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1 Soil Microbiology, Ecology and Biochemistry, Fifth Edition

2

3 **Chapter 16. Advancing Quantitative Models of Soil Microbiology, Ecology, and Biochemistry**

4

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6

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18 **Non-print items**

19

20 **ABSTRACT**

21 Rapid advances in soil biology are increasingly reflected in mathematical models. From
22 molecular to global scales, models contribute to fundamental understanding and prediction of
23 critical soil processes, such as carbon sequestration. Recent models explicitly incorporate
24 microbial control over soil carbon and nutrient cycling, an approach that offers greater
25 biological realism but raises new challenges in model parameterization and stability. Although
26 they have proliferated at community and ecosystem scales, microbial-explicit models have yet
27 to be incorporated into most Earth system models. Applying soil models across scales requires
28 integration with data to support parameterization and validation using approaches such as
29 Bayesian data assimilation. To catalyze future progress, we recommend breaking down barriers
30 between modeling and empirical disciplines while broadening access to the computational
31 infrastructure that supports soil biological modeling.

32

33 **KEYWORDS**

34 Bayesian data assimilation, biogeochemistry, carbon use efficiency, ecosystem, extracellular
35 enzyme, microbial decomposition, mineral stabilization, model intercomparison, model
36 validation, soil carbon

37

38 I INTRODUCTION

39 Soils host diverse biological communities, including plants, animals, and microbes. Together,
40 these communities provide benefits essential for ecosystem functioning and human well-being.
41 Decomposition of organic matter—primarily driven by microbes—regenerates nutrients that
42 support plant growth in agricultural and unmanaged systems. In turn, plant growth and
43 microbial transformations of organic matter enhance soil carbon (C) sequestration that
44 mitigates greenhouse gas emissions from human activities.

45
46 At the same time, the biological services provided by soils are vulnerable to human-caused
47 environmental change (Cavicchioli et al., 2019; Jansson and Hofmockel, 2020). For example,
48 there is concern that global warming will stimulate metabolic activity in soils, weakening C
49 sequestration and potentially turning soils into a net source of greenhouse gases (Davidson and
50 Janssens, 2006). Given these concerns, soil microbes and biological processes are topics of
51 intense research interest.

52
53 Improvements in sequencing technologies and other approaches for probing biological diversity
54 and functioning have led to rapid advances in fundamental knowledge of soil ecology (Bahram
55 et al., 2018). In parallel with these empirical advances, mathematical models of soil systems
56 have blossomed recently (Allison, 2017; Wieder et al., 2015). Foundational models of soil
57 biogeochemistry developed during the 1980s and 1990s have been joined by a new generation
58 of biologically-inspired models starting in the early 2000s. Since then, these models have
59 increased in scale and complexity.

60
61 Still, there is room for additional model improvement and intellectual development. Large-scale
62 models fail to replicate fundamental patterns in soil biogeochemical pools and fluxes (Todd-
63 Brown et al., 2014, 2013; Wu et al., 2018). Many of the most recent models with updated
64 biological mechanisms have not been tested extensively. The field of soil ecological modeling
65 has come a long way, but the pathway to addressing soil-relevant challenges with models
66 remains uncertain.

67
68 In an effort to elevate the relevance and impact of soil modeling, this chapter aims to
69 summarize the current state of the art while providing guidance for next steps to advance the
70 field. We discuss some of the main reasons for engaging in soil modeling and then review
71 selected modeling approaches from molecular to global scales. This review does not attempt to
72 be exhaustive, and we focus our attention primarily on advances from the past 5-10 years,
73 especially since the publication of Parton et al. (2015). The chapter concludes with
74 recommendations for model-data integration and future intellectual development.

75 76 II JUSTIFICATION FOR MODELING

77 As with empirical approaches, soil scientists use models to address a range of different goals
78 and questions. Models play an important role in advancing fundamental understanding of soil
79 processes by representing concepts and mechanisms in a quantitative framework. For instance,
80 the priming effect is a common biological mechanism in soil whereby addition of fresh organic
81 matter stimulates, or “primes,” the decomposition of existing soil C that may be older and more

82 resistant to decay (Fontaine et al., 2004). Soil researchers have developed models that
83 represent this mechanism, thereby quantifying the magnitude and impact of priming effects in
84 soil systems (Guenet et al., 2016).

85
86 Models are also useful for generating hypotheses. Koven et al. (2015) used a depth-resolved
87 version of the Community Land Model (CLM4.5BGC) to simulate permafrost thaw and its effects
88 on ecosystem C balance. This version of the model is notable for incorporating fundamental
89 understanding of how soil processes vary with depth, a crucial concept in frozen soils with
90 seasonal changes in active layer thickness. Moreover, CLM4.5 represents nitrogen (N) dynamics
91 which likely play into C-climate feedbacks. In response to climate warming, Koven et al.'s (2015)
92 modeling study suggested that the positive effects of N release on plant productivity and
93 associated C storage would be outweighed by the negative effects of permafrost thaw and
94 increased microbial metabolism with soil warming. This outcome is a testable hypothesis that
95 can be addressed with laboratory, field, and global change experiments (Mack et al., 2004; Xue
96 et al., 2016).

97
98 More broadly, models can help guide experimental work. A conceptual paradigm proposed by
99 Blankinship et al. (2018) calls for better integration between theory, models, and
100 measurements. This aim could be partially achieved by aligning modeled mechanisms and
101 outcomes with experimental data. For example, models of soil biogeochemistry include a wide
102 array of pools ranging from largely inert to mineral-associated organic matter and highly
103 dynamic microbial biomass. Aligning these pools with the chemical composition of real soils
104 provides a rationale for exploiting cutting-edge organic matter fractionation and
105 characterization approaches, such as NMR, X-ray microspectroscopy, and pyrolysis gas
106 chromatography-mass spectroscopy (Kalbitz et al., 2003; Lehmann et al., 2008; Quideau et al.,
107 2005). Likewise, recent advances in modeling microbial diversity can drive new approaches for
108 analyzing sequencing and other datasets that probe the functioning of microbial communities.
109 Building a model can generate practical guidelines for distilling, organizing, and processing the
110 information contained in complex 'omics datasets.

111
112 Scaling is another relevant application of soil models (Allison, 2017; Wieder et al., 2015). Nearly
113 all of the grand challenges facing soils at the global scale require knowledge of emergent
114 properties arising from smaller spatial scales and shorter time scales. At the molecular level,
115 cells exchange metabolites, enzymes catalyze reactions, and organic compounds interact with
116 mineral surfaces. At cellular to ecosystem scales, these molecular processes combine into
117 emergent biological properties such as growth and respiration. All the way up to the global
118 scale, biological systems interact with soil physical properties to determine outcomes like C and
119 nutrient balance. Modeling offers a quantitative, rational approach for representing key
120 emergent properties at ever-increasing scales. Nested sets of models can, for example, provide
121 insight on how Michaelis-Menten enzyme kinetics at the molecular level scale up to control
122 organic matter decomposition rates at the community scale (Tang and Riley, 2013; Wang and
123 Allison, 2019).

124

125 Models are also the primary tool available to scientists for making predictions, particularly in
126 the context of global environmental change (Bradford et al., 2016; Todd-Brown et al., 2012). In
127 many studies, the goal of prediction complements other modeling aims such as advancing
128 fundamental understanding, generating hypotheses, and scaling up. Although predictions
129 remain highly uncertain, soil models offer the potential to apply empirical and theoretical
130 advances to simulate C and nutrient pools at the scale of the entire planet, decades or centuries
131 into the future. Such models can provide answers to scientists and decision makers concerned
132 about the future state of soils, including the capacity to store C in the face of climate and land
133 use change (IPCC, 2019). The increasing prominence of model outputs in Intergovernmental
134 Panel on Climate Change reports and policy making emphasizes prediction as a relevant, if not
135 always singular, goal of model development.

136

137 **III MODELING APPROACHES**

138 Across scales, including the ecosystem scale, differential equation models are often applied to
139 track soil biogeochemical pools and fluxes. Sierra and Müller (2015) described a general
140 framework for this type of soil model based on first principles of mass balance, substrate
141 dependence, heterogeneity of decomposition rates, chemical transformations, variation in
142 environmental drivers, and interactions among soil pools. Nearly all existing models of soil
143 biogeochemistry fit under this general framework, allowing for rigorous comparison of stability
144 and mathematical properties across models.

145

146 Differential equation models like RothC and CENTURY emerged in the late 1970s and 1980s
147 (Jenkinson and Rayner, 1977; Parton et al., 1988), embracing the principles of mass balance and
148 substrate dependence as envisioned by Olson (1963) with organic matter decaying in
149 proportion to its concentration. These models further included the principle of heterogeneity
150 by representing different pools of organic matter with different decay rates. Transfers among
151 the pools were allowed, following the principle of chemical transformations, and decay rates
152 were functions of temperature and moisture levels, consistent with the principle of varying
153 environmental drivers. Bosatta and Ågren (1985, 1999) generalized the principle of
154 heterogeneous decomposition in their theory of continuous organic matter quality which was
155 intended to better reflect the complexity and diversity of soil organic compounds.

156

157 Models like RothC and CENTURY have some convenient mathematical properties, but they omit
158 the fundamental principle of interacting soil pools in Sierra and Müller's (2015) framework.
159 Commonly known as "linear" or "first-order," differential equation models without complex
160 dependencies among pools can be readily represented in matrix form and solved analytically
161 (Xia et al., 2013). They also tend to be mathematically stable, meaning that pool sizes and fluxes
162 do not oscillate as the system returns to steady-state following perturbation. Despite these
163 advantages, linear models simplify or omit mechanisms of interaction among organic matter
164 pools, such as enzymatic degradation driven by microbial decomposers. Rather, the biological
165 roles of microbes in linear models are assumed to be "implicit" (Schimel, 2001).

166

167 An alternative approach to account for the principle of soil pool interactions is to make
168 microbial mechanisms mathematically "explicit." The idea of microbial control over soil

169 biogeochemical processes dates back to at least Waksman (1927). In the late 1970s, O. L. Smith
170 proposed a complex model of soil microbial biogeochemistry that included many of the
171 features described by Sierra and Müller's (2015) general framework but did not receive much
172 attention (Smith, 1979a, 1979b). More recently, there has been an explosion of microbially
173 explicit model development and applications (Abramoff et al., 2018; Allison et al., 2010;
174 Fontaine and Barot, 2005; Schimel and Weintraub, 2003). Although they attempt to represent
175 biological mechanisms with higher fidelity, challenges remain with the stability, interpretability,
176 and scaling of microbially-explicit models (Wang et al., 2014). Efforts to analyze microbial
177 processes with models at different scales could help address some of these challenges (Allison,
178 2012; Kaiser et al., 2014).

179
180 Dynamical differential equation models are valuable for representing fundamental processes,
181 but predictive statistical models are a valuable alternative approach. Process-based models
182 with many differential equations require careful parameterization, otherwise they may be
183 mathematically unstable or generate inaccurate predictions. If accurate prediction is the goal,
184 rather than representing mechanisms, statistical models can be very useful, assuming sufficient
185 training data are available. Rapid development of machine learning techniques has made it
186 possible to extrapolate soil properties across time and space based on training data and
187 algorithms such as neural networks and random forest. For example, this approach has been
188 used to determine the global age of soil C based on radiocarbon profiles (Shi et al., 2020) and to
189 map soil C stocks across Scotland (Aitkenhead and Coull, 2016).

190
191 New approaches have started to combine features of process-based and probabilistic modeling.
192 Rather than representing explicit pools of C, Waring et al.'s (2020) PROMISE model tracks the
193 flow of individual C molecules through a heterogeneous soil system. Molecules undergo
194 transformations and movements based on soil parameters, proximity to microbes and
195 enzymes, and stochastic processes. In this way, molecules with different chemical properties
196 vary in transit time such that the total soil C pool contains a distribution of residence times. This
197 modeling framework requires relatively few assumptions and parameters while replicating
198 emergent properties of soil C more accurately than pool-based models. It also incorporates
199 mass balance and interactions among soil compounds, consistent with the six key principles
200 identified by Sierra and Müller (2015).

201

202 **IV MODELING ACROSS SCALES**

203 **A Cellular/Molecular**

204 Molecular interactions, both within and outside cells, underlie all soil biotic and abiotic
205 processes. Key interactions include metabolic pathways within microbial cells along with
206 sorption/desorption, enzymatic catalysis, and molecular diffusion outside of cells. Molecular-
207 scale interactions between organic molecules and soil minerals contribute to the physical
208 protection of soil organic matter (Schmidt et al., 2011), whereas extracellular enzyme activity
209 catalyzes decomposition of polymeric molecules (Burns et al., 2013). Many of these interactions
210 are represented in models at larger scales.

211

212 Metabolic pathways can be represented with flux balance models that simulate how specific
213 substrates are metabolized in microbial cells. In ¹³C metabolic flux analysis (¹³C-MFA), isotopic
214 labeling experiments provide models with information to estimate intracellular metabolic
215 fluxes. Together with ¹³C fingerprinting to pinpoint central metabolic pathways and RNA-seq to
216 complement the results of ¹³C-MFA, Varman et al. (2016) uncovered the lignin degradation
217 pathway of the bacterium *Sphingobium sp.* SYK-6. Environmental constraints and microbial
218 community interactions must also be considered when modeling microbial metabolism. Jansson
219 and Hofmockel (2018) defined the term metaphenome as the product of microbial functions
220 that are expressed given abiotic and biotic environmental constraints. Flux balance models can
221 be used to determine how microbial metaphenomes will respond to different environmental
222 conditions and perturbations.

223
224 Information on molecular mechanisms can be used to quantify and better represent emergent
225 properties in models. Carbon use efficiency (CUE) describes the proportion of C converted to
226 microbial biomass and results from a combination of multiple metabolic processes. Hagerty et
227 al. (2018) suggested modeling CUE explicitly to account for its dependence on microbial growth
228 and C allocation processes, including costs of extracellular enzyme production and substrate
229 assimilation. By representing these additional cellular processes, the accuracy of larger-scale
230 models with static CUE parameters could be improved.

231
232 Enzymes are biochemical catalysts involved in many molecular transformations that occur in
233 soil (Burns et al., 2013). Microbes secrete extracellular enzymes outside the cell to obtain
234 resources from complex biopolymers which are abundant in soils and litter. Given their role as
235 bio-catalysts targeting soil organic matter, extracellular enzyme activity represents a
236 mechanism of interaction between soil pools, namely microbial biomass and organic polymers.
237 The Michaelis-Menten equation describes this activity, which often represents the initial and
238 rate-limiting step in microbial decomposition. The Michaelis-Menten equation predicts reaction
239 velocity (dC/dt) as a function substrate concentration (C) based on two parameters: the
240 maximum velocity (V_{max}) at unlimited substrate concentration and the half-saturation constant
241 (K_M), which is the substrate concentration at $\frac{1}{2} V_{max}$:

$$242$$
$$243 \quad dC/dt = V_{max} \cdot C / (K_M + C)$$
$$244$$

245 V_{max} and K_M can be experimentally determined and used to parameterize models. German et al.
246 (2012) used experimental data on Michaelis-Menten enzyme kinetics obtained from enzyme
247 assays to build a decomposition model and determine the temperature sensitivity of
248 extracellular enzymes. They found that both V_{max} and K_M are temperature-sensitive and the
249 level of sensitivity is enzyme-specific.

250
251 Michaelis-Menten theory was extended in the Dual Arrhenius Michaelis-Menten (DAMM)
252 model (Davidson et al., 2012). DAMM represents the interaction between Arrhenius and
253 Michaelis-Menten kinetics at the scale of enzyme active sites to predict CO₂ production from
254 soil. The model accounts for temperature, moisture, and oxygen limitation effects on the
255 metabolism of soluble C substrates. Model predictions aligned well with laboratory

256 measurements of extracellular enzyme activity at different temperatures and field
257 measurements of soil respiration across seasons. DAMM was later extended to incorporate
258 microsite variation in substrate concentrations and applied to predict not only soil respiration
259 but also CH₄ and N₂O fluxes (Sihi et al., 2020).

260

261 The Reverse Michaelis Menten (RMM) and Equilibrium Chemistry Approximation (ECA)
262 equations have emerged as additional options to explicitly model enzyme kinetics (Moorhead
263 and Weintraub, 2018; Tang, 2015). The RMM equation describes the reaction velocity as a
264 function of enzyme concentration (E) where K_E is the enzyme concentration at $\frac{1}{2} V_{max}$:

265

$$266 \quad dC/dt = V_{max} \cdot E / (K_E + E)$$

267

268 This equation is a better fit for situations in which substrate available for enzyme binding is
269 limiting. Such situations may be common in soils, and therefore RMM was included in one of
270 the first microbial-explicit models of soil C and N dynamics (Weintraub and Schimel, 2003).

271

272 The ECA considers both free substrate and enzyme limitations by accounting for mass balance
273 constraints. Michaelis-Menten and RMM kinetics are special cases of the ECA (Tang, 2015):

274

$$275 \quad dC/dt = k \cdot E \cdot C / (K_{ES} + C + E)$$

276

277 where k is a rate constant, and $1/K_{ES}$ is the apparent substrate affinity of the enzyme. The ECA is
278 more widely applicable than the Michaelis-Menten and RMM due to its ability to consider a
279 wider range of substrate-to-enzyme ratios. These ratios can shift in soil systems, and the ECA
280 accounts for those changes by converging to either Michaelis-Menten or RMM kinetics (Wang
281 and Allison, 2019). However, the ECA is more complex and requires additional data for
282 parameterization, so the simpler Michaelis-Menten and RMM formulations may be better fits
283 in some environmental contexts.

284

285 **B Population**

286 As microbes consume substrates to obtain energy and nutrients, population size increases,
287 resulting in changes in substrate demand and decomposition ability. Monod growth is an
288 established model used to describe microbial growth given substrate availability (Parton et al.,
289 2015). Analogous to Michaelis-Menten kinetics, the specific growth rate (μ') is a function of
290 substrate concentration (S), where μ_{max} is the maximum potential growth rate and K_t is the
291 Monod constant, or substrate concentration at $\frac{1}{2} \mu_{max}$:

292

$$293 \quad \mu' = \mu_{max} \cdot S / (K_t + S)$$

294

295 Under the assumption that initial microbial biomass is much greater than initial substrate
296 concentration, the Monod equation can be simplified to the Michaelis-Menten equation. The
297 Monod equation does not account for density dependence, so other models such as the logistic
298 equation may be more appropriate if resources limit microbial population growth.

299

300 **C Community**

301 Moving up in scale, multiple models represent interacting populations of microbes, and many
302 of those also include physical features of the environment. Georgiou et al. (2017) found that
303 introducing density-dependent growth of microbial biomass in decomposition models of
304 varying complexity reduced divergence between model predictions and experimental
305 observations. Density-dependent growth accounts for community-level mechanisms, such as
306 competition and spatial limitations, though the exact parameterization may vary across biomes
307 and should be experimentally determined.

308

309 Multiple community-scale models have adopted trait-based approaches that focus on the
310 physiological characteristics of microbes. Analogous to some vegetation models, the Guild
311 Decomposition Model (GDM) represents three distinct microbial functional groups involved in
312 litter decomposition: opportunists that process available organic matter, decomposers that
313 break down holocellulose, and miners that degrade more chemically-resistant lignin polymers
314 (Moorhead and Sinsabaugh, 2006). The GDM is a differential equation model with explicit
315 degradation of substrate pools by the microbial functional groups following Michaelis-Menten
316 kinetics. The model also includes N which is often a limiting nutrient for fresh litter
317 decomposition. Overall, the GDM successfully simulated decomposition and successional
318 patterns consistent with observations.

319

320 The Microbial-Mineral Carbon Stabilization (MIMICS) model also represents microbial
321 functional groups along with mineral stabilization, making it suitable for application to soil
322 systems (Wieder et al., 2014). The functional groups in MIMICS distinguish r- versus K-selected
323 life histories, where r-strategists specialize on the degradation of low molecular weight
324 compounds and K-strategists process structural litter and chemically-protected compounds
325 relatively more efficiently. Like the GDM, MIMICS assumes Michaelis-Menten kinetics and
326 reproduces observed patterns, including litter decomposition rates and soil response to
327 disturbance.

328

329 Building on the idea of functional traits, other community-scale models represent interacting
330 populations and even individuals. The DEMENT model (Allison, 2012) assigns traits at random to
331 tens or hundreds of individual microbial taxa that compete and interact on a spatial grid (Fig.
332 16.1). Rather than assigning taxa to functional groups a priori, taxa with favorable trait
333 combinations for a given set of environmental conditions increase in abundance in the model
334 simulations. The model is individual-based, meaning that it tracks the locations of individual
335 cells or colonies that grow, divide, and disperse according to model assumptions and
336 parameters. DEMENT's unique structure allows for simulation of "virtual microbiome"
337 composition and functioning, including the cycling of C, N, and phosphorus. Once assigned, the
338 traits of individual taxa in DEMENT are fixed, but related models have allowed for trait
339 evolution within taxa (Allison, 2005; Folse and Allison, 2012).

340

341 [Insert Fig. 16.1 here]

342

343 Other models also represent microbial traits at the community scale. For example, an
344 individual-based model with trait-based functional groups interacting on a spatial grid predicted
345 tight cycling of N during litter decomposition, allowing the microbial community to maintain
346 CUE by overcoming stoichiometric imbalances (Kaiser et al., 2014). These findings, along with
347 applications of DEMENT (Allison, 2014), show that community-scale models are essential for
348 predicting emergent, and sometimes unexpected, properties of community functioning. At the
349 same time, challenges remain in translating genomic and physiological datasets into the trait
350 distributions required to parameterize these models.

351
352 Spatially-explicit models like DEMENT are designed to represent enzyme kinetics and microbial
353 interactions at appropriately small scales. Simulations with these models have provided insight
354 into the emergent properties of heterogeneous enzyme-substrate interactions occurring at sub-
355 micron scales, which could be useful for refining differential equation models operating at
356 larger scales (Wang and Allison, 2019). Similarly, modeling the heterogeneous spatial structure
357 of soil aggregates and associated microbial communities leads to more mechanistic prediction
358 of trace gas fluxes (Ebrahimi and Or, 2016). Like individual-based models, aggregate-based
359 models are useful for determining the scaling rules needed to incorporate heterogeneous soil
360 properties and microbial communities into larger-scale models (Wang et al., 2019).

361 362 **D Ecosystem**

363 Ecosystem-scale models of soil microbial and biological processes often include community-
364 level processes as well as inputs and outputs that interact with other ecosystem components
365 such as plants and minerals. Classical models such as RothC and CENTURY have long been
366 applied in an ecosystem context, and now microbial-explicit models are also being used at
367 ecosystem scales. Efforts to integrate these approaches are likewise gathering momentum. The
368 Millennial model combines the best of both classical and microbial-explicit models, including
369 microbial processes, mineral stabilization, aggregate dynamics, and soil pools that can actually
370 be measured (Abramoff et al., 2018).

371
372 Compared to classical ecosystem models, the techniques for developing and analyzing
373 microbial-explicit models are relatively similar. Like classical models, microbial-explicit models
374 require technical expertise to formulate differential equations that represent soil pools, fluxes,
375 and mechanisms of interest. For microbial-explicit models, those equations typically include
376 non-linear terms to represent the interaction between microbial or enzyme biomass and other
377 soil pools (Sierra and Müller, 2015). Microbial-explicit models should be evaluated for stability
378 and behavior across a range of relevant parameter values, much like classical linear models. For
379 some models, the mathematics involved in these analyses may be more complicated, especially
380 if there are no analytical solutions. However, complex microbial models can be solved
381 numerically, much like their classical counterparts. Therefore, researchers developing
382 microbial-explicit models will likely find the process familiar if they have experience with
383 classical models.

384
385 [Insert Fig. 16.2 here]
386

387 Microbial-explicit models represent key microbial traits such as CUE, microbial turnover, and
388 enzyme production that lead to different behaviors and predictions compared to microbial-
389 implicit models (Fig. 16.2). The Allison-Wallenstein-Bradford (AWB) model was proposed as a
390 relatively simple microbial-explicit model of soil C cycling at the ecosystem scale. In contrast to
391 the MIMICS model (as described in the Community section), the AWB model does not include
392 functional groups. Instead, it represents average traits of the whole microbial community, such
393 as CUE, enzyme kinetic parameters, and temperature sensitivities. Simulations with AWB
394 showed that the soil C response to 5°C warming depends on the temperature sensitivity of CUE.
395 Greater temperature sensitivity of CUE results in more stable soil C pools in response to
396 warming due to reductions in the biomass of microbial decomposers.

397
398 The Microbial-Enzyme-mediated Decomposition (MEND) model, developed by Wang et al.
399 (2013), is similar in structure to AWB but also accounts for mineral stabilization mechanisms.
400 MEND splits soil organic C (SOC) into particulate organic C (POC) and mineral-associated organic
401 C (MOC), both of which are converted into DOC via enzyme activity. DOC can adsorb onto or
402 desorb from MOC. The rate of breakdown into DOC is lower for MOC than POC, representing
403 the physical protection of soil organic matter (Schmidt et al., 2011). Still, MOC and POC respond
404 similarly to a step increase in temperature, meaning that MEND and AWB end up predicting
405 comparable SOC responses to warming.

406
407 Sulman et al. (2014) developed the Carbon, Organisms, Rhizosphere, and Protection in the Soil
408 Environment (CORPSE) model, which also explicitly represents microbes but has a somewhat
409 unique structure. Carbon in CORPSE can move between physically protected and unprotected
410 pools, but unlike in MEND, only unprotected C pools can be decomposed. Another difference
411 between CORPSE and MEND is that protected C pool sizes in CORPSE increase with clay
412 content. These differences emphasize a need for additional empirical studies that quantify
413 physical protection and the decomposition rates of protected SOC.

414
415 Soil models at the ecosystem scale differ substantially in their responses to plant C inputs.
416 Microbial-explicit models like AWB and CORPSE represent the priming effect, or increased
417 turnover of SOC in response to the addition of fresh plant C, documented in many empirical
418 studies (Bernal et al., 2016; Perveen et al., 2019). For example, Sulman et al. (2014) fitted
419 CORPSE to empirical data from free-air CO₂ enrichment experiments at Duke Forest and Oak
420 Ridge National Laboratory (ORNL). They found that the priming effect almost completely offset
421 increased litter input at Duke Forest. However, the model predicted that physical protection
422 was stronger at ORNL while the priming effect was much weaker, which corresponds with
423 observations at ORNL showing increased protection of SOC in soil microaggregates.

424
425 Ecosystem model development remains a very active area of research. Although there are
426 multiple microbial-explicit models available now, many of them still lack key mechanisms such
427 as spatial heterogeneity and cycling of N and other nutrients. When these mechanisms are
428 incorporated, model outcomes may change substantially. For example, the SCAMPS model
429 includes N dynamics and allows for variable C:N within the microbial community (Sistla et al.,
430 2014). This stoichiometric flexibility allows the microbial community to acclimate to warming,

431 resulting in greater losses of soil C through decomposition, especially in winter. The implication
432 is that soil C dynamics likely depend on interactions with nutrients mediated by decomposers
433 and plants.

434

435 **E Earth system**

436 Most Earth system models (ESMs) do not explicitly represent microbial communities. Of the 11
437 ESMs in the 6th Coupled Model Intercomparison Project (CMIP6), only one ESM explicitly
438 represents microbes (Arora et al., 2020). That model—GFDL-ESM4.1 from NOAA’s Geophysical
439 Fluid Dynamics Laboratory—represents soil C cycling using CORPSE.

440

441 Although they are not fully coupled, there have been efforts to run microbial-explicit models on
442 a global grid, forced with output from ESMs. Wieder et al. (2013) created a microbial-explicit
443 version of the Community Land Model (CLM) and compared its outputs with those from the
444 Daily CENTURY (DAYCENT) model and CLM4cn, a version of CLM with N cycling. Compared to
445 microbial-implicit CLM4cn and DAYCENT, microbial CLM predicted spatial patterns of steady-
446 state soil C that better aligned with global observations. Furthermore, a 20% increase in litter
447 inputs only increased global soil C temporarily due to priming effects in microbial CLM (Fig.
448 16.3). In contrast, soil C steadily increased in the microbial-implicit models CLM4cn and
449 DAYCENT. Global soil C responses to warming were also variable and mediated by the
450 temperature sensitivity of CUE as observed with the AWB model at the ecosystem level.

451

452 [Insert Fig. 16.3 here]

453

454 Hararuk et al. (2015) ran AWB and an ecosystem model by German et al. (2012)—which the
455 study called the GER model—on a global grid. Both models simulated steady-state global soil C
456 more accurately than the microbial-implicit CLM-CASA model. After calibrating the models
457 using a global soil C database, AWB and GER predicted faster declines in soil C compared to
458 CLM-CASA under the RCP 8.5 climate forcing scenario. Hararuk et al.’s (2015) analysis also
459 quantified the net outcome of decreasing CUE and the priming effect, allowing for key insights
460 into how these opposing processes ultimately influence soil C predictions.

461

462 **V MODEL-DATA INTEGRATION**

463 **A Uncertainty quantification**

464 As soil models continue to advance, they should be evaluated systematically for their
465 effectiveness in achieving research goals (Fig. 16.4). The process of reviewing and stress-testing
466 models against observations is termed “model validation” (Marzouk and Willcox, 2015).
467 Uncertainty quantification is a core part of model validation that involves assessment of model
468 variation, biases, limitations, and constraints that lead to deviations between the model and
469 the true, underlying data-generating processes. Uncertainty may arise from unknown values
470 and meanings of system parameters and inputs, potentially because parameters do not
471 correspond to measurable quantities. Related to parameter uncertainty, parametric variability
472 concerns the unknown effects of varying conditions on parameter and input values. Uncertainty
473 also stems from model discrepancy, or the intentional and unintentional assumptions and
474 simplifications separating a model from the actual processes it aims to represent.

475

476 [Insert Fig. 16.4 here]

477

478 Parameter uncertainty, parametric variability, and model discrepancy continue to be high for
479 soil biogeochemical models (Shi et al., 2018). Some soil models have parameters that facilitate
480 the functionality of the model, but do not have clear biological interpretations. For instance,
481 the AWB model assumes Arrhenius temperature dependence for SOC transformations, but the
482 associated activation energy parameters are not easy to measure directly (Allison et al., 2010;
483 Xie et al., 2020). Modeling temperature dependence also introduces parametric variability and
484 model discrepancy. Empirical studies confirm that parameters such as CUE and enzyme V_{max}
485 and K_M are temperature sensitive (Sinsabaugh et al., 2017, 2013), but the magnitude and
486 functional form of temperature dependency is still an active area of investigation (Alster et al.,
487 2020; Davidson et al., 2006).

488

489 Complex models have many parameters that may covary, making it difficult to constrain
490 parameter uncertainty (Sierra et al., 2015). Reducing this uncertainty requires that model
491 parameters are identifiable, such that change in parameter value causes an associated change
492 in variables predicted by the model. Sierra et al. (2015) proposed a collinearity index to quantify
493 the identifiability of a model—the higher the index, the lower the identifiability, and the more
494 difficult it is to find the true parameter values. Increasing the number of datasets used to
495 parameterize a model can increase identifiability of linear models and reduce overfitting,
496 thereby improving predictive accuracy. For microbial-explicit models, additional datasets
497 including microbial variables (e.g. soil enzyme activities, microbial biomass) might be needed to
498 increase parameter identifiability and reduce uncertainty.

499

500 Bayesian probabilistic frameworks are increasingly applied to interpret uncertainty in soil
501 models. Central to Bayesian uncertainty quantification and model validation are the processes
502 of Bayesian parameter estimation and inference, also known as data assimilation and
503 probabilistic/Bayesian inversion in the geosciences (Lahoz and Schneider, 2014). With these
504 approaches, the likely distribution of model parameter values for a given data set is estimated
505 and characterized. The numerical approximation of parameter distributions and model
506 likelihood estimation is carried out through Markov chain Monte Carlo (MCMC) simulation
507 methods (Christensen et al., 2006). Although the exact Monte Carlo simulation algorithm may
508 vary, most data assimilation frameworks include the following steps:

- 509 1. Choose model types and specific models to evaluate. In the case of soil biogeochemistry,
510 the assimilation of linear and non-linear ordinary differential equation models can be
511 compared (Xie et al., 2020).
- 512 2. Choose a dataset for comparison with model outputs.
- 513 3. Establish pre-inference probability density functions of model parameter values (known as
514 the “prior distributions” or “priors”).
- 515 4. Iteratively propose model parameter values to generate model outputs for computing
516 model likelihood for the given data set.

- 517 5. Approximate the distributions and probability density functions of parameter values that
518 correspond to better model fits to the data set (known as the “posterior distributions” or
519 “posteriors”).
- 520 6. Compare model likelihoods conditional on the data set with available and desired goodness-
521 of-fit metrics. The specific Monte Carlo algorithm will dictate the options available for
522 goodness-of-fit metrics.

523
524 “Exact” Bayesian Monte Carlo schemes comprehensively sample parameter values to compute
525 posterior distributions. These methods include traditional Gaussian random walk Metropolis-
526 Hastings MCMC and Gibbs samplers (McElreath, 2020), adaptive approaches derived from
527 evolutionary optimization algorithms such as differential adaptive evolution Metropolis (Vrugt,
528 2016), and the physics-inspired, momentum-driven family of Hamiltonian Monte Carlo
529 algorithms (Neal, 2011).

530
531 Statisticians have also been investigating “non-exact” Bayesian inference schemes that seek to
532 increase speed through approximation and simplification of parameter spaces. Non-exact
533 approaches include the approximate Bayesian computation (Alahmadi et al., 2021; Csilléry et
534 al., 2010) and variational Bayesian classes of methodologies (Blei et al., 2017; Ryder et al.,
535 2018). Goodness-of-fit methods range from simpler frequentist computations such as
536 coefficient of determination and maximum likelihood estimation to Bayesian metrics including
537 information criteria and cross-validation computations (Gelman et al., 2013). Fully Bayesian
538 goodness-of-fit metrics can be more stable than their frequentist counterparts and provide
539 more diagnostic information about overfitting and inference validity (Vehtari et al., 2016),
540 though there may be higher computational resource demands.

541
542 There have been several powerful applications of Bayesian parameter estimation to soil
543 biogeochemical models. Hararuk et al. (2014) integrated global soil C data into the C-only
544 version of the Community Land Model coupled with the Carnegie-Ames-Stanford Approach
545 submodel (CLM-CASA), while Ťupek et al. (2019) integrated respiration data from boreal forests
546 in Finland into the Yasso07, Yasso15, and CENTURY models. Both studies compared model
547 outputs before and after using a Bayesian data assimilation process to constrain model
548 parameters. In all cases, data integration resulted in model predictions that more closely
549 matched observations.

550
551 However, each of these studies has caveats. The soil C database used by Hararuk et al. (2014)
552 did not include time-series data, thereby necessitating a steady-state assumption about C pool
553 sizes. If this assumption is not accurate, estimates of model uncertainty may be difficult to
554 interpret. Ťupek et al. (2019) calibrated models with observed data but did not use an
555 independent dataset to validate model predictions, which can lead to model overfitting.
556 Maintaining separate training and validation datasets, a common practice in machine learning
557 approaches, can help avoid this problem (Botu et al., 2017).

558
559 Approaches like Bayesian data assimilation are most effective when extensive, multivariate
560 datasets are available for model calibration and validation across a range of ecosystems. For

561 example, field measurements of dryland soils have improved biogeochemical models of
562 ecosystem-specific C-cycling dynamics (Shen et al., 2016; Zhang et al., 2014). Going forward,
563 rapid advancements in remote and *in situ* environmental sensing tools like light detection and
564 ranging (LiDAR) (Kemppinen et al., 2018) and soil nutrient sensors (Burton et al., 2020) can
565 increase the availability of ecosystem-specific measurements at lower cost, higher resolution,
566 and greater sampling intensity than ever before.

567

568 **B Model intercomparison**

569 Model intercomparison goes hand-in-hand with model selection and data assimilation to
570 evaluate the behaviors and performance of different models relative to one another. For
571 instance, Li et al. (2014) compared 3 microbial-explicit models with a classical first order model
572 and found that steady-state SOC was much more responsive to varying temperature sensitivity
573 of CUE in the microbial-explicit models. In contrast, SOC stocks were largely independent of
574 microbial CUE in the first order model. This analysis points toward a need for additional
575 empirical research on how microbial CUE varies with temperature and other factors.

576

577 The application of Bayesian approaches to model calibration and selection can readily be
578 extended to model intercomparison. In their global analysis of soil C responses under RCP8.5,
579 Hararuk et al. (2015) used a Bayesian approach to show that the microbial-explicit models AWB
580 and GER better explained the spatial variation of steady-state soil C compared to the CLM-CASA
581 model. However, at least with some parameter values, the microbial-explicit models simulated
582 oscillations in soil C over time, which is an unrealistic behavior at ecosystem to global scales.

583

584 Xie et al. (2020) also applied a Bayesian approach to compare AWB with a classical model (Fig.
585 16.2). Both models were fit to a meta-analysis dataset on soil respiration response to warming
586 (Romero-Olivares et al., 2017) and compared using Bayesian goodness-of-fit metrics such as the
587 widely applicable information criterion (WAIC) and leave-one-out-cross validation (LOO). These
588 metrics account for the posterior distributions of parameter values after model fitting, and LOO
589 is a useful metric when limited data are available for model selection. Both models fit the meta-
590 analysis data reasonably well, but the simpler structure of the classical model led to slightly
591 better WAIC and LOO scores. These findings emphasize that model selection involves tradeoffs.
592 Simple models with few parameters may be calibrated to match observational datasets with
593 good validation scores, but these models may fall short in capturing the mechanistic details
594 needed to make accurate predictions across a broader range of soil ecosystems.

595

596 **VI RECOMMENDATIONS TO ADVANCE SOIL MODELS**

597 Despite recent progress, substantial barriers still prevent the widespread application of models
598 to grand challenges in soil biology. In particular, specialized language, expertise, and skill sets
599 can make it challenging to integrate modeling with other scientific approaches. This
600 specialization can be a barrier to information flow between modeling and empirical analyses.
601 Such issues can exacerbate the challenge of collecting data in a form that supports model
602 development, calibration, and validation. In addition, models can be difficult to access and
603 apply if recent versions, adequate documentation, and user interfaces are not available. Scaling
604 up models, for example to make Earth system predictions, can be limited by insufficient tools

605 for model selection and intercomparison. Approaches for model validation are still under
606 development and involve specialized knowledge of computational and statistical tools.

607

608 Overcoming these barriers would be beneficial. Predictive accuracy would increase for models
609 applied to simulate future soil C stocks, nutrient cycling, and climate change. Given that models
610 have multiple uses beyond prediction, broader community engagement in the science of
611 modeling would also advance fundamental knowledge across the disciplines of soil science,
612 biology, and biochemistry. To reap these benefits, we recommend the following steps:

- 613 ● Integrate modeling and empirical approaches. Rather than viewing modeling and empirical
614 activities as separate, we recommend co-developing models and empirical research.
615 Operationally, this means reconfiguring science teams so that researchers with modeling
616 expertise interact directly and frequently with empirical researchers. From the proposal
617 writing stage through model development and manuscript publication, scientists creating
618 models and collecting data should create spaces to develop a common language and align
619 research goals. By co-creating models and experiments, researchers can ensure that models
620 represent key processes, critical model parameters are measurable, and both model and
621 experimental outcomes are relevant to one another. Such cooperation would be
622 particularly helpful for incorporating complex 'omics datasets into trait-based community
623 models.
- 624 ● Collect more data. Relatively few time-series datasets are available for some soil variables,
625 such as C stocks, making it difficult to evaluate or avoid the steady-state assumptions often
626 made in biogeochemical models. Sparse data can also limit the possibility of separating data
627 into training versus validation subsets. Better integration between modeling and empirical
628 research could help fill some of these data gaps.
- 629 ● Cross-train researchers in modeling. To enable the interactions necessary for integration,
630 researchers should receive training in modeling perspectives and approaches. For example,
631 training activities such as workshops, short courses, and online modules can help students
632 acquire common vocabulary used in modeling. Conversely, students with a modeling
633 background can benefit from training activities focused on theory and empirical work. If
634 designed thoughtfully, seminars and courses can provide opportunities for students to get
635 comfortable communicating and collaborating across the modeling-empirical divide.
- 636 ● Improve accessibility to model code and analysis tools. The principles of F.A.I.R. data should
637 also apply to model code and outputs: findable, accessible, interoperable, and reusable
638 (Wilkinson et al., 2016). Code repositories such as GitHub and platforms such as the
639 Department of Energy's KBase can host code along with input/output files and user
640 interfaces to make models accessible. For new models, writing and documenting code in
641 widely-used, open-source formats such as R Markdown, Java, C++, and Jupyter Notebooks
642 for Python and other computer languages can promote interoperability and reusability. A
643 version control system is also important to ensure analyses from a prior model version can
644 be replicated. Regardless of the model or platform, researchers should always strive to
645 make model code and analyses publicly available with guidelines for reuse so that others
646 may validate, build upon, and broaden applications of existing models.
- 647 ● Plug-and-play models and datasets. Taking the principle of interoperability to another level,
648 we encourage the development of model testbeds that enable mixing and matching of

649 different models and datasets (Wieder et al., 2018). Ideally, such testbeds should allow for
650 modifications of model structure and input datasets. Testbeds can also facilitate
651 standardization of input/output protocols and datasets to enhance interoperability, thereby
652 avoiding tedious data reformatting procedures while also providing guidance on standards
653 that could be adopted by the broader soil science community.

- 654 ● Develop improved model selection and intercomparison tools. Moving beyond testbeds, the
655 research community would benefit from wider availability of model selection and
656 intercomparison resources. For example, the *soilR* package enables users to run simulations
657 with an array of differential equation models, including some that represent soil
658 radiocarbon (Sierra et al., 2012). Global intercomparison initiatives such as the Coupled
659 Model Intercomparison Project (CMIP) have also been tremendously valuable for comparing
660 Earth system models by establishing a standardized set of simulation scenarios and output
661 variables (Arora et al., 2020; Todd-Brown et al., 2013). As new tools for model inference
662 become available, they should be incorporated into intercomparison projects to enable
663 one-stop-shopping for model comparison and selection (Xie et al., 2020).

664

665 **VII CONCLUSION**

666 Within the last decade, models of soil systems have advanced substantially. There are now
667 many new approaches for representing microbial and biochemical processes in soil models. As
668 these new models came online, synthesis efforts placed them in the context of broad principles
669 that guide quantitative soil science across scales and ecosystems. We anticipate that these
670 advances will support further integration and unification of soil biological modeling in the next
671 5-10 years. Still, another modeling renaissance faces some significant challenges. Disciplinary
672 silos as well as difficulties in scaling models from genes to ecosystems must be overcome to
673 maximize the impact of recent model advances. Breaking down these barriers will require
674 better integration of modeling approaches into all branches of soil science. Our
675 recommendations to build computational infrastructure and train a new generation of
676 researchers well-versed in modeling can serve as an initial roadmap for integration. Following
677 our roadmap should help elevate models as powerful tools for tackling soil-related grand
678 challenges facing society, from food security to climate change.

679

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684

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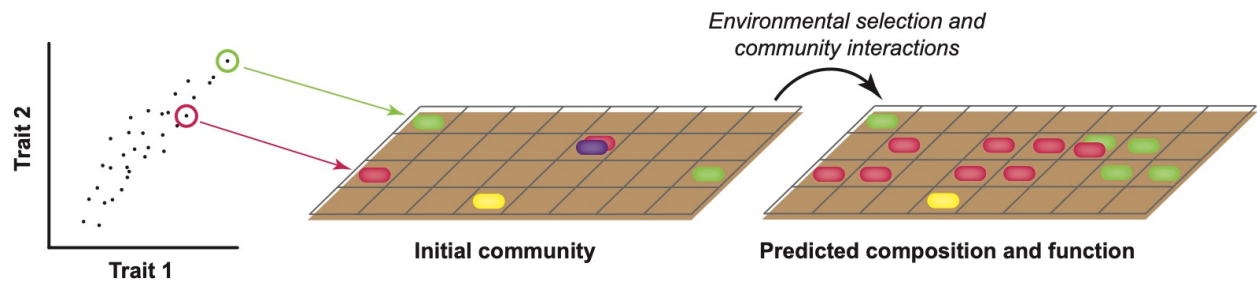
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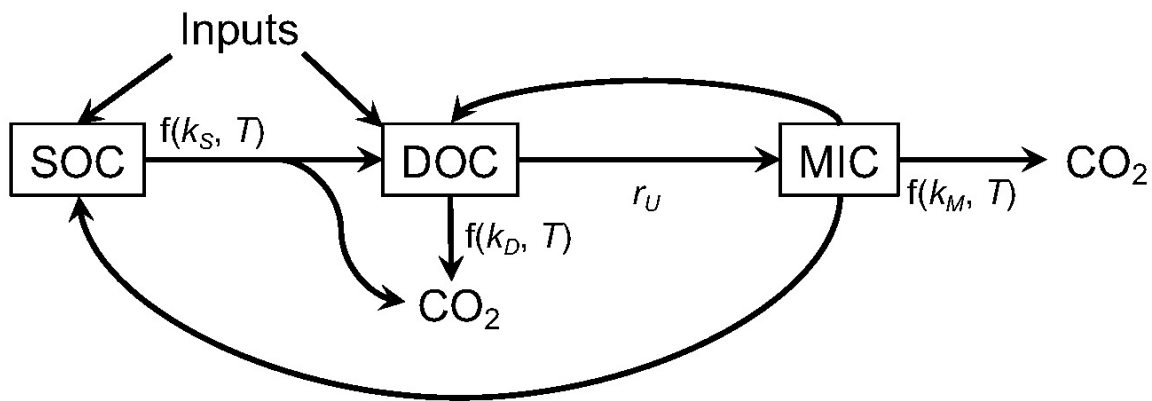


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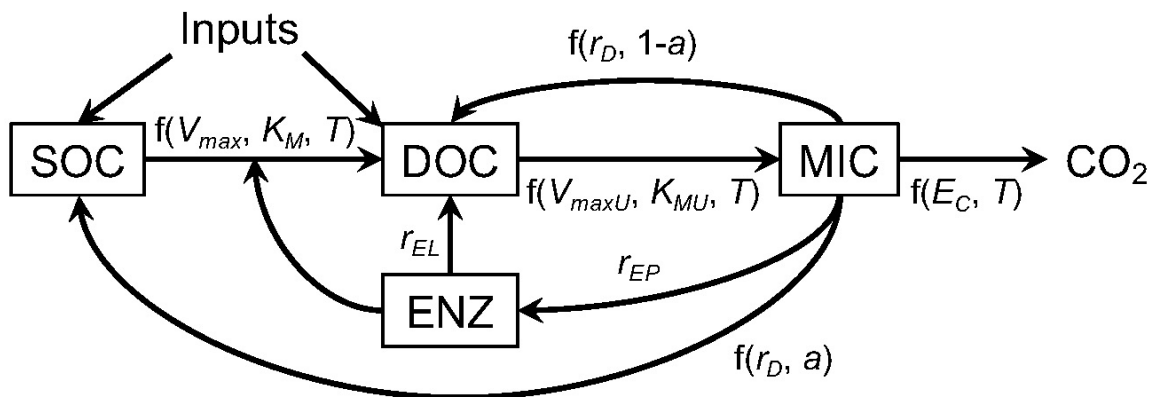
977 Fig. 16.1. Schematic of the Decomposition Model of Enzymatic Traits (DEMENT). Traits are
978 assigned to microbial taxa by drawing at random from empirically-based distributions. Taxa are
979 placed randomly on a spatial grid where they consume substrates, reproduce, disperse, and
980 interact over time. The model predicts community composition and function as taxon
981 abundances change due to environmental selection. Adapted from Allison (2012).

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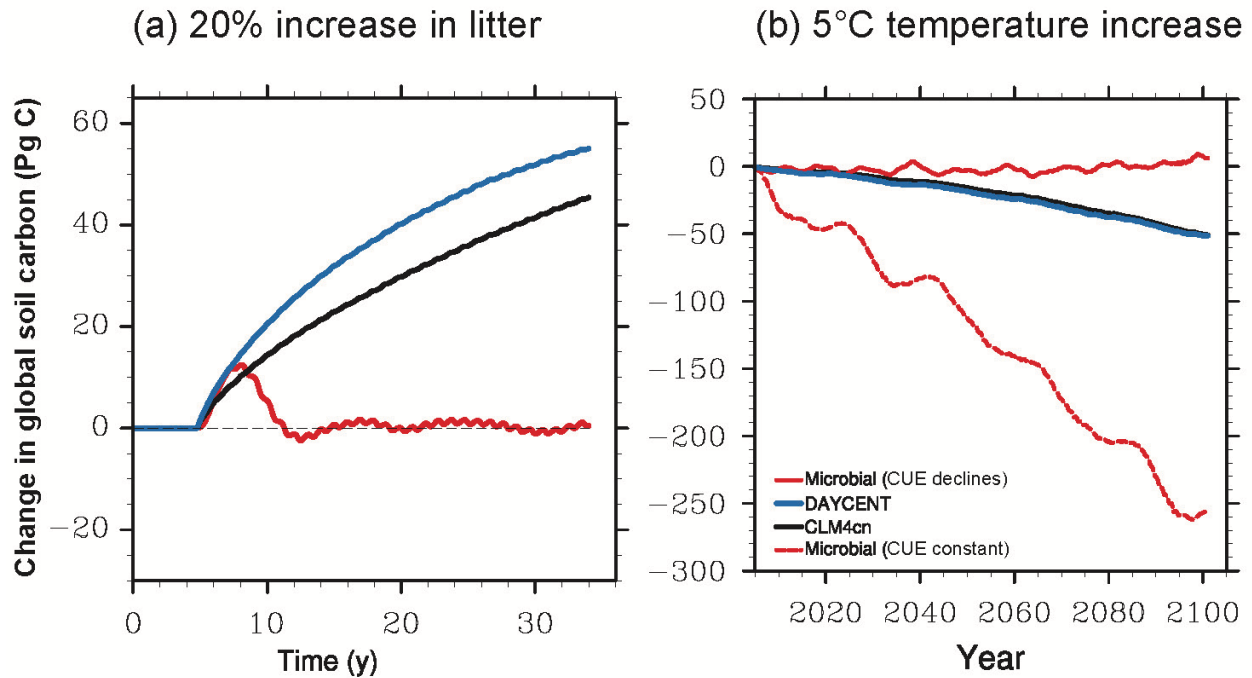
(a) Classical model



(b) AWB microbial model

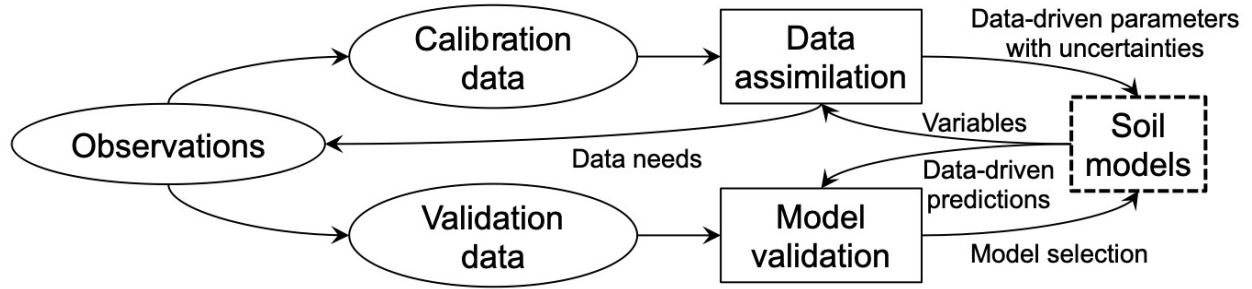


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 985 Fig. 16.2. A) Classical first-order linear model with microbial implicit transfers among pools. B)
 986 Allison-Wallenstein-Bradford (AWB) model with microbial-explicit interactions among pools of
 987 soil organic carbon (SOC), dissolved organic carbon (DOC), microbial biomass (MIC), and
 988 extracellular enzymes (ENZ). In the classical model, pool turnover depends on first-order decay
 989 constants (k_S for SOC, k_D for DOC, k_M for MIC) as well as DOC uptake by MIC (r_U). Turnover also
 990 depends on temperature (T). In the AWB model, SOC turnover is represented as a Michaelis-
 991 Menten process dependent on T and ENZ with parameters V_{max} and K_M . An analogous process
 992 describes DOC uptake by MIC with parameters V_{maxU} and K_{MU} . Carbon uptake is allocated to
 993 biomass versus respiration according to a carbon use efficiency parameter E_C . Enzymes are
 994 produced in proportion to MIC biomass at rate r_{EP} and are lost to the DOC pool at rate r_{EL} . MIC
 995 biomass dies at rate r_D and is partitioned into SOC versus DOC according to coefficient a .
 996 Partition coefficients are used in the conventional model but omitted from the figure for clarity.
 997 Adapted from Allison et al. (2010).
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Fig. 16.3. Soil carbon response of first-order and microbial-explicit models to A) increased litter inputs and B) warming at the global scale. Warming response in the microbial model depends on whether carbon use efficiency (CUE) declines or remains constant with increasing temperature. Adapted from Wieder et al. (2013).



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Fig. 16.4. Framework for model-data integration. Observations are used for validating model outputs or calibrating model parameters via data assimilation. Bayesian approaches can be used for data assimilation and model validation to obtain posterior parameter distributions and calculate indices of model fit that aid in model selection. Adapted from Wieder et al. (2015).