

**Key Points:**

- More than 70 microbial models have recently been developed to simulate soil carbon dynamics
- Diversity in model structures and parameters indicates uncertainty in translating current knowledge of microbial processes into models
- Data-driven model development and parameterization are highly recommended to improve the prediction of microbial models

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## 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 71 microbial models to characterize the microbial processes incorporated into SOC models and analyzed variations in mechanistic complexity. We revealed that (a) four processes (microbial-mediated decomposition, mineral interaction, microbial necromass recycling, and active and dormant microbial dynamics) are commonly incorporated in microbial models, (b) ~48% of models simulate only one microbial process (i.e., microbial-mediated decomposition) and 35% of models simulate two microbial processes: for example, microbial-mediated decomposition and mineral interaction, (c) more than 80% microbial models use nonlinear equations, such as forward Michaelis-Menten kinetics, to represent SOC decomposition, (d) the concept of persistence of SOC due to its intrinsic properties has been replaced by organo-mineral interaction (~39% of microbial models) that protects SOC from decomposition, and (e) various temperature and moisture modifiers and pH effects have been used to explain the environmental effect on microbial processes. 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.

**Plain Language Summary** Soil stores the largest amount of carbon (C) in land ecosystems and, thus, has the potential to regulate climate change. To understand soil C processes under climate change, researchers have developed numerous microbial models that focus on the role of microorganisms in soil organic carbon (SOC) decomposition. In this study, we reviewed 71 microbial models on how microbial processes are represented for their regulation of SOC dynamics. These models commonly include four processes: microbially mediated decomposition, mineral interaction, microbial necromass recycling, and dormancy of microbial activity. More than three-fourths of the models use nonlinear equations to describe the decomposition of SOC. The concept of SOC stability has shifted from chemical-based properties of SOC to interactions between SOC and minerals. Our review also revealed that microbial models vary greatly in representing environmental effects, such as temperature, soil moisture, and soil pH, on microbial processes. Finally, we recommend the use of data in guiding the future development of microbial models.

### 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<sub>2</sub> 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 1,417–1,469 Pg C (Hiederer & Köchy, 2011), which is nearly three times the amount of C stored in plant biomass (Schlesinger & Bernhardt, 2013) and two times 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 et al., 2016; Luo & Schuur, 2020).

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, Allison, et al., 2015). 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 resired  $\text{CO}_2$  is proportional to the soil C pool size (Davidson et al., 2014; Wieder, Allison, et al., 2015). These conventional SOC models implicitly represent microbial activities under the assumptions that (a) microbes respond so quickly to changes in substrate availability that their abundance never limits the decomposition rate (Schimel, 2001), (b) 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 (c) microbial communities have functional equivalence allowing them to optimally process the available SOC (Bradford & Fierer, 2012; Wieder, Allison, et al., 2015).

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). As a result, numerous microbial models have been developed 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. The microbial biomass pool is either represented as a decomposer of SOC or as a SOC substrate pool. 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, Parnas (Parnas, 1975), 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, and revealed that incorporation of 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 (Z. 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 (Z. Shi et al., 2018).

Although several studies have reviewed SOC models (Chertov et al., 2007; Frissel & Van Veen, 1981; Le Noë et al., 2023; Manzoni & Porporato, 2009; McGill, 1996; Molina & Smith, 1997; Paustian, 1994; Paustian et al., 1997; Smith et al., 1998; Wieder, Allison, et al., 2015; X. Xu et al., 2016), a comprehensive synthesis and analysis of microbial processes incorporated into SOC models is 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 71 microbial models developed over the last few decades (Table 1). To gather these models, we conducted a synthesis of published microbial models that simulate SOC decomposition, and we collected publications by searching keywords "SOC microbial model," "SOC model," "SOC decomposition model," and "litter decomposition" in ISI Web of Science and Google Scholar. In addition, we also used previously reviewed literature on the SOC models; for example, Manzoni and Porporato (2009) reviewed  $\sim 250$  biogeochemical models developed for C and nitrogen (N) cycling from 1933 to 2009, including both microbial and nonmicrobial models. Finally, all the collected models were thoroughly examined, and we selected those models for our study if they met the following two criteria: (a) models should simulate the C cycle in the soil (or coupled with other nutrients such as N), and (b) models should simulate at least one microbial biomass pool. If multiple versions of a microbial model are available with distinct formulations, we treated each version as a separate model. In the following sections, 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

**Table 1**

Microbial Models for SOC Decomposition and the Four Processes Incorporated Along With the Decomposition Formulation

Microbial model	Decomposition mechanism	Extracellular enzyme pool	Microbial-mediated decomposition	Active and dormant microbial dynamics	Mineral interaction	Microbial necromass recycling	References
DNDC	ZO	No	No	No	No	No	Li et al. (1994)
FOND	ZO	No	No	No	Yes	Yes	Fan et al. (2021)
GENDEC	ZO	No	No	No	No	Yes	Moorhead and Reynolds (1991)
LIDEL	ZO	No	No	No	No	Yes	Campbell et al. (2016)
MEMS v1.0	ZO	No	No	No	Yes	No	Robertson et al. (2019)
MOMOS	ZO	No	No	No	No	Yes	Pansu et al. (2010)
MySCaN	ZO	No	No	No	No	No	Orwin et al. (2011)
RothC	ZO	No	No	No	No	No	Coleman and Jenkinson (1996)
SOCRATES	ZO	No	No	No	No	No	Grace et al. (2006)
VERBERNE	ZO	No	No	No	Yes	No	Verberne et al. (1990)
Barot model	FO	No	Yes	No	No	No	Fontaine and Barot (2005)
Blagodatsky model	FO	No	Yes	No	No	No	Blagodatsky et al. (2010)
SYMPHONY	FO	No	Yes	No	No	No	Perveen et al. (2014)
CLM-Microbe	FMM	No	Yes	No	No	No	Wieder et al. (2013)
DecoBio v1.0	FMM	No	Yes	No	No	No	Xenakis and Williams (2014)
DEMENT	FMM	Yes	Yes	No	No	No	Allison (2012)
DORMANCY	FMM	Yes	Yes	Yes	No	No	He et al. (2015)
DORMANCY 2.0	FMM	No	Yes	Yes	No	No	Liu et al. (2019)
Ecosys	FMM	No	Yes	No	No	No	Grant et al. (1993)
Enzyme driven model	FMM	Yes	Yes	No	No	No	Allison et al. (2010)
Fatichi	FMM	Yes	Yes	No	No	No	Fatichi et al. (2019)
GDM	FMM	No	Yes	No	No	No	Moorhead and Sinsabaugh (2006)
German	FMM	Yes	Yes	No	No	No	German et al. (2012)
Hagerty	FMM	Yes	Yes	No	No	No	Hagerty et al. (2018)
He model	FMM	Yes	Yes	No	No	No	He et al. (2014)
Kaiser	FMM	Yes	Yes	No	No	Yes	Kaiser et al. (2014)
MEND	FMM	Yes	Yes	No	Yes	No	G. S. Wang et al. (2013)
MEND_dor	FMM	Yes	Yes	Yes	Yes	No	G. S. Wang et al. (2015)
MESDM	FMM	Yes	Yes	Yes	No	No	X. Zhang et al. (2022)
MIC-TEM-dormancy	FMM	Yes	Yes	Yes	No	No	Zha and Zhuang (2020)
MIC-TEM_Hao	FMM	Yes	Yes	No	No	No	Hao et al. (2015)
MIC-TEM_Zha	FMM	Yes	Yes	No	No	No	Zha and Zhuang (2018)
Millennial model	FMM	No	Yes	No	Yes	No	Abramoff et al. (2018)

**Table 1**  
*Continued*

Microbial model	Decomposition mechanism	Extracellular enzyme pool	Microbial-mediated decomposition	Active and dormant microbial dynamics	Mineral interaction	Microbial necromass recycling	References
MIMICS	FMM	No	Yes	No	Yes	No	Wieder et al. (2014)
MIMICS_D	FMM	No	Yes	No	Yes	No	H. Zhang et al. (2020)
MIMICS-CN v1.0	FMM	No	Yes	No	Yes	No	Kyker-Snowman et al. (2020)
MIMICS-DB	FMM	No	Yes	No	Yes	No	H. Zhang et al. (2020)
MIMICS-DBT	FMM	No	Yes	No	Yes	No	H. Zhang et al. (2020)
MIND	FMM	No	Yes	No	Yes	Yes	Fan et al. (2021)
ORCHIMIC v2.0	FMM	Yes	Yes	Yes	Yes	No	Y. Huang et al. (2021)
Parnas	FMM	No	Yes	No	No	No	Parnas (1975)
Resat	FMM	Yes	Yes	No	No	No	Resat et al. (2012)
SCAMPS	FMM	Yes	Yes	No	No	No	Sistla et al. (2014)
TRIPLEX_MICROBE	FMM	Yes	Yes	Yes	Yes	No	K. Wang et al. (2017)
Averill model	RMM	Yes	Yes	No	No	No	Averill (2014)
CMAX framework	RMM	No	Yes	No	No	No	X. Xu et al. (2014)
COMISSION	RMM	No	Yes	No	Yes	No	Ahrens et al. (2015)
EC1	RMM	Yes	Yes	No	No	No	Lawrence et al. (2009)
EC2	RMM	Yes	Yes	No	No	No	Lawrence et al. (2009)
EcoSMMARTS	RMM	Yes	Yes	Yes	No	Yes	Brangarí et al. (2020)
EEZY	RMM	Yes	Yes	No	No	No	Moorhead et al. (2012)
JSM	RMM	No	Yes	No	Yes	Yes	Yu et al. (2020)
Manzoni	RMM	No	Yes	No	No	No	Manzoni et al. (2021)
Millennial V2.0	RMM	No	Yes	No	Yes	No	Abramoff et al. (2022)
MIMICS-2	RMM	No	Yes	No	Yes	No	Wieder et al. (2019)
NCSOIL	RMM	No	Yes	No	No	No	Hadas et al. (1998)
Schimel model	RMM	Yes	Yes	No	No	No	Schimel and Weintraub (2003)
SOMic v1.0	RMM	No	Yes	No	Yes	No	Woolf and Lehmann (2019)
DAMM-MCNiP	ECA	Yes	Yes	No	No	No	Abramoff et al. (2017)
ORCHIMIC v1.0	ECA	Yes	Yes	Yes	Yes	No	Y. Huang et al. (2018)
RESOM	ECA	Yes	Yes	No	Yes	No	Tang and Riley (2015)
ReSom vNN	ECA	Yes	Yes	No	Yes	No	Abramoff et al. (2019)
ReSom vTD	ECA	Yes	Yes	No	Yes	No	Abramoff et al. (2019)
ReSom vTI	ECA	Yes	Yes	No	Yes	No	Abramoff et al. (2019)
ReSom vTN	ECA	Yes	Yes	No	Yes	No	Abramoff et al. (2019)
C-STABILITY	Multiplicative	No	Yes	No	No	No	Sainte-Marie et al. (2021)

Table 1  
Continued

Microbial model	Decomposition mechanism	Extracellular enzyme pool	Microbial-mediated decomposition	Active and dormant microbial dynamics	Mineral interaction	Microbial necromass recycling	References
MICNiT	Multiplicative	No	Yes	No	No	No	Blagodatsky et al. (2011)
CORPSE	Density-dependent	No	Yes	No	Yes	Yes	Sulman et al. (2014)
Phoenix	Density-dependent	No	Yes	No	Yes	No	McGill et al. (1981)
SOMIKO	Density-dependent	No	Yes	No	No	No	Gignoux et al. (2001)
MiFe	Logistic	No	Yes	No	Yes	No	Liao et al. (2022)

Note. FMM, Forward Michaelis-Menten; FO, First-order; RMM, Reverse Michaelis-Menten; ZO, Zero-order (The names of the models are determined based on two criteria: (a) if the model has a name in the original publication, that name will be used to represent the model; (b) if the model has no name, the last name of the first author will be used to name the model, e.g., Faticchi model). Models are grouped by their decomposition mechanisms.

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. Finally, 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.

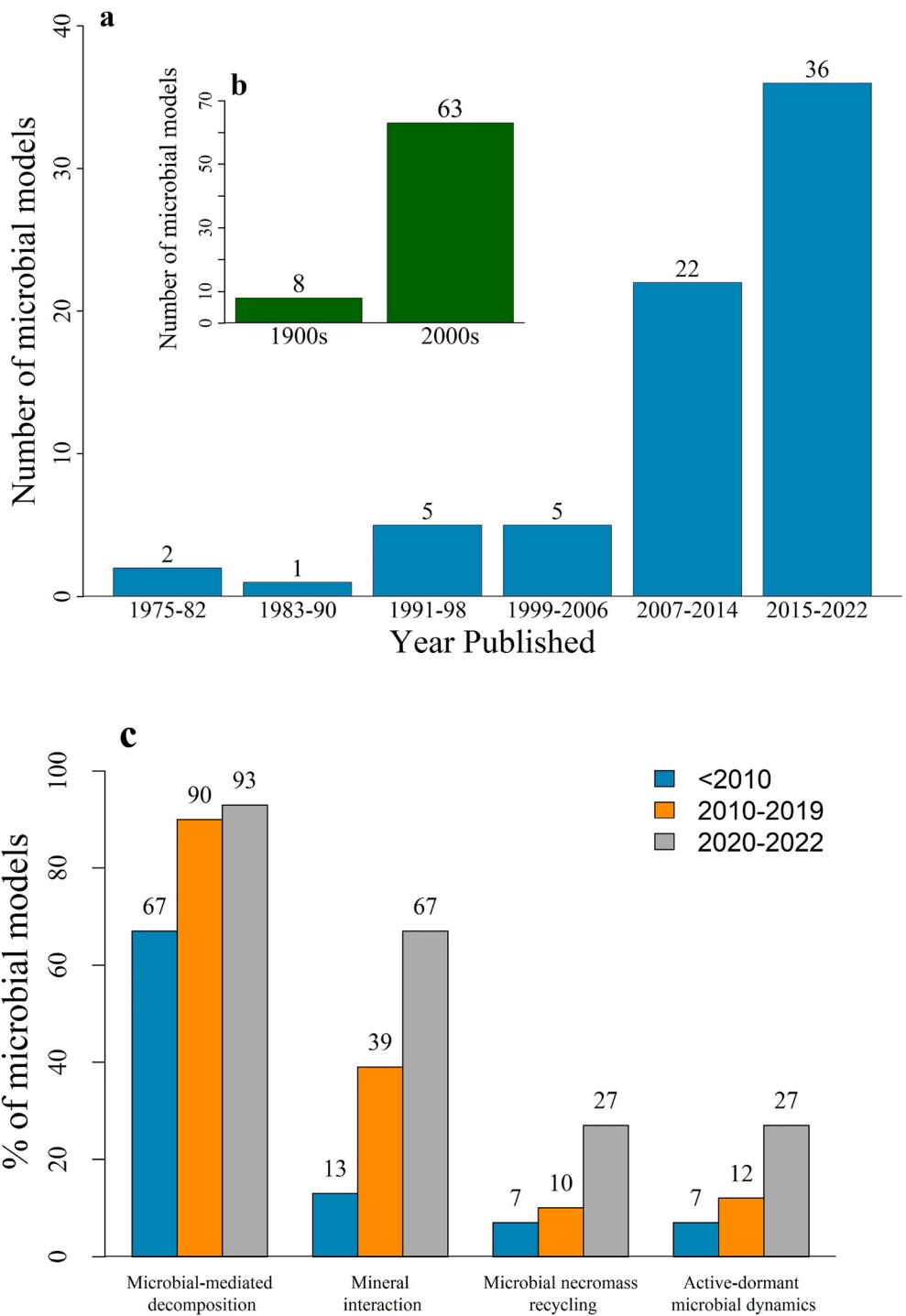
## 2. Historical Development of Microbial Models

Studies on the responses of organic matter (OM) decomposition to environmental factors have a long history, starting in the early 1930s (Manzoni & Porporato, 2009; Salter & Green, 1933; 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 (Figure 1a), and one of the first SOC microbial models was developed in 1975 (Parnas, 1975). This model 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 eight microbial models were developed during the last 25 years of the 20th century (Figure 1b), and the treatment of microbial biomass was often indistinguishable from the active pool of conventional SOC models, such as in VERBERNE, GENDEC, DNDC, and RothC microbial models. Microbial models started to receive more attention, mainly after Schimel and 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 account for 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). Instead, 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 advances 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; G. S. Wang et al., 2014). Thus, a significant increase in the trends of both the number of microbial models (Figures 1a and 1b) and the microbial processes controlling SOC decomposition was observed (Figure 1c). For example, 22 and 36 microbial models were developed during the periods of 2007–2014 and 2015–2022, respectively (Figure 1a). Microbial processes such as microbial necromass recycling and dynamic active-dormant microbial states are relatively less studied than the microbial processes related to decomposition and mineral association because of our recent but still developing understanding of microbial physiological states and the limitation in the measurement of microbial necromass and its physiological states *in situ* (Figure 1c).

## 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 (Minderman, 1968; Woolf & Lehmann, 2019). Such multipool 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



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

(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, Allison, et al., 2015).

Our review of the 71 microbial models revealed that four microbial processes are widely incorporated into SOC models: microbial-mediated decomposition, mineral interaction, microbial necromass recycling, and active and dormant microbial dynamics (Figure 2a; Table 1). Among the 71 microbial models, 61 models consider microbial

**Table 2**

Mathematical Formulations of the Four Processes: Microbial-Mediated Decomposition (Equations 1–18), Mineral Interaction (Equations 19–34), Microbial Necromass Recycling (Equations 35–41), and Active and Dormant Microbial Dynamics (Equations 42–46)

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; Faticchi; Hagerty; He model; Kaiser; MEND_dor; MESDM; MEND; MIC-TEM; Resat; SCAMPS; TRIPLEX_Microbe; DEMENT; ORCHIMIC v2.0
4. $D_c = V_{max} * Q_{10E}^{\frac{temp-15}{10}} * E * \frac{S}{K_m + S} * (120 - CN_{soil})$		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 <sub>2</sub> (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, MIMICS-2
11. $D_c = [1 + m_d(1 - \Gamma_s)] * \chi_t * V * S * \frac{E}{K_m + E}$	$M_d$ is coefficient of aggregate disruption; $\chi_t$ and $\Gamma_s$ are two moisture coefficients	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. $D_c = V_{max} * S * \frac{E}{K_{es} \left(1 + \frac{S}{K_{es}} + \frac{E}{K_{es}} + \frac{Min}{K_{me}}\right)}$	A function of S, E, and mineral particle (Min)	ReSOM; ReSOM vNN, ReSOM vTN, ReSOM vTD, ReSOM vTI
15. $D_c = k * \frac{1}{1 + K_1 \left(\frac{M}{S}\right) K_2} * M * f(T, W)$	Microbial density-dependent SOC decomposition	Phoenix
16. $D_c = \left(1 - e^{-k \frac{M}{S}}\right) S$	Exponentially related to microbial biomass (M)	SOMKO
17. $D_c = k * M * S$		C-STABILITY; MiCNiT
18. $D_c = \frac{\theta_1}{1 + e^{-\theta_2(t - \theta_3)}}$	$\theta_1, \theta_2, \theta_3$ are maximum rate, growth rate and lag phase	MiFe
19. Sorption = $K_{ad} * DOC * (q_{max} - C_{MAOM})$ Desorption = $K_{des} * C_{MAOM}$	The availability of sorption sites limits the sorption rate Langmuir isotherm	COMISSION

**Table 2**  
*Continued*

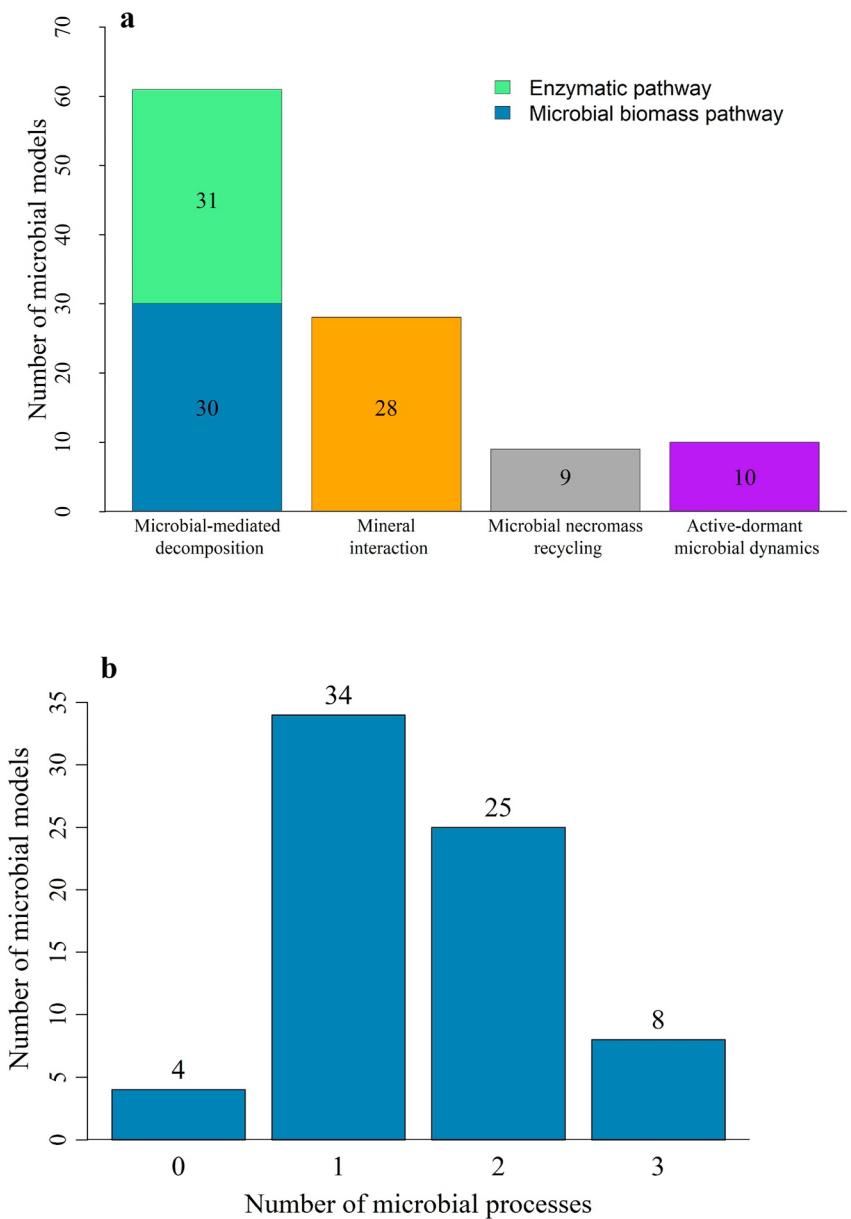
Equations	Ecological description	Models
20. $C_{\text{net\_sorption}} = \text{SOC} * f(\text{clay}) - \frac{C_p}{\tau}$	The rate of protected C formation is proportional to the amount of unprotected C pool. $\tau$ is the residence time of protected C.	CORPSE
21. Sorption = $K_{\text{ads}} * \text{SOC}_{\text{ac}}$ Desorption = $K_{\text{des}} * \text{SOC}_{\text{in}}$	$\text{SOC}_{\text{ac}}$ and $\text{SOC}_{\text{in}}$ are accessible and inaccessible SOC	C-Stability
22. $C_{\text{MAOM}} = (1 - f_{\text{BNF}}) * k_B * M$ $+ k * C_{\text{DN}} - R * K_{\text{NF}} * C_{\text{MAOM}}$	$k$ is the decomposition rate of microbes derived DOC ( $C_{\text{DN}}$ ) $R$ is the ratio of decomposition rate of $C_{\text{MAOM}}$ to fast pool of microbial necromass	FOND
23. Sorption = $K_{\text{ads}} * \text{DOC} * e^{-\frac{Ea}{R} \left( \frac{1}{T} - \frac{1}{T_{\text{ref}}} \right) * \frac{W}{dz}} * Q_{\text{max}}$ Desorption = $K_{\text{des}} * e^{-\frac{Ea}{R} \left( \frac{1}{T} - \frac{1}{T_{\text{ref}}} \right) * \frac{W}{dz}} * C_{\text{MAOM}}$	$dz$ is soil depth Langmuir isotherm	JSM
24. Net Sorption = $\text{DOC} * \left( \frac{\frac{(K * Q_{\text{max}} * \text{DOC}) - C_{\text{MAOM}}}{1 + (K * \text{DOC})}}{Q_{\text{max}}} \right)$	Sorption and desorption are not simulated separately, $Q_{\text{max}}$ maximum sorption capacity, Langmuir isotherm	MEMS v1.0
25. Sorption = $K_{\text{ads}} * \left( 1 - \frac{Q}{Q_{\text{max}}} \right) * \text{DOC}$ Desorption = $K_{\text{des}} * \left( \frac{Q}{Q_{\text{max}}} \right)$	$Q$ is adsorbed phase of DOC $K_{\text{ads}}$ and $K_{\text{des}}$ are sorption and desorption rate	MEND; MEND_dor; TRIPLEX_Microbe
26. Sorption = $\text{DOC} * \left( \frac{\frac{K_{\text{lm}} * Q_{\text{max}} * \text{DOC}}{1 + (K_{\text{lm}} * \text{DOC})} - C_{\text{MAOM}}}{Q_{\text{max}}} \right) f(T, W)$ $+ k_m * M * f(T, W) + k_b * f(T, W) (1 - p_a) *$ Desorption = $V_{\text{ma}} * \frac{C_{\text{MAOM}}}{K + C_{\text{MAOM}}} \left( 1 - \frac{C_{\text{aggregate}}}{A_{\text{max}}} \right) f(T, W)$ $K_{\text{lm}} = 10^{(-0.186\text{pH}-0.216)}$ $Q_{\text{max}} = \text{BD} 10^{(c_1 \log(\% \text{logclay}) + c_2)}$	$K_{\text{lm}}$ is binding affinity $Q_{\text{max}}$ is maximum sorption capacity $BD$ is bulk density $L$ is LMWC $A_{\text{max}}$ 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

**Table 2**  
*Continued*

Equations	Ecological description	Models
27. $\text{Sorption} = K_{\text{lm}} * \text{DOC} * \left(1 - \frac{C_{\text{MAOM}}}{Q_{\text{max}}}\right) f(W)$ $+ p_b k_{bd} * M^2 + (1 - p_a) k_b * C_{\text{aggregate}} * F(W)$ $\text{Desorption} = K_{\text{ld}} \frac{C_{\text{MAOM}}}{Q_{\text{max}}} + (1 - p_a) k_{\text{ma}} C_{\text{MAOM}} f(W)$ $K_{\text{lm}} = e^{-p_1 \text{pH} - p_2}$ $K_{\text{ld}} = e^{-p_3 \text{pH} - p_4}$ $Q_{\text{max}} = \text{depth} * \text{BD} \% \text{clay} \text{silt} * p_c$	$K_{\text{lm}}$ is the binding affinity $\% \text{clay} \text{silt}$ is the clay and silt content in percent and a coefficient ( $p_c$ ) $K_{\text{ld}}$ is desorption coefficient $\text{Depth}$ is site-level sampling depth in m $k_{\text{ma}}$ is the aggregate formation rate from MAOM $p_a$ is the proportion of aggregate C allocated to POM $\text{Langmuir isotherm}$	Millennial V2
28. $\text{Sorption} = f_1 * \text{Input} + f_2 * M$ $\text{Desorption} = 1.5 * 10^{-5} * k_d * e^{-1.5 * f_{\text{clay}}}$	$k_d$ is the coefficient of desorption rate	MIMICS, MIMICS-2 MIMICS-CN v1.0
29. $\text{Sorption} = f_1 * \text{Input} + f_2 * M$ $\text{Desorption} = 1.5 * 10^{-5} * k_d * e^{-1.5 * f_{\text{clay}}} * e^{k_{dp} * C_{\text{MAOM}}}$	$K_{dp}$ is the coefficient for tuning the relationship between the desorption and $C_p$ pool.	MIMICS-D
30. $\text{Sorption} = f_1 * \text{Input} + f_2 * M$ $\text{Desorption} = 1.5 * 10^{-5} * k_d * e^{-1.5 * f_{\text{clay}}} * e^{k_{dp} * C_{\text{MAOM}}} * e^{k_{bs} * BS}$	$k_{bs}$ is the coefficient of soil base saturation impact on desorption	MIMICS-DB
31. $C_{\text{net\_sorption}} = (1 - f_{\text{BNF}}) * k_B * M - R * \frac{V_{\text{max}} * M * C_{\text{MAOM}}}{K_M + C_{\text{MAOM}}}$	$f_{\text{BNF}}$ 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 $C_{\text{MAOM}}$ to fast pool of microbial necromass	MIND
32. $\text{Sorption} = K_{\text{ads}} * \text{DOC} * e^{-\frac{Ea_{\text{ads}}}{R} \left( \frac{1}{T} - \frac{1}{T_{\text{ref}}} \right)} * \left(1 - \frac{C_{\text{MAOM}}}{Q_{\text{max}}} \right)$ $\text{Desorption} = K_{\text{des}} * e^{-\frac{Ea_{\text{des}}}{R} \left( \frac{1}{T} - \frac{1}{T_{\text{ref}}} \right)} * \left( \frac{C_{\text{MAOM}}}{Q_{\text{max}}} \right)$	Function of temperature Arrhenius equation	ORCHIMIC v1.0; ORCHIMIC v2.0
33. $Q_{\text{max}} = \frac{x}{m} = k * C^{1/n}$	X is grams of OM adsorbed, m is weight of soil, k is sorption constant, C is DOC	Phoenix
34. $\text{Sorption} = f_{\text{sorb}} * k * \text{DOC}$ $\text{Desorption} = f_{\text{desorb}} * C_{\text{MAOM}}$	$f_{\text{sorb}}$ is the sorption coefficient, k is the rate constant for the combined processes of microbial uptake and sorption	SOMic v1.0
35. $V_{\text{max},N} * C_N * \frac{M/C_N}{K_m + M} * f(W)$	$C_N$ is microbial necromass C	CORPSE
36. $k^{\text{CR}} * \chi_a * \text{CR}$	$k^{\text{CR}}$ is decay rate of cell residue (CR)	EcoSMMARTS
37. $\frac{V_{\text{max},N} * M * C_N}{K + C_N}$	$V_{\text{max},N}$ is maximum assimilation rate	MIND
38. $k_{\text{NF}} * C_{\text{NF}}$	$k_{\text{NF}}$ is the decomposition rate of microbial necromass ( $C_{\text{NF}}$ )	FOND, MOMOS

**Table 2**  
*Continued*

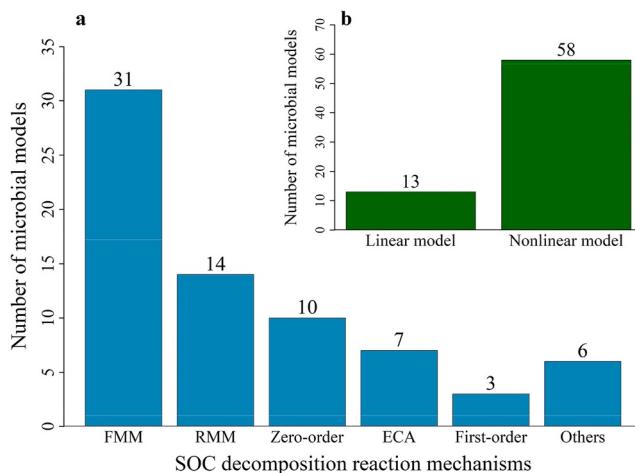
Equations	Ecological description	Models
39. $k * M * f(T, W, N)$	$F(T, W, N)$ is the function of temperature, moisture and nitrogen limitation)	GENDEC
40. $V_{\max} * M_{\text{res}} * \frac{E}{K_m + E} * f(T, W)$	$M_{\text{res}}$ is the microbial residues	JSM
41. $\frac{V_{\max} * N * E * C_N}{K + C_N}$		Kaiser
42. $R_{a-d} = k_{\text{tran}} * 1/(1 + \left(\frac{Se_{\text{sample}}}{Se_{\text{half}}}\right)^b) * B_a$ $R_{d-a} = k_{\text{tran}} * 1/(1 + a * \left(\frac{Se_{\text{half}}}{Se_{\text{sample}}}\right)^b) * B_d$	$k_{\text{tran}}$ is the maximum transition rate constant, $Se_{\text{sample}}$ is effective moisture saturation of sample, $Se_{\text{half}}$ is the saturation at which $R$ equals $0.5 * K_{\text{tran}}$ . $B_a$ and $B_d$ are active and dormant microbes, respectively.	DORMANCY 2.0
43. $R_{a-d} = k_i * (1 - \chi_a \xi_c) * B_a$ $R_{d-a} = k_d * \Gamma_m * \xi_c * B_d$	$k_i$ and $k_d$ are the maximum specific cell activation and deactivation rates. $\chi_a$ is the coefficient of water stress, $\xi_c$ is the saturation coefficient of DOC, $\Gamma_m$ is the coefficient of drought-legacy on microbes.	EcoSMMARTS
44. $\begin{cases} S_{\text{MBC}} = B_d \cdot \frac{dW}{dt} & \text{when } \frac{dW}{dt} > 0 \\ S_{\text{MBC}} = (B_a + B_{\text{MBC}_{WP}}) \cdot \frac{dW}{dt} & \text{when } \frac{dW}{dt} < 0 \end{cases}$	$S_{\text{MBC}}$ is microbial biomass transformation rate due to water content, $C_{\text{MBC}_{WP}}$ is potential active microbial biomass, respectively.	MESDM
45. $R_{a-d} = \left[1 - \frac{\text{DOC}}{(K_D + \text{DOC})}\right] * m_R * B_a$ $R_{d-a} = \left[\frac{\text{DOC}}{(K_D + \text{DOC})}\right] * m_R * B_d$	$m_R$ is the specific maintenance rate of $B_a$	ORCHIMIC v1.0; ORCHIMIC v2.0; MEND_dor; TRIPLEX_Microbe
46. $R_{a-d} = (1 - \phi) * m_R * Q_{10M}^{\frac{\text{temp}-15}{10}} * B_a$ $R_{d-a} = \phi * m_R * Q_{10M}^{\frac{\text{temp}-15}{10}} * B_d$	$\phi$ is the directly accessible substrate for microbial assimilation	DORMANCY; MIC-TEM-dormancy



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

biomass as a decomposer of SOC (Figure 2a). However, it should be noted that our study is not solely centered on the microbial models that represent microbial biomass as a decomposer of SOC. As a result, in the remaining 10 models, although they simulate a distinct microbial biomass pool, the microbial biomass is not explicitly represented as a decomposer; instead, it functions as a substrate pool (see Section 3.1.1). Among the 71 microbial models, 28 models regulate the availability of SOC for decomposition by explicitly simulating SOC interaction with the mineral surface (mineral interaction). Herein, microbial necromass recycling, simulated by 9 out of 71 models, refers to the formation of a microbial necromass pool resulting from the death of microbes. This pool follows a decomposition rate different from those other SOC pools. On the other hand, active-dormant dynamics (simulated by 10 out of 71 models) describe simultaneous changes in the physiology of microbial biomass in response to environmental stress (Figure 2a).

We noted that an individual model may not simulate all these four microbial processes. Instead, almost half of the models (48%) simulate only one microbial process, with microbial-mediated decomposition being the most



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

biomass-mediated decomposition (Figure 2a; Table 1). 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).

In contrast, there is no such an ENZ pool in microbial biomass-mediated decomposition models. 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 the model structures and the process representations (Figure 2a).

Further, we classified the microbial-mediated decomposition of SOC into six types based on the equations used: (a) zero-order, (b) first-order, (c) Forward Michaelis-Menten (FMM), (d) Reverse Michaelis-Menten (RMM), (e) Equilibrium Chemistry Approximation (ECA), or (f) Other (Figure 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 (Figure 3b; Table 1).

### 3.1.1. Zero-Order Microbial Model

In the zero-order microbial model, SOC decomposition is not a function of microbial biomass, although the model simulates a discrete microbial biomass pool. Instead, microbial biomass is only incorporated in the model to represent a highly decomposable C pool that has a fast turnover rate. Hence, the formulation is termed zero-order with respect to microbial biomass, emphasizing the independence of SOC decomposition from microbial biomass. SOC decomposition may be a function of the 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 71 models we reviewed, 10 models simulate microbial biomass as one (e.g., FOND, GENDEC, LIDEL, MEMS v1.0, MOMOS, RothC, and 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

commonly simulated process, followed by microbial necromass recycling and mineral interaction (see Table 1). About 35% of models simulate two microbial processes simultaneously, and the most common combinations of the processes simulated are microbial-mediated decomposition paired with either mineral interaction or active-dormant microbial dynamics (Figure 2b; Table 1). In this section, we focus on the detailed analyses of these four microbial processes incorporated into most microbial models.

### 3.1. Microbial-Mediated Decomposition of SOC

Microbial-mediated decomposition is a critical process in the soil C cycle because it is the primary pathway through which  $\text{CO}_2$  fixed by plants is returned to the atmosphere (X. Zhang et al., 2022). Therefore, microbial models have taken diverse approaches to represent the decomposition process (Figure 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  $\text{CO}_2$  through respiration (Sinsabaugh et al., 2008; X. Zhang et al., 2022). Two pathways are used to represent the decomposition of SOC: enzymatic-mediated and microbial

model) of the SOC pool (Figure 3a). However, the microbial component is 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 (Equation 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 decomposition coefficients of difference C pools that determine the apparent decomposition rate (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, which may alter SOC decomposition (Fang et al., 2005).

### 3.1.2. First-Order Microbial Model

In the first-order microbial models, the decomposition of SOC depends linearly on the size of the microbial biomass pool (Equation 1 in Table 2). Only 3 of the 71 microbial models (Barot, Blagodatsky, and SYMPHONY models) used first-order kinetics for microbial biomass (Figure 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 Blagodatsky and SYMPHONY models (Blagodatsky et al., 2010; Fontaine & Barot, 2005; Perveen et al., 2014). These models consider that the decomposition of recalcitrant SOC is limited by the ENZs instead of the quantity of substrate and assume 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 (Equation 1 in Table 2), resulting in first-order kinetics with respect to the microbial biomass.

### 3.1.3. Forward Michaelis-Menten

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. The tight coupling between the substrate and biological processes is necessary, in particular, when modeling short-term C and N dynamics (Blagodatsky et al., 1998), even it might also be relevant in medium-term (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, that is, the decomposition rate saturates as the substrate available for decomposition rises (Wieder, Allison, et al., 2015). In FMM kinetics, the SOC decomposition rate varies linearly with the microbial biomass (or enzyme pool) and nonlinearly with the substrate. Currently, the representation of SOC decomposition in microbial models is dominated by FMM kinetics: 31 out of 71 microbial models (~44%) used the FMM kinetics for SOC decomposition (Equations 2–6 in Table 2).

### 3.1.4. Reverse Michaelis-Menten

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 (a) the size of the SOC pool is sufficiently large such that the amount of ENZ (or microbial biomass), rather than the substrate, is the rate-limiting factor for SOC decomposition, (b) the maximum binding capacity of enzymes is proportional to the concentration of the substrate, and (c) the resulting decomposition rate is proportional to the amount of bound enzyme (Moorhead & Weintraub, 2018; Schimel & Weintraub, 2003). The Averill model, CMAX framework, COMISSION, EC1, EC2, EcoSMMARTS, EAZY, JSM, Manzoni, Millennial v2.0, MIMICS-2, NCSOIL, Schimel model, and SOMic v1.0 models have all adopted RMM kinetics for the SOC decomposition (Tables 2). However, some of these models, such as the CMAX framework, COMISSION, CORPSE, JSM, Manzoni, Millennial v2.0, MIMICS-2, NCSOIL, and SOMic v1.0, do not separately simulate the ENZ pool 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 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,  $S$  is the substrate, and  $E$  is the ENZ concentration.

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

It should be noted that the decomposition rate in Equation 2 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 Equation 2 is reduced to RMM (Tang & Riley, 2013). ReSOM and its subsequent versions, DAMM-MCNiP and ORCHIMIC v1.0, used the ECA mechanism (Equations 7, 13–14 in Table 2).

### 3.1.6. Other Mechanisms

Although the mechanisms mentioned above are the most commonly used in microbial models, some alternative mechanisms have been used in some instances. For example, CORPSE, Phoenix, and SOMKO models use microbial density-dependent SOC decomposition and assume that the high ratio of microbial C to structural C slows down the activity of microbes because of increased competition among microbes for nutrients and space (Gignoux et al., 2001; McGill et al., 1981) or that decomposition rate does not increase with further increase in microbial biomass due to substrate limitation (Sulman et al., 2014) (Equations 12, 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, and with the decomposition of SOC varying linearly with both microbial biomass and substrate (Equation 17 in 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 capture the observed nonlinear patterns of lignin decomposition (W. Huang et al., 2019) well. 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 the observed  $\text{CO}_2$  release from lignin decomposition than models assuming either first-order or FMM (Equation 18 in Table 2).

## 3.2. Mineral Interaction

SOC interaction with mineral surfaces is a critical process for the stabilization of SOC because plant-derived 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 (Y. 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-mediated 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., 2007, 2015; 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, 28 out of 71 microbial models explicitly represent the mineral interaction with SOC (Figure 2a; Table 1). However, not all of these 28 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, that is, C is transferred from MAOM to DOC (Equations 20, 22, 24, 31 in Table 2).

Environmental and biotic controls on sorption vary 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 depends on the amount of DOC available, the availability of sorption sites, and the sorption capacity (Equations 19–34 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, and ORCHIMIC (v1.0 and v2.0) introduced temperature modifiers for the sorption process (Equations 23, 26, 32 in Table 2). Only JSM and Millennial (both versions) models simulated the effect of soil moisture on the sorption process (Equations 23, 26–27 in Table 2). In most of the microbial models that simulate mineral interaction, particulate organic carbon (POC) and DOC compete for the mineral surfaces. However, in some microbial models, such as FOND, Millennial (both versions), MIMICS (v1–4), and MIND, microbial necromass also competes for the mineral surfaces (Equations 22, 26–31 in Table 2).

Environmental and biotic controls on desorption also vary among models but in less complex ways than their controls on sorption. Microbial models such as COMISSION, JSM, MEND, MEND\_dor, Millennial (both versions), MIMICS(v1–v6), MIND, ORCHIMIC (v1.0 and v2.0), and SOMic v1.0 explicitly represented the desorption process (Equations 19, 23, 25–30, 32, 34 in Table 2). The desorption mainly depends on the amount of C sorbed to the mineral surfaces and  $Q_{\max}$ . However, some models modulate the desorption process by adding temperature (JSM, Millennial, and ORCHIMIC (v1.0 and v2.0) or moisture functions (JSM, Millennial, and Millennial v2.0).

### 3.3. Microbial Necromass Recycling

Although the microbial models reviewed in this study consider the carbon pool of microbial biomass separately and simulate microbial decay (mortality) as a first-order process, most microbial models reviewed do not explicitly represent the microbial necromass pool with a different decomposition rate from plant residue.

The microbial necromass pool mainly consists of microbially derived SOC, such as dead microbes and extracellular compounds released from the dead microbes, that has a faster decomposition rate than the plant residues (Y. Huang et al., 2018). For example, in the MIND model, a separate microbial necromass pool is simulated with a different decomposition rate from plant residue. In contrast, in a model such as the Millennial model, a fraction of microbial necromass and plant residues (such as root exudates and leaf leachate) enter into the same C pool, that is, low molecular weight carbon, which follows the same decomposition pattern (Abramoff 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) (X. 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 derived 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 (<5% 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 (a) 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), (b) the chemical composition of microbial necromass is not labile, (c) 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 previous studies, the contribution of microbial necromass to SOC can range from 24% to 80% of SOC (Khan et al., 2016; Liang & Balser, 2011; Liang et al., 2019; 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 9 out of 71 microbial models, including CORPSE, EcoSMMARTS, FOND, GENDEC, JSM, Kaiser, LIDEL, MIND, and MOMOS, explicitly represent a separate microbial necromass pool under the assumption that the decomposition of microbial necromass is similar among different microbial groups, but different from that of plant residues. However, the mechanistic representation of microbial necromass in a microbial model still poses some challenges 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 physiological state: 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, 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; G. S. Wang et al., 2014).

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 (G. S. Wang et al., 2014). In microbial models, generally, there are two methods used to depict physiological states (G. S. Wang et al., 2014): 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). Similarly, only 0.02%–19.1% and 9.2%–24.2% of total microbial biomass are in active states in the subkurgan paleosols 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 inaccurate estimates of total live microbial biomass, leading to inaccuracies in model parameterization and forecasts of SOC (G. S. Wang et al., 2014).

In our review, only 10 out of 71 models explicitly simulate microbial transformation between active and dormant states (Brangarí et al., 2020; Gignoux et al., 2001; He et al., 2015; Y. Huang et al., 2018; Y. Huang et al., 2021; Liu et al., 2019; G. S. Wang et al., 2015; K. Wang et al., 2017; Zha & Zhuang, 2020; X. Zhang et al., 2022; Table 1). SOMKO is 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 (G. S. Wang et al., 2014) into the MEND model (Wang et al., 2013). Following G. S. 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: (a) the dormancy ( $B_{a \rightarrow d}$ ) and reactivation rates ( $B_{d \rightarrow a}$ ) are proportional to the active and dormant biomass pool sizes, respectively; (b) when substrate concentration is very high,  $B_{a \rightarrow d} \rightarrow 0$  and  $B_{d \rightarrow a} \geq 0$ ; (c) when substrate concentration is very low,  $B_{a \rightarrow d} \geq 0$  and  $B_{d \rightarrow a} \rightarrow 0$ ; and (d) 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; G. S. Wang et al., 2014). 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; X. Zhang et al., 2022).

#### 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 71 models we reviewed, 41 include temperature, 26 include soil moisture, and 7 include pH.

*Temperature.* In the microbial models, the temperature dependency of microbial processes was simulated using four mathematical functions: (a)  $Q_{10}$  functions, (b) Arrhenius functions, (c) Generalized Poisson function, and (d) 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 (X. Zhang et al., 2014). Only the SOMic v1.0 model was found to use a Generalized Poisson function, which is taken from the CENTURY model, 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). In addition, only the Millennial model uses the arctangent function, the temperature response function from the DAYCENT model, which predicts a decline in temperature sensitivity with increasing temperature (Abramoff et al., 2018).

*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,

**Table 3**  
*Environmental Control on Microbial Processes*

Model	Temperature	Moisture	pH	Note
DORMANCY	$Q_{10}^{(T-15)}/10$	$\phi = \frac{SolubleC * dLiq * \theta^3}{K_s + SolubleC * dLiq * \theta^3}$	N/A	$\phi$ is the directly accessible SOC used for dormancy; $dLiq$ is diffusion coefficient of substrate
EcoSMMARTS	N/A	$\chi_t = \left( \frac{\theta_w}{\theta_s} \right)^{\gamma_t}$ $\chi_a = \frac{1}{\theta_w + \theta_0} \exp \left( \frac{2 \ln(\theta_w - \theta_0) - \left[ \ln \left( \frac{(\theta_w - \theta_0)}{0.5 \theta_f c - \theta_0} \right) \right]^2}{2} \right)$	N/A	$\chi_t$ and $\chi_a$ are coefficients of tortuosity and water-stress, respectively
MEMS v1.0	$Q_{10} = 2, T_{ref} = 13.5\text{ C}$	N/A	N/A	
GENDEC	$2 < Q_{10} > 3$ $T_{ref} = 25\text{ C}$	$\alpha - \mu \log(-\Psi)$	N/A	$\alpha$ and $\mu$ are intercept and slope of soil moisture effect on decay rate, $\Psi$ is soil water potential
MOMOS	$Q_{10}^{(T-T_{opt})}/10$	$a + b \theta / \text{WHC}$	N/A	Moisture correction factor ( $f(\theta)$ ) 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); Schimel model ( $f(T)$ only)	$f(T) = e^{\frac{-Ea}{R} \left( \frac{1}{T} - \frac{1}{T_{ref}} \right)}$ $T_{ref} = 285.15\text{ K}$	$\max [0.25, \min (1, -1.1 * \theta^2 + 2.4 * \theta - 0.29)]$	$f = \frac{-(\text{pH} - \text{pH}_{\text{opt}})^2}{(\text{pH}) = e^{-\frac{\text{pH}_{\text{sen}}^2}{R}}}$ $\text{pH}_{\text{opt}} = 6$ $\text{pH}_{\text{sen}} = 1.66$	$R$ is ideal gas constant, $\Theta$ is soil moisture (%), $\text{pH}_{\text{opt}}$ is optimal pH for substrate decomposition $\text{pH}_{\text{sen}}$ is the sensitivity parameter of substrate decomposition
SOCRATES	$Q_{10}$ Temp factor, $TF = 0.177e^{(0.069T)}$	$0.0598 * \text{MAP}^{0.279}$	N/A	$T$ is mean annual air temperature (C)
MySCaN	$e^{(3.36 * \frac{(T-40)}{(T+31.79)})}$	N/A	N/A	Temperature response: Arrhenius function
ReSOM	$K_{EQ}(T) = K(T_0) e^{\left[ \frac{-\Delta G_{EQ}}{R} \left( \frac{1}{T} - \frac{1}{T_0} \right) \right]}$ $K_{NEQ}(T) = K_{NEQ}(T_0) \frac{T}{T_0} e^{\left[ \frac{-\Delta G_{EQ}}{R} \left( \frac{1}{T} - \frac{1}{T_0} \right) \right]}$ $f_{act} = \frac{1}{1 + e^{\left( \frac{-n\Delta G_E}{RT} \right)}}$	N/A	N/A	$K_{EQ}$ is temperature-dependent equilibrium reactions; $K_{NEQ}$ is temperature dependent nonequilibrium reactions; $f_{act}$ temperature dependent fraction of active enzyme ReSOM vTN: $K_{EQ} = 0$ ReSOM vTD: In eq $K_{EQ}(T), \Delta G_{EQ} = -20\text{ kJ/mol}$ ReSOM vTI: In eq $K_{EQ}(T), \Delta G_{EQ} = 20\text{ kJ/mol}$
DAMM-MCNiP	$e^{\frac{-Ea}{RT}}$	$\text{SOC} * \text{Frac} * dLiq * \theta^3$	N/A	Frac and $dLiq$ are the fraction and diffusion coefficient of unprotected SOC, respectively; $\theta$ is volumetric water content

**Table 3**  
*Continued*

Model	Temperature	Moisture	pH	Note
DEMENT (f(T) only); Ecosys	$f(T) = e^{\frac{-Ea}{RT}}$	$f(w) = \frac{w}{c+w}$	N/A	Arrhenius equation for temperature response variable. w and c are percent water content on a dry weight basis and at which microbial activity is at half its optimal value, respectively.
CORPSE	$e^{\frac{-Ea}{RT}}$	$(\theta/\theta_{sat})^3(1 - \theta/\theta_{sat})^{2.5}$	N/A	
Millennial	$\frac{t_2 + \frac{t_3}{\pi} \tan[\pi(T-t_1)]}{t_2 + \frac{t_3}{\pi} \tan[\pi t_4(T_{ref}-t_1)]}$	$\frac{1}{1+w_1 e^{(-w_2 RWC)}}$	$10^{(-0.186pH-0.216)}$	$t_1$ and $t_2$ are x-axis and y-axis locations of the inflection point (°C), respectively, $t_3$ is the distance from maximum to minimum point and $t_4$ is the slope 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 °C)
Millennial v2.0	$a_x e^{-\frac{Ea}{R(T+273.15)}}$	$\left(\frac{\theta}{\varphi}\right)^{0.5}$	$K_{lm} = e^{-p1pH-p2} K_{ld}$	$K_{lm}$ and $K_{ld}$ are binding affinity and desorption coefficient, $p1$ and $p2$ are sorption coefficient, $\theta$ is volumetric water content, $\varphi$ is matric potential, Arrhenius equation
CMAX framework	$f(T) = \begin{cases} 0, & T \leq T_{s_{min}} \\ \frac{T-T_{s_{ref}}}{Q_{10s}^{10}}, & T > T_{s_{min}} \end{cases}$	$A = \frac{\log\left(\frac{M_{min}}{M}\right)}{\log\left(\frac{M_{min}}{M_{max}}\right)}$ $1, M_{min} \leq M \leq M_{max}$	N/A	$T_{s_{min}}$ and $T_{s_{ref}}$ are minimum and reference temperatures for the substrate decomposition. $M_{min}$ and $M_{max}$ are the minimum and maximum moisture for substrate decomposition
CLM-Microbe; Enzyme-driven model; German; He model; MIC-TEM-Zha; Hagerty; MESDM; DAMM; SCAMPS	$V_{max} = V_{max0} * e^{\left(-\frac{Ea}{R*(temp+273)}\right)}$ $K_m = K_{mslope} * temp + K_{m0}$	N/A	N/A	Arrhenius equation
MIC-TEM-Hao	$V_{max} = V_{max0} * e^{\left(-\frac{Ea}{R*(temp+273)}\right)}$ $K_m = K_{mslope} * temp + K_{mod}$	DOC*dLiq*θ³	N/A	DOC is dissolved organic carbon
MIMICS; MIMICS-2; MIMICS-CN v1.0; MIMICS-D; MIMICS-DB; MIMICS-DBT	$V_{max} = e^{(V_{slope}*T+V_{int})} * a_v * V_{mod}$ $K = e^{(K_{slope}*T+V_{int})} * a_k * k_{mod}$	$(\theta/\theta_{sat})^3(1 - \theta/\theta_{sat})^{2.5}$	N/A	Arrhenius equation. Only MIMICS-2 uses moisture scalar

**Table 3**  
*Continued*

Model	Temperature	Moisture	pH	Note
JSM	$f(T, W) = e^{-\frac{E_a}{R} \left( \frac{1}{T} - \frac{1}{T_{ref}} \right)} * \frac{\theta}{\theta_{f_c}}$	N/A	N/A	Arrhenius equation
DecoBio v1.0:MIC-ITEM-DORMANCY	$Q_{10}^{\frac{T-15}{4791}}$	N/A	N/A	
RothC	$\frac{106.06}{1+e^{(T+18.27)}}$	$(-20 + 1.3 (\%clay) - 0.01 (\%clay)^2)$	N/A	
SOMIC v1.0	$f(T) = f_i \left( \frac{T_{max}-T}{T_{max}-T_{opt}} \right)^2 e^{0.2 \left( 1 - \left( \frac{T_{max}-T}{T_{max}-T_{opt}} \right)^{2.63} \right)}$ $f_i = 4.99$ $T_{max} = 45^{\circ}\text{C}$ $T_{opt} = 35^{\circ}\text{C}$	If $\text{and} > 0.444 \text{max\_md}$ , $\theta = 1.0$ If $\text{and} \leq 0.444 \text{max\_md}$ $\theta = 0.2 + 0.8 \frac{\text{max\_md}}{0.556 \text{max\_md}}$	N/A	Max_md is maximum possible soil moisture deficitGeneral Poisson function for temperature modifier
	EC1, EC2	$\frac{\text{WHC}}{60\%}$	N/A	Temperature was kept constant during laboratory incubation experiment; Water Holding Capacity (WHC)

diffusion is constrained by thin and discontinuous water films (Abramoff et al., 2017; Abs & Ferrière, 2020; Sihi et al., 2018). Diverse 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 consider the effect of soil pH on microbial processes. 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).

## 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 in most ESMs (Woolf & Lehmann, 2019). Moreover, the microbial models were intended to represent the SOC dynamics better than the conventional SOC model (Y. P. Wang et al., 2014) 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, such as the lack of experimental evidence for the rate-limitation processes, the lack of observational data to constrain model parameters, and the spin-up problem in microbial models, which will be discussed in this section. Finally, we finish it by providing some recommendations for future model improvements.

### 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 reported 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 limit 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; X. 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 (G. S. Wang et al., 2013). In addition, observational data of pool size is critical to constrain rate processes (T. Xu et al., 2006). However, the inability to simultaneously measure active, dormant, and dead microbial biomass in situ (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., 2013; Wieder, Allison, et al., 2015; Wieder, Grandy, et al., 2015) or assumed by the researchers (G. S. Wang et al., 2013). While laboratory data provide valuable insights into microbial processes under controlled conditions and help to constrain model parameters, challenges remain in understanding the effects of real-world environmental conditions or land management practices on the parameters related to microbial processes. As model parameterization is one of the three elements toward realistic model predictions (Luo & Schuur, 2020), the research community needs to collect observational data for estimating model parameters.

### 5.3. The Spin-Up Problem in Microbial Models

Setting up initial values of all C pools is crucial before a model can be used for any analyses (Xia et al., 2012). These initial values can be estimated based on observations (Luo & Reynolds, 1999) or assumed to be at a steady state. The steady state is usually achieved by spin-up methods that perform long model simulations for a long time until there is no trend of change in pool sizes over multiple years of repeated climate forcing (M. Shi et al., 2013). Several spin-up approaches have been used, including accelerated decomposition, native dynamics, and semi-analytical steady-state solutions. Attaining a steady state is computationally expensive, particularly for global model simulations and when integrating more biogeochemical processes (Thornton & Rosenbloom, 2005), and these approaches have yet to be tested on microbial models. Recently, an analytical steady-state solution has been developed and applied to microbial models to substantially reduce the computation cost of spin-up (Georgiou et al., 2017; Tao et al., 2023).

### 5.4. 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 contribute to a better-constrained model (Keenan et al., 2013; Richardson et al., 2010). Additionally, to achieve reliable predictions of SOC dynamics, it is crucial to validate models against independently collected long-term time-series datasets (Le Noë et al., 2023). This approach could help optimize the accuracy and reliability of model predictions. Thus, coordinated efforts between modelers and empiricists can return data maximally useful to constrain a model. 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 complexity reduction techniques that can simplify complex models without the loss of key model processes or the ability to integrate empirical data. Some commonly used model complexity reduction techniques include conversation analysis, nondimensionalization, 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 data set (Marschmann et al., 2019).

## 6. Summary

During the past three decades, SOC models have increasingly considered microbial controls on C cycling. Although the first microbial model was developed in the 1970s, our review shows that the majority of microbial

models were developed after 2000, likely in sync with the accelerated innovation of molecular techniques to study soil microbes. Most microbial models incorporated one or more of four microbial processes: microbial-mediated decomposition, mineral interactions, microbial necromass recycling, and active and dormant microbial dynamics. Among the four processes, microbial necromass recycling and dormancy were the least studied. The 71 microbial models reviewed mostly incorporated the three major environmental factors: soil temperature, moisture, and pH on the sorption capacity of minerals and/or SOC availability to microbes.

The diversity in mathematical equations and parameterization implies the presence of challenges in translating the theoretical understanding of microbial processes into models. Alternative to the approaches primarily based on conceptual and theoretical understanding, microbial models and their parameterization can be directly derived from experimental data (i.e., data-driven modeling approach). For example, the microbial-iron (MiFe) interactive model was developed from laboratory soil incubation data sets by testing three alternative model structures and parameter estimation with data assimilation (Liao et al., 2022). Future development of microbial models could benefit from coordinated research between modelers and empiricists to use empirical data to constrain the model structure and parameters and use models to guide experimental studies. Moreover, future research may employ statistically rigorous methods, such as data assimilation, to improve the model performance by optimizing parameterization and selecting alternative model structures.

## Data Availability Statement

No data were used in producing this manuscript; materials in the figures and tables are properly cited and referred to in the reference list.

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