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## REVIEW

Emerging relationships among microbes, soil carbon storage and climate change

# Uniting the scales of microbial biogeochemistry with trait-based modelling

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## Abstract

1. Below-ground microbial communities drive some of Earth's largest biogeochemical fluxes, yet they represent a major source of uncertainty in global biogeochemical models. This review synthesizes recent advances in trait-based soil carbon modelling in order to identify how empirical observations of microbial traits can inform the next generation of soil carbon models.
2. We identify four key perspectives from which trait-based models have investigated the role of microbes in soil carbon fluxes, ranging from the largest to the smallest scales of biological organization: (i) Earth system models, which have recently begun to incorporate microbial traits at a global scale; (ii) ecosystem models, which relate microbial carbon cycling to other trophic levels and element cycles; (iii) models from community ecology, which link theories of species diversity to ecosystem cycles; and (iv) models of fine-scale physiology, which mechanistically represent traits at the individual level.
3. Highlighting the contributions of diverse trait-based modelling approaches, we caution that this diversity makes it challenging to link perspectives at different scales. The meaning of a trait depends both on the structure of the model in which it occurs and on the scale treated by the model. Thus, reapplying a fine-scale trait at a broader scale may make incorrect predictions, an issue we illustrate quantitatively using model simulations.
4. With these challenges in mind, we highlight several ways to synthesize the scales of microbial biogeochemical modelling: (i) quantitatively, using mathematical scaling techniques, (ii) empirically, by applying experiments to test relationships between scales and (iii) conceptually, by identifying key traits and processes across scales.
5. Taking full advantage of trait-based modelling, ecologists will thus be able to incorporate multiple perspectives to better predict carbon cycling in a changing world.

## KEYWORDS

carbon cycle, community ecology, earth system modelling, ecosystem ecology, mathematical modelling, soil microbes, traits

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## 1 | INTRODUCTION

Through their microscopic interactions with plants and soil, below-ground microbial communities drive some of the planet's most powerful biogeochemical fluxes: As dominant members of the soil biota, microbes perform the bulk of soil respiration (Bond-Lamberty & Thomson, 2010); as mutualistic partners of most plant species, symbiotic microbes receive a generous share of the carbon fixed by plants (Hobbie & Hobbie, 2006). However, our limited understanding of these carbon fluxes threatens our ability to forecast global change (Terrer et al., 2016)—most Earth system models (ESMs) used for climate prediction, for instance, fail to directly model the biology of microbes (Bradford et al., 2016).

Like many challenges facing global change scientists, this is at its core a problem of scale. The recent explosion of trait-based approaches in microbial ecology has provided a unifying framework to understand the forces shaping microbial communities (Crowther et al., 2014) at soil's smallest scales. Applying conceptual advances in plant ecology, this paradigm uses traits to prioritize generalizable mechanistic insight. While incorporating such detail may be a way towards more robust models of carbon cycle feedbacks, it also requires grappling with the immense diversity, cryptic underground lifestyles and complex community dynamics of soil microbes. Thus, making global predictions calls for ecologists to synthesize local insight into microbial processes into a general understanding of what drives global biogeochemical fluxes (Crowther et al., 2019; Fry et al., 2019).

Trait-based mathematical models offer one promising path to generality. Although trait-based experimental approaches have already provided ways to link the detail of microbial communities with their functional attributes (Crowther et al., 2014; Treseder & Lennon, 2015, e.g.), researchers applying these perspectives must choose from a multitude of traits (Dawson et al., 2019), then grapple with the even greater number of species on which to measure them. Thus, there is a need to know which traits matter most, and how to measure them at scales that can inform global understanding (Fry et al., 2019). This is where mathematical modelling can contribute: The generality offered by mathematical models clarifies the consequences of individual traits at larger scales. By simplifying our understanding of microbial communities, these models synthesize general insight into global biogeochemistry (Zakharova et al., 2019).

Here, we review how mathematical models have applied traits to represent the role of microbes in global biogeochemistry. Focusing on the role of microbes in terrestrial carbon cycling, we discuss commonalities and differences across scales and identify opportunities for synthesis. We begin by reviewing the four key perspectives from which models have investigated the biogeochemical role of microbes (section 'Four scales of microbial biogeochemistry'), discussing developments at the scales of (i) the Earth system, (ii) the ecosystem, (iii) the community and (iv) microbial physiology. In the next section ('The unresolved problem of scale in trait-based models'), we identify challenges in linking scales to derive mechanistic global insight. Using specific examples, we discuss how traits help conceptually unify these scales, but also caution that traits must often be interpreted differently

when used at different scales. Synthesizing these current approaches, the final section of this review ('Unifying the scales of microbial biogeochemistry') discusses how microbial ecologists can integrate theoretical and empirical approaches to further understand the role of microbes in global biogeochemistry. By translating lower-level traits representing easily measured organismal processes to higher-level parameters that predict ecosystem function, mathematical modelling can provide a blueprint for incorporating mechanistic microbial traits into generalizable models at the largest scale.

## 2 | FOUR SCALES OF MICROBIAL BIOGEOCHEMISTRY

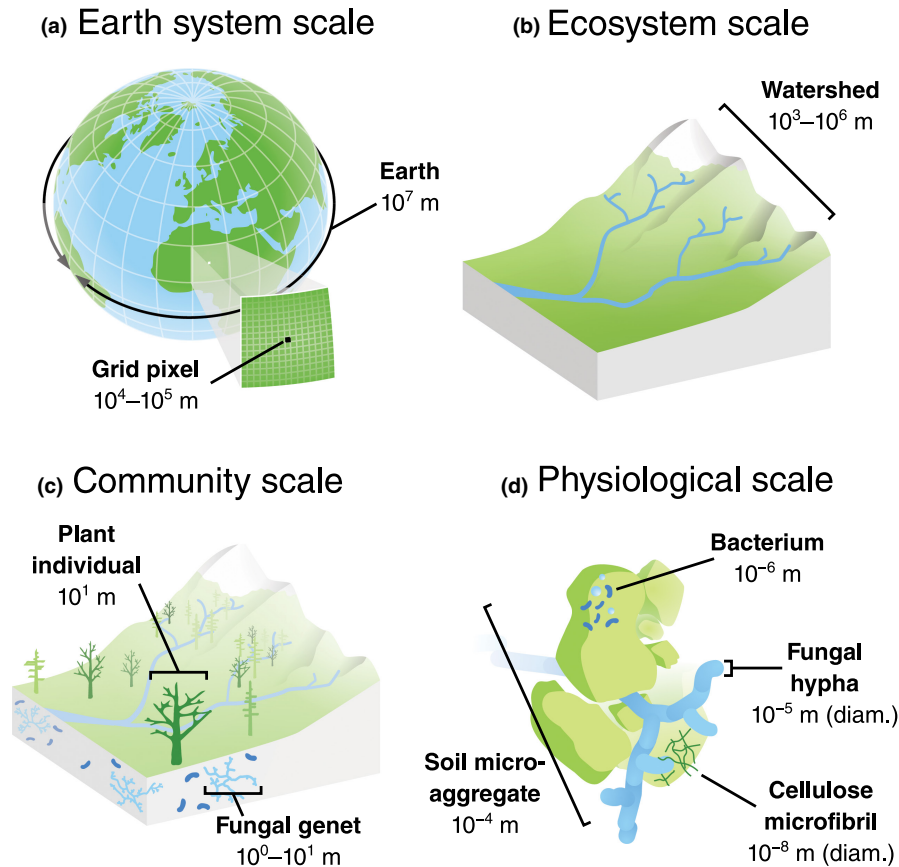
Trait-based modelling may address microbial biogeochemistry at four scales (Figure 1). First, at the *Earth system* scale, modelling microbial biology has the potential to improve quantitative predictions of global climate. Second, the related *ecosystem* perspective considers the same ecosystem fluxes, but its models aim not only to make quantitative predictions but also to understand the conceptual importance of microbial processes. Third, the *community* perspective draws on a rich body of community ecology theory to investigate how biogeochemical processes mediated by microbes affect the composition and function of soil communities. Finally, a *fine-scale physiological* perspective explicitly models the microscopic interactions between microbes and their environments.

Here, we use the term 'trait' to refer to properties that (a) can be measured for organisms or communities and (b) capture biotic variation in drivers of global biogeochemistry. As traditionally applied in plant ecology, traits achieve their predictive power by quantifying physiological processes linked to growth, reproduction and survival (Violle et al., 2007). Trait-based approaches to broad-scale microbial questions (e.g. Wieder, Allison, et al., 2015) may extend the trait concept beyond its most restrictive definitions (i.e. continuous-valued measurements of individual organisms; McGill et al. 2006), but such traits remain rooted in physiological mechanism. Typically, traits enter into quantitative models as *parameters*, fixed values constrained by empirical measurements or tuned by model builders, though they may also be treated as dynamic variables or as distributions.

Although the four perspectives we identify are not mutually exclusive, we use them to survey the trait-based modelling literature (with reference to the specific representative models in Figure 2 and Box 1) and identify how it has quantitatively addressed common research questions. Although microbes perform diverse metabolic roles in soil, we focus here on carbon cycling and microbial respiration, as these are the processes best represented across all four scales.

### 2.1 | The Earth system perspective: How much carbon do microbes move globally?

Earth system models are large simulations used to project climate change. Summarizing knowledge about global change drivers



**FIGURE 1** Four perspectives on microbial biogeochemistry and their associated spatial scales, spanning 16 orders of magnitude ( $10^{-8}$ – $10^7$  m). (a) At the Earth system scale, models represent the Earth's entire surface ( $\sim 10^7$  m) using grid cells with resolutions  $\sim 10^4$ – $10^5$  km (Schneider et al., 2017). (b) The ecosystem scale focuses on broad-scale flows of energy and material through ecosystems. One operational definition of the ecosystem is the watershed (Likens et al., 1970),  $\sim 10^3$ – $10^6$  m. (c) The community scale is defined by the scale of its constituent organisms: for example, a plant individual (represented here by a tree canopy  $\sim 10^1$  m) and a fungal genet ( $\sim 10^0$ – $10^1$  m, measured for ectomycorrhizal fungi of the genus *Suillus*; Hirose et al., 2004). (d) The physiological scale involves the fine-scale structure of microbial organisms and their environment. We show a soil microaggregate ( $\sim 10^{-4}$  m) with attendant fungal hyphae ( $\sim 10^{-5}$  m) and bacteria ( $\sim 10^{-6}$  m) (Wilpiszski et al., 2019). Much smaller is the nanoscale structure of cellulose, made up of microfibrils  $\sim 10^{-8}$  m in diameter (Heinze & Liebert, 2012)

across disciplines, they are the level which most directly informs policy and decision-making. Whereas the earliest global climate models focused on atmospheric and oceanic processes, successive generations have included an increasing number of biological processes (Dahan, 2010). Nonetheless, the nature of these models limits the degree of biological detail that is feasible. On the one hand, Earth system models demand immense computational resources; thus, their spatial resolution must be relatively coarse (currently, most use cells of 10–100 km; Schneider et al., 2017) and their components should be quick to compute. On the other hand, Earth system models aim to make robust quantitative predictions; accordingly, model builders prefer to include responses that can be quantified from empirical data or deduced from well-understood physical laws. Unfortunately, many processes fail to meet these requirements: They may be challenging to simulate due to their fine spatial scale or computational complexity; especially in the case of biological processes, they may be too poorly understood to represent confidently. As a result, models use the technique of *parameterization*, where simpler high-level parameters are tuned

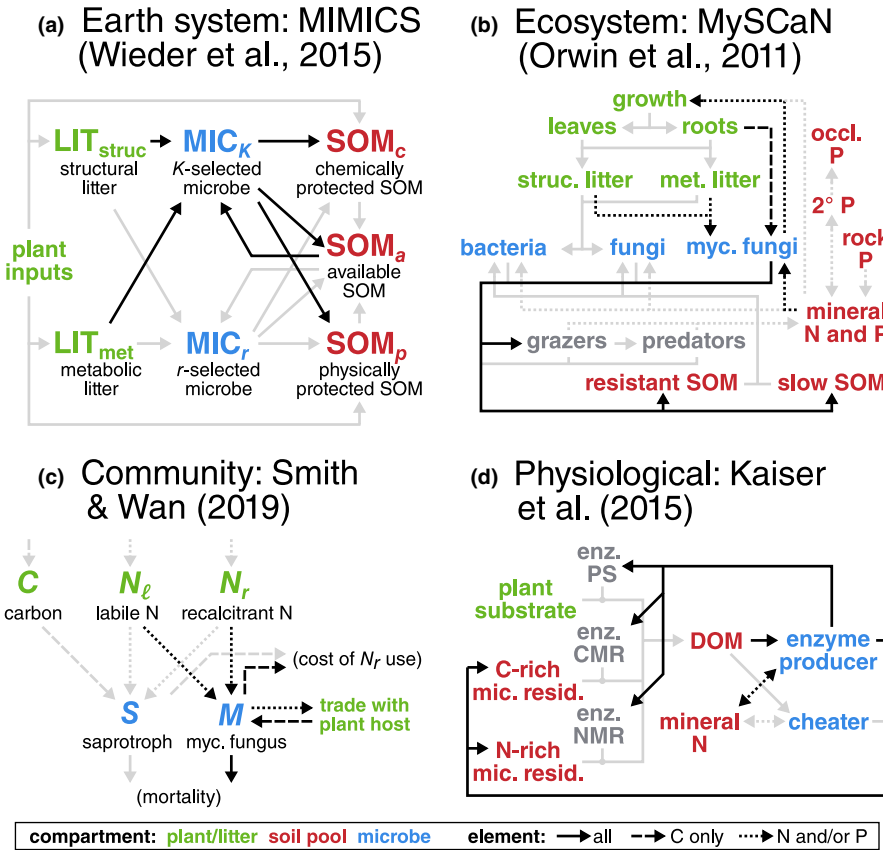
to approximate the effect of complex or unknown lower-level mechanisms.

### 2.1.1 | State of the art: From first-order to microbially explicit models

At present, Earth system models parameterize soil carbon cycling without considering microbial control of organic matter breakdown. Instead, these models represent the breakdown of organic matter as a *first-order process*, depending only on the size of a stock of carbon substrate ( $C_{\text{sub}}$ ) according to an environmentally determined linear *decay constant* ( $k$ ):

$$\text{change in carbon stock} = \text{carbon inputs} - \text{decay constant} \cdot \text{standing carbon stock}$$

$$\frac{dC_{\text{sub}}}{dt} = I_1 + I_2 + \dots - \underbrace{k_{[\text{decay}]}(\alpha, T, \dots)}_{\text{(function of soil moisture, temperature, etc.)}} \cdot C_{\text{sub}} \quad (1)$$



**FIGURE 2** Representative biogeochemical models illustrating each of the four scales. Here we show the entire structure of each model, as detailed in Box 1.1-1.4. Black arrows indicate fluxes appearing in the equations for microbial biomass, which are provided later in Box 2.1-2.4. (a) The Microbial-Mineral Carbon Stabilization model (Earth system). Abbreviation: SOM, soil organic matter. (b) Mycorrhizal organic nutrient uptake and carbon storage (ecosystem). Abbreviations: 2°, secondary; met., metabolic; myc., mycorrhizal; occl., occluded; struc., structural. (c) Resource ratio theory and litter decomposition (community). (d) Social dynamics within decomposer communities (physiological). Abbreviations: mic. resid., microbial residue; enz. PS/CMR/NMR, enzyme attacking plant substrate/C-rich/N-rich microbial residue; DOM, dissolved organic matter

This structure was used in almost all Earth system models from the Sixth Assessment Report from the Intergovernmental Panel on Climate Change (Berardi et al., 2020). Although varying the first-order decay constant captures a limited degree of feedback between climate and decomposition, this simple approach omits many known controls of decomposition (Allison et al., 2010). Nonetheless, no entire Earth system model run to date has directly represented microbial control of soil carbon (Berardi et al., 2020), though one (IPSL-CM6A-LR; Guenet et al., 2016) indirectly represents microbial priming effects.

To address these challenges, a newer generation of soil submodels explicitly represents microbial control of soil carbon. A common approach uses *Michaelis-Menten kinetics*: The substrate ( $C_{sub}$ ) breaks down at a rate proportional to microbial biomass ( $C_{mic}$ ). Increasing substrate availability also increases this rate, but the relationship saturates according to the microbial uptake traits  $V_{max}$  (maximum rate per unit biomass) and  $K_m$  (the half-saturation constant):

change in carbon stock = inputs – microbial biomass · uptake rate per unit biomass

$$\frac{dC_{sub}}{dt} = I_1 + I_2 + \dots - C_{mic} \cdot \frac{V_{max} \cdot C_{sub}}{K_m[\text{half saturation}] + C_{sub}} \quad (2)$$

saturating function of substrate C  
 when  $C_{sub}$  large,  $\approx V_{max}$   
 when  $C_{sub}$  is  $K_m$ ,  $= \frac{1}{2} V_{max}$

Although the Michaelis-Menten response can be rigorously derived for the kinetics of certain enzymes, its application to microbial activity relies on assumptions that may not be appropriate for all systems.

For instance, Schimel and Weintraub (2003) proposed that the related *reverse Michaelis-Menten kinetics* may be more appropriate when microbial enzymes compete for a limited number of substrate-binding sites. In either case, a third trait, the *microbial growth efficiency* ( $\epsilon$  or MGE), determines the fraction of carbon uptake that becomes microbial biomass. Sometimes, this fraction may also be labelled carbon use efficiency (CUE), though this term encompasses a broader range of definitions (Manzoni et al., 2018; Sinsabaugh et al., 2013).

In an early application of Michaelis-Menten decomposition to Earth system modelling, Wieder et al. (2013) showed that incorporating microbial control of decomposition improves models' ability to reproduce observed soil carbon stocks, but identified carbon use efficiency as a key uncertainty. Related approaches have incorporated extracellular enzyme production (Hararuk et al., 2015), carbon protection by mineral particles (Sulman et al., 2014) and basic ecological differentiation between fast- and slow-growing microbes (Wieder, Grandy, et al., 2015); we illustrate the last model (Figure 2a; Box 1.1) as an example of an Earth system modelling-focused approach.

### 2.1.2 | Future directions: Towards Earth system models with 'microbial traits'

Although the current generation of Earth system models uses first-order decay kinetics, and thus lacks microbial traits, the next

### BOX 1 Comparing four representative models of microbial biogeochemistry

Traits in microbial models of biogeochemistry can only be understood in relation to models' overall structure, which in turn reflects the questions motivating research at different scales. To illustrate these connections, we present one model of microbial biogeochemistry for each scale (Figure 2). The models at the Earth system (1.1) and community (1.3) scales are relatively simple, reflecting their predictive and theoretical aims, respectively. Meanwhile, the ecosystem (1.2) and physiological (1.4) models employ greater complexity thanks to their greater focus on realism.

- 1. The Microbial-Mineral Carbon Stabilization model (Earth system).** Developed to predict soil carbon stocks at the Earth system scale, MIMICS (Wieder, Grandy, et al., 2015) focuses on soil microbial responses to elevated temperature and litter (Figure 2a). A system of ordinary differential equations represents dynamics of two microbial biomass pools ( $MIC_r$ ,  $MIC_k$ ), two litter pools (metabolic  $LIT_{met}$  and structural  $LIT_{str}$ ) and three soil organic matter pools (available  $SOM_a$ , chemically recalcitrant  $SOM_c$  and physically protected  $SOM_p$ ). Two groups of microbes, fast-growing *r*-strategists ( $MIC_r$ ) and slow-growing *K*-strategists ( $MIC_k$ ), compete for carbon.
- 2. Mycorrhizal organic nutrient uptake and carbon storage (ecosystem).** To investigate the effect of mycorrhizal organic nutrient uptake on ecosystem-level carbon storage, Orwin et al. (2011) synthesized a model of ecosystem carbon, nitrogen and phosphorus cycling (the MySCaN model, Figure 2b). MySCaN tracks 37 state variables across seven soil layers. These represent carbon, nitrogen and phosphorus contents of 11 organic compartments representing plants, litter, microbial guilds, soil fauna and soil organic matter classes; each has flexible stoichiometry, constrained by traits. Four state variables represent mineral nitrogen and phosphorous pools.
- 3. Resource ratio theory and litter decomposition (community).** Applying the resource ratio framework of Tilman (1982), Smith and Wan (2019) consider competition between ectomycorrhizal (*M*) and saprotrophic fungi (*S*) for two pools of nitrogen: labile ( $N_l$ ) and recalcitrant ( $N_r$ ) (Figure 2c). A third resource pool accounts for decay dynamics: litter carbon (state variable *C*), used by the saprotroph but not by the ectomycorrhizal fungus; this pool's fate thus indicates whether ectomycorrhizal fungi suppress decay.
- 4. Social dynamics within decomposer communities (physiological).** Kaiser, Franklin, et al. (2015) built a spatially explicit individual-based model to determine how social dynamics between enzyme-producing and 'cheater' microbes affect decomposition (Figure 2d). Microbes, dissolved inorganic nitrogen and dissolved organic matter move within a grid of microsites ( $10 \mu m \times 10 \mu m \times 10 \mu m$ ); within cells, the model considers plant substrate, dead microbial biomass (N-rich and C-rich microbial remains) and extracellular enzymes.

generation of these large models is likely to take advantage of trait-based approaches to explicitly model microbial control of decomposition (Berardi et al., 2020). Nonetheless, the microbially explicit approach presents challenges: Trait values may be tricky to parameterize, and even fundamental questions of model structure remain unsettled. Unlike first-order decay constants, which have been quantified extensively using decomposition experiments, the conceptually defined pools and traits of many microbially explicit models cannot be constrained by literature values and must instead be fit from carbon stock data (Abramoff et al., 2018). As a result, there is considerable uncertainty in the microbial trait parameters of models such as MIMICS (Wieder, Grandy, et al., 2015). In turn, this produces high uncertainty in model outputs, further exacerbated by several structural uncertainties (Shi et al., 2018). On the one hand, models disagree on the choice between the two forms of Michaelis–Menten dynamics, which encode opposite assumptions about whether microbes (forward) or substrate sites (reverse) primarily limit decomposition. On the other hand, the shared formulation of microbial turnover in most next-generation models produces unrealistic oscillations in microbial biomass (Georgiou et al., 2017). Fortunately, as Earth system models begin to incorporate microbes as drivers of

decomposition, insights from other modelling perspectives may be able to clarify key uncertainties.

## 2.2 | The ecosystem perspective: How do microbial fluxes affect ecosystem function?

Next, we discuss the ecosystem modelling perspective. Like the Earth system perspective, this approach considers fluxes between different ecosystem compartments at broad spatial scales. However, rather than seeking the minimal complexity needed to make quantitative forecasts, the systems analysis approach of ecosystem modelling also seeks conceptual understanding of how microbial fluxes affect entire ecosystems. As these models are run over smaller spatial scales and do not act as components of larger modelling efforts, they may incorporate more complexity while remaining tractable. Additionally, since they do not only aim to make quantitative predictions, ecosystem models can explore the effects of processes that are too poorly understood to parameterize in Earth system models. Nonetheless, the close methodological relationship between modelling at the ecosystem and Earth system scales means that model

features first used at the ecosystem scale are often adopted to improve global predictive models.

Fundamentally, ecosystem modelling aims to understand emergent properties of the 'ecosystem' taken as an integrated whole. To do so, it builds *compartment models* tracking the flow of one or more properties (e.g. energy, nutrients) between several homogeneous compartments (e.g. plants, litter, soil microbes); as such, it assumes the distribution of these properties within compartments is insignificant for the dynamics of the system as a whole (Eriksson, 1971). This approach has long been used to model carbon cycling (e.g. Eriksson & Welander, 1956, without an explicit microbial pool); one ecosystem model in particular, CENTURY (Parton et al., 1987), and its extension DAYCENT (Parton et al., 1998) set the standard for modelling decay as a first-order process, now forming the basis for the soil component of most current Earth system modelling efforts (Berardi et al., 2020).

### 2.2.1 | State of the art: Multiple element cycles, multiple trophic levels

More recent ecosystem models, on the other hand, incorporate the findings of a new biogeochemical paradigm in which soil microbes are active drivers of varied soil carbon transformations. To do so under the compartment model framework, they track more properties (e.g. nutrients) per compartment or increase the number of compartments (e.g. types of organisms). As such, ecosystem modelling efforts have produced hundreds of carbon cycle models at an exponentially increasing pace (Manzoni & Porporato, 2009). In particular, recent ecosystem models have used an increased number of traits to investigate the effect of nutrient stoichiometry on microbially driven carbon cycling, and to include a richer set of trophic processes affecting microbes, such as food web interactions and symbiotic nutrient exchange.

Since soil microbes' carbon and mineral requirements do not match the composition of their substrate, microbial biogeochemistry depends on ecological *stoichiometry*: the constraints relating different element cycles within ecosystems. While global models of nitrogen and phosphorus cycling have been applied to predict plant growth under increased CO<sub>2</sub> (Zaehle et al., 2014; Zhu et al., 2019), more basic questions remain regarding soil microbial stoichiometry. Challenging the traditional experimental conclusion that nitrogen does not limit soil microbial growth, the foundational model of Schimel and Weintraub (2003) showed that changes in resource utilization may keep respiration constant even when microbes are nitrogen limited. Subsequent work has extended this approach to show how stoichiometric traits may drive a broader range of carbon transformations: for instance, the priming effect, whereby organic matter breakdown increases with the addition of carbon sources (Perveen et al., 2014, with two guilds of microbes; Cheng et al., 2014, focusing on root exudates; and Kyker-Snowman et al., 2020, at the Earth system scale). Beyond models focusing on heterotrophic respiration, work at the ecosystem scale has developed an increasingly

sophisticated understanding of the role of soil microbes in varied biogeochemical transformations such as nitrogen, phosphorus and methane cycling (Niu et al., 2016; Xu et al., 2016), and integrating a full suite of microbial processes into broad-scale models remains a field of active development (e.g. Nevison et al., 2022). Here too, trait-based approaches like those we review for carbon cycling provide important ways forward.

Ecosystem models have also begun to pay increasing attention to interactions between soil microbes and other trophic levels. For instance, there is growing recognition that soil fauna may affect soil microbial responses to global change (Grandy et al., 2016). Building upon early ecosystem models of the soil food web (Patten, 1972), recent work has highlighted the importance of functional redundancy (Zheng et al., 1997) and interactions between below- and above-ground food webs (Zou et al., 2016). Another focus of recent ecosystem modelling is the mutualism between mycorrhizal fungi and their plant hosts, though its combination of stoichiometric and trophic processes has been particularly challenging to represent. Accordingly, recent ecosystem models have used widely divergent structures to represent this reciprocal flux, ranging from plant-controlled (the MySCaN model of Orwin et al., 2011, illustrated in Figure 2b and Box 1.2), to a 'biological marketplace' (Franklin et al., 2014) or even fungus-controlled (Baskaran et al., 2017), yielding contrasting predictions regarding plant productivity.

### 2.2.2 | Future directions: Scaling ecosystem models up and down

Models designed from the perspective of ecosystem ecology use more complex structures (e.g. Box 1.2) to encode stoichiometric and trophic interactions; accordingly, they employ a more complicated suite of traits. Thus, important questions remain before current advances in ecosystem modelling can be applied globally. Many of the processes they represent are poorly understood: There are no standard model formulations for soil fauna (Grandy et al., 2016) or mycorrhizal exchange, for instance. Furthermore, as global models incorporate microbial processes beyond heterotrophic respiration (reviewed in e.g. Niu et al., 2016; Xu et al., 2016), interactions between biogeochemical cycles will become another important uncertainty. Nonetheless, judicious use of ecosystem modelling has the potential to identify minimal model structures and traits that may be applied at a global scale. The minimalistic SYMPHONY model (Perveen et al., 2014), for example, was designed with this aim in mind and thus captures priming using only five model compartments and eight parameters. Even models too complex for direct application to the Earth system scale may identify key traits for broader application: The fraction of plant photosynthate allocated to mycorrhizal fungi, for instance, emerges in multiple complex ecosystem models (Baskaran et al., 2017; Orwin et al., 2011) as a trait controlling ecosystem-level consequences of mycorrhizal exchange. Since ecosystem models summarize processes at lower scales, efforts to validate them for predictive purposes can also take advantage of work at finer resolutions.

## BOX 2 Microbial traits in four representative models

For each of the models described in Figure 2 and Box 1, we provide the equation (or algorithm) determining microbial biomass and highlight the microbial traits employed. In all cases, traits are represented as fixed biological parameters (names or descriptions given in italics).

### 1. The Microbial-Mineral Carbon Stabilization model (Earth system)

The *r*- and *K*-selected microbes differ in *uptake ability* (Michaelis–Menten constants  $V_{\max[i,\text{pool}]}$ ,  $K_{m[i,\text{pool}]}$ ), *growth efficiency* ( $\text{MGE}_{[i,\text{pool}]}$ ) and *biomass turnover* ( $\tau_{[i]}$ ). Thus, per capita growth of functional group *i* (*r* or *K*) is given by the differential equation:

$$\frac{1}{\text{MIC}_i} \cdot \frac{d\text{MIC}_i}{dt} = \overbrace{\text{MGE}_{[i,\text{met}]} \cdot \frac{V_{\max[i,\text{met}]} \cdot \text{LIT}_{\text{met}}}{K_{m[i,\text{met}]} + \text{LIT}_{\text{met}}}}^{\text{metabolic litter utilization}} + \overbrace{\text{MGE}_{[i,\text{str}]} \cdot \frac{V_{\max[i,\text{str}]} \cdot \text{LIT}_{\text{str}}}{K_{m[i,\text{str}]} + \text{LIT}_{\text{str}}}}^{\text{structural litter utilization}} + \overbrace{\text{MGE}_{[i,\text{a}]} \cdot \frac{V_{\max[i,\text{a}]} \cdot \text{SOM}_a}{K_{m[i,\text{a}]} + \text{SOM}_a}}^{\text{available SOM utilization}} - \overbrace{\tau_{[i]}}^{\text{turnover}} \quad (4)$$

Each microbe produces chemically distinct necromass, determined by three traits for *necromass composition* ( $f_{c[i]}$ ,  $f_{a[i]}$ ,  $f_{p[i]}$ ), and varies in its *enzymes' ability to access recalcitrant SOM* ( $\text{KO}_i$ ).

### 2. Mycorrhizal organic nutrient uptake and carbon storage (ecosystem)

At each time step, the change in nitrogen in mycorrhizal fungal biomass is:

$$\Delta N_{\text{myc}} = N_{\text{lit}} \cdot \overbrace{\frac{M_{\text{myc,lit}} \cdot C_{\text{myc}}}{K_{m,\text{myc,lit}} + C_{\text{myc}}} \cdot \max\left(2 - I_{\text{myc,lit}}^{(\text{C:N})} / (\text{C:N})_{\text{lit}}, 0\right)}^{\text{litter nitrogen uptake}} - \overbrace{N_{\text{myc}} \cdot M_{\text{N}}^{(\text{transf})} \cdot (1 - R_{\text{leaf,N}}) \cdot 5 \left(1 - (\text{C:N})_{\text{myc}} / I_{\text{myc,transf}}^{(\text{C:N})}\right)}^{\text{nitrogen transfer to plant}} - \overbrace{\tau_{\text{myc}} \cdot N_{\text{myc}}}_{\text{death}} \quad (5)$$

Similarly to other models, Michaelis–Menten *nitrogen uptake traits*  $M_{\text{myc,lit}}$ ,  $K_{m,\text{myc,lit}}$  and a *turnover rate*  $\tau_{\text{myc}}$  control cycling. Flexible *fungal and litter stoichiometry*  $(\text{C:N})_{\text{myc}}$ ,  $(\text{C:N})_{\text{lit}}$  necessitates additional traits: critical stoichiometric ratios for *nitrogen uptake*  $I_{\text{myc,lit}}^{(\text{C:N})}$  and for *resource exchange*  $I_{\text{myc,transf}}^{(\text{C:N})}$  plus *nitrogen transfer ability*  $M_{\text{N}}^{(\text{transf})}$ .

### 3. Resource ratio theory and litter decomposition (community)

The constant stoichiometry of fungal biomass constrains ectomycorrhizal carbon and nitrogen uptake, so that ectomycorrhizal growth is:

$$\frac{1}{M} \cdot \frac{dM}{dt} = \overbrace{L_M + R_M - X - D}^{\text{nitrogen flux}} = \overbrace{\chi \cdot X - \rho_M \cdot R_M - D}^{\text{carbon flux}} \quad (6)$$

For nitrogen,  $L_M$ ,  $R_M$  represent uptake of the labile and recalcitrant pools, up to a maximum determined by (linear) *labile and recalcitrant nitrogen uptake ability*  $r_{\ell M}$ ,  $r_{r M}$ ;  $X$  represents nitrogen traded to plants. For carbon, the trading rate  $\chi$  determines carbon return from the plant and the *cost of recalcitrant nitrogen use*  $\rho_M$  determines losses due to recalcitrant nitrogen uptake. *Death*  $D$  removes carbon and nitrogen from the biomass pool. Fully specified equations are obtained by optimizing uptake and trading to maximize growth.

### 4. Social dynamics within decomposer communities (physiological)

For each grid cell, microbial biomass is updated in the following six steps:

- Mortality according to *catastrophic mortality probability*  $m$ , with *necromass composition fractions*  $F_{\text{CC}}$ ,  $F_{\text{NC}}$  and  $F_{\text{DOM}}$
- C and N uptake: organic nutrients according to *uptake ability*  $U_{\text{adj}}$  and inorganic N up to 95% (species-independent) of the pool.
- Maintenance respiration*  $R_{\text{maint}}$ : if C is insufficient, the microbe respire biomass or dies.
- Investment in enzyme synthesis*  $E_{\text{fr}}$ , with *fractions of enzymes attacking each resource pool*  $E_{\text{FPS}}$ ,  $E_{\text{ICMR}}$ ,  $E_{\text{INMR}}$ . Enzymes follow species-independent Michaelis–Menten kinetics ( $k_{m,x}$ ,  $k_{\text{cat},x}$ ).
- Growth with a certain *fraction of carbon respired*  $R_{\text{ge}}$ , limited by C:N ratio  $M_{\text{CN}}$ .
- Colonization of an adjacent site if growth exceeds *maximum size*  $S_{\text{max}}$ .



## 2.3 | The community perspective: How can interspecies interactions affect ecosystems?

Community ecology looks within communities, the living components of ecosystems, and applies a rich body of theory to study species and their interactions. Due to this emphasis on generalizable theory, models from the community perspective often prioritize conceptual understanding over quantitative prediction, adopting simple structures amenable to theoretical analysis. Although community processes may indeed underpin ecosystem patterns, quantitative synthesis between the community and ecosystem perspectives remains elusive, in part due to incongruous theoretical underpinnings: Community models may overlook energy and nutrient flows in order to focus on species diversity, while ecosystem models must drastically simplify this very diversity in order to confront the broad scale of the cycles they investigate (Loreau, 2010). In mathematical terms: Community models may subsume physical processes determining growth into a few abstract parameters (e.g. self-limitation, mortality or resource supply), while ecosystem models may collapse functionally diverse organisms into a single state variable (e.g. microbial biomass). While incorporating a full complement of interacting species into ecosystem models might increase realism, such improvements in mechanistic detail can rapidly increase complexity and impair efforts to fit and validate these models. As a result, global change ecologists must often make a difficult choice between two mutually exclusive perspectives.

### 2.3.1 | State of the art: Bridging communities and ecosystems with consumer–resource theory

Resource-based models of species interactions (MacArthur & Levins, 1967; Tilman, 1982) may provide an important link between the theories of community ecology and the global change questions from ecosystem and Earth system perspectives. Alongside more traditional phenomenological models (such as the Lotka–Volterra models), these *consumer–resource models* provide a mechanistic foundation for species interactions by incorporating one or more resources (e.g. prey, environmental factors or abiotic nutrients). At their most general, such approaches model resource inputs  $I$  and uptake by two or more species with populations  $N_1, N_2, \dots$ :

$$\text{change in resource} = \text{input} - \text{uptake from consumers} \quad \frac{dR}{dt} = \underbrace{I(R, \dots)}_{\text{input function}} - \underbrace{u_1(R, \dots) \cdot N_1}_{\substack{\text{resource uptake} \\ \text{by species 1}}} - \underbrace{u_2(R, \dots) \cdot N_2}_{\substack{\text{resource uptake} \\ \text{by species 2}}} - \dots \quad (3)$$

Because species differ in their per capita resource uptake  $u_1, u_2, \dots$  (according to one or more traits in the model), competition may result in species coexistence or extinction. The community outcome, in turn, determines the system's final resource dynamics. Thus, this approach leverages a small number of traits to provide a fundamental link between community structure and resource dynamics (Zakharova et al., 2019). In one of its classic applications to

community ecology, for example, MacArthur (1969) used it to show that competition tends to maximize the utilization of resources. In an early application of the framework to plant–soil microbe interactions, Miki et al. (2010) demonstrated fundamental links between soil microbe functional diversity and plant coexistence. Linking consumer–resource theory to large-scale carbon cycling, Smith and Wan (2019) subsequently investigated whether competition between ectomycorrhizal and saprotrophic fungi can suppress litter decay (the so-called Gadgil effect). Extending the classic ‘resource ratio’ (or  $R^*$ ) model of Tilman (1982), this approach (summarized in Figure 2c and Box 1.3) provided general mathematical conditions relating litter and fungal traits to resource dynamics, highlighting ectomycorrhizal recalcitrant nitrogen uptake and plant litter recalcitrance as key traits determining litter decomposition.

### 2.3.2 | Future directions: Applying the community–ecosystem synthesis to soil microbes

Taking advantage of shared methodologies including consumer–resource dynamics, recent theoretical developments in plant ecology have synthesized community theory with ecosystem questions to investigate functional consequences of biodiversity (reviewed in Loreau, 2010). Although empirical studies have already emphasized importance of soil microbial diversity for ecosystem function (van der Heijden, 1998), relatively few community models (e.g. Loreau, 2001; Miki et al., 2010) have applied this conceptual synthesis to model soil microbial communities. Despite the potential of this emerging theory to inform larger scale models of microbial biogeochemistry, conceptual issues remain. In comparison to the plant communities where such work has already been applied, microbial communities have much higher species richness and thus more complex dynamics. The metabolic diversity of microbes produces a much more complex set of interactions (Muscarella & O'Dwyer, 2020) than occur between plants. Accordingly, existing model structures may be difficult to relate to empirical measurements, or fail to capture mechanisms specific to soil microbes. Consumer–resource models, for instance, permit only a limited degree of species coexistence (Tilman, 1982) and do not explicitly represent the physical processes controlling resource availability. Thus, the theoretical community ecology of soil microbes may move

forward in two ways: first, by finding specific questions to which existing models can be adapted (Miki et al., 2010; Smith & Wan, 2019) and second, by seeking tractable model structures that capture microbe-specific processes (e.g. Muscarella & O'Dwyer, 2020). In both cases, such efforts may take advantage of perspectives not only from within community ecology but also from mechanistic models at even smaller scales.

## 2.4 | The physiological perspective: How do the physiology and spatial distribution of microbes affect carbon cycling?

Incorporating the most mechanistic detail, the physiological perspective considers microbial individuals and their interaction with the microscopic world. Thus, in contrast to broader scale models employing homogeneous pools (i.e. compartment modelling), fine-scale models must adopt mathematical frameworks that directly include heterogeneity. *Individual-based modelling*, for instance, tracks individual organisms and their distribution in space through a series of discrete time steps, allowing them to more realistically represent the basic biology of individuals (Judson, 1994). In contrast, methodologies including *partial differential equation models* (Holmes et al., 1994), *integrodifference equations* (Lutscher, 2019) and *integral projection models* (Merow et al., 2014) use continuous mathematical distributions to model the traits, locations and/or abiotic environments of organisms. These approaches have long been applied to model microbial growth from a physiological perspective (Boswell & Davidson, 2012; Ferrer et al., 2008), often applying some representation of carbon dynamics towards this aim (e.g. Paustian & Schnürer, 1987). Nonetheless, the development of fine-scale models of soil carbon dynamics with the explicit intention of improving global change projections remains a field of active development.

### 2.4.1 | State of the art: Applying fine-scale microbial perspectives to carbon cycling

Soil microbes interact with an incredibly spatially and chemically complex soil environment, which models at the fine scale have begun to link to soil carbon cycling. Such approaches have been applied to explicitly study microbial enzymes (Forney & Rothman, 2007) and the three-dimensional structure of soil (Nguyen-Ngoc et al., 2013). From a more theoretical perspective, Bosatta and Ågren (1985) applied an integrodifference model with carbon 'quality' as a continuous spectrum to demonstrate the importance of substrate quality for microbial stoichiometry, an approach later extended e.g. to vertical spatial structure (Bosatta & Ågren, 1996) and microbial physiology (Sainte-Marie et al., 2020). In another demonstration that the stoichiometry of soil biogeochemical cycles varies according to microscale processes, Kaiser et al. (2014) used an individual-based model to show that microscale interactions between microbial functional groups can overcome the effects of nitrogen limitation.

Recent research has also shown the importance of social dynamics between competing microbes that can only be explicitly modelled using a spatial framework. Using an individual-based model of soil organic matter breakdown by microbial enzymes, Allison (2005) showed that spatial structure allows 'cheater' microbes (which benefit from extracellular enzymes produced by other microbes) to locally dominate, decreasing decomposition efficiency. Subsequent work by Kaiser, Franklin, et al. (2015) using a similar individual-based

model (summarized in Figure 2c and Box 1.4) showed that this process can also induce soil nitrogen retention and organic matter build-up, while Evans et al. (2016) applied the model to provide a novel mechanistic explanation for the poorly understood Birch effect (a pulse of microbial respiration observed upon rewetting of dry soils).

### 2.4.2 | Future directions: Generalizing insights from fine-scale models

While spatially and chemically explicit models excel at encoding mechanistic detail, they employ mathematical frameworks not directly compatible with the compartment modelling approach applied at the three larger scales. Nonetheless, as our theoretical and empirical understanding of fine-scale soil processes improves, such models have the potential to inform global predictive efforts. Developments in the related field of vegetation modelling offer one glimpse of the path forward. Informed by fine-scale plant physiology and demography, the Ecosystem Demography (ED) approach of Moorcroft et al. (2001) built a stochastic individual-based model of forest tree growth, using discrete functional types to capture trait variation, then quantitatively scaled this into an ecosystem-scale partial differential equation model. Numerous adaptations of this approach (reviewed in Fisher et al., 2018) have produced dynamic vegetation models (DVMs) applied at regional to global scales. Although similar transformations of fine-scale microbial models may one day inform large-scale prediction, doing so will require an understanding of the microbial processes and traits that control biogeochemical fluxes across scales.

## 3 | THE UNRESOLVED PROBLEM OF SCALE IN TRAIT-BASED MODELS

Functional traits have been highlighted as a way towards increased generality in ecological models, yet applying this insight requires identifying which functional traits matter. Furthermore, the large number of processes, questions and models of microbial biogeochemistry has spawned a large selection of traits and trait definitions across scales. Although the four scales we review above have each produced useful insight into carbon cycling, it remains challenging to synthesize these insights across all scales. In this section, we discuss commonalities that may help unify these disparate scales. In order to highlight obstacles to conceptual progress, we also discuss current limitations of trait-based modelling approaches. Using the four illustrative models summarized above (Figure 2; Box 1) as a case study, we show how traits control microbe-mediated carbon cycling in each model (Box 2) and discuss what it means for models at different scales to be 'trait-based' (subsection 'Four trait-based models: a case study'). Although similar traits are indeed used at different scales, we caution that such traits nonetheless have very different ecological interpretations, complicating efforts to combine modelling

perspectives and to inform models using empirical measurements (subsection 'Pitfalls of scaling traits').

### 3.1 | Four trait-based models: A case study

What does it mean for models at different scales to be 'trait-based'? In [Box 2](#), we address this question by using model equations to examine the microbial traits used in the four representative models. Though these models do not represent all possible modelling choices or all traits, we use this exercise to illustrate general ways in which trait-based modelling varies by scale. In particular, we focus on how scale determines the interpretation of traits that measure similar processes.

The diverse motivations and structures of our four representative models translate to divergent approaches to microbial traits. Models with more pools require a correspondingly larger number of traits (e.g. MIMICS in [Box 2.2](#)); similarly, models aiming for greater realism choose traits more closely tied to physiology (e.g. the physiological model in [Box 2.4](#)). Nonetheless, we identify key commonalities between each model's set of traits. Broadly, traits fall into four categories, as detailed in [Table 1](#): resource acquisition (including enzyme production, enzymatic activity and nutrient uptake), resource use (allocation of resources to growth and other physiological processes), mortality (death or turnover of microbial biomass) and recycling (composition of dead microbial biomass as it moves to other model pools).

The four models use similar traits to represent related processes. Resource (carbon or nutrient) uptake involves some process with Michaelis–Menten kinetics in all models except the community model of Smith & Wan (2019), though the linear uptake constant there may be derived as an approximation to a Michaelis–Menten response. Similarly, all four models implement some form of fixed per-capita mortality—the turnover rates of MIMICS and MySCaN, the death rate of Smith and Wan (2019) and the catastrophic mortality probability of Kaiser, Franklin, et al. (2015)—though MySCaN and Kaiser, Franklin, et al. (2015) also include additional specific mechanisms of mortality (grazing and starvation, respectively). As such, key traits identified at one scale may serve as starting points for the analysis of models at other scales. Nonetheless, we caution that such similarity may disguise two subtle but important distinctions in the interpretation of model traits:

1. **Context dependence: Microbial traits must be interpreted within the context of other modelling decisions.** Since model traits are abstractions that aggregate multiple lower-level processes, their precise meaning depends on the set of processes included in a specific model. For instance, though MIMICS (Earth system) and MySCaN (ecosystem) each include traits parameterizing Michaelis–Menten carbon uptake, as well as growth efficiency on acquired carbon, only MySCaN explicitly represents nitrogen stoichiometry. Accordingly, the maximum uptake rate ( $V_{\max}$ ) trait and growth efficiency of MySCaN determine microbial growth in the theoretical absence of nitrogen limitation; in contrast, the corresponding traits in MIMICS implicitly include the effect of mineral nutrient limitation. Indeed, in simulations testing MIMICS against nitrogen deposition experiments, Wieder, Grandy, et al. (2015) vary the maximum uptake and growth efficiency traits depending on nitrogen levels. Thus, researchers should consider the entire suite of traits and processes in a model before determining how to use empirical data to parameterize and test a model.
2. **Scale dependence: The meaning of microbial traits varies across scales.** In some cases, similarly named traits parameterize aggregated responses in large-scale models, but directly represent local processes in smaller scale models. For instance, the Michaelis–Menten traits in the MySCaN and MIMICS models parameterize the carbon uptake of the entire microbial pool, but those of Kaiser, Franklin, et al. (2015) (physiological) directly correspond to enzyme kinetics. Although these two sets of traits can be related quantitatively, they should not be considered identical (a point which we explore below). Additionally, even when traits do measure the same process, they cannot be considered identical when model pools are differently defined. All traits in the ecosystem and Earth system examples, for instance, concern the complete microbial compartment, while those in the community model describe populations of contrasting functional guilds, and those in the physiological model apply to microbial individuals. Because traits cannot simply be reapplied or averaged when moving from smaller to larger scales (explored below), scale creates unresolved challenges (Geyer et al., 2016) when synthesizing trait-based microbial models with each other and with empirical data.

### 3.2 | Pitfalls of scaling traits

A key strength of the trait-based approach is the potential to quantitatively link models to other models and to experimental data (Fry et al., 2019). Yet, as our case study above highlights, making these quantitative connections requires accounting for differences in trait definitions at different scales. We illustrate quantitative incompatibilities between trait definitions at different scales using a series of simulations ([Figure 3](#); [Appendix S1](#)). Starting with a model at a finer scale—(a) ecosystem, (b) community or (c) physiological—we attempt to predict the system's behaviour at a broader scale by naively reapplying lower-level traits. In each case, such extrapolation fails due to emergent processes (Bradford et al., 2017; Wilson & Gerber, 2020) that must be explicitly included in order to make accurate predictions.

Using experiments to parameterize trait-based models may also be complicated by scale. The definition of model pools may be difficult to reconcile with experimental approaches: resource pools intended to capture the complexity of resource dynamics in soil (e.g. accessible and protected soil organic matter) often lack precise chemical definitions (Abramoff et al., 2018), preventing direct measurement of corresponding traits. Indeed, all four representative

TABLE 1 Summary of traits from four representative models

Process	Representative model	Traits
Resource acquisition	Earth system: MIMICS (Wieder, Grandy, et al., 2015; Box 2.1)	Michaelis–Menten carbon uptake ( $V_{\max}$ , $K_m$ ) (substrate-specific), enzymatic access to recalcitrant soil organic matter
	Ecosystem: MySCaN (Orwin et al., 2011; Box 2.2)	Michaelis–Menten nitrogen uptake, critical carbon:nitrogen ratio for nitrogen uptake
	Community: Smith & Wan, 2019 (Box 2.3)	Linear nitrogen uptake ability (substrate-specific), carbon cost of recalcitrant nitrogen use
	Physiological: Kaiser, Franklin, et al., 2015 (Box 2.4)	Investment in enzyme production, ratios of enzymes for different pools, uptake ability per unit biomass, <i>Michaelis–Menten carbon breakdown (enzyme-specific; no variation by species)</i>
Resource use	Earth system: MIMICS	Substrate-specific microbial growth efficiencies
	Ecosystem: MySCaN	Critical carbon:nitrogen ratio for mycorrhizal exchange
	Community: Smith	Carbon cost of recalcitrant nitrogen use, <i>growth efficiency inherent in definition of model units (no variation by species)</i>
	Physiological: Kaiser	Maintenance respiration per unit biomass, fraction of carbon allocated towards growth that is respired, microbial carbon:nitrogen ratio, maximum size before microbial division
Mortality	Earth system: MIMICS	Biomass turnover rate
	Ecosystem: MySCaN	Biomass turnover rate, susceptibility to grazing
	Community: Smith	<i>Death rate (no variation by species)</i>
	Physiological: Kaiser	Catastrophic mortality probability, maintenance respiration per unit biomass
Recycling	Earth system: MIMICS	Necromass composition ratios (available:recalcitrant:protected soil organic matter)
	Ecosystem: MySCaN	<i>Necromass composition ratio (slow:resistant organic matter, no variation by functional group)</i>
	Community: Smith	<i>[no biomass recycling: necromass leaves the system]</i>
	Physiological: Kaiser	Necromass composition ratios (carbon-rich:nitrogen-rich:dissolved organic matter)

models tuned the value of one or more traits, rather than relying solely on empirical measurements. Furthermore, even when model pools are measurable, the scaling challenges illustrated in our model-based simulations (Figure 3) may make it challenging to measure traits at the correct scale. For instance, since diverse microbial communities may be challenging to directly manipulate, experimental work at community and ecosystem scales often measures processes at the level of the entire microbial pool (e.g. total respiration in a soil sample) rather than the demographic and physiological rates defined in finer scale models.

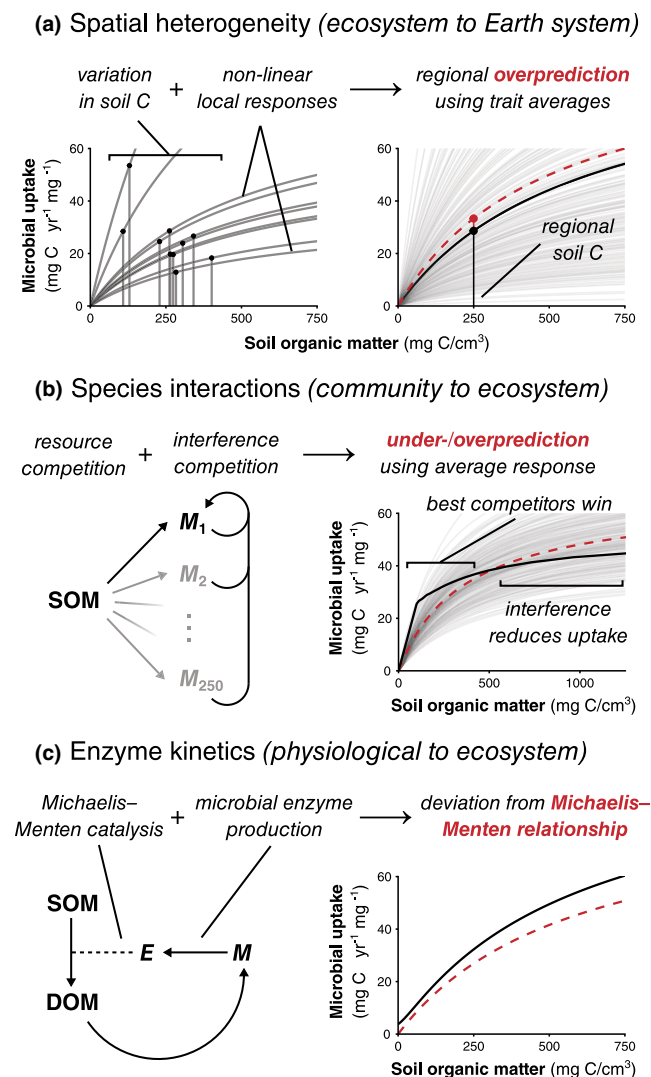
## 4 | UNIFYING THE SCALES OF MICROBIAL BIOGEOCHEMISTRY

Despite the difficulties posed by incompatible trait definitions across scales and between models and experiments, trait-based modelling remains a powerful tool for synthesizing a robust understanding of soil microbial biogeochemistry in the face of global

change. In particular, we discuss how quantitative modelling efforts can directly investigate multiple scales, how collaboration between model-driven work and empirical research can improve our understanding of biogeochemistry, and finally how work from different perspectives can improve conceptual understanding and drive model development. Though we focus here on soil carbon cycle modelling, our general recommendations can also apply to other microbial processes, especially as models increasingly represent them at broad scales.

### 4.1 | Quantitative: Linking scales with mean-field approaches

Although the challenge of modelling multiple scales means that few studies quantitatively link more than one scale, newer mathematical tools provide model builders with the possibility of robustly drawing these connections. One productive insight into biogeochemical modelling has been to apply tools used in physics (e.g.



**FIGURE 3** Simulations (Appendix S1) demonstrating challenges of upscaling trait-based models. In each panel, lower-level mechanisms cause the response of carbon uptake to levels of soil organic matter (SOM; solid black line) to deviate from predictions made using simplifying assumptions (dotted red line). (a) Spatial heterogeneity among local sites leads to incorrect predictions at the regional scale. We vary local soil SOM (vertical lines) and microbial responses (curves) randomly (left panel). Averaging 1000 sites (right panel), we find that uptake is systematically less than predicted using average traits. (b) Species interactions cause emergent responses. We simulate resource and interference competition between 250 microbial species ( $M_1, \dots, M_{250}$ ) with a randomly distributed responses to SOM (grey curves). At low SOM, the community outperforms the average response because resource competition selects the best competitors; at high SOM, strong interference instead suppresses uptake. (c) Production of an extracellular enzyme ( $E$ ) converting SOM to dissolved organic matter (DOM) in a classic physiological model (Allison et al., 2010; left) creates non-Michaelis-Menten uptake response (right), despite the Michaelis-Menten kinetics of the enzyme itself (dashed red line)

statistical mechanics) to investigate the bulk behaviour of systems where individual interactions are complex and highly numerous. These approaches, producing so-called *mean-field models*, vary in

complexity and frequency of application within ecology (Morozov & Poggiale, 2012). In community ecology, for instance, such techniques have had a long and productive history. In what was later termed *modern coexistence theory*, Chesson (2000) provided a framework for understanding the role of spatial and temporal heterogeneity in species coexistence; thanks to its generality, this theory provided a unifying framework for models of coexistence (Barabás et al., 2018). A related approach (Barbier et al., 2018) uses techniques from statistical physics to predict community properties from average interactions within a community; here, traits are not fixed parameters but rather statistical distributions. Indeed, application of such techniques to global microbial biogeochemistry has demonstrated that they might be used in Earth system contexts to capture local-scale heterogeneity (Wilson & Gerber, 2020).

Another potential solution, termed *targeted simulation*, is used elsewhere in Earth system modelling to simplify physical processes that are too computationally expensive to explicitly model at a global scale. Used, for example, to represent cloud dynamics (Grabowski & Wang, 2013), targeted simulation uses high-resolution mechanistic simulations to determine a value for a parameter that approximates the process in a lower-resolution model. As our ability to model soil microbial communities at the finest scales improves, such an approach—or extensions that leverage statistical estimation or machine learning (Fry et al., 2019; Schneider et al., 2017)—may provide a way to derive higher-level trait values from simulations incorporating fine-scale experimental data.

## 4.2 | Empirical: Synthesizing models and experiments across scales

As we have cautioned in this review, the traits used in quantitative models of biogeochemistry are not necessarily the same as the ones accessible to empirical researchers. Indeed, unlike the experimentally determined first-order decay constants in current Earth system models, microbial traits in most next-generation soil submodels cannot be empirically measured (Abramoff et al., 2018). Though the quantitative and conceptual strategies highlighted above may mitigate this problem, it remains clear that more reliable representation of Earth system modelling in soil processes will require better empirical information to validate model structures and constrain model parameters, which currently contribute high uncertainty to soil models (Todd-Brown et al., 2013).

Improved empirical techniques may offer one route to better trait measurements. High-resolution scanning technologies may inform models at microscopic scale (Nguyen-Ngoc et al., 2013), improving our understanding of individual-level physiological traits, while new methods for tracing nutrient flow in biotic interactions may determine which organismal traits control the mycorrhizal symbiosis (Kaiser, Kilburn, et al., 2015; Whiteside et al., 2009). Applied to models designed to include more measurable pools (Abramoff et al., 2018), such physiological information could ultimately inform more realistic Earth system predictions.

Some of the challenges in connecting empirical traits to model parameters concern scale. Ecosystem-, community- and individual-level traits, for instance, are not directly substitutable despite their similarities. By highlighting some of the ways in which trait definitions depend on scale, we hope to motivate empiricists to design targeted studies that specifically address scaling challenges. In particular, a *model community* approach has successfully been used in plant ecology to quantify the effects of community composition on ecosystem function. Though most work on soil microbes has focused on single species or on entire natural communities, increasing ability to culture these cryptic organisms and constantly growing genomic repositories may help researchers design model soil communities (Bengtsson-Palme, 2020) that mechanistically explore linkages between individual- and community-level traits.

### 4.3 | Conceptual: Unifying theories of microbial biogeochemistry

Though quantitative and empirical approaches provide a promising new approach to linking scales, the most important contribution of trait-based modelling to date has been conceptual. Community-scale approaches (e.g. *r*-/*K*-selection life-history theory) have already informed the design of ecosystem- and Earth system-scale models, for instance, by motivating the definition of model compartments (e.g. the *r*- and *K*-selected microbial pools of Wieder, Grandy, et al., 2015). Development of plant models offers a glimpse into the potential of trait-based microbial modelling. Decades of conceptual advances in plant functional ecology are now succinctly summarized in the handful of trait-based plant functional types used in current Earth system models (Wullschlegler et al., 2014). As fine-scale models identify the most important local mechanisms driving biogeochemistry, a theory of microscale effects on carbon cycling will similarly be able to inform high-level approximations to these processes at the Earth system scale. Mechanistic understanding of the priming effect, for instance, has already been incorporated into an Earth system model run (Guenet et al., 2016), albeit without explicit representation of the microbes responsible for the effect. At the ecosystem scale, Perveen et al. (2014) found that guild-level stoichiometric differences were key for reproducing a carbon priming effect, while from a community perspective, Smith & Wan (2019) found that nitrogen uptake traits were the driver of mycorrhizal suppression of decay.

Deriving conceptual insight into model traits is therefore important at all scales of modelling. Because complex models are harder to simulate and analyse, we thus suggest that model builders working at all scales should investigate the minimal level of model complexity needed to produce realistic dynamics. Though many models use Michaelis–Menten kinetics to represent carbon uptake, for instance, some instead employ linear uptake (e.g. Perveen et al., 2014; Smith & Wan, 2019) and few models at the ecosystem scale have compared the two formulations.

In line with empiricists' efforts to work with a more consistent set of traits (Dawson et al., 2019; Treseder & Lennon, 2015), we expect that that consensus on key parameters will emerge among model builders, along with an awareness of how these parameters depend on scale. Working in this direction, Geyer et al. (2016) highlighted carbon use efficiency as a key determinant of soil carbon storage, but identified three different versions of the concept at different scales: a species-specific physiological trait, a community-level value (corresponding most closely to 'microbial growth efficiency' as reviewed here) and an ecosystem-level measurement. In tandem with our other recommendations, conceptual synthesis may thus provide a framework that links scales and connects models to experiments.

## 5 | CONCLUSION

Global environmental change challenges modern ecology to develop new ways of looking at living systems. A changing climate affects all levels of biological organization: from single molecules, to whole species, to the entire biosphere. Therefore, understanding carbon cycling under global change requires ecologists to understand the interactions between these levels. Taking advantage of the ability of trait-based modelling to unite these scales, quantitative ecologists may be poised to incorporate multiple perspectives to better predict carbon cycle feedbacks. By clarifying verbal hypotheses, identifying traits that matter most, and showing how these traits relate to lower level mechanisms, mathematical modelling has the potential to synthesize theoretical and empirical perspectives on microbial biogeochemistry across scales.

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The authors have no conflicts of interest to declare.

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J.W. and T.W.C. conceived the study; J.W. conducted the simulations and wrote the manuscript with input from T.W.C. Both authors contributed to revision and gave final approval for publication. This research was funded by grants to T.W.C. from DOB Ecology and Bernina Initiative.

### DATA AVAILABILITY STATEMENT

No data appear in the manuscript.

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