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## OPINION

# Microbial evolution—An under-appreciated driver of soil carbon cycling

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## Abstract

Although substantial advances in predicting the ecological impacts of global change have been made, predictions of the evolutionary impacts have lagged behind. In soil ecosystems, microbes act as the primary energetic drivers of carbon cycling; however, microbes are also capable of evolving on timescales comparable to rates of global change. Given the importance of soil ecosystems in global carbon cycling, we assess the potential impact of microbial evolution on carbon-climate feedbacks in this system. We begin by reviewing the current state of knowledge concerning microbial evolution in response to global change and its specific effect on soil carbon dynamics. Through this integration, we synthesize a roadmap detailing how to integrate microbial evolution into ecosystem biogeochemical models. Specifically, we highlight the importance of microscale mechanistic soil carbon models, including choosing an appropriate evolutionary model (e.g., adaptive dynamics, quantitative genetics), validating model predictions with 'omics' and experimental data, scaling microbial adaptations to ecosystem level processes, and validating with ecosystem-scale measurements. The proposed steps will require significant investment of scientific resources and might require 10–20 years to be fully implemented. However, through the application of multi-scale integrated approaches, we will advance the integration of microbial evolution into predictive understanding of ecosystems, providing clarity on its role and impact within the broader context of environmental change.

## KEYWORDS

biogeochemistry, carbon cycle, evolution, global change, microbe

## 1 | INTRODUCTION

Modern biological research has made substantial advances in predicting the ecological impacts of global change, with a central focus on understanding biosphere-climate feedbacks. These insights are typically derived from the environmental responses of either

ocean phytoplankton, shifts in vegetation function and patterns, and to a lesser extent, alterations in soil microbial biomass and activity (Crowther et al., 2019; Dutkiewicz et al., 2009; McDowell et al., 2020). Yet, a critical knowledge gap remains around the influence of evolution, particularly local environmental adaptation, on contemporary ecosystem processes (Abs et al., 2023; Urban

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et al., 2020). Microbes are especially pertinent to this discourse because of their high potential for rapid evolutionary responses and their impact on regulating global biogeochemical processes (Falkowski et al., 2008). Here we argue that microbial evolution is mostly ignored in current global biogeochemical cycle research; yet it can potentially strongly affect carbon (C) cycling, especially in response to climate change, and as such should be represented in future models (Figure 1). We further assert that a thorough exploration of microbial evolution's impact on biogeochemistry is not only scientifically interesting but also vital for constraining model parameters and constructing robust models rooted in empirical data.

We illustrate this point by focusing on the influence of microbial evolution on the soil-climate feedback, as soils harbor the largest reservoir of terrestrial organic C. Furthermore, the dynamics of soil organic C (SOC) can either exacerbate climate change through increased respiration of organic matter, thereby releasing carbon dioxide (CO<sub>2</sub>) to the atmosphere, or mitigate climate change through increased C storage in microbial biomass or mineral-associated soil organic matter (Kallenbach et al., 2016; Woolf & Lehmann, 2019). Soil microbes also interact with plants through nutrient exchange and competition, which affect both plant C cycling and soil C inputs (Stuart Chapin et al., 2009). Thus, changes in microbial functional traits regulating these processes, particularly those subject to high selective pressures, could alter soil CO<sub>2</sub> emissions and, in turn, affect climate.

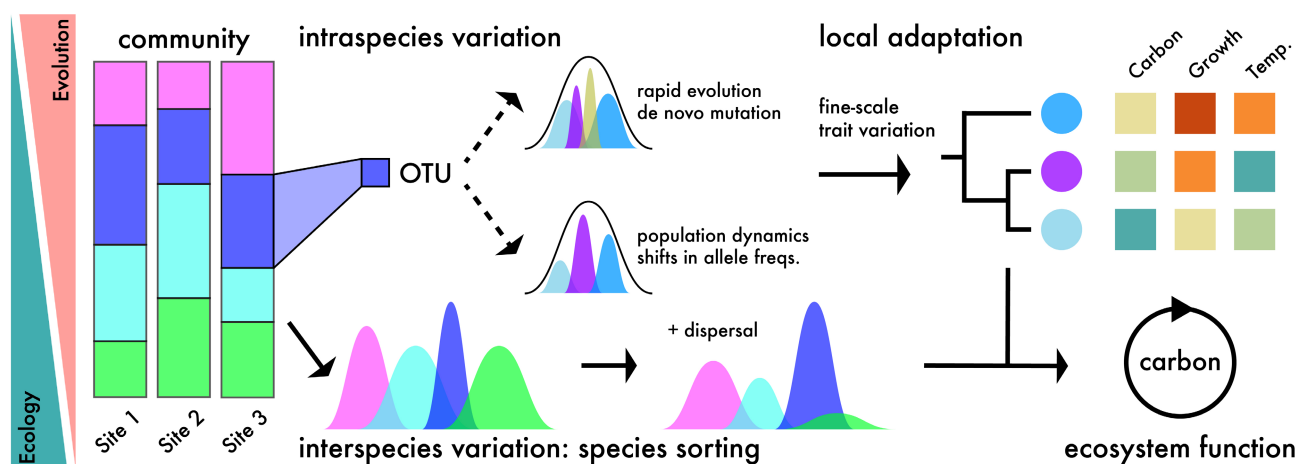
In this perspective article, we review the current state of knowledge about microbial adaptation to climate change and soil C biogeochemistry, and propose future directions regarding how to better integrate the impact of microbial evolution on soil carbon cycling in predictive models. First, we build a conceptual framework for defining microbial evolution in the context of soil carbon cycling. Second,

we develop our main hypothesis that microbial adaptation can strongly change the response of soil CO<sub>2</sub> fluxes to climate change by synthesizing empirical evidence on how microbial evolution affects the soil C response to climate change. Finally, we provide a roadmap for how to integrate microbial evolution into ecosystem biogeochemical models.

## 2 | CONCEPTUAL FRAMEWORK TO INVESTIGATE MICROBIAL EVOLUTION

### 2.1 | The traditional ecology–evolution divide is not appropriate for microbes

Microbial responses to environmental change are unique because ecological and evolutionary processes often occur simultaneously along a spatiotemporal continuum (Cohan, 2006; Loreau et al., 2023). For example, temporal turnover of soil fungi in ~1 week is equivalent to spatial turnover of taxa across 100 km (Averill et al., 2019). The distinction between evolution, defined as changes in allele frequencies within a population, and ecology, defined as changes in taxonomic abundances within a community, might be less relevant for microbes compared to larger organisms (Fraser et al., 2009; Rosselló-Mora & Amann, 2001). This reasoning centers around the challenges in delineating microbial taxonomic units that limit our capacity to distinguish between ecological and evolutionary processes. The uncertainty of what constitutes a microbial taxon and, by extension, a population (the fundamental unit of evolution), complicates studies of inter- and intraspecific interactions. Microbes do not abide by the traditional biological species concept: they reproduce asexually and exchange genetic material across disparate taxonomic lineages via



**FIGURE 1** Impact of microbial eco-evolutionary dynamics with consequences for ecosystem function. Communities across sites are composed of different operational taxonomic units (OTUs), a proxy for microbial species (here four OTUs are represented for simplicity). Yet, OTUs mask millions of years of evolutionary divergence, precluding insights into the evolutionary dynamics of microbial populations or other adaptive responses. When a community responds to environmental change, a continuum of ecological (i.e., interspecies variation) and evolutionary responses (i.e., intraspecies variation) shift taxonomic (species) and genetic (alleles) frequencies within the community. Shifts in functional traits (e.g., carbon degradation and temperature response) across taxa or within populations can be assessed by the degree of phylogenetic conservation to predict the overall functional response of the community.

horizontal gene transfer (HGT), which further convolutes evolutionary signals (Doolittle, 1999).

Ecological and evolutionary feedbacks in microbial systems likely operate on similar timescales. Microbial communities (microbiomes) are capable of responding to environmental change within a span of weeks, and on similar time scales, keystone niche constructing taxa can significantly reshape community functions such as organic matter recycling and creation of soil structure. Additional ecological processes such as succession and dispersal, are rapid and widespread in microbiomes with the potential to alter evolutionary and successional trajectories through the introduction of new alleles and/or introducing novel intra- and interspecific interactions (Bassar et al., 2021; Yoshida et al., 2003). As such, recent frameworks suggest shifting the focus from disentangling ecological and evolutionary processes to quantifying the diverse mechanisms by which compositional shifts occur across timescales and how they affect community function (Martiny et al., 2023) (Figure 2).

## 2.2 | Alternative framework: Historical versus contemporary processes

While there may be no clear divide between ecological and evolutionary processes in microbiomes, it is instructive to distinguish between historical and contemporary evolution. Historical evolution encapsulates the cumulative evolutionary pressures spanning tens to hundreds of millions of years, a process that governs trait variation among taxa that contribute to differential geographic distributions (i.e., phylogeography). In contrast, contemporary evolution denotes the ongoing adaptive responses within populations to environmental change, which takes place on the timescales of months to decades.

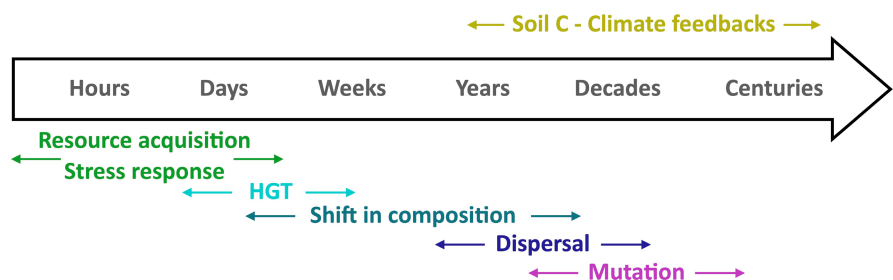
Different evolutionary processes operate across a wide range of timescales; however, mutations remain the source of new genetic variation. In microbes, it is estimated that there are ~1 million mutations per day in 1 g of soil (Wielgoss et al., 2013). Most of these random mutations will either be deleterious, synonymous, or emerge in noncoding regions, and only a small fraction proves advantageous under specific environmental conditions. Even in these rare instances, advantageous mutations must proliferate from a single cell to other individuals within a population to alter evolutionary dynamics. This process can occur through gene-specific (Chase et al., 2019; Shapiro et al., 2012) or genome-specific sweeps (Bendall et al., 2016) within a population that ultimately contribute to ecological differentiation between

populations (Arevalo et al., 2019). Whether this genetic exchange occurs among closely-related strains (via homologous recombination) or HGT among disparate lineages, the rapid acquisition of advantageous genes or entire genomic segments provides a genetic reservoir that is adaptive to environmental fluxes (Polz et al., 2013). Even so, transferred regions must provide a selective advantage to proliferate from low to high frequency within a population and, in the case of HGT, overcome costs of assimilating foreign genes (Baltrus, 2013; Gophna et al., 2004). Historical evolution is therefore expected to be mostly driven by long-term processes such as trait selection, while contemporary evolution might be mainly driven by faster processes such as HGT and shifts in population and allele frequencies.

## 2.3 | Historical evolution is needed to predict contemporary evolution

Historical and contemporary evolution are intertwined as historical environmental conditions constrain the potential for current and future changes. To predict how microbial evolutionary dynamics affect C cycling (i.e. contemporary evolution on a time scale of decades to centuries), we must concurrently consider the historical selective pressures that contribute to extant genetic diversity. For instance, historical evolutionary divergence governs contemporary patterns of functional diversity and biogeography, including at the population level, and constrains the potential for changes in allele frequencies in response to contemporary or future environmental change (Averill et al., 2016; Lehmann et al., 2020; Strickland et al., 2015). This effect of historical evolution on adaptive responses (at the community or population level), termed “legacy effect” is most evident in transplant studies, where microbiomes from one historical environment are transplanted into a new environment (Chase et al., 2021; Glassman et al., 2018). In these studies, communities originating from historically distinct climates degraded leaf litter differentially when transplanted into a common climate. However, legacy effects can vary across systems or be context-dependent; for example, historical evolutionary patterns may either impede (Brockhurst et al., 2007) or, conversely, facilitate adaptation (Blazantin & Turner, 2021) to new conditions. To predict the direction and intensity of historical evolution's impact on contemporary evolution in a specific location, the next steps could involve focusing on particular legacy effects and testing them through transplant or common garden experiments, or identifying patterns in data that indicate the legacy effects of a particular system.

**FIGURE 2** Timescales of microbial response processes and C cycling. Environmental fluctuations and soil–plant feedbacks that drive microbial responses occur at all temporal scales along this gradient. Source: Adapted from Abramoff et al. (2018). HGT, horizontal gene transfer.



### 3 | RATIONALE FOR INTEGRATING MICROBIAL EVOLUTION INTO BIOGEOCHEMICAL MODELS

#### 3.1 | Evidence for rapid microbial evolution under laboratory conditions

The impact of microbial evolution on short-term C cycling has been empirically observed with lab-based evolution experiments. In these experiments, microbes are exposed to a strong selective pressure (e.g., temperature or C substrate) while controlling other external factors. Famously, Travisano and Lenski (1996) demonstrated that microbial C metabolism evolved in response to differential substrate availability (glucose and citrate) insomuch that some evolved *Escherichia coli* populations escaped historical evolutionary constraints via de novo mutations to use citrate, a novel substrate for this taxon. Even in eukaryotic microbes, Romero-Olivares et al. (2015) showed that fungal strains adapted to variable temperatures exhibited higher fitness when compared to the ancestor on time scales of 6 months. Therefore, evolution might quickly alter or generate novel response traits under new environmental conditions, such as expected with climatic changes.

#### 3.2 | Integration of ecological interactions

Although experimental evolution studies are useful, they can be difficult to extrapolate to field settings (Chen et al., 2023). For one, these experiments are typically run under idealized conditions and eliminate confounding, yet important, ecological interactions that would otherwise occur in natural communities. For example, strains are often evolved in monocultures under a single environmental stressor (e.g., temperature) while maintaining nutrient-rich media, thereby eliminating competition and other resource limitations. Omitting these interactions could have evolutionary consequences; for instance, Rodríguez-Verdugo and Ackermann (2021) demonstrated by evolving a two species community, in which the presence of another species modified evolutionary trajectories, ultimately resulting in changes to the biodegrading function of the microbial system (Rodríguez-Verdugo, 2021).

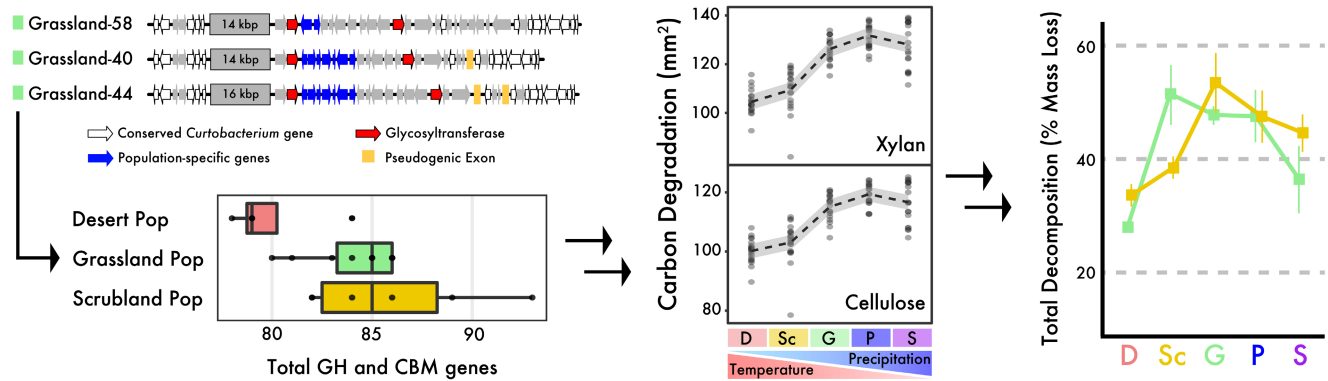
Likewise, long-term interactions with other organism types, such as plants, in field settings could significantly influence microbial evolutionary trajectories. For instance, laboratory studies indicate that microbial carbon use efficiency (CUE) decreases with warming (Wang et al., 2021). However, field studies demonstrate the opposite relationship (Ye et al., 2019), and the precise role of microbial evolution in this context remains elusive. Additionally, experimental evolution studies typically span only a few months to a maximum of a couple of years, whereas longer-term field experiments revealed microbial responses continue to vary on a decadal scale. For example, in a global change warming experiment, forest soils undergoing increased temperature (+5°C) alternately exhibited higher and lower

respiration rates than control plots, again with a limited understanding of the role of microbial evolution (Melillo et al., 2017). Finally, laboratory experiments have cultures that are often grown in shaking flasks, maximizing local dispersal for individuals in the population thereby increasing the opportunity for genetic exchange and intra-specific competition. Especially when considering the high spatial heterogeneity in soils, extrapolating evolutionary dynamics and the rates at which they occur from lab-based experiments might not reflect natural conditions.

To better represent the diversity of microbial communities and account for ecological interactions, some laboratory studies have recently employed synthetic communities (Li et al., 2022). However, these lab-based assessments likely minimize or completely remove dynamic environmental conditions, such as temperature and moisture fluctuations corresponding to diel cycles, seasonal climatic variation, and spatial heterogeneity in soils. In order to account for environmental heterogeneity, Chase et al. (2021) conducted a field experiment in which they assessed adaptive responses to environmental change by monitoring both a single soil isolate alongside entire soil communities that were reciprocally transplanted across an elevation gradient. By tracking mutational responses in the isolate along with compositional shifts within the community, the combination of ecological and evolutionary responses to new climates resulted in changes in C decomposition of organic matter (Figure 3). Because these eco-evolutionary processes occurred on relatively fast timescales (within 18 months), we must reconsider how we model C cycling traits in biogeochemical models.

### 4 | ROADMAP TO INTEGRATE MICROBIAL EVOLUTION IN BIOGEOCHEMICAL MODELS

There is a history of including at least some aspects of microbial ecology in soil modeling (e.g., Allison, 2012; Wieder et al., 2014); however, there is a pressing need for greater focus on evolutionary models that complement ecological models. Consequently, this discussion will emphasize evolution (though less integrated), yet the outlined approaches actually model eco-evolution. To integrate microbial evolutionary processes in the context of ecosystem or global C cycling, we suggest a multi-scale modeling approach. At the micro-scale, mechanistic models identify environmental parameters that influence metabolic trade-offs and other evolutionary pressures on the genes and traits mediating C cycling (e.g., glycoside hydrolase [GH] enzymes, as shown in Figure 3). At the ecosystem and global scales, biogeochemical models must incorporate microbial-vegetation-climate feedbacks to predict soil C stocks. This approach has already been successfully applied in vegetation models (Williams et al., 1997), but not yet for microbial systems. Here we propose a roadmap for such an approach to investigate the effect on C cycling of microbial evolution in response to climate change, bridging the gap between micro- and global scales.



**FIGURE 3** Population dynamics contribute to ecosystem functioning. *Curtobacterium* genomes from soil (proxy for individuals) within a population recombine population-specific regions (proxy for gene flow) related to carbon utilization. These evolutionary processes contribute to differences in carbon utilization enzymes (e.g., glycoside hydrolases [GH] and carbohydrate binding modules [CBM]) between populations (Pop) that are maintained across geographic locations. Upon conducting a reciprocal transplant experiment across a climate gradient, each geographic site selected for traits within *Curtobacterium*; for example, colder, wetter sites selected for *Curtobacterium* species with increased degradation of cellulose and xylan (data from Chase et al., 2021). At the completion of the transplant experiment, eco-evolutionary processes manifested as differences in total decomposition at the community level (data from Glassman et al., 2018). Sites along the climate gradient differ in temperature and precipitation ranging from desert (D, red), scrubland (Sc, yellow), grassland (G, green), pine oak (P, blue), and subalpine (S, purple) habitats. In the right panel, decomposition rates by microbes historically adapted to Sc and G conditions are compared along the climate gradient for simplicity.

#### 4.1 | Modeling evolution in mechanistic microscale soil models

Along with obtaining long-term microbiome data from natural communities, mathematical and numerical approaches can be employed to predict evolutionary responses. These predictions serve to inform empirical hypotheses on evolutionary rates and impacts on C cycling (Lässig et al., 2017). This section reviews existing modeling approaches, most of which have not yet been applied to microbial biogeochemical models. These approaches can either be used directly to predict community-level trait responses or in a two-step approach that predicts population-level evolutionary responses, which are then integrated into a community model to predict community-level trait responses.

##### 4.1.1 | Optimization of metabolic processes

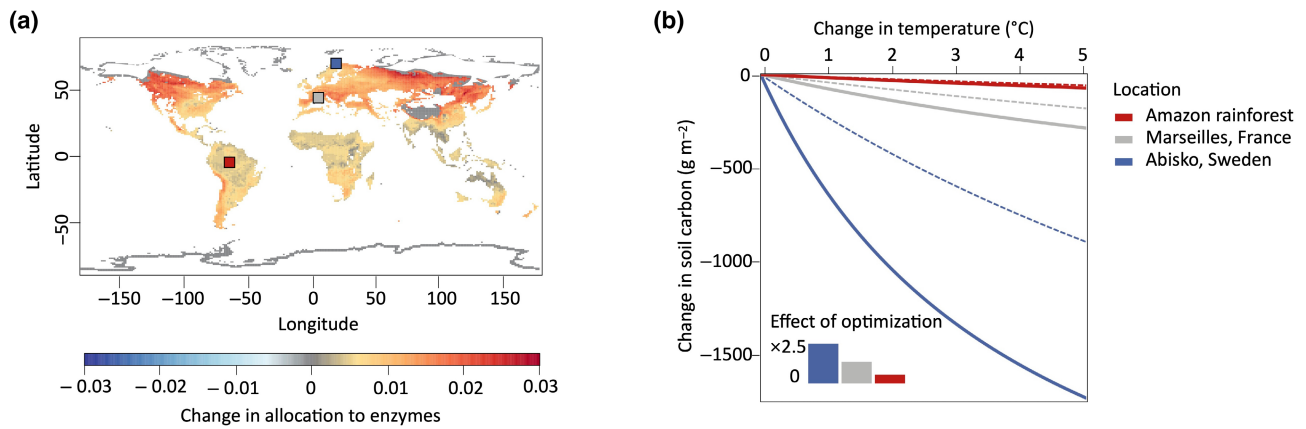
One approach is to represent evolutionary processes implicitly by assuming microbial fitness will be maximized via optimization of microbial metabolic processes. The simplest models based on this idea assume evolution of a representative microbe—that is, they neglect interspecific variability in the community (Allison, 2014). With this assumption, the cumulative evolutionary dynamics results in a community of microbes all similarly adapted to specific environmental conditions, inasmuch that different taxa can be treated mathematically neutral as a homogeneous population. This assumption leads to rapid predictions of microbial trait distributions and how these traits affect rates of C cycling. However, in these minimalist models, microbial diversity and the ecological and evolutionary responses by specific microbial taxa, such as the potential for diversification and

adaptation, are absent altogether. Therefore, this method is particularly applicable for modeling microbial communities with very simple ecological interactions.

The level of mechanistic detail varies in these models, from those optimizing metabolic networks (Feist & Palsson, 2010) to those focusing on emergent traits at the community level. For example, CUE (C allocated to growth as a fraction of substrate uptake) could be considered as an adaptive emergent trait that is under selection to maximize growth rates given some level of nutrient availability (Allison, 2014). Under limited nutrient availability, high CUE is assumed to increase nutrient demand and allocation for growth, further exacerbating nutrient limitations in the community. Thus, to maximize growth, microbes need to upregulate CUE with increasing nutrient content of organic substrates or inorganic nutrient availability—a pattern predicted by a simple mathematical model that is largely consistent with empirical observations (Manzoni et al., 2017).

Along the same lines, extracellular enzyme production can be optimized to acquire or degrade polymeric carbohydrates to maximize growth rate. Optimal enzyme production is modeled as a balance between the energetic cost of enzyme production and the gains from acquiring carbon substrate for growth and other metabolic products. In this way, a simple growth versus yield trade-off model predicts for and scales between enzyme production rate or CUE and SOC (Abs et al., 2020; Calabrese et al., 2022).

Temporal aspects of resource acquisition can also be predicted from the simple assumption that resource investment maximizes cumulative growth throughout the decomposition processes (as opposed to maximizing growth at any time point or at steady state) (Manzoni et al., 2023). Maximum growth is achieved when resource acquisition is upregulated with increasing substrate availability, such that the highest resource acquisition costs and the highest returns



**FIGURE 4** Effect of microbial adaptation modeled with adaptive dynamics on soil C stocks (Abs et al., 2022). (a) The effect of adaptation to global warming by 2100 is heterogeneous in space, with the strongest effect in cold regions. (b) Change in soil C stocks as a function of temperature, with (solid line) or without (dashed line) microbial adaptation, in three locations that differ by their initial temperature (Amazon rainforest, Marseilles in France, and Abisko in Sweden). *Source:* Reproduced from Abs et al. (2022).

occur early during decomposition, whereas costs are minimized in the later phases when returns are decreasing. A similar approach can be adopted to study microbial resource acquisition strategies when decomposing chemically heterogeneous substrates in which different compounds interact. For example, microbial growth can be maximized by starting lignin decomposition earlier in lignin-rich litter types, to allow access to hydrolysable C, despite the higher costs of production and maintenance of oxidative enzymes (Chakrawal et al., 2024).

#### 4.1.2 | Quantitative genetics

A second approach to modeling evolution is quantitative genetics (QG), which predicts shifts in allele frequencies (Henry et al., 2021). Despite its potential, this method has not been used to study the influence of microbial evolution on soil C because QG models typically exclude ecological feedback. In these models, ecological impacts are often reduced solely to population density (i.e., frequency-dependent) without consideration for species or environmental interactions (Lion, 2018). Despite this limitation, there has been growing interest in this method over the past half-century, particularly in the realms of frequency-dependent selection and rapid evolutionary responses. These explorations in other systems include predator-prey models, some of which incorporate microbial components (e.g., host-phage dynamics) (Abrams, 2001; Abrams et al., 1993; Day, 2005; Iwasa et al., 1991; Lion, 2018; Lion et al., 2023; Slatkin, 1980). The lack of QG models in microbial ecology might be more of a disciplinary divide rather than a technical challenge. Given the adaptability of these tools [e.g., explicit resource dynamics (Lion, 2018)], the integration of QG with microbial ecology poses a promising opportunity to quantify the relationships among microbial evolution, functional traits, and ecosystem processes.

#### 4.1.3 | Adaptive dynamics

A third approach, known as adaptive dynamics, uses a mathematical framework based on eco-evolutionary game theory. This approach assumes that population and resource dynamics adaptively impact fitness at arbitrary time intervals, resulting in incremental eco-evolutionary changes (Geritz et al., 1998; Kisdi & Geritz, 2010). By incorporating competition for resources (e.g., carbon and nutrients; space) between evolved and ancestral strains, this method captures some of the complex dynamics of ecological and evolutionary processes occurring within microbial communities. For instance, Abs et al. (2022) applied adaptive dynamics to predict the eco-evolutionary dynamics of microbial communities in response to global warming, specifically focusing on allocation to enzyme production as a trait (Figure 4). Their findings revealed that warming reduces the likelihood of cheating for soluble resources, leading to a higher investment in enzyme production. Consequently, this shift resulted in a nearly twofold increase in global soil C loss by 2100 due to microbial eco-evolution. It is important to note that adaptive dynamics is most suitable for modeling the evolution of populations through mutations, assuming small trait variance, asexual reproduction, and low variation rates.

#### 4.1.4 | Partial differential equations with explicit mutation process

The fourth approach explicitly models the mutation process. The advantage of this method is that it incorporates eco-evolutionary feedbacks without assuming that evolution occurs at a significantly slower rate than ecological processes. These models are based on partial differential equations (PDEs) describing mutation as a diffusion process in the trait space (Bouin et al., 2012; Leman et al., 2014).

While mathematicians have long been using these models, their adoption by ecologists has been limited. One explanation might be that these models do not provide analytical solutions, and are therefore hard to interpret biologically. One proposed resolution to this issue involves reframing the model as a set of moment equations. In doing so, the model's focus shifts from describing the dynamics of the whole trait distribution to tracking the mean and the variance of that distribution (Bolker & Pacala, 1997; Turelli & Barton, 1990). However, this approach demands that higher order moments are small enough to be ignored—referred to as “moment closure approximations” (Grenfell et al., 1995). An alternative strategy for mitigating the shortcomings associated with PDEs involves employing Hamilton–Jacobi equations. With Hamilton–Jacobi equations, like in QG, the trait distribution must be denser around the mean, but mutations do not have to be rare like in adaptive dynamics. However, these equations share some of the limitations of adaptive dynamics, albeit to a lesser extent, including a requirement that mutations occur at a slower rate than ecological processes (Jing et al., 2017). To identify the optimal analytical method, it is crucial to determine how to represent ecological processes relative to evolutionary ones, and vice versa. Shen and Clairambault (2020) have offered an excellent review of various models, detailing the insights that each model can deliver.

#### 4.1.5 | Numerical individual based models

In the last approach, numerical models trace the behavior of individual microbes. Despite their heightened realism, these models come at the expense of increased complexity, rendering them analytically intractable (Levin, 1992). Nonetheless, this approach can serve as an efficient exploratory tool. For instance, Folse and Allison (2012), proposed an implementation of evolutionary dynamics that incorporated the effects of spatial heterogeneity on microbial taxa and substrate diversity. This model revealed patterns in microbial spatial distributions; for example, cooperation among the same types of microbes resulted in aggregation, whereas cooperation between different types led to filamentous patterns. This approach provides insights for ecological and ecosystem-level interpretations considering higher diversity correlated with slower substrate decay rates due to the synergistic interactions resulting in individuals producing fewer enzymes. Hence, despite their complexity, numerical models have effectively uncovered phenomena in environmental and evolutionary biology that govern microbiome functioning.

Given observed differences in lab and field empirical data, there exists a parallel argument for integrating environmental heterogeneity into modeling approaches. Theoretical and modeling studies have demonstrated that spatial heterogeneity can sustain the evolutionary production of public goods, such as extracellular degrading enzymes (Abs et al., 2020; Allison, 2005), and promote microbial diversity (Stump et al., 2018). Soil exhibits strong spatial structure (Young & Crawford, 2004), and recent research has indicated its influence on soil C dynamics at both the pore scale (Kaiser et al., 2015;

Wang & Allison, 2019) and global scale (Abs et al., 2022; Tang & Riley, 2014). The need to account for spatial heterogeneity, a feature which is ignored in ecosystem and global models, is a challenge addressed in Section 4.3. Overall, we note that there are still few studies investigating the emergent properties of spatial heterogeneity on evolutionary dynamics of soil microbes with mechanistic microscale soil models. Numerical models have the limitation of not providing exact analytical solutions, which can make interpretation and deeper understanding of underlying principles challenging. Nevertheless, spatially explicit and analytical models may converge as analytical spatially explicit models are developed (Chakrawal et al., 2020; Leman et al., 2014).

#### 4.2 | Validation with omics data

We cannot easily predict or validate evolutionary trajectories using plot- or field-scale observations of fluxes and C stocks because they aggregate over the functioning of diverse microbial communities (e.g., Figure 3). However, a skyrocketing number of omics datasets provide opportunities for fine scale resolution of microbial ecological and evolutionary patterns at sites around the globe (Allen White et al., 2017). Omics data refer to large-scale datasets generated from high-throughput technologies that cover multiple layers of biological information, such as gene sequences, transcripts (gene expression), proteomes, and metabolomes. The most robust outcomes will likely emerge from integrating these multiple layers through multi-omics strategies to understand the relationship between genetic and realized potential of a microbiome (Hultman et al., 2015; Jansson & Baker, 2016). A key need is to derive microbial parameters from these datasets, while ground truthing with genomic data, though the computational approaches remain a work in progress.

Several emerging quantitative approaches have attempted to translate genomic data into microbial life history strategies. The Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt) software is often employed to extrapolate functional traits from amplicon data based on clustering of the 16S rRNA gene into operational taxonomic units (<https://picrust.github.io/picrust/>). The DEBmicrotrait model predicts functional traits from sequenced genomes or metagenome-assembled genomes (Karaoz & Brodie, 2022). Finally, the data-driven COMETS model predicts metabolic pathways from genomic data, information that can be used to generate hypotheses about the impact of individual microbes on ecosystem function (Dukovski et al., 2021). However, most environmental microbiomes are largely understudied and lack representative isolates to determine phenotypic traits, especially in soil systems (Choi et al., 2017).

Given that environmental microbiomes are highly diverse and largely lack cultured representatives to inform metabolic models, computational tools rely on the conservation of traits and metabolic pathways. As such, determining how to interpret microbiome functional data is dependent on the trait of interest, as traits are conserved at varying phylogenetic levels (Martiny et al., 2015). Highly

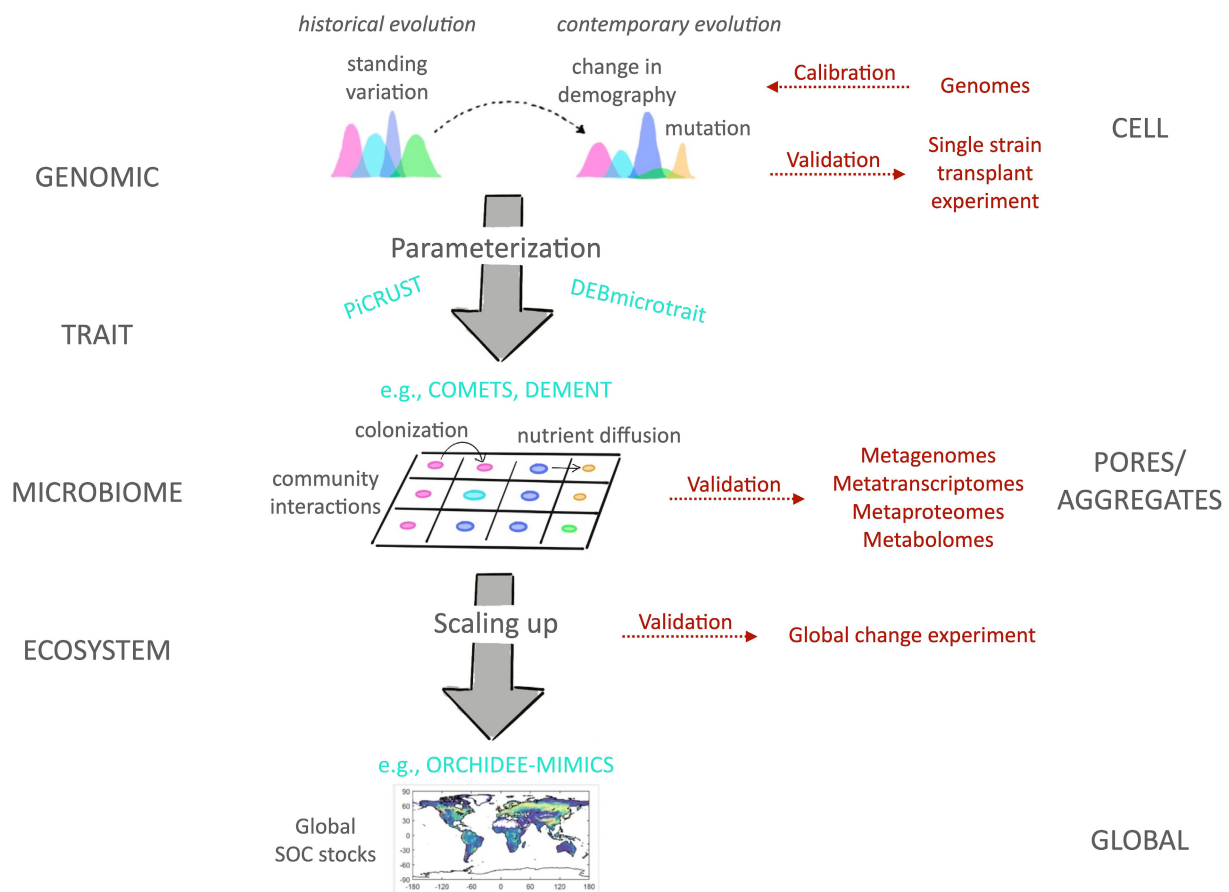
conserved traits like pH tolerance can be adequately captured by surveying the entire community at broad taxonomic depths. Simpler traits, such as those related to C utilization as represented by the composition of GH genes, are less conserved and can vary among closely-related microbial lineages, especially within OTU designations based on 16S rRNA similarity (Chase et al., 2017, 2018; Scales et al., 2022). The statistical models we present here might work at different taxonomic levels to generate global maps of trait values. If we assume a space-for-time substitution and no legacy effects, these maps could then be used to validate the theoretical predictions of trait adaptation to global change obtained with the methods presented in Section 4.1.

### 4.3 | Scaling up from microscale to global scale

Eco-evolutionary models, which operate at the microscale, provide a foundation to extrapolate to larger scales that encompass soil cores, plots, and ecosystems. Upscaling from micrometers to 1000s of km is very challenging and has not been achieved yet, to the best of our knowledge. However, accomplishing this upscaling would be a game changer, as it would enable the study of evolutionary effects on

global C cycling. The integration of microbial evolution is currently a focal point in the advancement of soil biogeochemical models. (Crowther et al., 2019) anticipate that the forthcoming generation of models will account for continuous variation in traits—similar to ongoing efforts in vegetation models (Harrison et al., 2021; Kattge & Knorr, 2007; Lombardozzi et al., 2015). Martiny et al. (2023) highlighted the impracticality of assuming invariant microbial response functions, given their dependency on microbial communities and the specific processes—and their rates—at work. Further, Cruz-Paredes et al. (2023) discovered that these response functions depend not only on variables like annual mean temperature but also on the specific process, such as growth or respiration.

To incorporate microbial evolutionary processes into ecosystem models, it may be helpful to begin with a microbial explicit ecosystem model. Several such models have been developed in the past decade, including CORPSE (Sulman et al., 2014), MILLENNIAL (Abramoff et al., 2018, 2022), and MIMICS (Wieder et al., 2014, 2015). While these models typically do not mechanistically represent microbial evolution through mutations or HGT due to their small number of idealized microbial functional groups, it is possible to implicitly represent microbial evolution. Fixed trait values, such as CUE, can be replaced with a function that considers both present and past abiotic



**FIGURE 5** Conceptual framework of the integration of microbial evolution into ecosystem models across levels of biological organization (left) and spatial scales (right). In red are the data that can be used to calibrate or validate models at different scales. SOC, soil organic carbon.

conditions. This function could be estimated by aggregating outputs from the microscale models outlined in Section 4.1 at the kilometer scale. While this approach has been applied in vegetation modeling (Williams et al., 1997), its application to soil microbial C models has yet to be explored.

Validation of the effects of microbial adaptation on soil C cycling can be accomplished by comparing model outputs—with and without evolution—with observations from soil incubations or ecosystem-scale studies. These observations would include measurements of soil respiration, litter decay rates, microbial biomass and growth rates, and soil C and nitrogen (N) pools (Bonan et al., 2013), and ideally experimental treatments (e.g., C amendments, warming, rainfall manipulation). For example, the outcomes of eco-evolutionary processes could manifest themselves as different trajectories of litter decomposition (e.g., Chakrawal et al., 2024) or different temperature sensitivities of microbial growth and respiration (e.g., Allison, 2014) compared to those predicted by models neglecting eco-evolutionary processes. This approach allows for an examination of whether microbial evolution influences C dynamics in idealized systems without plants (soil incubations) or whole ecosystems including vegetation. Microbial explicit soil models are now being coupled with vegetation models to describe whole ecosystems. For instance, the integration of MIMICS with the Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE) model has enabled investigations into the interactions between microbial biomass and C dynamics (Terrer et al., 2021). The same needs to be done with microbial models integrating microbial evolution.

## 5 | CONCLUSION

We proposed a definition of evolution suitable for linking microbial processes to ecosystem- and global-scale biogeochemistry. This definition includes ecological processes confounded with evolutionary ones, and is useful for integrating microbial evolution into large-scale biogeochemical models (Figure 5). In summary, our roadmap for this integration includes the following:

- Select a microscale mechanistic model of SOC decomposition.
- Select an evolutionary model depending on the characteristics of the microbial community (e.g., adaptive dynamics if variation at the population level can be ignored, otherwise QG if variation at the individual level can be ignored, otherwise a numerical individual-based model).
- Validate model predictions with omics data.
- Scale microbial adaptation to the ecosystem level, either by replacing parameters in existing ecosystem microbial models by functions predicted by the microscale one, or by building a new ecosystem microbial model from aggregating the microscale one, or by fully coupling the microscale model and a land surface model.
- Validate larger-scale model predictions with ecosystem scale measurements.

We acknowledge that this is an ambitious roadmap; the proposed steps might take 10–20 years to be implemented. However, through these integrated approaches, researchers will gain insights into the magnitude and mechanisms of evolutionary effects on soil C cycling, thereby improving predictions of microbial evolutionary consequences for biogeochemistry on a changing planet.

### AUTHOR CONTRIBUTIONS

**Elsa Abs:** Conceptualization; writing – original draft; writing – review and editing. **Alexander B. Chase:** Writing – review and editing. **Stefano Manzoni:** Writing – review and editing. **Philippe Ciais:** Writing – review and editing. **Steven D. Allison:** Writing – review and editing.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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