumptions we made to facilitate good agreement with LIDET observations exerted negligible effects on steady-state SOM pools, while other assumptions had significant influence. For example, our assumption that soils at both sites contained ten percent clay had no bearing on litter decomposition dynamics because, as parameterized, clay fraction only modifies steady-state SOM pools. In contrast, assumptions about the metabolic fraction of litter inputs exert significant influence over litter decomposition dynamics by modifying the steady-state size of all simulated pools. Specifically, decreasing f_{met} generates comparable total microbial biomass pools, but with a larger proportion of biomass in the oligotrophic (MIC_K) community. The oligotrophic community decomposes leaf litter more slowly, resulting in lower rates of mass loss (Wieder, unpublished data). More broadly, any parameter that modifies the steady-state size of microbial biomass pools will strongly influence temporal dynamics of the model, although such modifications may have little or no effect on steady-state soil C storage.

3.2 Steady-state soil C pools: influence of litter inputs

Soil C pools in MIMICS vary as a function of litter quality and soil texture (Fig. 3), with high metabolic fraction of litter providing the widest range of steady-state values (from 5.2 to 26.3 mg C cm^{-3} in low clay and high clay soils, respectively). In soils with low clay content (< 0.3 clay fraction) receiving low quality litter inputs (< 0.2 f_{met}) the chemically protected SOM pool was larger than the physically protected SOM pool, however, in all other cases the majority of SOM was found in the physically protected SOM pool. Reducing litter inputs 10 % directly reduced the size of microbial biomass pools 10 %, with no changes to the size of steady-state litter or SOM pools.

At steady-state total litter pool size (the sum of LIT_m and LIT_s) was inversely related to the fraction of metabolic inputs; ranging from 2.3 to 4.1 mg C cm^{-3} (with high and

low f_{met}, respectively). The proportion of total litter found in the metabolic litter pool increased exponentially with increasing f_{met}. Total microbial biomass pool size was relatively invariant with litter quality and soil clay content ($\sim 0.12\,\mathrm{mg\,C\,cm^{-3}}$); however, the relative abundance of MIC_r increased from approximately 9 % of the total microbial biomass pool with low quality liter inputs, to nearly 45 % with high quality litter inputs (Fig. 4a).

3.3 Steady-state soil C pools: influence of microbial physiology

We assumed microbial functional types control the Michaelis–Menten kinetics of litter mineralization. In contrast, the physical soil environment exerts strong control over half saturation constant of SOM mineralization, with modest differences in the V_{max} driven by microbial functional types (Table 1). Thus, MIMICS illustrates how functional differences between microbial functional types can regulate the fate of C substrates and affects steady-state SOM pools, either directly or indirectly. We illustrate these dynamics with a series of sensitivity analyses where we perturb individual parameters 10 % and document their effect on steady-state soil C pool simulated by MIMICS.

Litter quality determines the relative abundance of microbial functional types in MIMICS. These results, however, depend on the competitive dynamics between microbial functional types that are directly related to assumptions made about the catabolic potential, MGE, and turnover rates of MIC_r and MIC_K communities (Fig. 4a). For example, reducing the catabolic potential of litter mineralization for the copiotrophic community, (MIC_r; either by reducing V_{max}, or increasing K_m) reduces the relative abundance of MIC_r by 1–3 % across soil textures. This decline in MIC_r abundance indirectly feeds back to steady-state SOM pools (Fig. 4b) because we also assumed that the turnover of MIC_r is greater than MIC_K. Thus, reducing the relative abundance of MIC_r indirectly reduced inputs of microbial residues to SOM pools, reducing total soil C storage. Reductions in soil C storage associated with the kinetics of litter C mineralization, however, are distal to the production of microbial residues that build SOM in MIMICS. Instead,

parameters like MGE and microbial turnover are proximal to the production of microbial biomass and exert greater influence over soil C dynamics (Fig. 4).

Carbon substrates and microbial physiology likely determine the efficiency by which different microbial functional types convert assimilated C into microbial biomass (Sinsabaugh et al., 2013; Lipson et al., 2009; Pfeiffer et al., 2001; Russell and Cook, 1995). We explore this theory by decreasing the MGE of MIC_r communities 10 % (see Lee and Schmidt, 2014). This modification concurrently reduces the relative abundance of the MIC_r community 3–10 %, with greater reductions in high substrate quality environments (Fig. 4a). These results indicate that assumptions made about tradeoffs between microbial growth rates and MGE may be important in structuring competitive interactions between microbial functional types. The relative abundance of microbial functional types relates to the community physiological function, which in turn influences soil C dynamics. In this example, reducing the relative abundance of the MIC_r community by reducing its MGE can either increase or decrease soil C storage (Fig. 4b). In low quality resource environments ($f_{met} < 0.25$) reducing MIC_r abundance reduces rates of SOM turnover and can lead to modest increases in SOM pools by as much as 1 %. In high quality resource environments ($f_{met} > 0.25$) reducing the relative abundance of MIC_r communities reduces inputs of microbial residues to SOM pools with over a 3 % declines in steady-state soil C storage.

Modifications that reduce the kinetic capacity and growth efficiency of the MIC_r community reduce the relative abundance of this community. Shifts in community composition largely influence SOM dynamics via interactions with the production of microbial residues that govern the fate of C in MIMICS. Not surprisingly, increasing microbial turnover of the MIC_r community 10 % also reduces the relative abundance of this functional type 3–13 % (Fig. 4a). This directly increases inputs of microbial residues to SOM pools and generally increases soil C storage, with greater SOC accumulation in clay rich environments that stabilize microbial residues (Fig. 4b). Thus, in MIMICS we assume microbial functional types can govern the fate of C substrates assimilated. Microbial growth efficiency and turnover are proximal to the production of microbial

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biomass and microbially derived inputs to SOM pools. Accordingly, these parameters have larger influence over the relative abundance of microbial functional types and soil C stabilization.

4 Discussion

We outline a framework for integrating litter quality, functional differences in microbial physiology and the physical protection of microbial byproducts in forming stable SOM in a process-based numerical model (Fig. 1; Table 1). Our approach simulates observed climate and litter quality effects on average rates of leaf litter decomposition (Fig. 2), providing a robust validation for the MIMICS parameterizations governing the kinetics of litter decay. Although further analyses are needed to test our soil C results against field data, MIMICS allows us to begin exploring theoretical interactions between substrate quality, microbial community abundance, and the formation of stable SOM. Initial results from MIMICS suggest that soil C stabilization may be greatest in environments with high metabolic inputs and clay rich soils (Fig. 3); results that aligns with recent experimental evidence and conceptual models of SOM formation that highlight the production and stabilization of microbial residues on minerals surfaces (Cortufo et al., 2013; Miltner et al., 2012; Kleber et al., 2011; Grandy and Neff, 2008; Marschner et al., 2008). Further, our results suggest that proximal controls over the production of microbial biomass and residues, MGE and microbial turnover, provide an important mechanism by which microbial communities may influence SOM dynamics in mineral soils (Fig. 4). The extent to which variation in MGE and turnover can be constrained by observations remains uncertain, but overcoming this technical challenge may be critical in resolving potential effects of microbial functional diversity in soil biogeochemical models.

While MIMICS provides insights into the interaction between SOM dynamics and microbial physiology, it also presents a platform for evaluating the key differences between traditional and microbial modeling approaches (summarized in Table 2). Traditional soil

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biogeochemistry models simulate the turnover of SOM based on the *implicit* representation of microbial activity (Schnitzer and Montreal, 2011; Berg and McClaugherty, 2008). In both traditional and microbial explicit approaches MGE determines the fraction of assimilated C that enters receiver pools. Although MGE is typically fixed in traditional models, modifying MGE directly effects pool size but not flux rates (Frey et al., 2013; Tucker et al., 2013). In contrast, MGE and microbial turnover regulate both pool size and rates of litter and SOM turnover in microbial explicit models. Moreover, in the MIMICS framework, there is a feedback whereby differences in the relative abundance of microbial functional types influences litter decomposition and soil C storage (Fig. 4).

4.1 Litter inputs and SOM formation

The quantity of litter inputs are positively related with steady-state SOM pool sizes in traditional biogeochemistry models (Todd-Brown et al., 2013). In contrast, the quantity of litter inputs is completely unrelated to steady-state SOM pool size in microbial explicit models. This feature appears to be characteristic of microbial explicit models (German et al., 2012; Wang et al., 2013; Wieder et al., 2013b). Instead, litter quantity determines the size of microbial biomass pools, in agreement with observational data (Fierer et al., 2009). In MIMICS, larger microbial biomass pools increase input rates of microbial residues to SOM pools, but they also accelerate rates of C turnover in a "priming effect". This phenomenon occurs when new C inputs result in the accelerated turnover of native SOM (Phillips et al., 2011; Kuzyakov, 2010). Recognizing the potential for priming to have a disproportionally strong effect on SOM dynamics in microbial explicit models we created a physically protected SOM pool (Fig. 1). This provides a mechanism whereby increasing litter inputs could increase inputs of microbial residues to SOM pools to a greater extent than larger microbial biomass pools could mineralize extant SOM, at least in clay rich soils. However, microbial biomass still directly affects inputs and losses from SOM, suggesting that MIMICS likely overemphasizes the role of biological processes in what should be physically dominant SOM stabilization mechanisms. The extent to which priming decreases SOM with increasing litter inputs is unknown, but

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there are an increasing number of studies showing that increases in litter inputs do not increase or may even decrease soil C (Sulzman et al., 2005; Nadelhoffer et al., 2004; K. Lajtha, personal communication, 2013; but see also Leff et al., 2012). While the relationships between C inputs, microbial biomass pools, and SOM are a controversial element of microbial-explicit models and require clarifications, they do have their basis in both experimental evidence and theory.

In traditional models, increasing litter quality causes declines in soil C storage with greater partitioning into pools with faster turnover times (Wieder et al., 2013a; Schimel et al., 1994). In MIMICS, increasing the chemical quality of litter inputs increases the relative abundance of the copiotrophic microbial community (MIC_r) with faster kinetics (Table 1; Fig. 4a), a result that qualitatively aligns with observations (Waring et al., 2013; Nemergut et al., 2010; Rousk and Bååth, 2007). Our results indicate that the combined effects of accelerated litter turnover and increasing microbial inputs on SOM depends on soil texture, with maximum soil C storage occurring in high clay soils receiving high quality litter inputs (Fig. 3). These divergent projections between traditional and microbial models highlight the importance of considering potential interactions between microbial physiology and the physical soil environment.

Explicit representation of physical protection of SOM in MIMICS provides a mechanism to form stable SOM via mineral stabilization of microbial byproducts (Six et al., 2002; Sollins et al., 1996). Thus, high turnover of MIC_r communities can actually build stable SOM in resource rich environments when those microbial byproducts are physically stabilized in finely textured soils (Fig. 3). Currently, we combine the physical protection mechanisms of aggregation and mineral associations (Grandy and Robertson, 2007; Mikutta et al., 2006; Six et al., 2002; Hassink, 1997) into the same functional pool (SOM_p; Fig. 1). Given the potential differences in the long-term stabilization of various protection mechanisms, further analyses are needed to evaluate the model structures and parameterizations to better simulate diverse stabilization mechanisms across larger spatial and temporal scales.

4.2 Microbial physiology

Microbial physiological traits related to growth and biomass production are key elements in determining input rates of microbial residues to SOM. The deficit of empirical data relating soil C stabilization to MGE and microbial turnover presents challenges to moving beyond these theoretical concepts; however, MIMICS introduces a framework to explore how microbial physiological tradeoffs may influence relative community abundance and soil C dynamics. Although highly reductionist, simplifying the metabolic and life history strategies of belowground communities into broad categories relating to microbial physiology provides a tractable path forward to begin exploring how microbial community structure and abundance may affect soil biogeochemical processes (Miki et al., 2010). While the temperature responses of Michaelis–Menten kinetics are based on observational data (German et al., 2012), the model presented here provides numerous avenues to explore how less well-defined microbial characteristics respond to the physical and chemical soil environment and how changes in those responses may mediate biogeochemical processes. For example, we have made certain assumptions about the effectiveness of microbial functional types in mineralizing different C substrate pools (Table 1). While broadly based on microbial physiological theory (Fierer et al., 2007), these assumptions establish competitive interactions between copiotrophic and oligotrophic microbial communities that structure the relative abundance of microbial functional types at steady-state (Fig. 4).

Key physiological parameters in MIMICS include the Michaelis–Menten kinetics of substrate mineralization (V_{max} and K_m), the efficiency by which microbial communities turn C substrates into biomass (MGE), and the rate of microbial turnover (τ). The importance of microbial physiology in determining soil C dynamics remains uncertain; especially in mineral soils where physical access to C substrates, and not microbial catabolic potential, limit rates of SOM mineralization (Schimel and Schaeffer, 2012). Thus, the extent to which physiological differences between microbial functional groups determine the fate of C remains speculative (Cotrufo et al., 2013; Schimel and Schaeffer, 2012),

but MIMICS suggests that proximal factors controlling the production and turnover of microbial biomass (MGE and τ) will mediate soil C dynamics (Fig. 4). These characteristics of microbial explicit models show similarities with key drivers determining steady-state SOM pools in traditional models (environmentally sensitive turnover rates, the quantity of litter inputs and MGE; Todd-Brown et al., 2013, Xia et al., 2013); although, these parameters can elicit contrasting responses in different modeling frameworks.

In traditional and microbial models MGE influences soil biogeochemical responses to perturbations, an observation that initiated a surge of interest in quantifying and understanding factors that influence MGE (Frey et al., 2013; Sinsabaugh et al., 2013; Tucker et al., 2013; Manzoni et al., 2012; Bradford et al., 2008). In traditional models, reducing MGE increases the fraction of assimilated C lost to heterotrophic respiration rates without modifying rates of C mineralization from donor pools. This causes an overall reduction in SOM pools (Frey et al., 2013). In microbial models, reducing MGE also increases the fraction of mineralized C lost to heterotrophic respiration and reduces the size of microbial biomass pools. However, reducing microbial biomass pools concurrently slows rates of substrate mineralization (Eq. 1) and may result in no net change in steady-state SOM pool size (Wieder et al., 2013b). In MIMICS, MGE has no direct effect on steady-state SOM dynamics. Instead, MGE strongly affects steady-state SOM pools by influencing the relative abundance of microbial functional types (Fig. 4), which determines both microbial turnover and SOM mineralization kinetics. This feature is absent in microbial models lacking explicit microbial functional types (Wieder et al., 2013b), and shows that understanding the response of MGE to perturbations may be important in resolving questions of microbial competition, physiological tradeoffs, community composition and soil biogeochemical function at multiple scales.

Physiological differences in catabolic potential between microbial functional types become less important in mineral soils where soil texture determines the half-saturation constant for SOM mineralization (Table 1). Instead, the allocation of microbial biomass into the chemically and physically protected pools becomes more important in determining microbial influence on SOM dynamics (Schimel and Schaeffer, 2012; Fig. 4). In

sandy soils, with low physical protection of SOM, microbial communities have easier physical access to SOM pools and biochemical protection is more important in stabilizing SOM. In MIMICS, low litter quality environments favor oligotrophic microbial communities, which have slower kinetics and turnover. While MIC_K still allocate C to the physically protected pool, the combination of litter chemical recalcitrance and lower microbial kinetics results in more litter byproducts entering the chemically protected pool. This leads to greater C storage in low clay soils receiving low quality litter inputs (Fig. 3). With increasing clay content, microbial access to C become restricted as physical protection increases. Accordingly, soil C storage is maximized in high clay soils that have greater microbial turnover that is allocated to physically protected pools (i.e., high quality litter inputs).

These examples highlight the importance of τ in determining the amount of microbial control over soil C cycling, although our inability to quantify the flow of C from microbes into SOM (Simpson et al., 2007), and rates of microbial growth and turnover (Blagodatskaya and Kuzyakov, 2013; Rousk and Bååth, 2011; Blazewicz and Schwartz, 2011), limit numerical approaches to simulating microbial physiology (*sensu* Elliott et al., 1996). Thus, estimating microbial turnover and its potential response to the soil environment remains a huge source of uncertainty in microbial models that has not been readily assessed with current experimental techniques.

More broadly, microbial models would benefit from stronger theoretical and empirical understanding of microbial physiological response to perturbations. A growing body of literature documents site-level microbial community shifts and physiological responses to environmental change drivers (Lee and Schmidt 2014; Stone et al., 2012; Dijkstra et al., 2011; Manzoni et al., 2011; Nemergut et al., 2010; Carney et al., 2007; Waldrop et al., 2004). More broadly, sampling across wide geographic gradients (Ramirez et al., 2012) and meta-analyses (Janssens et al., 2010; Liu and Greaver, 2010) provide useful summaries of observations and offer broad targets that models should be expected to replicate. Confidence in model projections can be improved if parameterizations for microbial physiology across gradients or in response to perturbations draw on robust

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empirical relationships. This goal seems feasible for parameterizations of Michaelis–Menten kinetics and MGE (German et al., 2012; Frey et al., 2013; Lee and Schmidt, 2014). Developing similar empirical relationships to resolve community effects on the fate of microbial turnover products remains a challenge, although new approaches may

5 offer key insight (e.g., Fierer et al., 2012b). The degree to which microbial communities effect soil C dynamics in mineral soils (Schimel and Schaeffer, 2012) likely depend on such data.

MIMICS provides a tractable test bed for exploring the implementation of microbial-based soil biogeochemical concepts across scales. Our new microbial-based model,

10 MIMICS, demonstrates how to incorporate the effects of belowground metabolic and biological diversity on biogeochemical cycles through the explicit representation of microbial functional types, parameterized by functional tradeoffs in physiological strategies. We also introduce a framework for simulating effects of litter chemical quality and physical stabilization of SOM in microbial explicit models. Further model develop-

15 ments should include soil environmental drivers that modify rates of biogeochemical processes and microbial community composition (e.g., nitrogen availability, soil pH, hydrology, oxygen availability, land management practices, etc.). These developments demand collaboration between observational and modeling communities, and will benefit from the synthesis of datasets that can be used to parameterize and evaluate pro-

20 cesses simulated across gradients and in response to perturbations. Despite these challenges, we see the potential for significant steps forward in advancing and refining out theoretical understanding of soil biogeochemical cycles and the implementation of that theory in processed-based models.

Supplementary material related to this article is available online at

25 **http://www.biogeosciences-discuss.net/11/1147/2014/bgd-11-1147-2014-supplement.pdf.**

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Table 1. Model parameter descriptions, values, and units used in the MIMICS model.

Parameter	Description	Value	Units
f_{met}	Partitioning of litter inputs to LIT_m	0.85–0.013 (lignin × N^{-1})	–
f_i	Fraction of litter inputs directly transferred to SOM	0.02, 0.3 × $e^{(-4 \times fmet)}$ [a]	–
V_{slope}	Regression coefficient	0.063 [b]	$\ln(mg\,C_s\,(mg\,MIC)^{-1}\,h^{-1})\,°C^{-1}$
V_{int}	Regression intercept	5.47 [b]	$\ln(mg\,C_s\,(mg\,MIC)^{-1}\,h^{-1})$
a_V	Tuning coefficient	8×10^{-6} [b]	–
V_{mod-r}	Modifies V_{max} for each substrate pool entering MIC_r	10, 2, 6, 2 [c]	–
V_{mod-K}	Modifies V_{max} for each substrate pool entering MIC_K	2, 2, 2, 2 [d]	–
K_{slope}	Regression coefficient	0.017 [b,e]	$\ln(mg\,C\,cm^{-3})\,°C^{-1}$
K_{int}	Regression intercept	3.19 [b]	$\ln(mg\,C\,cm^{-3})$
a_K	Tuning coefficient	10 [b]	–
K_{mod-r}	Modifies K_m for each substrate pool entering MIC_r	0.125, 0.5, P_{scalar}, C_{scalar} [c]	–
K_{mod-K}	Modifies K_m for each substrate pool entering MIC_K	0.5, 0.25, P_{scalar}, C_{scalar} [d]	–
P_{scalar}	Physical protection scalar used in K_{mod}	$1/(2.5 \times e^{(-3 \times fmet)})$	–
C_{scalar}	Chemical protection scalar using in K_{mod}	$1/(1.4 + 0.2(f_{clay}))$	–
MGE	Microbial growth efficiency for substrate pools	0.6, 0.3, 0.6, 0.3 [f]	$mg\,mg^{-1}$
τ	Microbial biomass turnover rate	$6 \times 10^{-4} \times e^{(0.9 \times fmet)}$, 3×10^{-4} [g]	h^{-1}
f_c	Fraction of τ partitioned to SOM_c	$0.2 \times e^{(-2 \times fmet)}$, $0.4 \times e^{(-3 \times fmet)}$ [g]	–

[a] For metabolic litter inputs entering SOM_p and structural litter inputs entering SOM_c, respectively.

[b] From observations in German et al. (2012), as used in Wieder et al. (2013).

[c] For LIT_m, LIT_s, SOM_p, and SOM_c fluxes entering MIC_r, respectively.

[d] For LIT_m, LIT_s, SOM_p, and SOM_c, fluxes entering MIC_K, respectively.

[e] Used to calculate all K_m values, except for LIT_s entering MIC_r and MIC_K, which used 0.027.

[f] For C leaving LIT_m, LIT_s SOM_p, and SOM_c, respectively.

[g] For MIC_r and MIC_K, respectively.

Table 2. Main effects of major model components in traditional soil biogeochemical models based on theories of chemical recalcitrance and the MIMICS microbial model.

| Component	Traditional model	MIMICS model
Litter quality	Determines partitioning to pools with different turnover times. SOM pools decline with increasing f_{met}.	Determines partitioning to LIT pools and the relative abundance of MIC communities. Variable SOM pool response to f_{met}.
Litter quantity	Determines SOM pool size.	Determines MIC pool size.
Soil texture	Modulates turnover constants and partitioning of SOM between pools. No explicit representation of physical protection.	Explicitly represents physical protection of SOM. Provides a mechanism for microbial byproducts to build stable SOM.
Reaction kinetics	Environmentally sensitive. Determines turnover of C pools.	Temperature sensitive. Along with MIC pool size determines substrate turnover. Structures competitive dynamics between MIC_r and MIC_K.
MGE	Determines fraction of C lost between pool transfers, no effect on rates of C mineralization.	Determines fraction of C lost in transfers to MIC pools and MIC pool size. Thus, MGE affects rates of C mineralization and competitive dynamics between MIC_r and MIC_K.
τ	Implicitly simulated as part of reaction kinetics.	Explicitly simulated. Determines microbial control over SOM formation in mineral soils
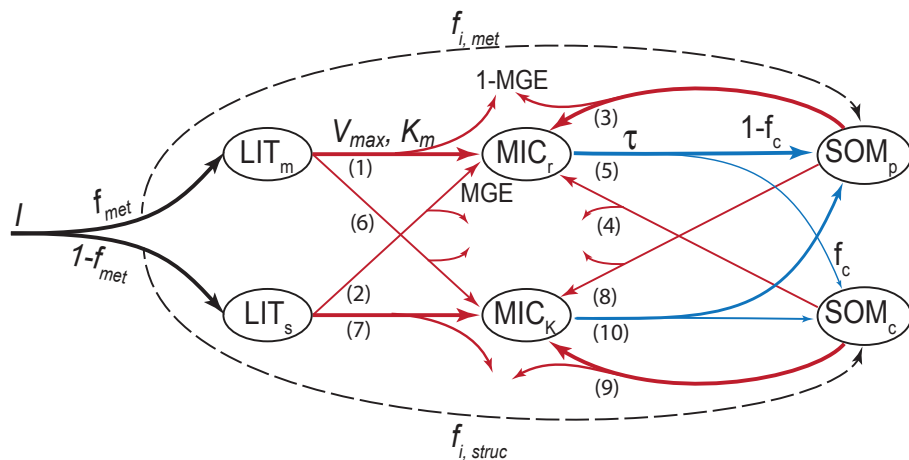
Fig. 1. Litter, microbial biomass and soil organic matter (SOM) pools and carbon flows represented in MIMICS. Litter inputs (I), (black lines) are partitioned into two litter pools based on litter quality (f_{met}). Litter pools in the model correspond to metabolic and structural litter (LIT$_m$ and LIT$_s$, respectively). Rates of decomposition (red lines) are controled by temperature sensitive Michaelis–Menten kinetics derrived from observational data (German et al., 2012) that are modified by microbial functional type and on C-substrate pool quality. Microbial functional types correspond to copiotrophic and oligiotrophic growth strategies (MIC$_r$ and MIC$_K$, respectively; Fierer et al., 2007). Microbial growth efficiency (MGE) determines the partitioning of C fluxes entering microbial biomass pools vs. heterotrophic respiration. Turnover of the microbial biomass pools (τ), (blue lines) depend on microbial functional type, and are partitioned into physically and chemically protected SOM pools (SOM$_p$ and SOM$_c$, respectively based on f_c). Decomposition of C from SOM pools also follows Michaelis–Menten kinetics, with clay fraction increasing the half-saturation constant for both pools, but especially SOM$_p$. A fraction of litter inputs (f_i), (dashed black lines) bypasses litter and microbial biomass pools, and is directly transferred to SOM pools. Numbers below each flux correspond to equations listed in Appendix A. See Appendix A for a more detailed description of equations governing C fluxes in MIMICS.
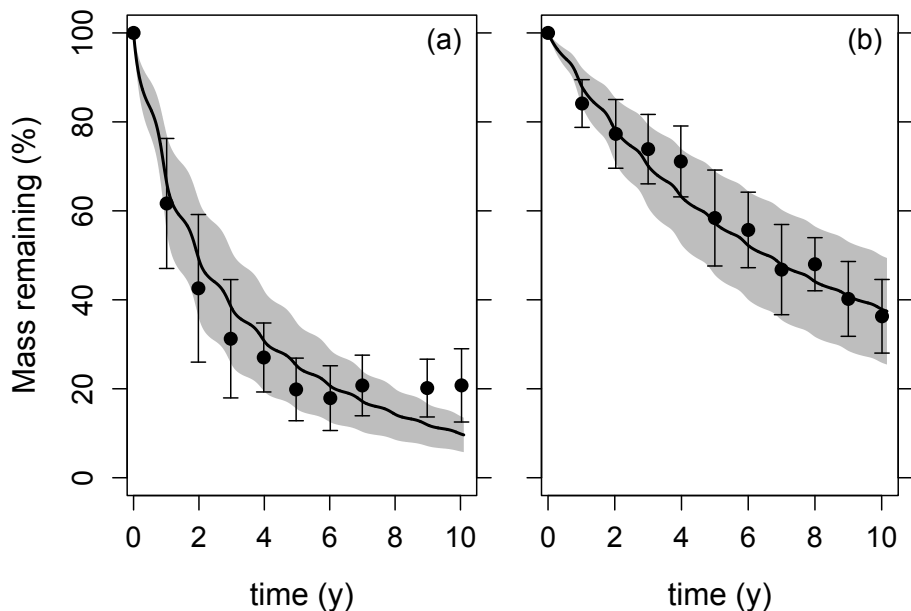
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Fig. 2. Observed and modeled leaf litter decomposition dynamics at **(a)** Harvard Forest and **(b)** Bonanza Creek Long Term Ecological Research sites. Closed circles show mean percent mass remaining of six leaf litter types decomposed over ten years as part of the LIDET study (Parton et al., 2007; Bonan et al., 2013; mean ± 1 SD). Similarly, solid lines indicate the mean percent mass remaining (± 1 SD, shaded region) of the six leaf litter types predicted by MIMICS forced with a climatology of observed mean daily soil temperature at each study site. Model parameters were calibrated to fit observations from Harvard Forest (Table 1). The same parameters were used to evaluate model output at the Bonanza Creek site. In observations and simulations the range of variation shows the effects of litter quality on rates of litter mass loss.
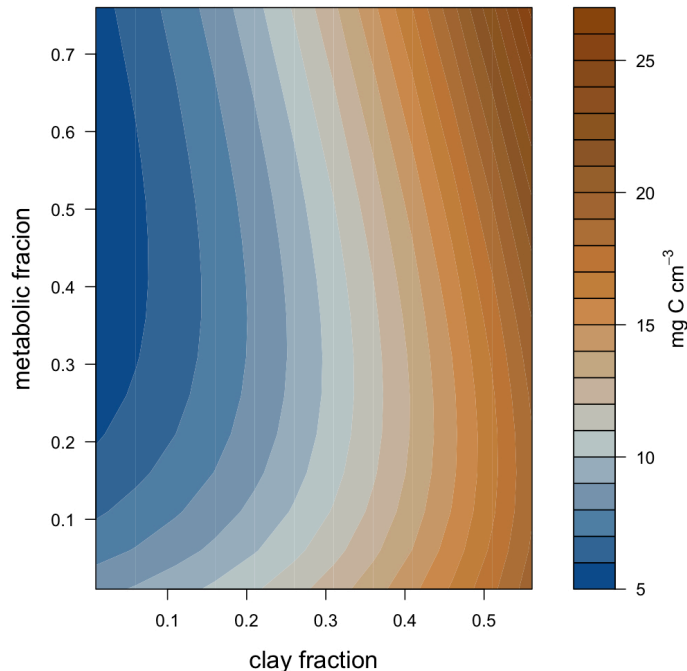
Fig. 3. Steady-state soil organic matter pools (mg C cm^{-3}, 0–30 cm) that are simulated by MIM-ICS across hypothetical sites with a range of clay content and litter quality at 15 °C with litter inputs of 160 g C m^{-2} yr^{-1}. Low clay soils store more C when receiving low quality litter inputs, whereas high clay soils store more C with high quality litter inputs.
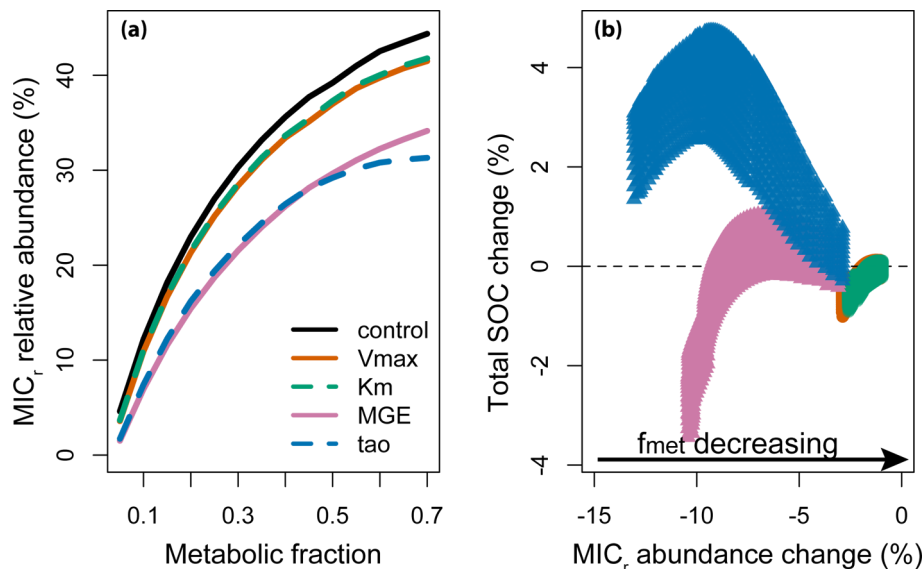
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Fig. 4. Proximal controls over the production and turnover of microbial biomass (MGE and τ) in MIMICS have larger influence over the relative abundance of microbial functional types and steady-state SOM dynamics. **(a)** The relative abundance of the copiotrophic community (MIC$_r$/total microbial biomass × 100) as a function of litter quality (f_{met}) in base simulations (black line; parameters as in Table 1) and in response to: 10 % reductions in catabolic potential of the MIC$_r$ community consuming litter C substrates (reducing V_{max}, orange line; increasing K_m, green line); simulating substrate and community effects on MGE (by reducing MGE of MIC$_r$ 10 %; pink line); and increasing turnover (τ) of the MIC$_r$ community by 10 % (blue line). **(b)** Differences between the base simulation and modifications described in panel **(a)** on the percent change in steady-state SOM pools vs. the change in the MIC$_r$ relative abundance.