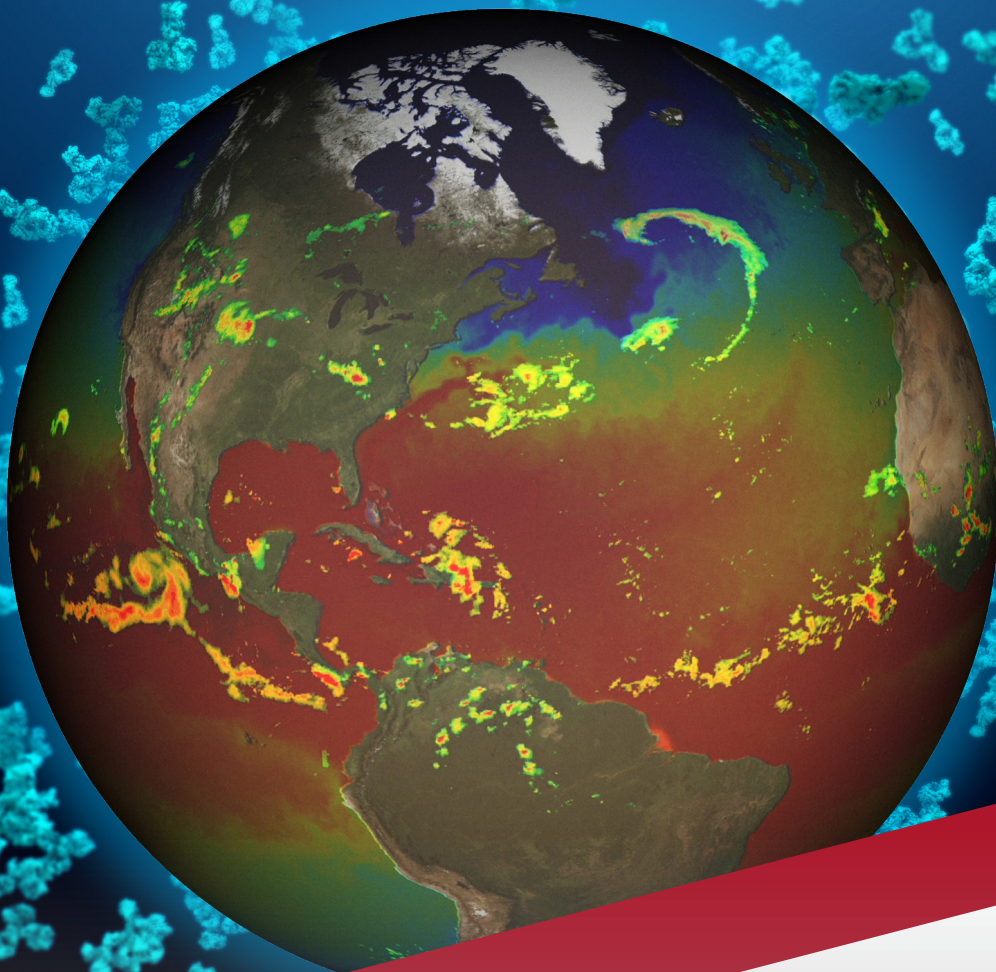


COLLOQUIUM REPORT



Microbes in Models: Integrating Microbes into Earth System Models for Understanding Climate Change



AMERICAN
SOCIETY FOR
MICROBIOLOGY

AMERICAN
ACADEMY OF
MICROBIOLOGY
RECOGNIZING SCIENTIFIC EXCELLENCE

Microbes in Models: Integrating Microbes into Earth System Models for Understanding Climate Change

Report on an American Academy of Microbiology Virtual Colloquium held on December 6 & 8, 2022.

GOVERNORS, AMERICAN ACADEMY OF MICROBIOLOGY

Arturo Casadevall, M.D., Ph.D., Chair
Johns Hopkins Bloomberg School of
Public Health

Vanessa Sperandio, Ph.D., Chair-Elect
The University of Texas Southwestern
Medical Center

Carey-Ann Burnham, Ph.D.
Washington University School of
Medicine

Gail H. Cassell, Ph.D.
Harvard Medical School

Lynn Enquist, Ph.D.
Princeton University

Mary Estes, Ph.D.
Baylor College of Medicine

Susan Golden, Ph.D.
University of California San Diego

Jay T. Lennon, Ph.D.
Indiana University

Denise Monack, Ph.D.
Stanford University School of Medicine

Barbara E. Murray, M.D.
University of Texas Health Science
Center at Houston

Susan E. Sharp, Ph.D.
Copan Diagnostics

Susan Weiss, Ph.D.
University of Pennsylvania

Henry Neal Williams, Ph.D.
Florida A&M University

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Lawrence Berkeley Lab and Ronin
Institute

Naomi M. Levine, Ph.D.
University of Southern California

Jennifer B.H. Martiny, Ph.D.
University of California, Irvine

COLLOQUIUM PARTICIPANTS

Steven D. Allison, Ph.D.
University of California, Irvine

Arturo Casadevall, M.D., Ph.D.
Johns Hopkins Bloomberg School of
Public Health

Philippe Ciais, Ph.D.
Le Laboratoire des Sciences du Climat
et de l'Environnement, France

Kristen M. DeAngelis, Ph.D.
University of Massachusetts Amherst

John P. Dunne, Ph.D.
National Oceanic and Atmospheric
Administration Office of Oceanic and
Atmospheric Research Geophysical
Fluid Dynamics Laboratory

Serita D. Frey, Ph.D.
University of New Hampshire

Christine Hawkes, Ph.D.
North Carolina State University

Bruce Hungate, Ph.D.
Northern Arizona University

Swamini Khurana, Dr. rer. nat, M.S.
Stockholm University

Stephanie N. Kivlin, Ph.D.
University of Tennessee, Knoxville

Stefano Manzoni, Ph.D.
Stockholm University

Adam Martiny, Ph.D.
University of California, Irvine

Jennifer Pett-Ridge, Ph.D.
Lawrence Livermore National
Laboratory

James Tremper Randerson, Ph.D.
University of California, Irvine

Mamta Rawat, Ph. D.
National Science Foundation

Adriana L. Romero-Olivares, Ph.D.
New Mexico State University

David Talmy, Ph.D., MMath, MRes
University of Tennessee

Jinyun Tang, Ph.D.
Lawrence Berkeley National
Laboratory

Katherine Todd-Brown, Ph.D.
University of Florida

Meike Vogt, Ph.D.
Eidgenössische Technische Hochschule
(ETH) Zürich

Ying-Ping Wang, Ph.D.
Commonwealth Scientific and
Industrial Research Organisation
(CSIRO) Environment

Will Wieder, Ph.D.
National Center for Atmospheric
Research, Climate and Global
Dynamics Laboratory

Emily Zakem, Ph.D.
Carnegie Institution for Science

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Executive Summary

Climate change is altering the planet and threatens humanity. Earth system models simulate the planet's physical, chemical, and biological processes to help scientists understand current environmental changes and make projections for Earth's future, which can inform society's responses to combat and mitigate climate change's negative effects. Climate change will fundamentally change life on Earth, including microorganisms. Microbes will also influence climate change by driving biogeochemical cycles through the consumption and production of greenhouse gasses. Thus, explicitly including microbial processes into Earth system models can improve model projections. However, fully understanding the feedbacks between climate change and microbes, and then including those processes into Earth systems models, is a major challenge.

This report is based on the deliberations of experts who participated in a virtual colloquium on 6 and 8 December, 2022, organized by the American Academy of Microbiology, which is the honorific leadership group and think tank within the American Society for Microbiology. At the colloquium, these experts from the climate and microbial sciences attempted to clearly articulate current knowledge gaps of the two fields. As a result, the participants compiled a list of top ten challenges to better incorporate microbial processes into Earth system models. Solving these challenges requires new thinking and approaches. Transdisciplinary efforts have the potential to propel science—and society—towards combating climate change.



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Introduction

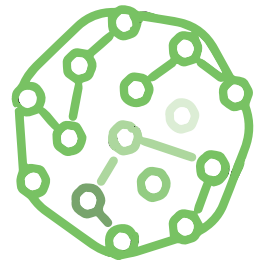
“Climate change impacts and risks are becoming increasingly complex and more difficult to manage” according to a recent Intergovernmental Panel on Climate Change (IPCC) report. With an estimated 3.3 to 3.6 billion people living in areas that are highly vulnerable to climate change, mathematical models are useful tools to refine the complexity of climate change into more manageable terms. These in turn help inform planning strategies and mitigation actions to tackle the pressing threat of climate change to humanity. Thus, **climate models** and **Earth system models** are vital to understanding and projecting climate change’s effects.

Accurate models are important for informing climate projections to guide policies. Climate models have historically been skillful in their predictions and projections of physical climate changes, for example, projected surface temperature warming is consistent with observations (Stouffer and Manabe 2017; Hausfather et al. 2019). However, as climate change leads to new environmental changes, the accuracy of existing models for the future dynamics of ecosystems is unclear. Going forward, the most informative models will be those that best represent major transformations of carbon and nutrients. The key to understanding Earth’s future may come from the world’s smallest creatures—microorganisms.

Microbes include **viruses, bacteria, archaea, fungi, protozoa, and algae** that are found all across Earth. Though individually small, microbes greatly influence climate change through nutrient cycling and green-

house gas production and consumption. The essential microbial processes that contribute to the global climate and biogeochemistry feedback include those controlling the dynamics of CO_2 , CH_4 , N_2O , NO_x , NH_3 , inorganic phosphorus, organic matter, and to a lesser extent H_2 and CO (Galloway et al. 2014). There are nearly 4,250 Gt of biologically active organic carbon stored in Earth’s land and oceans, and microbes are major drivers of carbon and nutrient fluxes in these ecosystems (Friedlingstein et al. 2021). Even small changes to the rate that these large pools are cycled have the potential for significant impacts to climate.

Currently, the Earth system models that are intended to inform climate change adaptation and mitigation strategies show high uncertainty in their representation of land-atmosphere greenhouse gas exchanges under climate change scenarios. Additionally, marine models are not currently able to accurately assess the role of plankton diversity and plankton networks for specific marine ecosystem services or biogeochemical functions, such as nitrogen fixation or carbon export, and thus cannot reliably assess the resilience of these systems to environmental and climate change. Thus, lack of full consideration of microbes and their activities in Earth system models can be sources of uncertainty (Berardi et al. 2020). Reducing model uncertainty while building confidence in model projections is critical as we contend with alterations to Earth’s operating systems in a changing world to inform policy or conservation measures to



Accurate models are important for informing climate projections to guide climate and land use policies

WHAT ARE MODELS?

Models are mathematical representations of the world, often represented as a series of **differential equations** that track one or more state variables (e.g., carbon concentration or stock, nutrient concentration, living biomass of microorganisms, and energy transport) through time. Models can resolve a range of time scales, such as hourly, daily, and yearly, and can be run for spatial scales ranging

from microsite (e.g., soil pore and aggregate), to plot or site, all the way to the globe (Figure 1). The term “Earth system models” refers to global scale models, which are composed of coupled submodels representing the major components of the Earth system (atmosphere, land, sea ice, and oceans). This report specifically considers Earth system models.

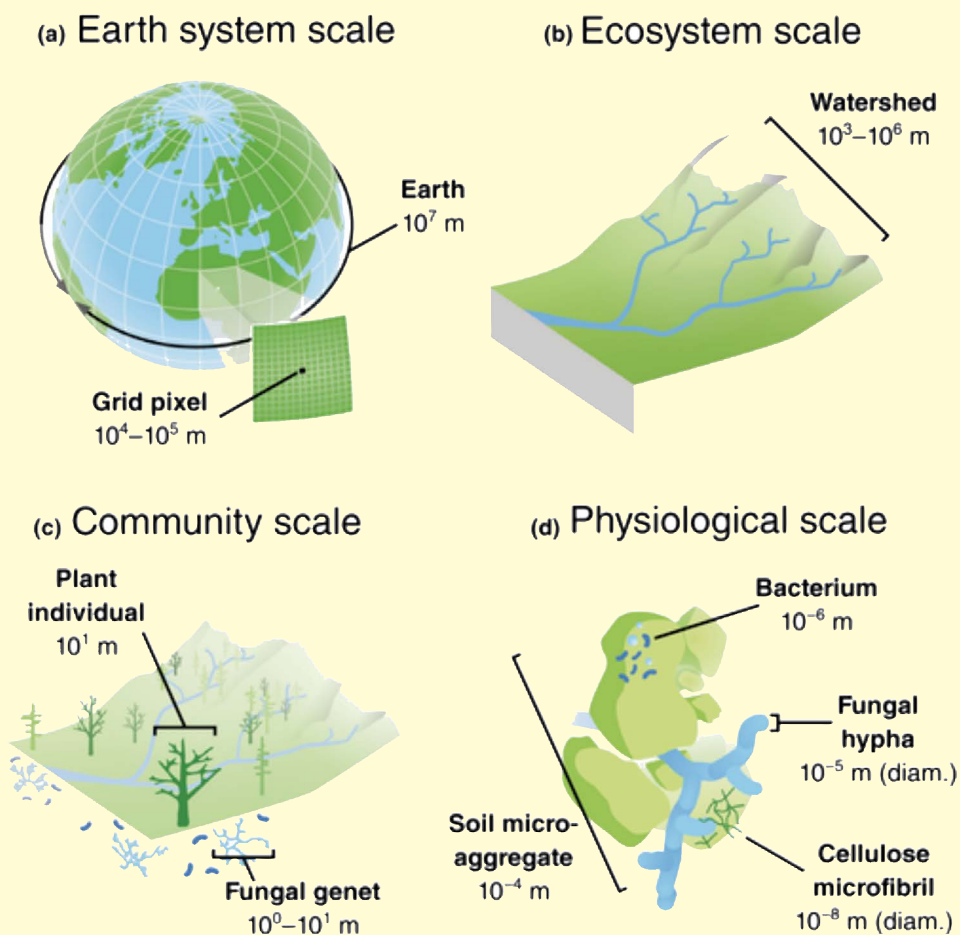


Figure 1. Example of four spatial scales of models, which span 16 orders of magnitude, and their associated microbial biogeochemistry (Wan and Crowther 2022).

Models are informed by fundamental theories of physics, chemistry, and biology. Model equations often contain free **parameters**, which are scalar values that modify model compartments of information, known as pools, or the rates of transformation between model pools. Parameter values are often derived from the scientific literature or estimated from large datasets and/or targeted experiments (Zhang et al. 2017; Post et al. 2017).

Models can be updated by adding new pools, new equations modifying existing pools, and/or new parameters that modify existing transfers between

pools. For example, older soil models such as Century and Roth-C contain only soil pools, but newer models contain a microbial biomass pool and sometimes also a pool that represents extracellular enzymes. These pools also have equations that define transfers from microbial biomass to other pools, such as uptake of substrates, decomposition of plant material, release of carbon dioxide, and transfer of dead microbial biomass into soil pools. Each of these transfers is defined by an equation that contains one or more parameters describing the rate of transfer, which is defined using data, theory, or experiments.

protect these systems (Bradford et al. 2016) and can be achieved through broader engagement among scientific disciplines.

Explicit incorporation of microbial processes into models improves model prediction and reduces model uncertainty for terrestrial systems (Wieder et al. 2015; Guo et al. 2020; Wang et al. 2021). Including even rudimentary parameterizations of microbial processes improves model representation of contemporary soil carbon (Wieder et al. 2013). In ocean biogeochemical models used in Earth system models, the growth of explicitly resolved **phytoplankton** (phototrophic microbes) functional-types allowed models to capture the magnitude and distribution of marine primary productivity, linking marine carbon and nutrient cycling (Quéré et al. 2005; Moore et al. 2001; Séférian et al. 2020). More highly resolved trait-based representations of microbial phytoplankton also generated more realistic biogeographic patterns (Follows et al. 2007), though the diversity of phytoplankton types included in Earth system models is much lower than used by models aimed at resolving biogeographical patterns. Wholly taking microbial activities into consideration could be critical for developing more accurate predictive climate models that are needed to help manage climate change's impacts.

In addition to improving the accuracy of models to inform climate change mitigation strategies, the inclusion of microbial processes into models has the potential to help scientists understand how microbes are **adapting** and **acclimating** to environmental changes resulting from climate change. Climate change impacts all life, including microbes. As temperature, humidity, precipitation, acidity, and the frequency and intensity of natural disturbances (such as hurri-

canes, fires, and droughts on land and eddies, heat waves, and dust deposition in the oceans) change, microorganisms and their local associated communities, known as **microbiomes**, will respond accordingly. Environmental stress can lead to unknown and emergent responses from microbes. Microbial community composition, structure, and activity may alter when adapting to combined abiotic and biotic stressors becoming more intense with climate changes (Smith et al. 2022). Models that take microbial processes into account can help predict how microbes will respond and how such changes feedback into climate change.

Incorporating microbial processes into models is not an easy task. First, microbes are orders of magnitude smaller than the 10s of kilometer grids used in global Earth system models. Thus, scaling up processes from the microscale to the macroscale is a challenge. Second, there is often a mismatch between the types of data and the temporal and spatial resolution of the data collected in the field and the pools and processes and scales resolved in the models. Thus there is a need for improved integration of microbial data and models. The fields of microbiology, climate science, and computational modeling all annotate and use data differently, making it hard to facilitate transdisciplinary endeavors. In addition, it is unclear how to account for microbes' ability to adapt or acclimate to a changing environment on timescales that are relevant to Earth system models. Finally, once microbial processes are included, this increases degrees of freedom that in turn can increase the uncertainty of model projections. It can be difficult to find the correct balance between simulations which incorporate more known microbial processes with the additional computing power needed to include these processes. Fortunately,



Climate change impacts all life, including microbes.

advances in sequencing techniques, computational biology, and machine learning are providing new approaches for making rapid progress toward better representing microbiomes in Earth system models.

In 2011, the American Academy of Microbiology, the honorific leadership group and scientific think tank within the American Society for Microbiology, sought to bring microbiologists and modelers together by hosting the colloquium entitled “Incorporating Microbial Processes Into Climate Models”. Recommendations resulting from that colloquium included choosing a few specific biogeochemical cycles to serve as demonstration projects; assessing current data

collection and developing a monitoring and data collection strategy; validating processes to integrate data collection, modeling, and experimentation; and providing incentives for collaborations and interdisciplinary training. Since that colloquium, the technology and available data have greatly improved in climate science, mathematical modeling, and microbiology, prompting another gathering to discuss future progress.

On 6 and 8 December 2022, the American Academy of Microbiology convened another colloquium entitled “Microbes in Models: Steps for Integrating Microbes into Earth System Models for Understanding Climate Change.” Climate modelers and microbiologists highlighted the most pressing barriers and knowledge gaps to overcome in order to include microbial activities in climate models more effectively and make more skillful predictions (Figure 2). The colloquium participants focused mostly on Earth system models that related to land and oceans because those are the major compartments where microorganisms are most critical to biogeochemical transformations. However, the participants acknowledged that many of the discussion points are relevant to smaller-scale site-level models as well.

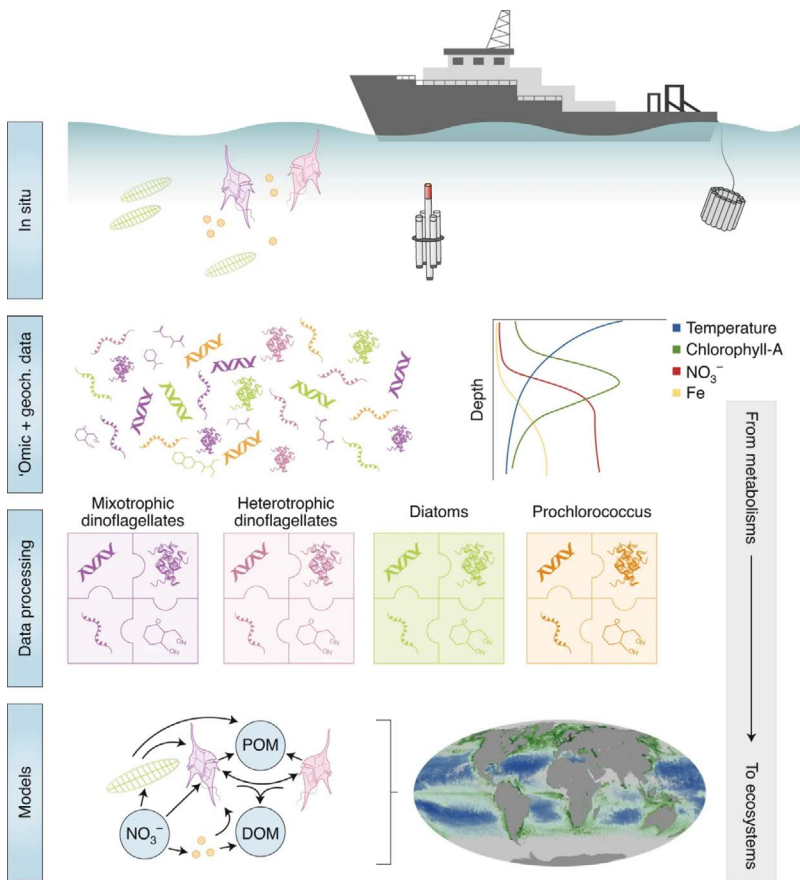


Figure 2. Example of linking marine microbial metabolisms to biogeochemical cycling in the oceans (Levine and Leles 2021).

Top Research Challenges

Are microbes necessary to predict future climate?

Given the central role that microbes play in global biogeochemistry, the explicit consideration of microorganisms in models may lead to more accurate models that can better predict climate under future scenarios.

Earth system models used for projections of climate change have typically not included explicit representation of microorganisms responsible for the mineralization of organic carbon pools and other relevant biogeochemical transformations. For example, though most Coupled Model Intercomparison Project (CMIP6) ocean biogeochemical models resolve the biomass of explicit microbial phytoplankton and zooplankton populations, only a few models now resolve explicit heterotrophic bacterial populations (Séférian et al. 2020; Le Quéré et al. 2016). Microbial activities involve complex interactions at the microscale between thousands of species and their environment. Some choice about how to reduce this complexity in Earth system models is required, given that representing the full complexity of microbial communities is not possible due to both conceptual and practical limitations. As our understanding of microbial communities expands, Earth system models are increasing in complexity and have the capacity for incorporation of more detailed, mechanistic descriptions of microbially mediated processes. In answering how far should we climb up this hierarchy, perhaps the following is the first question: should microbes be explicitly resolved in climate models at all?

Global Earth system models generally lack explicit microbial representation (other than phytoplankton). A first

step would be to include microbial pools and fluxes into Earth Systems Models. Beyond this, models may explicitly track the biomass of different functional groups. Arguments for such expansion include (i) the incorporation of critical interactions within microbial communities and food webs, (ii) potential feedbacks between microbial systems and climate, and (iii) the need for explicit representation of microbial biomass to better connect sequencing data and other observations to biogeochemical cycling parameterizations in models. The main argument against such expansion is that incorporating detailed descriptions of processes, when the parameterizations and parameter values for those processes remain uncertain, can add uncertainty to the models and may not improve model predictions (Anderson 2005).

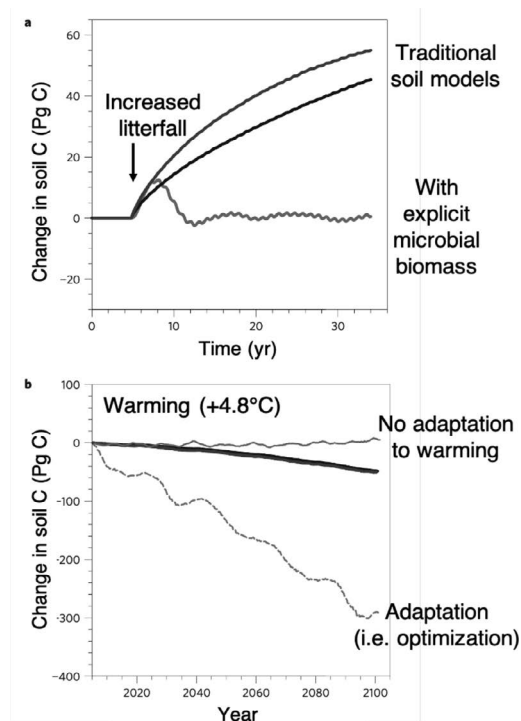
The answer to this debate is not simply a “yes” or “no”. The primary objective of these models is to understand and predict how the Earth system responds to anthropogenic greenhouse gas emissions. Since microbes underlie key processes shaping this response, the question is not simply whether or not to include microbes, but rather what degree of complexity should be used to describe them. This degree of complexity ranges from the most simplistic descriptions, such as **first-order rate constants** for the decomposition of organic matter pools



The primary objective of climate models is to understand and predict how the Earth system responds to anthropogenic greenhouse gas emissions

(i.e., an implicit description of microbial dynamics), to the full resolution of the thousands of microbial species that contribute to ecosystem processes, like decomposition (i.e., an explicit description). Physical climate scientists grapple with a similar argument about the appropriate spatial resolution of models (Held 2005). In the climate dynamics field, a hierarchical approach to modeling physics at high spatial resolution has become useful (Jeevanjee et al. 2017). Analogously, process modeling studies could follow a hierarchical approach to considering varying degrees of mechanistic, rather than spatial, resolution. Establishing quantitatively sound justifications for the appropriate degree of complexity to include in Earth system models would be extremely useful (Benedetti et al. 2023). Such studies would inform climate model developers about the best path to take so that decisions related to which microbial processes to include are made based on the best guess possible bolstered by process modeling studies.

Figure 3. (a) Response of steady-state soil C pools for conventional soil biogeochemistry models (black and blue lines) and a model with microbial processes explicitly included (green lines) to a 20% global increase in litterfall beginning in year five. (b) Response to a 4.8° increase in mean global temperature by 2100, projected by ensemble member one of CESM simulations for RCP 8.5 used in CMIP5 experiments from 2006 to 2100. For the microbial model, either microbial growth efficiency (MGE) changes with temperature (solid green line) or microbial communities adapt to increasing temperatures without changing MGE (dashed green line). Modified from Wieder et al. 2013.



For example, a soil modeling study embracing an analysis of model hierarchy supports both sides of the debate. The explicit resolution of microbial biomass qualitatively changed the response of the soil carbon pool to increased input (litterfall) (Wieder et al. 2013) (Figure 3). The dynamic biomass pool increased as a feedback to the input increased so that the standing stock of carbon returned to previous levels after five years. This is in contrast to results with an implicit representation (by a first-order rate constant and thus no feedback) where the standing stock continued to increase for decades. However, there was a drawback: uncertainty in how one of the microbial growth parameters changes with long-term global warming produced a wide range of responses in the soil carbon stock, from a negligible change to a loss of 300 Pg C by 2100. Notably, the latter response assumed that the microbial population adapted to warming, and thus that the microbial growth efficiency did not change with warming in the long term.

If models are to be expanded to include microbes explicitly, computational cost will increase significantly and much additional work will be required of model developers to properly parameterize the new state variables. Therefore, it will benefit the community if the decision about such an expansion is made deliberately, with a solid research foundation suggesting the way forward. Such research would allow us to progress from qualitative arguments about whether or not to include microbes based on individual opinions to quantitative arguments for how the explicit resolution of microbial populations changes model estimates of, for example, climate and greenhouse gas emissions.

2 Tradeoffs in model complexity

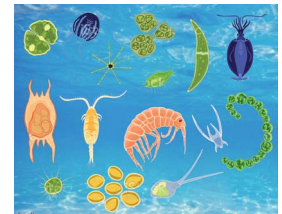
Modern Earth system models are already large and complex and introducing more parameters and processes can increase the uncertainty of their projections, potentially making them less useful.

We need to develop a robust understanding of the cost and benefits of adding microbial processes to Earth system models. Increased complexity in Earth system models comes with a tradeoff between more realistic and outcome-rich simulations and increased computational and human resource costs. A key decision is how much interactive coupling is needed, and with which level of complexity. Coupling is critical if microbial feedbacks are (i) important for climate forcing, such as significantly changing natural sources or sinks of greenhouse gases under climate change, and (ii) occurring at a timescale that matches the climate simulation, typically decadal to centennial timescales. Thus, a robust framework would include an assessment of the magnitude of feedback compared to human emissions as well as the response time-scale.

Ocean biogeochemical models have explicitly incorporated phytoplankton dynamics for the past two decades, but there is currently still a debate over the level of microbial complexity needed in those models (Friedrichs et al. 2007). In terrestrial biogeochemical models, microbial communities are more often implicitly represented. The existing soil biogeochemical modules in Earth system models often adopt the CENTURY-like microbially implicit formulation (e.g., Koven et al. 2013; Wang et al. 2010; Zhu et al. 2019), with a series of connected carbon pools, with prescribed decomposition rates modulated by environmental conditions. Although these models have included many processes and are quite detailed in terms of

parameterizations, their predictive performances have often been poor. Specifically, due to their assumption of instantaneous microbial response to environmental conditions, their predictions often exhibit less variability than benchmark datasets reveal (Carvalhais et al. 2014). When evaluating an ensemble of models for simulated global fluxes and stocks, Earth system models typically demonstrate a wide range of values with standard deviations of about 50% or more of their mean values (Varney et al. 2022; Hoffman et al. 2014). Furthermore, for the same processes, such as the temperature and moisture sensitivity of soil heterotrophic respiration, the models often use empirical response functions derived from different observations, which disagree with each other significantly (Sierra et al. 2015).

Explicitly incorporating microbial processes, for instance, through microbial interactions with plants and diverse types of substrates, may help resolve some of these variable biogeochemical responses to environmental changes (Wieder et al. 2014). However, since there are many types of microbes and corresponding substrates (Dubey et al. 2019), careful process selection is needed. New microbial pools or higher resolution (time and/or space) greatly increase the computational power required. Adding complexity also allows for more solutions to both current and future climate and ecosystem conditions. However, we commonly lack microbial observations to robustly select between outcomes. Thus, we may reduce model fidelity by adding complexity.



Ocean biogeochemical models have explicitly incorporated phytoplankton dynamics for the past two decades

3

Microbial functional groups

Climate change modelers often handle biological complexity by using functional group classifications (e.g., plant and phytoplankton functional groups). Similar efforts could be applied to other microorganisms by lumping taxa into functional groups based on their metabolism, or in a less categorical fashion by expressing functional activities in relation to a continuous range of environmental drivers, such as temperature, oxygen, and moisture.

In the ocean, photosynthetic microbes form the base of the marine food web. As such, once carbon cycle dynamics were explicitly added to climate models, ocean biogeochemical modelers needed to tackle the challenge of incorporating microbes. The classic way that this is done is using plankton functional types (PFTs), which are akin to plant functional types used in terrestrial ecosystem models (Moore et al. 2001; Quéré et al. 2005). These broad categories of microbial groups have allowed ocean biogeochemical models to capture first-order dynamics in carbon and nutrient cycling. However, even the state-of-the-art Earth system models (e.g., CMIP6) only incorporate a handful of PFTs, typically between two and five (Séférian et al. 2020). Heterotrophic microbes (bacteria and archaea) are either not explicitly incorporated into marine biogeochemical models or are represented as one to a few bacterial pools. This pales in relation to the known diversity of marine microbes. Trait-based models (e.g., Follows et al. 2007) incorporate large numbers of microbial groups (hundreds) but at increased computational cost. We currently lack a good framework for expanding how we define functional groups to allow us to incorporate the known diversity of marine microbes. This is particularly important for heterotrophic microbes where biogeochemical function and rates of carbon cycling can vary significantly based on community composition (e.g., Carlson et al. 2004).

Explicit representation of microbial communities has typically been absent in the terrestrial component of Earth system models. This arises from the lack of knowledge of how functional archetypes of soil microbial communities are distributed at the global scale, high degree of dormancy and functional redundancy exhibited by microbial populations, and the importance of emergent properties of mixed microbial communities that remain impossible to capture with existing methods of investigation. It is safe to assume that biomes defined by plant communities are not an adequate proxy for belowground microbial diversity and community composition (Vasar et al. 2022).

Functional groups could help organize microbial biodiversity into categories that describe qualitatively different ways microbes affect carbon cycling and other processes mathematical models are used to predict. Functional groups reduce the complexity of microbial biodiversity, making the modeling computationally tractable. Functional groups are useful when different organisms live according to different rules, perhaps because of a capacity to use particular substrates (e.g., O_2 vs NO_3^- as an electron acceptor), strategies for acquiring resources (e.g., rapid resource assimilation vs slow and efficient growth), or ways to tolerate stress (e.g., UV or salt resistance). Some groups are categorical, such as the ability to use a resource or not.

Others describe continuous axes of trait variation, such as growth rate and efficiency (Barton et al. 2012; Litchman and Klausmeier 2008; Edwards et al. 2012; Edwards et al. 2016). Some have narrow evolutionary histories, like bacterial methanotrophs and nitrifiers, where the presence of a gene confers functional group membership. Still others aggregate across suites of traits broadly distributed across all domains of life, like the central metabolic network. Proposed schemes for functional groups for heterotrophic microbes include copiotrophs vs. oligotrophs, maximizing yield, resource assimilators, or stress tolerance. Other frameworks are based on enzyme functional groups and metabolic pathways (Koch 2001; Wang et al. 2013; Malik et al. 2020; Wutzler et al. 2022; Zakem et al. 2020) Additionally, for soil microbes, distinguishing saprotrophs from mycorrhizae could provide insight into the pathways of C input and fate in soil.

The evidence is compelling that the biodiversity of microorganisms be-

longs in biogeochemical models, yet it is not clear how best to organize functional groups or under what conditions one functional schema would work better than another. Functional groups can be organized by genetic capacity for specific functions (methanogenesis, nitrogen fixation, denitrification, and lignin breakdown) which relate directly to biogeochemical fluxes. Alternatively, microbial physiological traits could directly inform rates of microbial transformations. For example, the 16S rRNA copy number can be used as a surrogate for the suite of traits encoding protein production and capacity for rapid growth (Li et al. 2019). Because organisms in populations are the units of natural selection, functional groups could also be organized by phylogenetic relationships (Morrissey et al. 2016; Dang et al. 2021). While categorical groupings may be easier to model, they may not be better supported by data than continuous functions representing trait variation. It is therefore critical to consider not only which schema may be appropri-



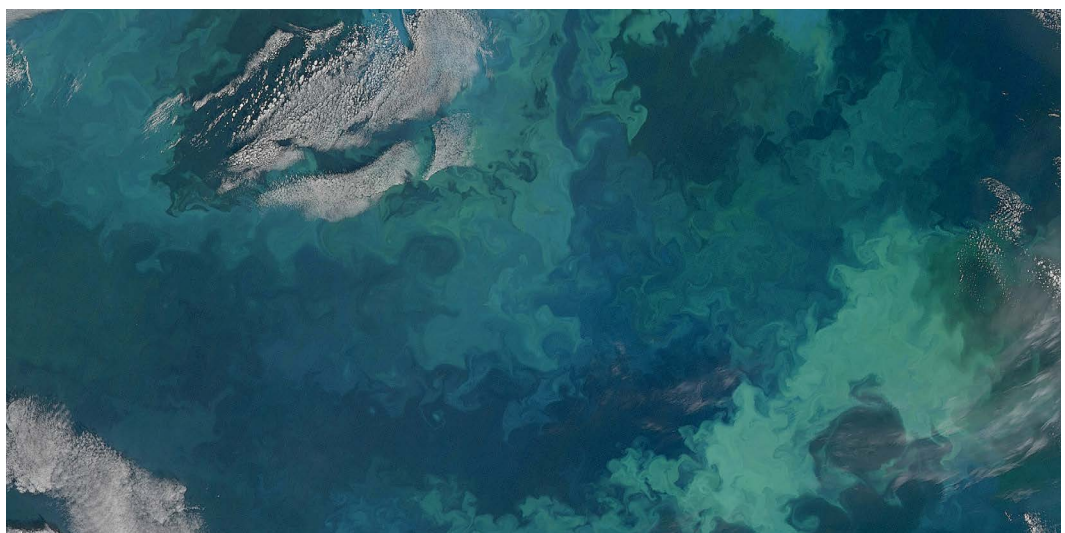
Figure 4. Microbes may behave differently in pure cultures compared to their growth in natural ecosystems, as represented by the racing microbes. Image by Victor Leshyk, Center for Ecosystem Science and Society at Northern Arizona University (Ecos).

ate, but also methods for comparing across schemata for different applications where it is necessary to simplify soil microbial diversity using functional groups or axes.

Proposed schemes for dividing microorganisms into functional groups are speculative, concerning how microorganisms live and grow in nature based on inferences from genome analyses, and on observations in pure cultures in the laboratory, such as assays of growth rates, resource requirements and flexibilities, and responses to changing conditions. Laboratory-based assays assess functional potential—the capacity for organisms to perform. However, the behavior of organisms in culture does not necessarily translate to their performance in nature (Li et al. 2019)—performance that equates to the microbially mediated biogeochemistry that we hope to model with greater accuracy (Figure 4). Proposals and conceptual frameworks for microbial functional groupings have only rarely been tested against empirical evidence from the field. A critical next step in refining functional group schemes for microorganisms is to test the concepts against activity data (for example, Barnett et al. 2021; Stone et al. 2023), especially data collected under field

conditions, and doing so is increasingly possible despite their limitations and sensitivity to assumptions (Pold et al. 2020). Key will be to define metrics that can be measured and directly compared to model output, metrics like growth, growth efficiency, substrate assimilation, mortality, extracellular excretions, and necromass production, metrics that empiricists and modelers agree about.

With new ways to measure microbes in nature, as well as understanding what they are doing and how fast, the fields of both soil and marine biogeochemistry are poised to address many questions about how microorganisms affect element fluxes. Searching for functional groups, testing them against alternatives, and validating with field data will substantially advance the field. This is also important because climate models will give more useful projections of future climate if we discover impactful functional groups or axes of variation for microorganisms that better predict microbial feedbacks to the changing climate. More generally, discovering useful functional groups for microorganisms, or useful axes of functional variation, will substantially advance ecosystem modeling, making it more aware of the microbiology underpinning global element cycles.



The variations in color are caused by different species and concentrations of phytoplankton.

4 Microbial evolution

Short generation times, large population capacity, and the ability to share genetic material potentially allow microbes to evolve quickly in response to climate change. Including phenotypic variation and evolutionary adaptation in climate-related traits in models may impart resistance and resilience to microbial processes.

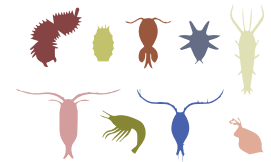
The composition of microbial communities often responds to environmental changes (Shade et al. 2012), but the short generation times and large population sizes of microorganisms mean that evolutionary forces may also play a role in their community dynamics. Process-based microbial models are challenging to parameterize partly because microorganisms acclimate and adapt, so their capacity to decompose, metabolize, and recycle organic matter varies through time in response to changes in environmental conditions and resource availability (Bang et al. 2018). This means that parameters describing the kinetics of carbon cycling in both terrestrial and marine environments also can vary over relatively short (acclimation) or long timescales (evolution and community composition changes). Capturing this variation might result in a large number of unspecified or unconstrained parameters, lowering a model's robustness.

Laboratory studies with marine phytoplankton have demonstrated that phytoplankton evolve under new environmental conditions relatively rapidly (approximately 300 generations or one to six years depending on generation time) (Aranguren-Gassis et al 2019; O'Donnell et al 2018; Schluter et al 2016; Walworth et al 2016; Schaum et al 2018; Barton et al. 2020), suggesting that marine phytoplankton are likely able to adapt readily to anthropogenically induced changes (Collins et al. 2020). Despite this likelihood, explicit representation of evolutionary dynamics is absent from global climate models (Ward et al 2019). In the ocean, an additional level of complexity is

that marine microbes are transported by the ocean currents throughout the global oceans (Hellweger et al. 2014; Doblin and Seville 2016; Jonsson and Watson 2016). These physical dynamics can play a significant role in selective pressure experienced by microbes and thus the rate of adaptation (e.g., Walworth et al. 2020; Ward et al. 2021). One modeling study suggested that adaptation to increased ocean pH could result in significant shifts in phytoplankton community composition (Dutkiewicz et al. 2015). Despite recent advances in our understanding of how marine microbes adapt to environmental shifts, evolutionary processes have not yet been well incorporated into Earth system models and so we have a limited understanding of the impact of marine microbial acclimation and adaptation for marine carbon cycling (Le Gland et al. 2021).

Soil microbial models accounting for acclimation and adaptation assume that microorganisms are adapted to the current environmental conditions (instantaneous optimization) (Manzoni et al. 2017) or consider temporal variations in microbial traits that maximize microbial fitness over a prescribed time interval (dynamic optimization) (Manzoni et al. 2023). These approaches are complementary rather than mutually exclusive and might yield different insights into microbial responses over different spatial and temporal scales.

Experiments and observational studies demonstrate a range of heritable genomic responses to climate variation. In a common garden experiment set along an elevational and climate



Explicit representation of evolutionary dynamics is absent from global climate models



To what degree adaptation occurs depending on substrate type or soil and environmental conditions is not well understood

gradient from desert to subalpine, transplanted *Curtobacterium* communities converged after 18 months towards native communities, accompanied by genomic mutations associated with local adaptation (Chase et al. 2021). Thirty years of climate warming was shown to affect **codon usage bias** in six lineages of bacteria, with other lineage-specific effects on carbon and nitrogen-metabolism genes (Choudoir et al. 2023). Some lineages have a deeper reserve of genes that may be shared within a population by gene transfer events, and environmental stress can lead to even a rarely occurring gene to sweep through a population due to stress (Vernikos et al. 2015). Stressors including acidity, heat, drought, and salt stress all led to reductions in genome gene richness of *Bradyrhizobium diazoefficiens* (Simonsen 2022). Further analysis of these genes showed that gene loss was stress or environment specific. This is consistent with independent observations that warmer and drier soils tend to have bacteria with smaller genomes (Liu et al. 2023). Climate stress may also affect gene flow through plasmid transfer, mistranslation of tRNAs, or viral sharing of genomic information (Trubl et al. 2018).

Heritable variation may also be epigenetic, though these dynamics are not well described in natural environments yet. Variations in stress response may originate through changes in gene expression that vary within populations due to epigenetic adaptation, a memory response in cells that can last generations (Andersson 2016). In bacteria, a memorylike response is seen as a version of local adaptation to stressful environmental conditions. For example, *E. coli* shows a coupled transcriptional response to lower redox and increasing temperature, environmental changes that signal a transition to the digestive tract; this response can be decoupled in the laboratory when signals are presented separately, suggesting that cells are able to interpret

frequency of or variation in environmental changes (Mitchell et al. 2009).

Quantifying adaptive responses in microbial communities is fundamental for modeling responses to global warming (Toseland et al. 2013). For example, warming causes heterotrophic respiration to increase, but the rate of increase in short-term incubation experiments is steeper than observed along climatic gradients, even after removing the effect of reduced substrate availability in warmer conditions in soils (Dacal et al. 2019). Along similar lines, microbial carbon use efficiency decreases with increasing temperature in short-term incubations, but less so if microbes are adapted to warmer conditions, and microbial respiration in soils decreases over time in warming conditions (Romero-Olivares et al. 2017). Also, microbial communities use carbon more efficiently during drying-rewetting cycles when adapted to drier climate (Leizeaga et al. 2020). Current models neglect these evolutionary effects, possibly leading to overestimating soil respiration responses to warming and respiration pulses at rewetting. However, to what degree adaptation occurs depending on substrate type or soil and environmental conditions is not well understood.

Approximating adaptive dynamics so that they can be embedded into current model structures and determining at which scale adaptive processes should be modeled (species, functional group, or even at the community level) are ongoing challenges. Efforts are needed to expand our quantitative understanding of how different groups of microbes evolve in response to climate change. Arguably, most studies to date have focused on bacteria and eukaryotic protists (algae). More information about the evolution of fungi and viruses is needed to get a holistic overview of how microbial communities are adapting as a whole (van Diepen et al. 2016).

5 Spatial scale

The average microorganism is approximately $1 \mu\text{m}^2$, while the typical grid size of an Earth system model is 22 orders of magnitude greater. Spatial interpolation of microbial abundances and processes is a major challenge for incorporating microbes into climate change models.

Physical models of the climate system typically develop mathematical parameterizations for subgrid processes that cannot be resolved by their relatively coarse spatial resolution. Similar approaches may be required for representing microbial physiology in Earth system models (Figure 5). Even cutting edge physical models at very high resolution (kilometer scale) cannot resolve the spatial scales that are relevant for microbial processes. Instead, more meaningful information could be generated by more faithfully representing abiotic subgrid heterogeneity in land models, both laterally and vertically (Torres-Rojas et al. 2022), and subsequently developing parameterizations of microbially driven processes that are informed by relationships between microbial functional traits and their environmental sensitivities (Wieder et al. 2015; Lipson and Xu 2019; Chen et al. 2022; Evans et al. 2022).

The issue of spatial scale is relevant for both marine and terrestrial systems. Recent efforts by marine researchers in data synthesis and statistical and numerical modeling highlight the fact that the spatiotemporal integration scale of biological information on plankton occurrences, abundances, or metagenomic data matters for the identification of the dominant biotic or environmental drivers of plankton community structure, diversity, and biogeography. This leads to an interesting divergence between the main drivers of community structure and diversity as identified in mechanistic models (e.g., Henson et al. 2021;

Dutkiewicz et al. 2020), those derived from macroecological studies using species distribution models (e.g., Benedetti et al. 2021), those identified

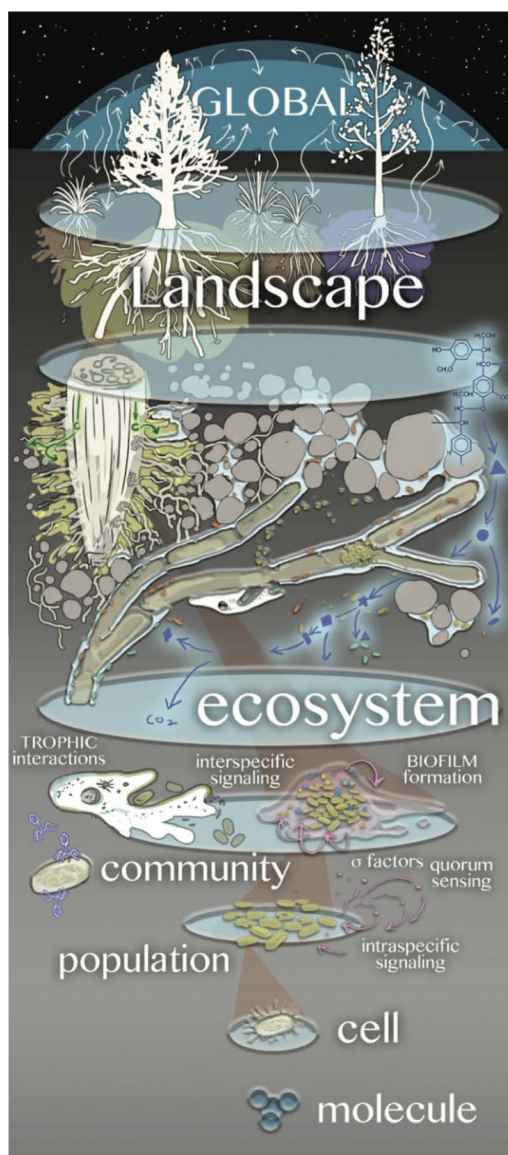


Figure 5. Illustration of the range of scales—from molecular to global—through which microorganisms influence the Earth system. Image by Victor Leshyk, Center for Ecosystem Science and Society at Northern Arizona University (EcoSS). (BERAC 2017)

as dominant in new synthesis work on metagenomic data (e.g., Guidi et al. 2016), and those derived in larger-scale data analysis efforts (e.g., Beaugrand 2009). Such a scale-dependence is also known to exist for terrestrial communities, where macroecological modeling studies show that biotic interactions and dispersal limitation matter at small spatio-temporal scales, but large-scale environmental factors such as temperature and precipitation emerge as prime drivers of community assembly as the integration scale increases (Thuiller et al. 2015). Whereas numerical ocean and climate models are often calibrated with physiological and trait data from laboratory studies at small scales, and new metagenomic samples integrate the community structure across some tens to hundreds of liters of samples, global macroecological machine learning and species distribution models integrate data at the global scale across decades, ocean basins, and sampling expeditions, which may explain the differences in the dominant drivers of community assembly emerging in each of these methods.

Functional relationships can also be derived from smaller-scale models in a tiered modeling approach. For example, microsite models with explicit

representation of microorganisms can be used to define scaling relationships between environmental variables and processes that affect large-scale biogeochemistry, such as decay rates of bioavailable carbon pools, microbial carbon use efficiency (Saifuddin et al. 2019) and microbial turnover (Georgiou et al. 2017). Starting from micro-scale models and integrating their results in space is important because process rates at the macro-scale can depend on micro-scale heterogeneities. For example, the non-linear microbial kinetics used in microbial-explicit models change their mathematical structure once applied at soil core or large scales (Chakrawal et al. 2020). Sharing information between models at different scales (e.g., using mathematical upscaling techniques) may alleviate the lack of understanding between microbial traits and biogeochemical function in microbial ecology.

Scale-dependent numerical models will help us overcome this challenge to generate better climate projections, and to better understand key aspects of microbial community dynamics—“who” lives where with “whom” and how these shifts might matter for specific ecosystem services.



6 Temporal scale

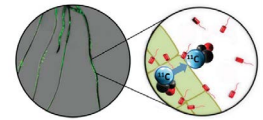
Many microbial processes occur on timescales of seconds to minutes, but environmental and energetic constraints can reduce the rates of metabolism and greatly extend the timescale at which microbial biomass pools turn over. The range of microbial persistence and lifespan must be addressed in order to accurately represent microbes in Earth systems models.

Microbial communities can be dynamic on short timescales (i.e., minutes to hours) where transcriptional and metabolic changes can rapidly alter community processes. Thus, *in situ* sampling of soil and ocean microbial communities represent single moments in time. While these snapshots provide insight into the immediate status of microbial community composition and activity (Moran et al. 2012), they provide limited insight into how communities change over time and what drives temporal changes.

Generation times of microbial taxa vary depending on the species, the resources available, as well as environmental conditions, allowing for high variability in microbial growth and biomass (Pold et al. 2017). Rousk and Baath (2011) summarized that fungal generation time could be as high as 600 days in wood, while bacterial generation time could be as low as 1 day in soil, with community averages for bacteria estimated to be closer to 2 weeks (Domeignoz-Horta et al. 2022). Additionally, temporal turnover of soil fungi in only approximately 1 week was the equivalent of spatial turnover of taxa across 100 km (Averill et al. 2019). In the surface ocean, marine microbes can grow rapidly, while in the deep ocean, growth rates are typically much slower. In addition, in many marine and groundwater systems, nutrients and energy are limiting environments resulting in high rates of dormancy (Bradley et al. 2020).

Microbial community composition can also shift rapidly in response to environmental changes. For example, surface microbial communities were seen to shift daily during a phytoplankton bloom (Needham and Furchman 2016). While these short-term fluctuations are not predictable, longer-term variability, such as seasonal cycles, has been shown to be reproducible (e.g. Cram et al. 2015; Ward et al 2017). In soil systems, some short-term successional or seasonal variation has been shown to be predictable (Blazewicz et al. 2020). Whether or not this temporal variation in composition matters for rates of carbon and nutrient cycling and trophic interactions is the classic problem of how composition translates into functional variation.

Developing model representations of microbial processes requires an understanding of what drives changes in microbial growth and activity over time—both what these shifts are and the timescales over which they occur. This is particularly challenging because the response of microbial species and communities to environmental stressors differs, even if these communities are from similar domains (e.g., soil) but from different biomes (Waring et al. 2021) or from different sampling points even in the same biome (Ofiti et al. 2022). Thus, understanding functional acclimation will require a temporal perspective. This can be seen in experiments that track microbial responses to altered environmental changes over multiple years. In



Developing model representations of microbial processes requires an understanding of what drives changes in microbial growth and activity over time

some cases, functional legacies persist based on historical climate for up to 4.5 years (Hawkes et al. 2017). Others find compositional shifts in response to experimental warming only after approximately 20 years (DeAngelis et al. 2015; Pec et al. 2021), but functional shifts occurred throughout, largely tracking substrate availability (Melillo et al. 2017). Longer-term studies with sampling at multiple temporal scales are needed to determine whether these unexpected responses are common and sufficiently durable to matter for far-term projections.

Given the challenges of accurately sampling temporal dynamics, research in both terrestrial and marine systems often invokes space-for-time substitution. This is when a site is sampled spatially to gain insight into temporal variability that might occur if a single site were sampled over an extended period of time. This approach has been effective in modeling climate change effects on plant diversity and genetic variation (Blois et al. 2013; Wogan and Wang 2018) and may also be useful for microbial processes (Glassman et al. 2018).

The diversity of microbial communities, environments, and responses to environmental changes makes it challenging for data scientists and modelers to synthesize these large microbial datasets being generated such that they identify appropriate microbial life cycle processes at the correct temporal scale along with parameters to incorporate in their earth system model of concern. Most models currently assume that microbial communities and associated functions respond instantaneously and consistently across a region to environmental change. In fact, Yang et al. argued that microbial explicit models are not relevant for earth system models as microbes adapt quickly in the

face of environmental change because ecosystems do not lose function when environmental conditions change over the span of several years (Yang et al. 2023). However, the speed of ecosystem functions may change with feedback being positive (Ofiti et al. 2022) or negative depending on temporal scale of interest. Thus, identification of the appropriate temporal scale is critical to evaluate the incorporation or rejection of microbial processes in earth system models. Long-term studies are also needed to understand both the actual response to change and any time lags in functional shifts. Such studies will allow us to determine whether these fine-scale microbial dynamics are needed for accurate forward projections and, if so, how these can best be incorporated into models.

Emphasizing the role of temporal variation in microbial community function requires a major shift in the culture of how microbial composition and function are measured and utilized in models. Correctly identifying the baseline temporal scale of microbial activity will enable modelers to accurately predict the response of microbes to change in environmental conditions. This may improve the accuracy of earth system models, especially if feedback loops are especially strong. In turn, the end users (such as forest management practitioners, policy makers, and agriculturalists) will be better equipped to make informed decisions for land-use/land-management techniques to maintain ecosystem services in the face of climate change. Finally, sufficient temporal studies across fine to coarse scales to determine the most appropriate scale for modeling are needed. Given the necessary timescales, funding opportunities must be expanded to support long-term work in contrast to the typical 3–5 year grant cycle.

7 Microbes on land and water

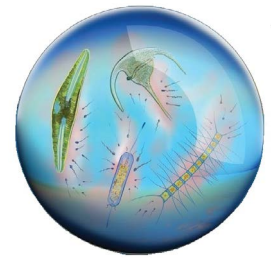
Though models often consider land and water as separate entities, integrating microbes into climate change models may foster intellectual exchange between these two research communities. Furthermore, the role of microbes at the land-water interface is increasingly being recognized as an important issue in climate change research.

While aquatic marine and terrestrial microbiologists often study similar types of questions, these communities have historically had very few intellectual exchanges. Unfortunately, this siloing means that much of the work of incorporating the general principles of metabolism and competition into models has been duplicated—there are no easy channels for communicating the advances in one community to the other community. Below we highlight some ways that these two communities overlap and some in which they are different.

Water is essential for life. In soils, microbes can persist in thinner films of water, or through the expression of traits associated with, for example, biofilm formation or dormancy. As most fundamental microbial processes thus basically occur in water or water films, in theory, many of the relationships controlling these processes can be shared across land and water models. However, there are three major differences in microbial activities in land and water that currently confound models in the climate change context.

1. Water is often a limiting resource on land but not in the ocean. Specifically, the presence of water in terrestrial systems has a fundamental influence on all aspects of productivity, oxidation reduction, and biogeochemical fluxes such as soil CH_4 and N_2O emissions (Luo et al. 2013) and H_2 uptake (Bertagni et al. 2021).
2. Ocean salinity constrains microbial osmotic balance, which has critical implications for biodiversity and ecosystem services under human freshwater extraction, intensification of the hydrological cycle, and sea level rise (Mau-bach et al. 2020). While osmotic balance is also important in soil systems, marine organisms must contend with constant high external salt content.
3. Physical mixing in the ocean generates spatial gradients in light, nutrient availability, and sometimes chemical status that span tens to hundreds of meters. These scales are enormous compared to the relatively compressed top meters of microbially active soil.

Both fields strive to identify unifying principles of nutrient cycling and energy flows, prey avoidance, and the importance of physical environmental constraints such as temperature on growth and grazing. Key to advancing our understanding is incorporation of these “principles,” as well as how they respond to perturbations such as climate warming, into numerical models. While the principles may be similar in the two systems, ocean models must capture oxidation-reduction transitions which occur over large spatial scales in the ocean interior (e.g. Algeo and Li 2020; Stanev et al. 2018) compared to the intense spatial and temporal heterogeneity and thin layers in soil systems (Boye et al. 2018).



Water is essential for life.

A primary scientific challenge is the robust characterization of how land and ocean systems will respond in terms of CO_2 , N_2O , CH_4 , and H_2 fluxes, the resulting impact on atmospheric composition, and the associated climate feedbacks. Central to addressing this challenge is the ability to balance the thermodynamic, hydrological, biogeochemical, and ecological factors associated with changing phases (frozen, liquid, and dry) and quantities (oxic-hypoxic-suboxic) of water in the context of climate warming and intensification of the hydrological cycle on microbial function and the subsequent carbon balance. The complex role of microbes in governing these interactive processes has only recently been modeled in ways suitable for representation in global earth system models (Sulman et al. 2014; Weider et al. 2014). Still, the most advanced of these representations still struggle to represent the global range of soil dynamics (Varney et al. 2022). Further, the land to river, estuary, and coast to pelagic ocean transition requires a vast array of microbial adaptations typically studied in separate disciplines. Understanding microbial interactions on land can be particularly valuable to apply to freshwater and saltwater systems in general by their breadth of environmental and ecological contributions over which they have been studied from cold to hot, wet to dry, fresh to hypersaline, and

mechanically tortuous, porous, and heterogeneous to uniform and interacting with a wide variety of macroflora and fauna and the implications for elemental stoichiometry.

Whether considering land or water, representation of emergent behavior requires not only inclusion of the relevant dominant and contributing processes, but also their overall/net effects that often compete in their influence on how the overall system evolves. This means that decisions on how the relative magnitude of processes are implemented in a model are critically important to the overall function. This challenge is particularly relevant in comparing the roles of microbes in land and ocean systems under climate change through the question of niche exclusion: where it exists, how it might emerge under changing environments, and how fast it might be relieved through migration, adaptation, or evolution. Hutchinson's (1961) Paradox of the Plankton remains as relevant today—why does so much microbial biodiversity persist together across Earth's environments, what are its limitations, and how do the ecological controls combine to determine how the Earth system will respond to climate change? Only by combining interdisciplinary fields in land and ocean microbial dynamics can these questions be answered before their implications for climate feedback are realized.



Understanding of microbial interactions on land can be particularly valuable to apply to freshwater and saltwater systems

8

Need for the “right” information

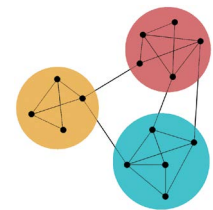
Microbiologists have access to cutting-edge technologies that are capable of generating massive amounts of data, and new statistical approaches are being developed so that high-dimensionality datasets can be more readily incorporated into ecosystem models. Applying these methods to larger-scale manipulative, distributed, or comparative field sites has the potential to further facilitate integration of microbial data into climate change models.

Earth system models commonly contain representations of carbon fixation by photosynthesis and release by aerobic respiration (e.g., Wenzel et al. 2014), but the “right” information, as the repertoire of metabolisms explicitly considered in models to include the diverse metabolic capabilities of bacteria, archaea, and fungi, is sorely lacking. On land, plants are responsible for photosynthesis, whereas in the oceans, photosynthesis is carried out by microbial life in the form of phytoplankton. The most recent Coupled Model Intercomparison Project (CMIP6, Tokarska et al. 2020) compared predictions by Earth system models that have a range of microbial complexity within them, with some more sophisticated models explicitly resolving diverse groups of phytoplankton and variable phytoplankton stoichiometry (Séférian et al. 2020). Photosynthesis and aerobic respiration are carried out by organisms in all domains of life, both on land and in the oceans. In contrast, microbially mediated production of methane and nitrous oxide is dominated by bacteria and archaea (Thompson et al. 2012). What many Earth system models are lacking is explicit inclusion of microbial metabolism associated with release of carbon dioxide (through aerobic respiration) and other greenhouse gases such as methane (through methanogenesis).

Lessons learned by Earth system modelers who have included ever

more complex representations of the plankton may provide lessons for those interested in identifying the right information to include a wider repertoire of microbial metabolisms in Earth system models. For instance, the UK iMarNet project compared the skill of seven biogeochemical models, covering a range of biological complexity, in predicting carbon dynamics on large scales (Kwiatkowski et al. 2014). This gave insight into which level of biological complexity was important for representing large-scale carbon dynamics in Earth system models. Similar approaches could be applied more broadly in terrestrial and ocean systems, with more explicit focus on the microbial metabolisms that have been largely overlooked in Earth system models.

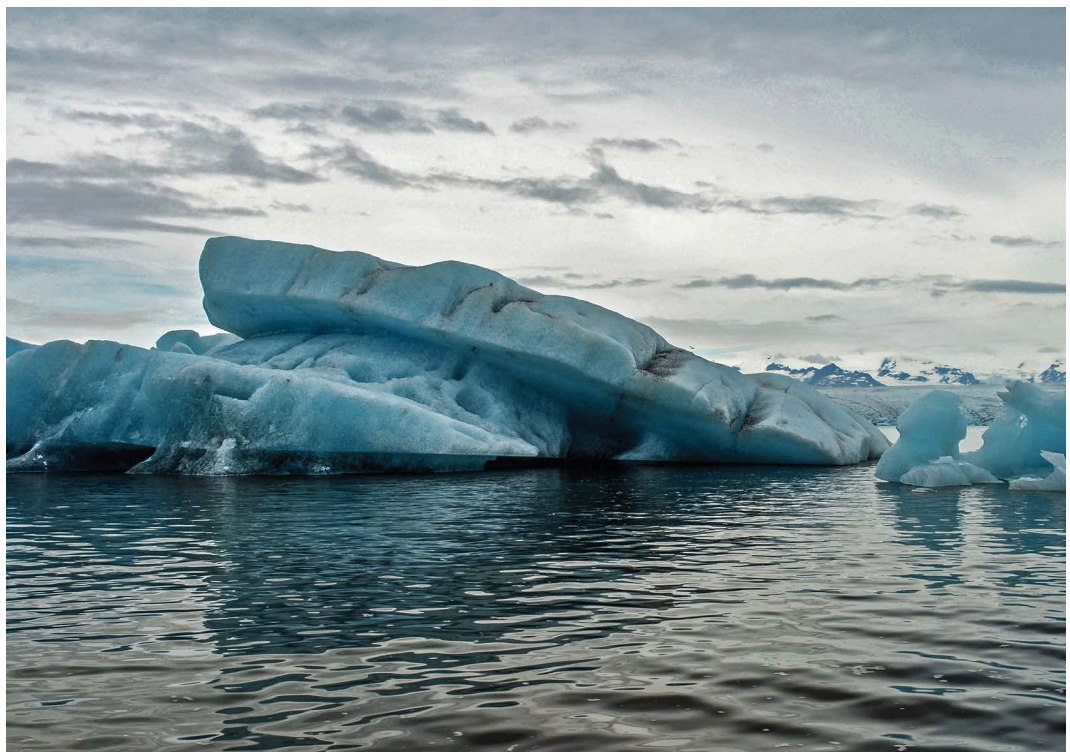
The question of what information is right is critical since without considerable effort toward identification of appropriate models and data, all other effort will be wasted. As a cautionary note, in 1991, Wally Broecker wrote an op-ed in the journal *Global Biogeochemical Cycles* entitled: “Keeping global change honest” (Broecker 1991). In it, he highlights potential for outsized representation of the importance of one field (such as biology) in Earth system function and how that practice “complicates an already murky situation.” Considering this context, it seems prudent for any concerted effort to expand representation of microbes in climate models to be led by close collaboration between geo-



The question of what information is “right” is critical

scientists and biologists. Only through interdisciplinary work can these efforts realistically assess which processes and mechanisms are appropriate and necessary for inclusion and identify appropriate experiments and data to inform model development. Indeed, it is not just any two communities. There are communities of ecosystem and biogeochemical modelers that couple microbes with global biogeochemical processes, who could act as a 'bridge' between microbiologists and climate modelers. The iMarNet project described above provides a case study when such cross-disciplinary collaboration has worked effectively. Cohesive transdisciplinary research will help direct effort efficiently and productively toward inclusion of microbial processes that are most likely to matter for Earth's climate.

Today, there are many interdisciplinary teams of researchers investing considerable effort to understand microbial controls on global biogeochemical cycles (Zakem et al. 2020). Many models coupling microbes and global biogeochemistry include representations of diverse microbiota. Such models are often simulated on large scales both in the ocean (Zakem et al. 2018) and on land (Braghiere et al. 2021), yet many processes within these models have not been incorporated into climate models. Identifying appropriate models and data to inform climate model parameterization will enable the field to recognize if and how diverse microbial metabolisms impact the Earth system function. A comprehensive answer to this question is not obvious with current knowledge.



9

Data harmonization

Efforts are needed to facilitate transdisciplinary endeavors, such as the development of ontologies that clearly define concepts and their interrelationships as well as efforts to structure and organize databases. These harmonization efforts can be used to bring together data from multiple sources needed to inform model prediction and policy.

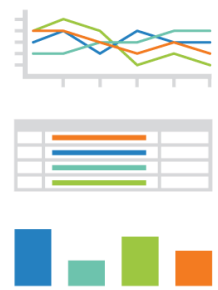
Any global model would need to be supported by data streams drawn from multiple sources. No single study or project could provide a complete picture of the global system due to the diversity of agents, processes, large spatial area, and extensive temporal coverage. Direct measurements of microorganisms include, -omics data, phenotypic (trait) information, and organic chemical characterization. In addition, abiotic variables that better reflect the immediate environment of microorganisms such as pore-space topology, aggregate dynamics, micro-temperature, redox conditions, and mineral-organic interactions could also be included. None of these measurements are unique or have emerged as a silver bullet that could motivate a unified global field campaign. However, many different studies are already collecting quite a range of microbial data, especially different types of -omics data (Stec et al. 2017).

Diverse data, which are data from multiple sources and specialties, present special informatics challenges that are distinct from “big data” challenges. Both the structure of the data tables and vocabulary used to describe the data (variable or column names and methodology used to collect the data) are unique to the purpose of the original data collected and idiosyncrasies of the data collector. This data diversity is desirable, reflecting new and innovative ways of looking at a complex system. However, common metadata tools to

place data in context with each other are needed (Samuel et al. 2021).

Metadata tools include community vocabularies, dictionaries, and ontologies. The development of these metadata tools has been uneven across the sciences. The genetics community quickly realized that their high-volume sequence data required strict and regular data formats and have been leaders in this space (Pesant et al. 2015). However, critical contextual information beyond base genetic information is often delivered as relatively poorly described “metadata,” which is often the primary data in nongenetic focused studies. Indeed, this metadata is exactly the biogeochemical information that is often of primary importance in global biogeochemical models. Biogeochemical focused ontologies are nascent at best and not developed enough to be leveraged in a data integration workflow. A current microbiome-focused effort is the National Microbiome Data Collaborative.

Semantic development to support data integration requires tighter collaborations across specialists and development of new communities to support these collaborations. Outside of genetics, development for microbial data annotations and metadata has typically focused on data discovery, not harmonization, and lacks critical methodological details needed for data harmonization (for example, ENVO bulk density). Developing these annotations (ontologies and other



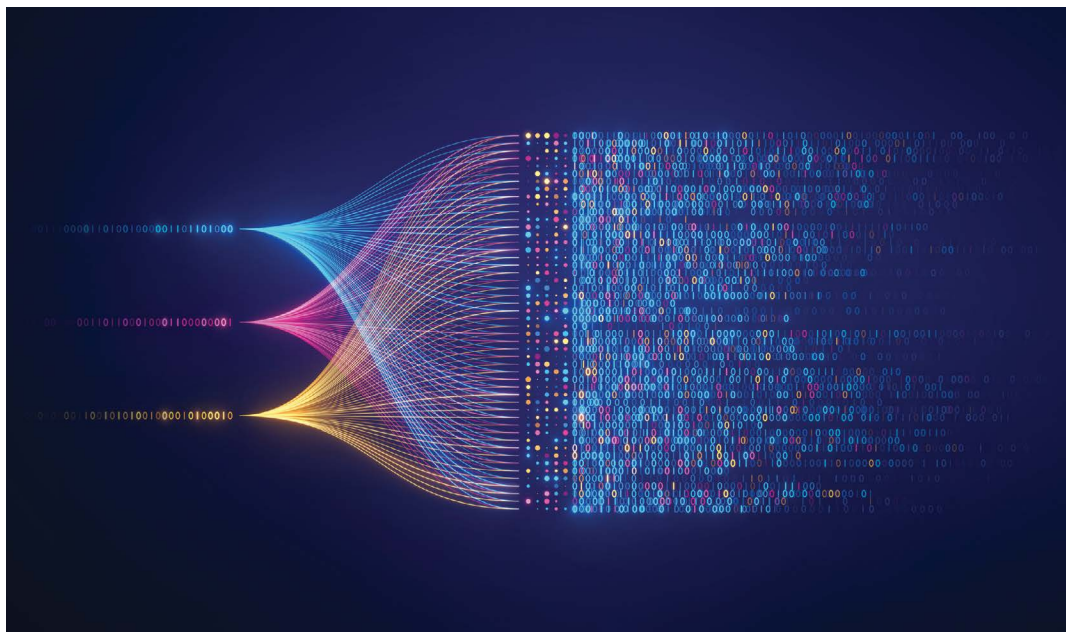
Any global microbial model would need to be supported by data streams drawn from multiple source

semantic resources) requires a close collaboration between data providers (experimentalists), data aggregators, knowledge engineers, and modelers. These collaborations require new incentive structures to promote initial development and ongoing maintenance of these resources as the field moves forward.

Developing data-centered communities of practice provides the social glue to support ontology development, annotation activities, and integration. This softer side of data science is critical for the success of these cross-disciplinary ontologies. Communities of practice would establish social norms around credit and attribution that currently are a barrier for some researchers sharing their data. They steward ontologies through scientific development, extending terminologies, and developing new data models as the field

moves forward. They also provide ongoing educational and collaboration opportunities to both early career and established researchers in how to work with diverse data streams.

A world where microbial, functional, and environmental data are fully harmonized lowers the barrier for scientific participation and discovery. Fully integrated data streams allow for innovative reuse of previously collected data and the formation of new cross-disciplinary collaborations. Data-centric communities of practice provide concrete platforms for cross-disciplinary collaboration using clear and precise semantic resources to break down disciplinary jargon. These communities establish new norms for collaboration that give credit and attribution to all researchers involved in the data processing pipeline to satisfy data hungry models.



10

Novel impacts on microbes

By including microbes in Earth system models, models may yield new insight into how climate change is affecting the distribution, abundance, and functionality of microbial life. This is important for the stability of managed and natural ecosystems and the services that they provide.

Thus far, we have discussed the challenges of integrating microorganisms into Earth or ecosystem models to improve their predictions. However, even if this integration does not change model predictions, it is important to recognize that climate change will impact microorganisms, their processes, and the services that ecosystems provide to humanity (Peralta et al 2014). Indeed, microorganisms control the majority, and often rate-limiting steps, of carbon and nutrient cycling (Falkowski et al 2008). Therefore, microbial processes will be largely responsible for ecosystem-level responses to global change, whether or not their feedback on climate alters current Earth system model predictions. Indeed, a recent American Academy of Microbiology colloquium report “Microbes and Climate Change - Science, People & Impacts” previously focused on enumerating these impacts.

Microbial community structure and composition are sensitive to a variety of global changes ranging from small-scale manipulations of nutrients and temperature to large-scale disturbances such as deforestation and storms. Understanding the mechanistic links between microbial composition and functioning would help to predict changes in ecosystem processes. While many studies document correlations between microbial composition and ecosystem processes (e.g., Bier et al. 2015), establishing causal relationships remains difficult.

Of course, tracking changes in the distribution and abundance of individual microbial species is unrealistic, given the diversity of microbial communities. One potential approach is to consider broader-scale assessments of microbial composition, considering, for instance, a handful of major groupings within a functional group as discussed above. In the oceans, for instance, understanding climate impacts on major clades of nitrogen-fixing microorganisms is clarifying the biogeographic patterns of nitrogen cycling (Zehr and Capone 2020).

On land, one such useful grouping may be to consider that arbuscular mycorrhizal fungal forests store less carbon than ectomycorrhizal fungal forests (Averill et al. 2014), with associated shifts in biogeochemical syndromes (Averill et al. 2019) and sensitivity to nitrogen deposition (Averill et al. 2018). Given that mycorrhizal plant and fungal distributions and vulnerabilities to climate change are now well-known (Davison et al. 2021; Kivlin et al. 2021; Steidinger et al. 2020), including mycorrhizal fungal associations could add realistic constraints to spatial and temporal dynamics of terrestrial carbon storage in a changing climate (e.g., Sulman et al. 2019; Braghiere et al. 2021).



It is important to recognize that climate change will impact microorganisms, their processes, and the services that ecosystems provide to humanity

Conclusions

Though invisible to humans, Earth processes are driven by microorganisms. The variation in species, traits, and function of microbes appears to be limitless. With microbes' many impacts on humans and the globe, explicit inclusion of their activities and processes into Earth system models is vital for managing the future effects of climate change.



Climate change is happening now

Earth's climate is changing and so are the rules governing how microbes interact with their environment (Melillo et al. 2014; Abs et al. 2020). Microbes living at higher temperatures metabolize faster, and these physiological changes can accompany changes in the community ecology of these microbiomes: some organisms become more dominant while others decline in abundance or cease to survive (Brown et al. 2004). Climate change stands to alter microbes in irreversible and unknown ways, which includes adaptation, expansion of biogeographical ranges, and many other life-history strategies (Ladau and Eloe-Fadrosh 2019). Because microbes affect humans and ecosystems in myriad ways, understanding how climate change affects microbes and microbiomes can help inform mitigation strategies.

However, fully understanding the feedback between climate change and microbes is difficult. Leveraging current and past observations while being open to incorporating future processes from a highly diverse set of domains remains a challenge. During the colloquium "Microbes in Models: Steps for Integrating Microbes into Earth System Models for Understanding Climate Change," participants discussed knowledge, infrastructure,

and communication gaps that exist. From that, the group developed and outlined their top 10 challenges for incorporating microbes into models as outlined above. Highlighting these major challenges gives scientists in both fields awareness of the transdisciplinary actions needed to overcome these challenges to propel science—and society in general—towards climate change solutions.

Developing a properly complex microbially explicit biogeochemical model that sufficiently accounts for the diversity of microbial communities and the physiological mechanisms underlying each individual microbial functional group has been a long-term goal for scientists working in various subdisciplines of earth sciences, but has yet to be achieved. The colloquium aimed to outline those challenges with the intention to bring attention and encourage the scientific community to work on finding solutions. As these challenges are better defined, addressing them will allow better integration of microbial biology into the predictive biogeochemistry capability of Earth system models, which will enable more robust quantification of the feedbacks between biogeochemistry and climate change. Each of these challenges will need more than one solution. The quest to find the answers for these challenges will likely require transdisciplinary research teams, new methods, and potentially a novel conceptual framework. Although more research is needed, newer research is arguably even more critical.

At least in science, one can't improve what one can't measure. One can't measure if there is no contextual

framework or model to do so. Therefore, as climate change will fundamentally change life on Earth, including that of microorganisms, it is critically important to bring the scientific communities together to address these transdisciplinary challenges. Though difficult, explicit and thoughtful inclusion of microbial

processes in Earth system models can aid in humanity's response to climate change. Expertise from diverse fields, such as climate science, computer modeling, ecology, and microbiology, working in harmony will be vital for finding solutions to the greatest threat facing society today.

Glossary

Acclimation: temporary and reversible changes that result from becoming accustomed to a new climate or to new conditions.

Adaptation: heritable physical or behavioral trait that serves a specific function and improves an organism's fitness or survival.

Algae: photosynthetic, eukaryotic organisms mainly found in aquatic environments.

Archaea: single-cell organisms that lack a nucleus (known as a prokaryote) that are similar but evolutionarily distinct from bacteria. Many have been found in extreme environments.

Bacteria: microscopic organisms that have only one cell and no nucleus.

Climate models: mathematical equations to characterize how energy and matter interact in different parts of the ocean, atmosphere, and land.

Codon usage bias: the phenomenon where specific codons are used more often than other synonymous codons during translation of genes.

Differential equations: equation that relates one or more unknown functions and their derivatives.

Earth system models: integrate the interactions of atmosphere, ocean, land, ice, and biosphere to estimate the state of regional and global climate under a wide variety of conditions.

First-order rate constants: proportionality constant in an equation that expresses the relationship between factors.

Fungi: eukaryotic organisms that belong to the Kingdom fungi. They can be unicellular or multicellular.

Microbiome: collection of all microorganisms in a location.

Parameters: numerical values that modify model variables, pools, and/or transformations and as a set influence model outcomes.

Phytoplankton: photosynthetic eukaryotes that are major providers of nutrients to aquatic food webs.

Protozoa: single-celled, eukaryotic microorganisms.

Virus: microscopic infectious agent that replicates only inside the living cells of an organism.

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This report is based on the deliberations of experts who gathered to discuss a series of questions developed by the steering committee. All participants had the opportunity to provide feedback, and every effort has been made to ensure that the information is accurate and complete. The contents reflect the views of the participants and are not intended to reflect official positions of the Academy or of American Society for Microbiology.

