Microbial Models for Simulating Soil Carbon Dynamics: A Review

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Abstract

Soils store the largest amount of carbon (C) in the biosphere, and the C pool in soil is critical to the global C balance. Numerous microbial models have been developed over the last few decades to represent microbial processes that regulate the responses of soil organic carbon (SOC) to climate change. However, the representation of microbial processes varies, and how microbial processes are incorporated into SOC models has not been well explored. Here, we reviewed 70 microbial models to characterize the microbial processes incorporated into SOC models and analyzed variations in mechanistic complexity. We revealed that (1) four processes (microbial decomposition, mineral interaction, microbial mortality, and transition between active and dormant microbial states) are commonly incorporated in microbial models, (2) ˜47% of models simulate only one (i.e., microbial decomposition) and 33% simulated two microbial processes: microbial decomposition and mineral interaction, (3) more than 80% microbial models use nonlinear mathematical equations, such as forward Michaelis-Menten kinetics, to represent SOC decomposition, (4) the concept of persistence of SOC due to its intrinsic properties has been replaced by organo-mineral interaction (˜39% of microbial models) that protects SOC from decomposition, and (5) various temperature and moisture modifiers and pH effects have been used to explain the environmental effect on microbial processes. Finally, we propose a roadmap for SOC model improvement. In the future, to realistically incorporate microbial processes into Earth System Models, it is imperative to identify experimental evidence on rate limitation processes and firmly ground model structure on the field and laboratory data.

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Microbial Models for Simulating Soil Carbon Dynamics: A Review

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Key Points:

1. Recent model development indicates a growing interest in incorporating microbial processes
2. Diversity in mathematical equations indicates uncertainty in translating current knowledge of microbial processes into models
3. Field observational data are critical to validate the mechanistic representation of microbial processes

Abstract

Soils store the largest amount of carbon (C) in the biosphere, and the C pool in soil is critical to the global C balance. Numerous microbial models have been developed over the last few decades to represent microbial processes that regulate the responses of soil organic carbon (SOC) to climate change. However, the representation of microbial processes varies, and how microbial processes are incorporated into SOC models has not been well explored. Here, we reviewed 70 microbial models to characterize the microbial processes incorporated into SOC models and analyzed variations in mechanistic complexity. We revealed that (1) four processes (microbial decomposition, mineral interaction, microbial mortality, and transition between active and dormant microbial states) are commonly incorporated in microbial models, (2) ~47% of models simulate only one (i.e., microbial decomposition) and 33% simulated two microbial processes: microbial decomposition and mineral interaction, (3) more than 80% microbial models use nonlinear mathematical equations, such as forward Michaelis-Menten kinetics, to represent SOC decomposition, (4) the concept of persistence of SOC due to its intrinsic properties has been replaced by organo-mineral interaction (~39% of microbial models) that protects SOC from decomposition, and (5) various temperature and moisture modifiers and pH effects have been used to explain the environmental effect on microbial processes. Finally, we propose a roadmap for SOC model improvement. In the future, to realistically incorporate microbial processes into Earth System Models, it is imperative to identify experimental evidence on rate limitation processes and firmly ground model structure on the field and laboratory data.

1. Introduction

Soils store the largest amount of organic carbon (C) in terrestrial ecosystems (Lehmann & Kleber, 2015). Thus, even a small change in soil C turnover could have significant consequences for atmospheric CO_2 concentrations and the stability of the global climate system (Luo et al., 2016; Schmidt et al., 2011). It is estimated that the global soil organic carbon (SOC) pool size at a depth of 1 m is 1417–1469 Pg C (Hiederer & Köchy, 2011), which is nearly three times the amount of C stored in plant biomass (Schlesinger & Bernhardt, 2013) and twice the amount of C in the atmosphere (Schmidt et al., 2011). Therefore, it is crucial to understand and simulate the critical processes underlying the dynamics of SOC to accurately forecast its responses to future changes in climate and land management (Amelung et al., 2020). However, the current process-based models have very high uncertainty in estimating the response of global SOC to climate change (Fan et al., 2021; Todd-Brown et al., 2013; Wieder et al., 2013). These uncertainties result partly from inadequate representations of ecosystem processes that control the exchanges of water, energy, and C between land ecosystems and the atmosphere (Hao et al., 2015; Wieder et al., 2013) and partly from the uncertainties in estimating the SOC model parameters (Abramoff et al., 2022; Luo & Schuur, 2020; Luo et al., 2016).

Developing models that accurately simulate belowground processes is challenging for soil, environmental, and earth sciences (Hinckley et al., 2014; Todd-Brown et al., 2013; Wieder et al., 2015a). Currently, SOC dynamics in Earth System Models (ESMs) are mostly represented by conventional SOC models that do not explicitly simulate microbial activity or soil microbial communities. Instead, these models strongly emphasize the relationship between SOC chemical recalcitrance and soil C storage (Wieder et al., 2014; Zeng et al., 2006), assuming that respired CO_2 is proportional to the soil C pool size (Davidson et al., 2014; Wieder et al., 2015a). These conventional SOC models implicitly represent microbial activities under the assumptions that (1) microbes respond so quickly to changes in substrate availability that their abundance never limits the decomposition rate (Schimel, 2001), (2) microbial and other ecosystem properties as expressed by parameters in models are invariant across wide environmental and edaphic conditions and through time (Luo & Schuur, 2020), and (3) microbial communities have functional equivalence allowing them to optimally process the available SOC (Bradford & Fierer, 2012; Wieder et al., 2015a).

Theoretically, it is known that microbial processes fundamentally regulate the decomposition and stabilization of SOC (Davidson et al., 2014). Therefore, in the past few decades, researchers have incorporated various microbial processes to improve the simulation of future C-cycle-climate feedback (Wieder et al., 2013) and as a result, numerous microbial models have been developed over the last few decades to simulate microbial regulation on the response of SOC to climate change. Here we define a microbial model as a soil biogeochemical model that simulates at least one discrete microbial biomass pool that controls the decomposition rate of SOC. Studies to date indicate large variations among microbial models in the capacity to simulate and predict SOC dynamics, possibly due to their variations in model structure and representations of various processes in models. Since the 1970s, many microbial models have been developed, for example, the Schimel model (Schimel & Weintraub, 2003), the enzyme-driven model (Allison et al., 2010), ReSOM (Tang & Riley, 2015), and MIND (Fan et al., 2021). Several studies have reported contrasting findings when SOC dynamics were compared between conventional and microbial models. For example, one study compared a conventional SOC model (similar to the CENTURY model) with microbial models (EC1 and EC2) to simulate soil respiration from a laboratory-based pulsed drying-rewetting experiment, revealed that microbial controls on SOC decomposition improved the model's ability to capture the observed pulsed soil respiration (Lawrence et al., 2009). However, other studies reported similar or amplified uncertainty in SOC responses to climate change when incorporating microbial control on SOC decomposition, which might be due to complex mechanisms in microbial processes and the challenges of parametrization (Shi et al., 2018; Sulman et al., 2018). For example, by selecting suitable environmental response functions and an improved parameterization method, conventional SOC models could also capture the pulse dynamics of soil heterotrophic respiration similarly well with microbial models (Zhou et al., 2021). In addition, the uncertainty of the MIMICS microbial model in projecting long-term SOC was >10 times greater than that in the conventional Century-type model, possibly because the complex model structure and a large number of parameters increased uncertainty due to feedback in the model dynamics (Shi et al., 2018).

Although several studies have reviewed SOC models (Chertov et al., 2007; Frissel & Van Veen, 1981; McGill, 1996; Molina & Smith, 1997; Paustian, 1994; Paustian et al., 1997; Smith et al., 1998; Wieder et al., 2015a; Xu et al., 2016), comprehensive synthesis and analysis of microbial processes incorporated into SOC models are lacking. Microbial models vary a lot in terms of representations of microbial processes and their incorporations into SOC models. To provide an overview of the status of microbial models, in this study, we reviewed 70 microbial models developed over the last few decades (Table 1). We first examine the history of microbial model development and the trend of the microbial processes incorporated. Then, we provide a comprehensive overview on each of the microbial processes that substantially overlap across microbial models and their mechanistic representations into SOC models. For each process, we include the mathematical equations adopted in the models and the environmental factors that influence them. We finish the review with the challenges associated with microbial models and some recommendations that would be beneficial for better model development in estimating SOC dynamics.

Table 1: Microbial models for SOC decomposition and the four processes incorporated along with the decomposition formulation. ZO: Zero-order; FO: First-order; FMM: Forward Michaelis Menten; RMM: Reverse Michaelis-Menten (The names of the models are determined based on two criteria: (1) if the model has a name in the original publication, that name will be used to represent the model; (2) if the model has no name, the last name of the first author will be used to name the model, for example, Fatichi model.)

Microbial Model	Decomposition mechanism	Microbial decomposition	Transition between active and dormant microbial state	Mineral interaction	Microbial mortality	References
Averill model	RMM	Yes	No	No	No	Averill (2014)
Barot model	FO	Yes	No	No	No	Fontaine and Barot (2005)
Blagodastsky model	FO	Yes	No	No	No	Blagodatsky et al. (2010)
CLM-Microbe	FMM	Yes	No	No	No	Wieder et al. (2013)
CMAX framework	RMM	Yes	No	No	No	Xu et al. (2014)
COMISSION	RMM	Yes	No	Yes	No	Ahrens et al. (2015)
CORPSE	RMM	Yes	No	Yes	Yes	Sulman et al. (2014)
C-STABILITY	Multiplicative	Yes	No	No	No	Sainte-Marie et al. (2021)
DAMM-MCNiP	ECA	Yes	No	No	No	Abramoff et al. (2017)
DecoBio v1.0	FMM	Yes	No	No	No	Xenakis and Williams (2014)
DEMENT	FMM	Yes	No	No	No	Allison (2012)
DNDC	ZO	No	No	No	No	Li et al. (1994)
DORMANCY	FMM	Yes	Yes	No	No	He et al. (2015)
DORMANCY 2.0	FMM	Yes	Yes	No	No	Liu et al. (2019)
EC1	RMM	Yes	No	No	No	Lawrence et al. (2009)
EC2	RMM	Yes	No	No	No	Lawrence et al. (2009)
EcoSMMARTS	RMM	Yes	Yes	No	Yes	Brangarí et al. (2020)
Ecosys	FMM	Yes	No	No	No	Grant et al. (1993)
EEZY	RMM	Yes	No	No	No	Moorhead et al. (2012)
Enzyme driven model	FMM	Yes	No	No	No	Allison et al. (2010)
Fatichi	FMM	Yes	No	No	No	Fatichi et al. (2019)
FOND	ZO	No	No	Yes	Yes	Fan et al. (2021)
GDM	FMM	Yes	No	No	No	Moorhead and Sinsabaugh (2006)
GENDEC	ZO	No	No	No	Yes	Moorhead and Sinsabaugh (2000)
German	FMM	Yes	No	No	No	German et al. (2012)
Hagerty	FMM	Yes	No	No	No	Hagerty et al. (2018)
He model	FMM	Yes	No	No	No	He et al. (2014)
JSM	RMM	Yes	No	Yes	Yes	Yu et al. (2020)
Kaiser	FMM	Yes	No	No	Yes	Kaiser et al. (2014)
LIDEL	ZO	No	No	No	No	Campbell et al. (2016)
Manzoni	RMM	Yes	No	No	No	Manzoni et al. (2021)
MEMS v1.0	ZO	No	No	Yes	No	Robertson et al. (2019)
MEND	FMM	Yes	No	Yes	No	Wang et al. (2013)
MEND_dor	FMM	Yes	Yes	Yes	No	Wang et al. (2015)
MESDM	FMM	Yes	Yes	No	No	Zhang et al. (2022)

MiCNiT	Multiplicative	Yes	No	No	No	Blagodatsky et al. (2011)
MIC-TEM_Hao	FMM	Yes	No	No	No	Hao et al. (2015)
MIC-TEM_Zha	FMM	Yes	No	No	No	Zha and Zhuang (2018)
MIC-TEM-dormancy	FMM	Yes	Yes	No	No	Zha and Zhuang (2020)
MiFe	Logistic	Yes	No	Yes	No	Liao et al. (2022)
Millennial model	FMM	Yes	No	Yes	No	Abramoff et al. (2018)
Millennial V2.0	RMM	Yes	No	Yes	No	Abramoff et al. (2022)
MIMICS	FMM	Yes	No	Yes	No	Wieder et al. (2014)
MIMICS_D	FMM	Yes	No	Yes	No	Zhang et al. (2020)
MIMICS-CN v1.0	FMM	Yes	No	Yes	No	Kyker-Snowman et al. (2020)
MIMICS-DB	FMM	Yes	No	Yes	No	Zhang et al. (2020)
MIMICS-DBT	FMM	Yes	No	Yes	No	Zhang et al. (2020)
MIND	FMM	Yes	No	Yes	Yes	Fan et al. (2021)
MOMOS	ZO	No	No	No	Yes	Pansu et al. (2010)
MySCaN	ZO	No	No	No	No	Orwin et al. (2011)
NCSOIL	RMM	Yes	No	No	No	Hadas et al. (1998)
ORCHIMIC v1.0	ECA	Yes	Yes	Yes	Yes	Huang et al. (2018)
ORCHIMIC v2.0	FMM	Yes	Yes	Yes	Yes	Huang et al. (2021)
Parnas	FMM	Yes	No	No	No	Parnas (1975)
Phoenix	Density-dependent	Yes	No	Yes	No	McGill et al. (1981)
Resat	FMM	Yes	No	No	No	Resat et al. (2012)
RESOM	ECA	Yes	No	Yes	No	Tang and Riley (2015)
ReSom vNN	ECA	Yes	No	Yes	No	Abramoff et al. (2019)
ReSom vTD	ECA	Yes	No	Yes	No	Abramoff et al. (2019)
ReSom vTI	ECA	Yes	No	Yes	No	Abramoff et al. (2019)
ReSom vTN	ECA	Yes	No	Yes	No	Abramoff et al. (2019)
RothC	ZO	No	No	No	No	Coleman and Jenkinson (1996)
SCAMPS	FMM	Yes	No	No	No	Sistla et al. (2014)
Schimel model	RMM	Yes	No	No	No	Schimel and Weintraub (2003)
SOCRATES	ZO	No	No	No	No	Grace et al. (2006)
SOMic v1.0	RMM	Yes	No	Yes	No	Woolf and Lehmann (2019)
SOMKO	Density-dependent	Yes	Yes	No	No	Gignoux et al. (2001)
SYMPHONY	FO	Yes	No	No	No	Perveen et al. (2014)
TRIPLEX_MICROBE	FMM	Yes	Yes	Yes	No	Wang et al. (2017)
VERBERNE	ZO	No	No	Yes	No	Verberne et al. (1990)

2. Historical Development of Microbial Models

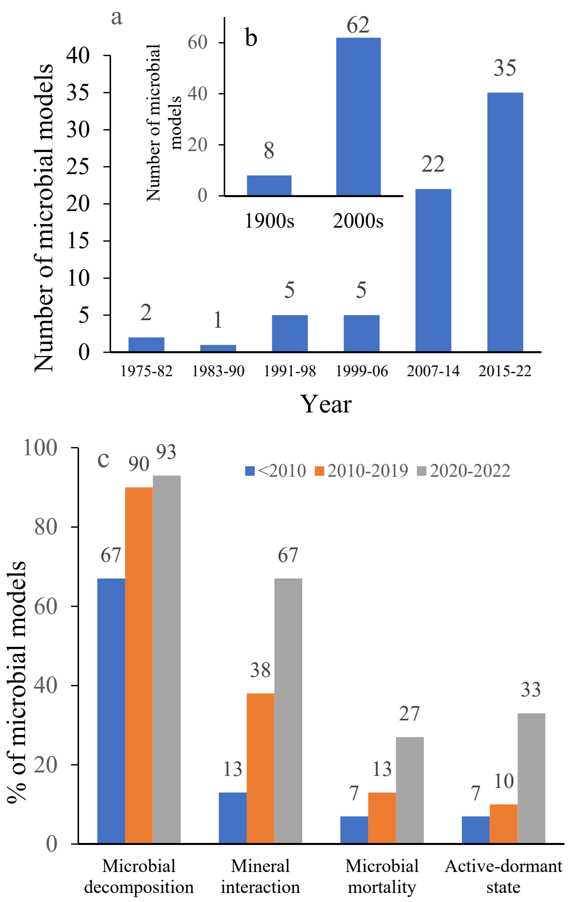

Figure 1: Historic development of microbial models since 1975 (a and b); Percentage of microbial models with consideration of major microbial processes. The percentage was calculated as the number of models considering each process divided by the total number of published models in each time period (c)

Studies on organic matter (OM) decomposition to environmental factors have a long history, starting in the early 1930s (Manzoni & Porporato, 2009; Wang & Allison, 2019), and SOC decomposition has been modeled as a first-order decay process since 1945 (Hénin & Dupuis, 1945). However, the integration of microbial biomass into the SOC model did not exist until the 1970s, and one of the first SOC microbial models was developed in 1975 (Parnas, 1975) that calculated litter decomposition as an explicit function of microbial biomass under the assumption that the decomposition of SOC is proportional to the growth rate of the soil microbial community. This approach dynamically linked microbial and litter pools. The development of microbial models was slow during the late 20th century. Only 8 microbial models were developed during the last 25 years of the 20th century (Fig 1b), and the treatment of microbial biomass was often indistinguishable from the active pool of conventional SOC models, such as VERBERNE, GENDEC, DNDC, and RothC microbial models. Microbial models started to receive more attention, mainly after Schimel and Weintraub (Schimel & Weintraub, 2003) proposed the Reverse Michaelis-Menten kinetics derived from the Langmuir sorption isotherm theory and explicitly represented the extracellular enzyme (ENZ) pool in their model. Subsequently, several studies explored additional ecological interactions between microorganisms and SOC. For example, it was previously thought that the long-term persistence of SOC was because of the recalcitrant chemical property of SOC, such as humic substances that were considered large, complex macromolecules and the most stable component of SOC (Lützow et al., 2006). However, recent studies suggested that the recalcitrant components represent only a small fraction of total OM, and the molecular property alone does not control the persistence of SOC (Kleber & Johnson, 2010; Sutton & Sposito, 2005). Rather, mineral surfaces predominantly influence the decomposition of SOC by altering SOC concentration and its mobilities (Greenland, 1965). Mineral particles in soil adsorb SOC onto its surfaces by forming various chemical bonds that prevent SOC accessibility from microbes (McGill et al., 1981; McLaren & Peterson, 1965), resulting in explicit consideration of the mineral interaction process in the models.

Likewise, relatively recent development in microbiology and genomics uncovered that under natural environmental conditions, soil microbes exist in three physiological states: dead, alive, and dormant microbes (Gignoux et al., 2001; Mason et al., 1986; Wang et al., 2014a). Thus, a significant increase in the trends of the number of microbial models (Fig. 1a and 1b) and consideration of microbial processes controlling SOC decomposition were observed (Fig 1c). For example, 22 and 35 microbial models were developed during the periods of 2007 to 2014 and 2015 to 2022, respectively (Fig 1a). Microbial processes such as microbial mortality and dynamic active-dormant microbial states are relatively less studied than the microbial processes related to decomposition and mineral association because of our recent knowledge development of microbial physiological states and the limitation in their measurements *in situ*.

3. Model Representation of Microbial Processes

Early on, empirical fitting of a first-order model to SOC decomposition required multiple pools so that fractions of SOC decayed with different turnover rates (Woolf & Lehmann, 2019). Such multi-pool models, derived from empirical results, reflect a conceptual paradigm that different types of SOC have different representative turnover rates. Although many microbial processes are suggested to be essential for controlling SOC cycling in the literature (Lehmann et al., 2020; Schmidt et al., 2011), there is less agreement about the best mathematical formulations to represent these processes (Table 2, (Sulman et al., 2018; Wieder et al., 2015a).

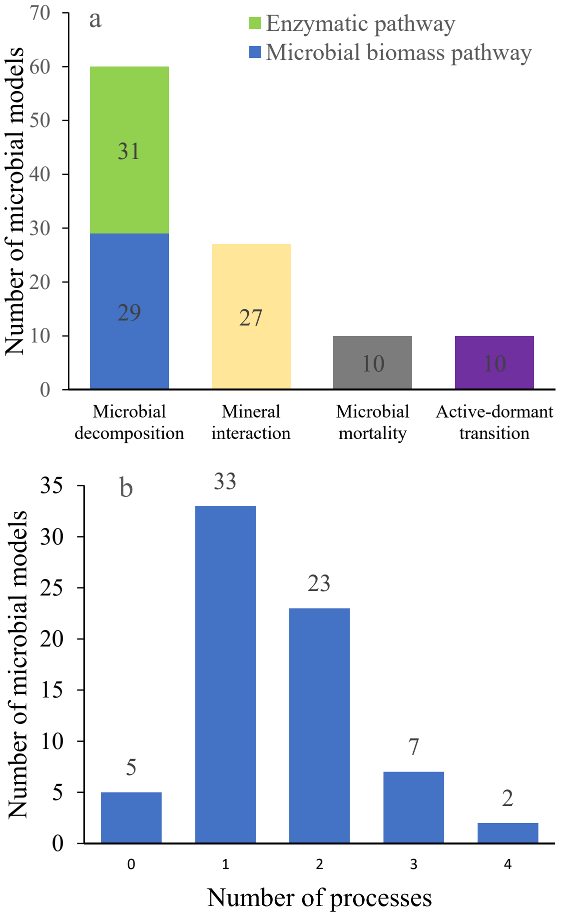

Figure 2: Number of microbial models (a) with major processes incorporated into microbial models; (b) simulating the number of microbial processes

Our review of the 70 microbial models revealed that four microbial processes are widely incorporated into SOC models: microbial decomposition, mineral interaction, microbial mortality, and transition between active and dormant microbial states (Fig 2a; Table 1). Among the 70 microbial models, almost 50% simulate two processes (i.e., microbial decomposition), and one-third of the microbial models simulate two processes in a single model. The combinations of the two processes are mostly between microbial decomposition and mineral interaction (Fig 2b;

Table 1). In this section, we focus on these four microbial processes that have been incorporated into most of the microbial models.

3.1 Microbial Decomposition of SOC

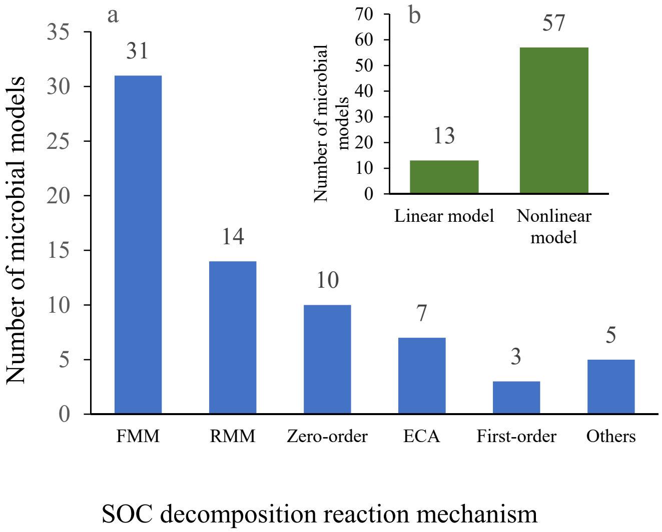

Figure 3: Number of microbial models (a) adopted various SOC decomposition reaction mechanisms; (b) representing linear and nonlinear decomposition kinetics

Microbial decomposition is a critical process in the soil C cycle because it is the primary pathway through which CO_2 fixed by plants is returned to the atmosphere (Zhang et al., 2022). Therefore, microbial models have taken diverse approaches to represent the decomposition process (Fig. 1c, Table 2). There is a consensus among microbial models that microbes produce ENZ to degrade complex SOC into dissolved organic carbon (DOC) through catalysis, take up DOC, convert the assimilated C into microbial biomass for growth, and release CO_2 through respiration (Sinsabaugh et al., 2008; Zhang et al., 2022). Two pathways are used for the representation of the decomposition of SOC: enzymatic- and microbial biomass-mediated decomposition (Fig 2a). The major difference between these two pathways is that enzymatic-mediated decomposition models simulate an explicit ENZ pool, assuming ENZ production is controlled by both substrate concentration and microbial community structure (Sistla et al., 2014) and directly couple SOC decomposition to the ENZ activity instead of microbial biomass (Table 2). For example, microbial models such as the Averill model, DAMM-MCNiP, DEMENT, DORMANCY, EC1, EC2, EcoSMMARTS, EEZY, Enzyme driven model, Fatichi, German, Hagerty, HE model, Kaiser, MEND_dor, MESDM, MIC-TEM_Hao, MIC-

TEM_Zha, MIC-TEM-dormancy, MEND, ORCHIMIC (v1.0, v2.0), Resat, RESOM (v1, v2, v3, v3, v4, v5), SCAMPS, Schimel model, and TRIPLEX_MICROBE (Table 1) consider a separate ENZ pool in addition to microbial biomass pool (Table 2). In contrast, microbial biomass-mediated decomposition models (e.g., Barot model, Blagodastsky model, C-Stability, CLM-Microbe, CMAX framework, COMISSION, CORPSE, DecoBio v1.0, DORMANCY 2.0, Ecosys, GDM, JSM, Manzoni, MiCNiT, MiFe, Millennial model, Millennial v2.0, MIMICS, MIMICS (v1, v2, v3, v4), MIND, NCSOIL, Parnas, SOMic v1.0, SOMKO, and SYMPHONY (Table 1) do not explicitly simulate the pool of ENZ. Instead, they implicitly assume the enzymatic catalysis of SOC to drive the rate of SOC decomposition. We consider these pathways to be separate processes in our analyses to preserve the uniqueness of their model structures and their process representations (Table 2).

Further, we classified the microbial decomposition of SOC into six types based on the equations used: 1) zero-order, 2) first-order, 3) forward Michaelis-Menten (FMM), 4) Reverse Michaelis-Menten (RMM), 5) Equilibrium Chemistry Approximation (ECA), or 6) Other (Fig 3a). Types 1 and 2 are linear-type whereas types 3-6 are nonlinear models. These formulations differ functionally with different fundamental assumptions on whether the decomposition of SOC is limited by substrate availability, microbial biomass (or ENZ), or both, and on how these components are linked with decomposition. For example, formulations 1 (i.e., zero-order) and 2 (i.e., first-order) are represented by simple mathematical equations (consisting of only one parameter). In contrast, the nonlinear microbial model family (i.e., formulations 3-6) is represented by various complex mathematical equations with a large number of parameters. It is worth to note that more than 80% of the microbial models used nonlinear kinetics (formulations 3-6) to represent SOC decomposition (Fig 3b; Table 1).

3.1.1 Zero-Order Microbial Model (ZO)

The zero-order microbial model is not a function of microbial biomass although the model simulates a discrete microbial biomass pool. Such a model may be a function of substrate as:

$$D_c = kS \quad (1)$$

where D_c is the rate of decomposition of C, S is the substrate of SOC, and k is the coefficient of the decomposition rate.

Of the 70 models we reviewed, 10 models simulated microbial biomass as one (e.g., FOND, GENDEC, LIDEL, MEMS v1.0, MOMOS, RothC, VERBERNE) or more components (e.g., bacteria and fungi pools in MySCaN, protected and unprotected microbial C in SOCRATES, labile and resistant microbial C in the DNDC model) of the SOC pool (Fig 3a). However, the microbial component was only taken as a substrate of decomposition rather than as a decomposer that could modify the rates of decomposition in these models. Thus, the SOC decomposition reaction rate becomes zero-order with respect to microbial biomass (Eq 1). This formulation is similar to the conventional SOC models in which each substrate with specific quality has its own microbial community associated with it, and the microbial community is presumably in equilibrium with the substrate most of the time. Therefore, decomposition is only limited by substrate (S) (McGill & Myers, 1987; Wutzler & Reichstein, 2008). Furthermore, the contribution of soil microbes to SOC decomposition is implicitly included in the apparent decomposition rate coefficients of different C pools (McGill, 1996; Paustian, 1994) when a model is parameterized. Due to this treatment of soil microbes, models are independent of temporal and spatial variations in the soil microbial community and may lack the flexibility to simulate the effects of land-use or climate change that impact soil microbial biomass and activities on SOC decomposition (Fang et al., 2005).

3.1.2 First-Order Microbial Model (FO)

In the first-order microbial models, the decomposition of SOC depends linearly on the size of the microbial biomass pool (Eq. 1 in Table 2). Only 3 (Barot, Blagodastsky, and SYMPHONY models) out of the 70 microbial models used first-order kinetics for microbial biomass (Fig 3a), as the assumption of this type of model, that is, the substrate is the only limiting factor for SOC decomposition was questioned in the Barot model and later was adopted in Blagodastsky and SYMPHONY models (Blagodatsky et al., 2010; Fontaine & Barot, 2005; Perveen et al., 2014). These models considered that the decomposition of recalcitrant SOC was limited by the extracellular enzymes instead of the quantity of substrate and assumed that the quantity of ENZ is proportional to the size of the microbial biomass pool. The SOC decomposition increases linearly with the size of the microbial pool (Eq. 1 in Table 2), resulting in first-order kinetics with respect to the microbial biomass.

3.1.3 Forward Michaelis-Menten (FMM)

The first-order (linear) models have been challenged on the grounds that SOC breakdown depends on the amount of SOC as well as on microbial components (Fang et al., 2005; Schimel & Weintraub, 2003), thus resulting in nonlinear decomposition rates. This tight coupling between the substrate and biological processes is necessary, in particular, while modeling short-term C and nitrogen (N) dynamics (Blagodatsky et al., 1998), while it might also be relevant in medium- (Whitmore, 1996) and long-term analyses (Smith et al., 1998). Based on the assumption that the decomposition rate of SOC is limited by the substrate or the microbial pool (or the enzyme pool), various mathematical equations were used to describe the decomposition of SOC (Table 2).

The FMM kinetics assumes that substrate availability is the rate-limiting factor in decomposition, i.e., the decomposition rate saturates as the substrate available for decomposition rises (Wieder et al., 2015a). In FMM kinetics, the SOC decomposition rate varies linearly with the microbial biomass (or enzyme pool) and nonlinearly with the substrate. The representation of SOC decomposition in microbial models was dominated by FMM kinetics: 31 out of 70 microbial models (~44%) used the FMM kinetics for SOC decomposition (Eqs. 2-6 in Table 2).

3.1.4 Reverse Michaelis-Menten (RMM)

In contrast to FMM kinetics, in RMM kinetics, the decomposition reaction rate changes linearly with the amount of substrate and saturates with the enzyme pool (or microbial biomass) (Schimel & Weintraub, 2003). The assumptions underlying the RMM kinetics are (1) the size of SOC pool is sufficiently large enough such that the amount of ENZ (or microbial biomass), rather than the substrate, is the rate-limiting factor for SOC decomposition, (2) the maximum binding capacity of enzymes is proportional to the concentration of the substrate, and (3) the resulting decomposition rate is proportional to the amount of bound enzyme (Moorhead & Weintraub, 2018; Schimel & Weintraub, 2003). The Averill model, CMAX framework, COMISSION, CORPSE, EC1, EC2, EcoSMMARTS, EEZY, JSM, Manzoni, NCSOIL, Schimel model, and SOMic v1.0 models have all adopted RMM kinetics for the SOC decomposition (Eqs. 7-12 in Tables 2). However, some of these models, such as the CMAX framework, COMISSION, CORPSE, JSM, Manzoni, NCSOIL, and SOMic v1.0, do not separately simulate ENZ pools but instead assume that ENZ production linearly depends on microbial biomass because it is challenging to measure ENZ production and these models focus on simulating C pools that are measurable.

3.1.5 Equilibrium Chemistry Approximation (ECA)

ECA is a relatively new decomposition mechanism proposed by Tang and Riley (2013). It was derived from the first-order approximation of the full equilibrium chemistry formulation of a consumer-substrate network that can account for multiple consumers (i.e., microbes and minerals) and multiple substrates as:

$$D_c = \frac{V_{max} * S * E}{k_m + S + E} \quad (2)$$

where V_{max} is the maximum decomposition rate, k_m is the half-saturation constant, and E is the extracellular enzyme

The assumptions underlying the ECA kinetics are (1) there is no binding between substrates or between consumers, and (2) once an enzyme-substrate complex is formed, it will not bind with another substrate or consumer to form new complexes (Tang & Riley, 2013). Eq. 2 demonstrates a reaction that has only one enzyme interacting with one substrate.

It should be noted that the decomposition rate becomes FMM when the substrate changes significantly while the enzyme concentration is much lower than the substrate, such that $k_m + E$ is almost constant. On the other hand, when the substrate concentration is much higher than the enzyme concentration, such that the microbial process barely changes the total substrate concentration in the temporal window of interest, $k_m + S$ is almost constant, and eq. 2 is reduced to RMM (Tang & Riley, 2013). ReSOM and its subsequent versions, DAMM-MCNiP and ORCHIMIC v1.0, used the ECA mechanism (Eqs. 7, 13-14 in Table 2).

3.1.6 Other Mechanisms

Although the mechanisms mentioned above were the most commonly used in microbial models, other mechanisms have been used in some instances. For example, Phoenix and SOMKO models use microbial density-dependent SOC decomposition and assume that the increase in the ratio of microbial C to structural C slows down the activity of microbes because of increased competition among microbes for nutrients and space (Eqs. 15-16 in Table 2). Subsequently, to avoid such a heavy nonlinear model parameterization and also assuming the low concentrations of SOC, some models (e.g., C-Stability and MiCNiT) use a multiplicative expression that still couples microbes and SOC, but the decomposition of SOC varies linearly with microbial biomass and substrate (Eqs. 17, Table 2) (Manzoni & Porporato, 2007). Furthermore, a recent study (Liao et al., 2022) was conducted to understand the most probable mechanisms behind the observed nonlinear patterns of lignin decomposition. The study reported that neither the conventional nor FMM nonlinear models could simulate the observed nonlinear patterns of lignin decomposition (Huang et al., 2019). Instead, the data-driven approach revealed that time-dependent growth and mortality functions expressed by logistic equations in the microbial-iron (MiFe) model better represented observed CO_2 release from lignin decomposition than models assuming either first-order or FMM (Eq. 18 in Table 2).

3.2 Mineral Interaction

SOC interaction with mineral surfaces is a critical process for the stabilization of SOC because plant- and microbially-derived SOC can be protected from decomposition through the formation of complex organo-mineral interactions (Abramoff et al., 2019). Sorption and desorption are the two processes that regulate the amount of DOC available to microbes for decomposition (Huang et al., 2018). The majority of SOC models simulate the mineral interaction implicitly by modifying the SOC decomposition rate with an empirical factor based on the clay fraction

(Abramoff et al., 2019; Coleman & Jenkinson, 1996; Sulman et al., 2014; Wieder et al., 2013). However, it is becoming increasingly clear that the persistence and decomposition of SOC are interconnected with the physical environment, organic–mineral interactions, and both local biotic and abiotic factors (Newcomb et al., 2017). In addition, a significant proportion of stable SOC is derived from simple C rather than chemically resistant compounds (Cotrufo et al., 2013), suggesting molecular structure alone does not control the long-term stability of SOC (Schmidt et al., 2011). Sorption is a rapid process that occurs within seconds to minutes and thus occurs more rapidly than microbial decomposition (Kothawala et al., 2008; Qualls & Haines, 1992). Therefore, the long residence time or the stabilization of SOC are commonly attributed to an interaction between DOC, microbially derived C, or intact plant compounds with mineral surfaces, which provide reactive sites for physical and chemical stabilization, thus preventing degradation of SOC by microbes (Grant et al., 2022; Kleber et al., 2015; Kleber et al., 2007; Lehmann & Kleber, 2015; Schmidt et al., 2011). Factors influencing the formation and stability of protected C include the chemistry of OM, texture, and structure of soils, physicochemical properties and abundance of soil minerals, pH, the ionic strength of the soil water, temperature, and moisture (Abramoff et al., 2018; Feng et al., 2016).

In our analysis, 27 out of 70 microbial models explicitly represented the mineral interaction with SOC (Fig 2a; Table 1). However, not all of these 27 models explicitly simulate the sorption and desorption processes simultaneously. For example, CORPSE, FOND, MEMS, MIND, and VERBERNE do not explicitly represent desorption; instead, they simulate the net sorption of C to mineral surfaces, meaning that when the mineral-associated organic matter (MAOM) pool reaches saturation, the net transfer of C from DOC to MAOM can be negative, i.e., C is transferred from MAOM to DOC (Eqs. 20, 21, 23, 30 in Table 2).

Environmental and biotic controls on sorption varied greatly among models. Factors considered that could influence the sorption process include DOC (or SOC), MAOM, maximum sorption capacity (Q_{max}, depending on clay and silt content), soil temperature and moisture, and microbial necromass (i.e., mass from microbial death and subsequent lysis and fragmentation of microbes). In most microbial models, the maximum sorption of SOC depended on the amount of DOC available, the availability of sorption sites, and the sorption capacity (Eqs. 19-33 in Table 2). Thus, the rate of SOC sorption increases when the DOC content is higher, and the sorption sites are unoccupied. In addition, models such as JSM, Millennial v1.0, and ORCHIMIC (v1.0 and v2.0) introduced temperature rate modifiers for the sorption process (Eq. 22, 26, 31 in Table 2). Only JSM and Millennial (v1.0 and v2.0) models simulated the effect of soil moisture on the sorption process (Eqs. 22, 25-26 in Table 2). In most microbial models, particulate organic carbon (POC) and DOC were competing for the mineral surfaces. However, in some microbial models, such as FOND, Millennial (v1.0 and v2.0), MIMICS (v1-4), and MIND, microbial necromass was also competing for the mineral surfaces (Eqs. 21, 25-30 in Table 2).

Environmental and biotic controls on desorption also varied among models but in less complex ways than their controls on sorption. Microbial models such as COMISSION, JSM, MEND, MEND_dor, Millennial (v1.0 and v2.0), MIMICS(v1-v5), MIND, ORCHIMIC (v1.0 and v2.0) and SOMic v1.0 explicitly represented the desorption process (Eq. 19, 22, 24-29, 31, 33 in Table 2). The desorption mostly depended on the amount of C sorbed to the mineral surfaces and Q_{max}. However, some models modulated the desorption process by adding temperature (JSM, Millennial (v1.0), and ORCHIMIC (v1.0 and v2.0) or moisture functions (JSM, Millennial v1.0, and v2.0).

3.3 Microbial Mortality

Although the microbial models reviewed in this study consider the carbon pool of microbial biomass separately, most microbial models did not explicitly represent the microbial necromass pool with a different decomposition rate from plant residue. For example, in the Millennial model, a fraction of microbial necromass and plant residues (such as root exudates and leaf leachate) enter into the same C pool, i.e., low molecular weight carbon, which follows the same decomposition pattern (Abramoff et al., 2018). The microbial necromass pool mainly consists of microbially derived SOC, such as dead microbes and extracellular compounds released from the dead microbes, that have a faster decomposition rate than the plant residues (Huang et al., 2018). Several studies reported that soil microbes have different structural and chemical compositions from plant litter, which could result in their different decomposition rates (Kögel-Knabner, 2002; Liang et al., 2017). For example, the global mean C:N ratio of microbial biomass (~7) (Xu et al., 2013) is much lower than that of plant litter (~53) (Yuan & Chen, 2009), which may cause decoupling of C and N if microbes prioritize SOC with high N content to meet their demands. Consequently, the microbial assimilation of high N-containing SOC for the growth of microbial biomass may lead to different decomposition rates between microbial necromass and plant residues because of varying chemical structures and characteristics of microbially- and plant-derived SOC (Kögel-Knabner, 2002; Liang et al., 2017). For example, in the GENDEC model, the decomposition rate of microbial necromass is higher than that of the plant residues because the N-content of microbial necromass is relatively higher than that of the plant residues (Moorhead & Reynolds, 1991).

Although the C pool size of active microbial biomass in the soil is minimal (<2% of total SOC, (Dalal, 1998), microbial necromass may accumulate over a long period of time, and it can contribute to a significant proportion of SOC if (1) the turnover rate of microbial biomass is higher than the input rate of plant litter (Liang et al., 2011; Simpson et al., 2007; Zhu et al., 2020), (2) the chemical composition of microbial necromass is not labile, (3) mineral matrix of the soil protects microbially derived SOC (Dwivedi et al., 2017; Mikutta et al., 2006; Miltner et al., 2012; Torn et al., 1997). According to the previous studies, the contribution of microbial necromass to SOC can range from 24-80% of SOC (Khan et al., 2016; Liang et al., 2019; Liang & Balser, 2011; Miltner et al., 2012). Therefore, the role of microbial necromass in the formation of SOC cannot be ignored when considering microbial biomass as a decomposer in microbial models (Fan et al., 2021; Kögel-Knabner, 2002).

It is widely known that different microbial groups differ in their chemical composition. For instance, the cell walls of fungi are composed of a high proportion of recalcitrant polymers (e.g., protein and melanin), whereas bacterial cell walls are made up of carbohydrates (Kögel-Knabner, 2002). However, despite the differences in the cell wall composition of microbial groups, the decomposition rates of necromass of different microbial groups in the soil have been found to be similar (Throckmorton et al., 2012). In our review, we found 10 out of 70 microbial models, including CORPSE, EcoSMMARTS, FOND, GENDEC, JSM, Kaiser, MIND, MOMOS, and ORCHIMIC (v1.0 & v2.0) explicitly represented a separate microbial necromass pool under the assumption that decomposition of microbial necromass is 1) similar among different microbial groups, but 2) different from that of plant residues. However, the mechanistic representation of microbial necromass in a microbial model still poses some challenges that is discussed in section 5.2.

3.4 Active and Dormant Microbial Dynamics

In a given environment, at any given time, microorganisms can be in any of the physiological states: active, dormant, or dead (Mason et al., 1986). Therefore, distinguishing these states in the microbial models may be important to modeling SOC accurately. The active fraction of microbial communities play a significant role in ecologically important processes like SOC decomposition and nutrient cycling (Blagodatsky et al., 2000). However, when environmental conditions are unfavorable for growth, for example, when there is not enough substrate, microbes may reduce metabolic activities from low to zero to prevent biomass loss and may enter into dormant states (Lennon & Jones, 2011; Stolpovsky et al., 2011). The dormant microbes do not play the same roles as those active microbes, and dormancy is considered an evolutionary strategy that preserves genotypes until conditions improve to allow replication (Price & Sowers, 2004). The maintenance cost of C in dormant microbes can be two to three orders of magnitude lower than that of metabolically active microorganisms (Anderson & Domsch, 1985a; Anderson & Domsch, 1985b).

It is important to represent active versus dormant microbes in microbial models to accurately simulate SOC dynamics, given the variations in substrate and environmental conditions over time and space. With seasonal variations in substrate availability, temperature, and moisture, many soils have slow SOC turnover rates. Even when some resources are abundant at a time, the spatial and temporal complexity of soils may lead to disproportionate distributions of other potentially limited resources, which can dramatically increase the dormancy rates. High dormancy rates may be a defining characteristic of soil systems when spatial and temporal complexity is paired with various resource distributions across species within a community. Therefore, an understanding of dormancy could improve the prediction on how active microbes contribute to ecosystem processes like decomposition and nutrient cycling (Blagodatsky et al., 2000; Wang et al., 2014a).

Despite the potential importance, it is challenging to study microbial dormancy because there is no single method available to measure individual microbial physiological states: active, dormant, or dead simultaneously; instead, a combination of various techniques has been used to quantify microbial states (Wang et al., 2014a). In microbial models, generally, there are two methods used to depict physiological states (Wang et al., 2014a): one is to separate total live microbial biomass into two pools: active and dormant (Table 1); and another is to directly regard the active fraction (i.e., a ratio of active to total live microbial biomass) as a state variable (Blagodatsky et al., 1998). However, despite the limited ability to distinguish between active, dormant, and dead microbial biomass, a wealth of studies suggest that in a given microbial community, the majority of microbes may be dormant under natural circumstances (Blagodatsky et al., 2000; Yarwood et al., 2013). For example, in a Typic Argiudoll soil from Argentinean Pampa, only 3.8–9.7 % of total microbial biomass is in the active state (Alvarez et al., 1998); however, 0.02–19.1 % and 9.2–24.2 % of total microbial biomass are in active states in the subkurgan paleosoils of different ages and modern background soils, respectively (Khomutova et al., 2004). Other studies reported that under natural soil conditions, the fraction of active microbial biomass is usually below 50% of total live microbial biomass (Lennon & Jones, 2011; Stenstrom et al., 2001; Van de Werf & Verstraete, 1987). Thus, not including dormancy from the microbially-driven ecosystem processes could result in incorrect estimates of total live microbial biomass, leading to inaccuracies in model parameterization and forecasts of SOC (Wang et al., 2014a).

In our review, only 10 out of 70 models explicitly simulated microbial transformation between active and dormant states (Brangarí et al., 2020; Gignoux et al., 2001; He et al., 2015; Huang et al., 2018; Huang et al., 2021; Liu et al., 2019; Wang et al., 2015; Wang et al., 2017; Zha & Zhuang, 2020; Zhang et al., 2022), (Table 1). SOMKO was one of the first microbial models that distinguish active and dormant microbial biomass (Gignoux et al., 2001). In SOMKO, the direction of net flux from the active to the dormant state depends on the maintenance requirement relative to substrate availability. If the substrate availability is less than the maintenance requirement, there is a positive net flux from the active to the dormant pool and vice versa. Later, MEND_dor introduced the rates of dormancy and reactivation of microbial biomass (Wang et al., 2014a) into the MEND model (Wang et al., 2013). Following Wang et al. (2013), a few more microbial models were developed by adopting the MEND_dor dormancy framework to simulate SOC decomposition. For example, ORCHIMIC (v1.0 and v2.0) and TRIPLEX_Microbe microbial models have incorporated the MEND_dor dormancy framework along with the following assumptions: (1) the dormancy ($B_{a\to d}$) and reactivation rates ($B_{d\to a}$) are proportional to the active and dormant biomass pool sizes, respectively; (2) when substrate concentration is very high, $B_{a\to d} \to 0$ and $B_{d\to a} \geq 0$; (3) when substrate concentration is very low, $B_{a\to d} \geq 0$ and $B_{d\to a} \to 0$; (4) both transformation processes are governed by the maximum specific maintenance rate for active microbes since the maintenance energy cost is the critical factor determining the dormancy strategy (Lennon & Jones, 2011; Wang et al., 2014a). Unlike the above-mentioned microbial models that consider the substrate dependence of dormancy, the microbial dormancy in the microbial models DORMANCY 2.0, EcoSMMARTS, and MESDM is also affected by soil moisture content (Table 2). Such microbial models were developed to simulate the soil respiration in soil moisture-limited conditions to capture the drying-rewetting effect (i.e., Birch effect) under the assumptions that the soil water content determines the overall microbial performance and changes in soil water content can alter the physiological state of a portion of the microbes (Brangarí et al., 2020; Zhang et al., 2022).

Table 2: Mathematical formulations of the four processes: Microbial Decomposition (Eqs. 1-18), Mineral Interaction (Eqs. 19-33), Microbial Mortality (Eqs. 34-37), and Transition between Active and Dormant States (Eqs. 38-42)

Equations	Ecological description	Models
1. $D_c = k*M$	A function of microbial biomass (M)	Barot model; BLAGODATSKY; SYMPHONY
2. $D_c = V_{max}*M*\frac{S}{K_m+S}$	The function of microbial biomass (M) and substrate(S)	Parnas; MIND; GDM; German; CLM-Microbe; MIMICS; MIMICS-CN v1.0; MIMICS-D, MIMICS-DB, MIMICS-DBT; Ecosys; DecoBio v1.0
3. $D_c = V_{max}*E*\frac{S}{K_m+S}$	Function of Extracellular enzyme (E) and substrate(S)	Enzyme-driven model; Fatichi; Hagerty; He model; Kaiser; MEND_dor; MESDM; MEND; MIC-TEM; Resat; SCAMPS; TRIPLEX_Microbe; DEMENT; ORCHIMIC v2.0
4. $D_c = V_{max}*\boldsymbol{Q}_{\boldsymbol{10E}}^{\frac{temp-15}{10}}*E*\frac{S}{K_m+S}*(120 - CN_{soil})$		DORMANCY; MIC-TEM-dormancy
5. $D_c = V_{max}*\frac{S}{K_s+S}*\frac{M}{K_m+M}*f(T, W)$	Double Michaelis-Menten kinetics	Millennial model
6. $D_c = k*M*\frac{C}{(K_C+C)}*\frac{O_2}{(K_{O_2}+O_2)}$	Function of DOC and O_2 (dissolved oxygen concentration in water)	DORMANCY v2.0; DAMM; MIC-TEM_Hao
7. $D_c = V_{max} * S* \frac{E}{K_m*f(T)+S+E} * f(pH, W, T, clay)$	Function of S, E, clay content, soil pH, temperature (T), and moisture (W)	ORCHIMIC v1.0
8. $D_c = k*S*\frac{M}{K_m+M}$	Reverse Michaelis-Menten. Millennial V2 includes moisture modifier function, f(W)	CMAX framework; NCSOIL; COMISSION; Millennial V2
9. $D_c = V_{max}*S*\frac{E}{K_m+E}$	A function of S and E	JSM; Schimel model; EEZY; Averill model; Manzoni; SOMic v1.0
10. $D_c = V_{max}*S*\frac{E}{K_m+E}*f(T, W)$	A function of S and E, T, and W	EC1, EC2
11. $D_c = V*S*\frac{E}{K_m+E}*f(W)$		EcoSMMARTS
12. $D_c = k*S*\frac{M/S}{K_m+\frac{M}{S}}*f(W)$	Function of S and ratio of M and S	CORPSE
13. $D_c = V_{max}*\frac{S*E}{K_m+S+E}$	ECA	DAMM-MCNiP
14. $D_c = \boldsymbol{V_{max}} * \boldsymbol{S} * \frac{E}{K_{es}(1+\frac{S}{K_{es}}+\frac{E}{K_{es}}+\frac{Min}{K_{me}})}$	A function of S, E, and mineral particle (Min)	ReSOM; ReSOM vNN, ReSOM vTN , ReSOM vTD, ReSOM vTI
15. $D_c = k*\frac{1}{1+K_1(\frac{M}{S})K_2} * \boldsymbol{M} * \boldsymbol{f(T,W)}$	Microbial density-dependent SOC decomposition	Phoenix
16. $D_c = (1-e^{-k\frac{M}{S}})S$	Exponentially related to microbial biomass (M)	SOMKO
17. $D_c = k*M*S$		C-STABILITY; MiCNiT
18. $D_c = \frac{\theta_1}{1+e^{-\theta_2(t-\theta_3)}}$	θ_1 , θ_2, θ_3 are maximum rate, growth rate and lag phase	MiFe
19. $Sorption = K_{ads}*DOC*(q_{max}-C_{MAOM})$ $Desorption = K_{des}*C_{MAOM}$	The availability of sorption sites limits the sorption rate Langmuir isotherm	COMISSION
20. $\boldsymbol{C_{net\_sorption}} = SOC*f(clay) - \frac{Cp}{\tau}$	The rate of protected C formation is proportional to the amount of unprotected C pool. τ is the residence time of protected C.	CORPSE
21. $C_{MAOM} = (1-f_{BNF})*k_B*M + k*C_{DN} - R*K_{NF}*C_{MAOM}$	k is the decomposition rate of microbes derived DOC (C_{DN})	FOND

	R is the ratio of decomposition rate of C_{MAOM} to fast pool of microbial necromass	
22. Sorption = $K_{ads}*DOC*e^{\frac{-Ea}{R}\left(\frac{1}{T}-\frac{1}{T_{ref}}\right)*\frac{W}{dz}}*Q_{max}$ Desorption = $K_{des}*e^{\frac{-Ea}{R}\left(\frac{1}{T}-\frac{1}{T_{ref}}\right)*\frac{W}{dz}}*C_{MAOM}$	dz is soil depth Langmuir isotherm	JSM
23. Net Sorption = $DOC*(\frac{(\frac{(K*Q_{max}*DOC)}{1+(K*DOC)})-C_{MAOM}}{Q_{max}})$	Sorption and desorption are not simulated separately, Q_{max} maximum sorption capacity, Langmuir isotherm	MEMS v1.0
24. Sorption = $K_{ads}*(1-\frac{Q}{Q_{max}})*DOC$ Desorption = $K_{des}*(\frac{Q}{Q_{max}})$	Q is adsorbed phase of DOC K_{ads} and K_{des} are sorption and desorption rate	MEND; MEND_dor; TRIPLEX_Microbe
25. Sorption = $DOC*(\frac{\frac{K_{lm}*Q_{max}*DOC}{1+(K_{lm}*DOC)}-C_{MAOM}}{Q_{max}})f(T, W) + k_m*M*f(T, W) + k_b*f(T, W)(1-p_a)*C_{aggregate}$ Desorption = $V_{ma}*\frac{C_{MAOM}}{K+C_{MAOM}}(1-\frac{C_{aggregate}}{A_{max}})f(T, W)$ $K_{lm} = 10^{(-0.186pH-0.216)}$ $Q_{max} = BD10^{(c_1\log(\%logclay)+c_2)}$	K_{lm} is binding affinity Q_{max} is maximum sorption capacity BD is bulk density L is LMWC A_{max} is the maximum capacity of C in soil aggregates k_m is sorption rate of microbial biomass k_b is rate of breakdown Langmuir isotherm	Millennial
26. Sorption = $K_{lm}*DOC*\left(1-\frac{C_{MAOM}}{Q_{max}}\right)f(W)+p_bk_{bd}*M^2 + (1-p_a)k_b*C_{aggregate}*F(W)$ Desorption = $K_{ld}\frac{C_{MAOM}}{Q_{max}} + (1-p_a)k_{ma}C_{MAOM}f(W)$ $K_{lm} = e^{-p1pH-p2}K_{ld}$ Q_{max} = depth*BD %claysilt*p_c	K_{lm} is the binding affinity %claysilt is the clay and silt content in percent and a coefficient (p_c) K_{ld} is desorption coefficient Depth is site-level sampling depth in m k_{ma} is the aggregate formation rate from MAOM p_a is the proportion of aggregate C allocated to POM Langmuir isotherm	Millennial V2
27. Sorption = $f_1*Input + f_2*M$ Desorption = $1.5*10^{-5}*k_d*e^{-1.5*f_{clay}}$	k_d is the coefficient of desorption rate	MIMICS MIMICS-CN v1.0
28. Sorption = $f_1*Input + f_2*M$ Desorption = $1.5*10^{-5}*k_d*e^{-1.5*f_{clay}}*e^{k_{dp}*C_{MAOM}}$	K_{dp} iss the coefficient for tuning the relationship between the desorption and C_p pool.	MIMICS-D (Kyker-Snowman et al., 2020)
29. Sorption = $f_1*Input + f_2*M$ Desorption = $1.5*10^{-5}*k_d*e^{-1.5*f_{clay}}*e^{k_{dp}*C_{MAOM}}*e^{k_{bs}*BS}$	k_{bs} is the coefficient of soil base saturation impact on desorption	MIMICS-DB
30. $C_{net\_sorption} = (1-f_{BNF})*k_B*M - R*\frac{V_{max}*M*C_{MAOM}}{K_M+C_{MAOM}}$	f_{BNF} is proportion of fast pool in microbial biomass, k_B is average mortality rate, M is microbial biomass R is the ratio of decomposition rate of C_{MAOM} to fast pool of microbial necromass	MIND (Fan et al., 2021)
31. Sorption = $K_{ads}*DOC*e^{\frac{-Ea_{ads}}{R}\left(\frac{1}{T}-\frac{1}{T_{ref}}\right)}*(1-\frac{C_{MAOM}}{Q_{max}})$ Desorption = $K_{des}*e^{\frac{-Ea_{des}}{R}\left(\frac{1}{T}-\frac{1}{T_{ref}}\right)}*(\frac{C_{MAOM}}{Q_{max}})$	Function of temperature Arrhenius equation	ORCHIMIC v1.0; ORCHIMIC v2.0

32.	$Q_{max} = \frac{x}{m} = k*C^{1/n}$	X is grams of OM adsorbed, m is weight of soil, k is sorption constant, C is DOC	Phoenix
33.	Sorption = f_{sorb} * k*DOC Desorption = $f_{desorb}*C_{MAOM}$	f_{sorb} is the sorption coefficient, k is the rate constant for the combined processes of microbial uptake and sorption	SOMic v1.0
34.	$D*B_a$	Death rate of microbes is fraction (D) of their active biomass (B_a)	ORCHIMIC v1.0; ORCHIMIC v2.0
35.	$C_N = D*M$	Function of mortality rate, and microbial biomass	CORPSE; MIND; FOND; EcoSMMARTS
36.	$(k_1+k_3)*M + k_2*\gamma$	k1, k2, k3, and γ are the minimum microbial death rate, growth-related microbial death rate, and mortality associated with the change in soil water potential, and microbial growth, respectively.	GENDEC
37.	$m = \frac{1}{M_{CS}}*m_f$	M_{CS} is the maximum cell size of a microbe, m_f is a factor relating mortality rate to the inverse of maximum microbial biomass	Kaiser
38.	$R_{a\text{-}d} = k_{tran}*1/(1+(\frac{Sesample}{Sehalf})^{b})*B_a$ $R_{d\text{-}a} = k_{tran}*1/(1+a*(\frac{Sehalf}{Sesample})^{b})*B_d$	k_{tran} is the maximum transition rate constant, Se_{sample} is effective moisture saturation of sample, Se_{half} is the saturation at which R equals $0.5*K_{tran.}$ B_a and B_d are active and dormant microbes, respectively.	DORMANCY 2.0
39.	$R_{a\text{-}d} = k_i*(1-\chi_a\xi_c)*B_a$ $R_{d\text{-}a} = k_d*\Gamma_m*\xi_c*B_d$	k_i and k_d are the maximum specific cell activation and deactivation rates. χ_a is the coefficient of water stress, ξ_c is the saturation coefficient of DOC, Γ_m is the coefficient of drought-legacy on microbes.	EcoSMMARTS
40.	$\begin{cases} S_{MBC} = B_d \cdot \frac{dW}{dt} & when\ \frac{dW}{dt} > 0 \\ S_{MBC=(B_a+B_{MBC_{WP}})\cdot\frac{dw}{dt}} & when\ \frac{dW}{dt} < 0 \end{cases}$	S_{MBC} is microbial biomass transformation rate due to water content, $C_{MBC_{WP}}$ is potential active microbial biomass, respectively.	MESDM
41.	$R_{a\text{-}d} = [1 - \frac{DOC}{(K_D+DOC)}]*m_R*B_a$ $R_{d\text{-}a} = \frac{DOC}{(K_D+DOC)}]*m_R*B_d$	m_R is the specific maintenance rate of B_a	ORCHIMIC v1.0; ORCHIMIC v2.0; MEND_dor; TRIPLEX_Microbe
42.	$R_{a\text{-}d} = (1-\phi)*m_R*Q_{10M}^{\frac{temp-15}{10}}*B_a$ $R_{d\text{-}a} = \phi*m_R*Q_{10M}^{\frac{temp-15}{10}}*B_d$	ϕ is the directly accessible substrate for microbial assimilation	DORMANCY; MIC-TEM-dormancy

4. Environmental Control on Microbial Processes

Many environmental factors affect microbial processes, including soil temperature, moisture, pH, redox potential, and oxygen availability. This review mainly focuses on soil temperature, moisture, and pH because they are commonly incorporated into microbial models (Table 3). Among the 70 models we reviewed, 38 included temperature, 12 included soil moisture, and 7 included pH.

Temperature. In the microbial models, the temperature dependency of microbial processes was simulated using four mathematical functions: (1) Q_{10} functions, (2) Arrhenius functions, (3) Generalized Poisson function, and (4) Arctangent function. Of these functions, the Arrhenius function is most widely used among most microbial models, followed by the Q_{10} function. The Arrhenius function represents an increase in SOC decomposition with temperature and dependence on substrate quality through the activation energy (Zhang et al., 2014). Only the SOMic v1.0 model was found to use a Generalized Poisson function, determined by fitting data from an incubation experiment conducted in the laboratory in which cellulose was labeled and decomposed at three different temperatures (Burke et al., 2003; Parton et al., 1987; Sorensen, 1981). Similarly, only the Millennial model was found to use the arctangent function, which predicts a decline in temperature sensitivity with increasing temperature (Abramoff et al., 2018). These two temperature response functions were taken from CENTURY and DAYCENT, respectively (Burke et al., 2003).

Moisture. Modeling the response of microbial communities to pulse moisture dynamics is challenging because moisture controls complex physical and biological interactions in soil and has significant direct and indirect impacts on the decomposition rates (Lawrence et al., 2009). Soil moisture is a critical factor controlling SOC decomposition because, at high water content,

O_2 becomes a limiting factor, whereas, at low water content, diffusion is constrained by thin and discontinuous water films (Abramoff et al., 2017; Abs & Ferrière, 2020; Sihi et al., 2018). Various mathematical functions were used to represent the responses of microbial processes to soil moisture; for example, the moisture response variables vary widely by including the function of soil water potential, water holding capacity, or soil water content (Table 3).

pH. A small number of microbial models considered the effect of soil pH on microbial processes (7 out of 70 models). Soil pH has a significant impact on mineral surfaces and SOC availability to microbes. At high pH, the sorption capacity of mineral surfaces is reduced drastically, which means that less SOC will be sorbed on the mineral surfaces, and most of the SOC will be available to microbes for decomposition (Abramoff et al., 2022).

Table 3: Environmental Control on Microbial Processes

Model	Temperature	Moisture	pH	Note
MEMS v1.0	Q_{10}=2, T_{ref} = 13.5 C			
GENDEC	2< Q_{10}>3 T_{ref} = 25 C	SM= α - µlog(-Ψ)	*N/A*	α and µ are intercept and slope of soil moisture effect on decay rate, Ψ is soil water potential
MOMOS	Q_{10}=2.2 T_{ref} =28 C	f(θ) = a + b θ/WHC	*N/A*	Moisture correction factor (f(θ)) WHC is water holding capacity, a and b range between 0 and 1
MIND; ORCHIMIC v1.0; ORCHIMIC v2.0; MEND; TRIPLEX-Microbe (f(T) & pH only); Microbial-Enzyme model (f(T) only)	f(T)=$e^{\frac{-Ea}{R}(\frac{1}{T}-\frac{1}{Tref})}$ T_{ref} = 285.15 K	f(θ)= max[0.25, min(1, -1.1*θ^2 + 2.4*θ -0.29)]	f(pH)= $e^{\frac{-(pH-pH_{opt})^2}{pH_{sen}^2}}$ pH_{opt} = 6 pH_{sen}= 1.66	R is ideal gas constant, Θ is soil moisture (%), pH_{opt} is optimal pH for substrate decomposition pH_{sen} is the sensitivity parameter of substrate decomposition
SOCRATES	Q_{10} Temp factor, TF= 0.177$e^{(0.069\mathrm{T})}$	Moisture factor, MF= 0.0598*$\mathrm{MAP}^{0.279}$	*N/A*	T is mean annual air temperature (C)
MySCaN	$e^{\left(3.36*\frac{(T-40)}{(T+31.79)}\right)}$	*N/A*	*N/A*	Temperature response: Arrhenius function
ReSOM	K_{EQ}(T)= K(T_0) $e^{[\frac{-\Delta G_{EQ}}{R}(\frac{1}{T}-\frac{1}{T_0})]}$ K_{NEQ}(T)= K_{NEQ}(T_0)$\frac{T}{T_0}e^{[\frac{-\Delta G_{EQ}}{R}(\frac{1}{T}-\frac{1}{T_0})]}$ f_{act}= $\frac{1}{1+e^{\left(-\frac{n\Delta G_E}{RT}\right)}}$	*N/A*	*N/A*	K_{EQ} is temperature-dependent equilibrium reactions; K_{NEQ} is temperature dependent non-equilibrium reactions; f_{act} temperature dependent fraction of active enzyme ReSOM vTN: KEQ=0 ReSOM vTD: In eq K_{EQ}(T), ΔG_{EQ} = -20 kJ/mol ReSOM vTI: In eq K_{EQ}(T), ΔG_{EQ} = 20 kJ/mol
DAMM-MCNiP; DEMENT; Ecosys; CORPSE	$e^{\frac{-Ea}{RT}}$	*N/A*	*N/A*	Arrhenius equation
Millennial	$\frac{t_2+\frac{t_3}{\pi}\mathrm{atan}[\pi(T-t_1)]}{t_2+\frac{t_3}{\pi}\mathrm{atan}[\pi t_4(T_{ref}-t_1)]}$	$\frac{1}{1+w_1e^{(-w_2RWC)}}$	$10^{(-0.186\mathrm{pH}-0.216)}$	t_1 and t_2 are x-axis and y-axis locations of the inflection point (℃), respectively t_3 is the distance from maximum to minimum point and t_4 is the slop of the line at the inflection point w_1 and w_2 are empirical parameters RWC relative water content T_{ref} is the reference temperature (30 ℃)
Millennial v2.0	$a_xe^{-\frac{Ea}{R(T+273.15)}}$	$(\frac{\theta}{\varphi})^{0.5}$	K_{lm}= $e^{-p1pH-p2}$ K_{ld}	K_{lm} and K_{ld} are binding affinity and desorption coefficient, p1 and p2 are sorption coefficient, θ is volumetric water content, φ is matric potential, Arrhenius equation
CMAX framework	$f(T)=\begin{cases}0, & T\leq Ts_{min}\\ Q_{10s}^{\frac{T-Ts_{ref}}{10}}, & T>Ts_{min}\end{cases}$	f(M) = $\frac{\log(\frac{M_{min}}{M})}{\log(\frac{M_{min}}{M_{max}})}$	*N/A*	Ts_{min} and Ts_{ref} are minimum and reference temperatures for the substrate decomposition M_{min} and M_{max} are the minimum and maximum

		when, $M_{min} \leq M \leq M_{max}$		moisture for substrate decomposition
CLM-Microbe; Enzyme-driven model; German; He model; MIC-TEM-Hao; MIC-TEM-Zha; Hagerty; MESDM; DAMM; SCAMPS	$V_{max} = V_{max0} * e^{(-\frac{E_a}{R*(temp+273)})}$ $K_m = K_{mslope} * temp + K_{m0}$	*N/A*	*N/A*	Arrhenius equation
MIMICS-CN v1.0; MIMICS-D; MIMICS-DB; MIMICS-DBT	$V_{max} = e^{(V_{slope}*T+V_{int})} * a_v * V_{mod}$ $K = e^{(K_{slope}*T+V_{int})} * a_k * k_{mod}$	*N/A*	*N/A*	Arrhenius equation
JSM	$f(T, W) = e^{\frac{-Ea}{R}(\frac{1}{T}-\frac{1}{Tref})} * \frac{W}{soil_{depth}}$	*N/A*	*N/A*	Arrhenius equation
DecoBio v1.0; DORMANCY; MIC-TEM-DORMANCY	$Q_{10}^{\frac{T-15}{10}}$	*N/A*	*N/A*	
SOMic v1.0	f(T)= $f_t\left(\frac{T_{max}-T}{T_{max}-T_{opt}}\right)^2 e^{\frac{0.2}{2.63}\left(1-\left(\frac{T_{max}-T}{T_{max}-T_{opt}}\right)^{2.63}\right)}$ $f_t = 4.99$ $T_{max} = 45$ ℃ $T_{opt} = 35$℃	If amd>0.444max_md, θ=1.0 If amd ≤0.444max_md $\theta = 0.2 + 0.8\frac{\max_{md} - amd}{0.556\max\_md}$	*N/A*	Max_md is maximum possible soil moisture deficit Generalized Poisson function for temperature modifier
EC1, EC2	*N/A*	$\frac{WHC}{60\%}$	*N/A*	Water Holding Capacity (WHC)

5. Challenges and Recommendations

Despite the diverse representations of microbial processes and appropriate simulations of the microbial responses to perturbations by microbial models, conventional SOC models remain the backbone of SOC modeling in most applications, including ESMs, partly because microbial models have not yet demonstrated their reliability to provide robust predictions over varying environmental conditions and long-time scales (Wieder et al., 2013; Woolf & Lehmann, 2019). Moreover, the microbial models were intended to represent the SOC dynamics better than the conventional SOC model (Wang et al., 2014b) with the belief that microbial models may be appropriate to describe the C cycling under variable environmental conditions (Schimel, 2001; Schimel & Weintraub, 2003). However, it poses several challenges, including (1) the lack of experimental evidence for the rate-limitation processes, (2) the lack of observational data to constrain model parameters, and (3) model complexity due to a large number of parameters.

5.1 Experimental Evidence for Rate-Limitation Processes in Microbial Models

It is known that SOC is decomposed mainly as a result of ENZ produced by microbes, and it has been demonstrated that microbes can degrade almost all SOC, irrespective of the chemical composition of SOC, if it is physically accessible to microbes (Kleber, 2010; Lützow et al., 2006; Woolf & Lehmann, 2019). Microbial models are mainly based on the assumption that the SOC decomposition rate is limited by either microbial biomass or ENZ or both (Allison et al., 2010). However, a few studies report that in soil, microbial activities do not limit the rate of SOC decomposition; instead, abiotic processes are rate-limiting (Kemmitt et al., 2008). A common way for abiotic processes to control SOC decomposition is through physical protection that limits microbial access to substrates (Dungait et al., 2012; Kemmitt et al., 2008; Schimel & Schaeffer, 2012). In contrast, a core assumption of conventional SOC models is that the biomass of microbes and their enzyme production never limits microbial processes, and microbial communities will always rapidly adapt to the available substrate and subsidence of environmental stress (Schimel, 2001). Thus, it is imperative to conduct experimental studies to examine the assumption on the rate limitation processes by microbial biomass or enzyme activity.

5.2 The Lack of Observational Data to Estimate Model Parameters

A lack of observational data is one of the most significant constraints to the validation of mechanistic descriptions of microbial processes and the parameterization of microbial models. Model development and data collection are generally separate activities, and their integration is critical for the advancement of science (De Kauwe et al., 2014; Luo et al., 2012; Peng et al., 2011; Xu et al., 2016). In addition, the performance of a model is usually assessed by comparing simulations against a set of empirical observations derived from independent experiments (Moorhead & Sinsabaugh, 2006). When processes are made explicit rather than implicit, it is essential to test the validity of those assumptions against the reality provided by data (Schimel, 2001). However, the incorporation of microbial processes increases the complexity of models and enlarges the number of model parameters, which can be challenging to empirically measure. For example, FMM, RMM, and ECA kinetics use two kinetic parameters, the maximum specific reaction rate (V_{max}) and half saturation constant (K_m). There are very few estimates of the K_m for enzyme pools in explicitly enzyme-represented microbial models (Lawrence et al., 2009; Moorhead & Sinsabaugh, 2006) or of the V_{max} or K_m for substrates (Wang et al., 2013). In addition, observational data of pool size is critical to constrain rate processes (Xu et al., 2006). However, the inability to measure active, dormant, and dead microbial biomass *in situ* simultaneously (see section 3.4) and difficulty in differentiating microbial necromass C from nonmicrobial C (Liang et al., 2019) present challenges in validating these processes. Similarly, the measurement and evaluation of the stability of various SOC-mineral interactions in different soils are challenging due to difficulty with the fractionation of SOC bound to different minerals *in situ* (Lützow et al., 2006). Therefore, most of the parameter values used by microbial models are primarily laboratory-based (Sulman et al., 2014; Wieder et al., 2015a; Wieder et al., 2013; Wieder et al., 2015b) or assumed by the researchers (Wang et al., 2013), which may not reflect the actual conditions in the field. As model parameterization is one of the three elements towards realistic model predictions (Luo & Schuur, 2020), the research community needs to collect observational data for estimating model parameters. When extensive SOC data were used to estimate spatially varying parameters, the conventional Community Land Model (CLM4.5) can well simulate spatial and vertical patterns of SOC storage over the US continent (Tao & Luo, 2022; Tao et al., 2020).

5.3 Potential Improvements of Microbial Models

While the incorporation of microbial processes increases model complexity, several strategies can reduce the mismatch between model complexity and observational data. First, we need targeted, precise data collection strategies because more data does not necessarily produce a better-constrained model. Coordinated efforts between modelers and empiricists can return data maximally useful to constrain a model (Keenan et al., 2013; Richardson et al., 2010). Second, inaccurate parameterization is emerging as one of the major causes of mismatches between models and data (Luo & Schuur, 2020). Therefore, model improvements should include optimization algorithms that calibrate model parameters with data, such as data assimilation techniques (Luo et al., 2016; Wang & Chen, 2013). Third, an alternative approach is model reduction techniques that can simplify complex models without the loss of key model processes or the ability to integrate real data. Some commonly used model complexity reduction techniques include conversation analysis, nondimensionalisation, model decomposition (Snowden et al., 2017), and Manifold Boundary Approximation Method (MBAM) (Transtrum & Qiu, 2014). For example, a recent study applied the MBAM technique to a highly complex microbial model to demonstrate the systematic reduction of model complexity to match the information content of different datasets and thereby could explain fundamental controlling mechanisms in each dataset (Marschmann et al., 2019).

6. Summary

During the past three decades, SOC models have increasingly considered microbial controls on C cycling to identify mechanisms that govern C fluxes. Although the first model was developed in the 1970s, our review of 70 microbial models revealed that the majority of microbial models were developed since 2000, likely in sync with the acceleration of molecular methods to study soil microbes. Most of the microbial models incorporated one or more of four microbial processes: microbial decomposition, mineral interactions, microbial mortality, or transition between active and dormant microbial states. Among the four processes, microbial mortality and dormancy were the least studied.

Our analysis synthesized a diverse suite of mathematical formulations used to represent microbial processes across the 70 models. For example, 18 types of mathematical expressions are used to describe the decomposition of SOC across the 70 microbial models. The majority of models used nonlinear equations, especially forward Michaelis-Menten kinetics. Similarly, 15 types of mathematical expressions were devised to explain mineral interactions. Most microbial models simulated sorption and desorption processes separately, while a few simulated net sorption. The numerical expressions for microbial mortality were similar across models, with mortality proportional to microbial biomass. The 10 models that simulated dormancy used one of 5 equations to describe the dynamics of active and dormant microbial states as a function of the environmental stresses of soil temperature and moisture.

We identified the three major environmental factors incorporated in the microbial processes: soil temperature, soil moisture, and the effect of soil pH on the sorption capacity of minerals and/or SOC availability to microbes. We propose that future model structures could benefit from the following considerations: (1) focusing on measurable soil pools so that model performance can be evaluated against observational data, for example, (2) utilizing model-data integration approaches to help identify the most probable mechanisms underlying system behavior, and (3) employing a rigorous statistical method, such as data assimilation, that helps improve the model performance by optimizing the model parameters.

In conclusion, advancements in microbial genomics and computational sciences have improved our understanding of the microbial processes governing SOC dynamics, and microbial models bloomed in the past few decades to incorporate such advanced understandings. However, the diversity in mathematical equations used to incorporate microbial processes and the lack of observational data to validate these processes limit the translation of the current knowledge on SOC processes into models. Thus, to realistically incorporate microbial processes into ESMs, a significant challenge for future research is to design experiments that could quantify the key processes involved in the formation of various SOC pools in different soils.

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