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# Microbes and Climate Change



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# Microbes and Climate Change

Report on an American Academy of Microbiology and American Geophysical Union Colloquium held in Washington, DC, in March 2016

The American Academy of Microbiology (Academy) is the honorific branch of the American Society for Microbiology (ASM), a nonprofit scientific society with nearly 48,000 members. Fellows of the Academy have been elected by their peers in recognition of their outstanding contributions to the microbial sciences. Through its colloquium program, the Academy draws on the expertise of these fellows to address critical issues in the microbial sciences.

The American Geophysical Union (AGU) galvanizes a community of Earth and space scientists that collaboratively advances and communicates science and its power to ensure a sustainable future. AGU is dedicated to the furtherance of the Earth and space sciences and to communicating our science's ability to benefit humanity.

This report is based on the deliberations of experts who gathered for a full day 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, ASM, or AGU.

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# Introduction

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Microorganisms have been changing the climate, and have been changed by the climate, throughout Earth's history. As we experience unprecedented environmental impacts from **climate change**, microorganisms will respond, **adapt**, and evolve in their surroundings. Because they have generation times as short as a few hours, they will do so at higher rates than most other organisms. This makes microbes ideal sentinels for understanding the effects of climate change on biological systems and the global **biogeochemical** cycles that microbes mediate. Scientists can study the effects of climate change on microbes to both understand and hopefully predict the future effects of climate change on all forms of life.

This colloquium brought together members of the American Society for Microbiology and the American Geophysical Union because understanding climate change impacts requires experts from many scientific disciplines. The collaboration between these two societies intermingled scientists

## Key terms used throughout text

**Adaptation (to climate):** the process of adjustment to actual or expected climate and its effects. In human systems, adaptation seeks to moderate or avoid harm or exploit beneficial opportunities. In some natural systems, human intervention may facilitate adjustment to expected climate and its effects. (*Agard et al. 2014*)

**Albedo:** a measure of the reflectivity of the Earth's surface.

**Biogeochemistry:** the study of biological, geological, chemical, and physical processes and reactions that influence the inventory of reactive elements at present and over Earth's history.

**Climate change:** change in the state of the Earth's climate resulting from the combination of biotic processes, variations in solar radiation, volcanic eruptions, and human activity.

Climate change can be identified (e.g., by using statistical tests) by shifts in the mean and/or the variability of its properties that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forces such as modulations of the solar cycles, volcanic eruptions, and persistent anthropogenic changes in the composition of the atmosphere or in land use. (*modified from the IPCC 2014 report definition; Agard et al. 2014*)

**Permafrost:** the frozen portion of soil and rock below the freezing point of water in polar and high alpine regions.

**Symbiont:** an organism living in a close and often long-term association with one or more organisms of different species.

knowledgeable about microbial contributions and responses to climate change across global settings (terrestrial polar regions; soil, agriculture, and freshwater; oceans) and able to think broadly about the functions of microbiomes.

Although scientists have been studying microbial ecosystems for many years, we realize we have much more to learn and understand about complex and interconnected microbial functions. The information in this report reflects the current understanding of microbes and our changing climate, as well as gaps and priorities for future study.

## Biogeochemical Processes and Climate Change

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Microbes form the backbone of every ecological system on Earth by controlling biogeochemical cycling of elements essential for life, such as carbon (C) and nitrogen (N). As part of these biogeochemical cycles, microbes both produce and consume heat-trapping gases (greenhouse gases), such as carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O). Over Earth's history, the climate has changed in response to changes in the abundance of greenhouse gases in the atmosphere.

The net effect of microbes on biogeochemical cycles has varied over geologic time, and microbes have both contributed to and mitigated changes in Earth's climate. The impact of microbes on these cycles is briefly described below.

**Carbon:** Microbes can either consume inorganic carbon as carbon dioxide (CO<sub>2</sub>) through photosynthesis or chemosynthesis, storing it as organic matter (cell mass), or consume organic matter through respiration, producing CO<sub>2</sub> or methane (CH<sub>4</sub>) as metabolic by-products and releasing these gases into the ocean or atmosphere. Microbes also prevent much of the methane produced in ecosystems from reaching the atmosphere through methanotrophy



Microbes like these in soil are central players converting carbon into greenhouse gases. *Image courtesy of Pacific Northwest National Laboratory.*

(consuming methane). Over time, as a result of changes in ecosystems, the balance between consumption and production of carbon dioxide and methane shifts (Fisher et al. 2014; Levine et al. 2011). The balance between microbial consumption and production of  $\text{CO}_2$  and other greenhouse gases determines whether a particular area is a net carbon source (produces inorganic carbon) or sink (consumes inorganic carbon).

**Nitrogen:** As with the carbon cycle, Earth's nitrogen pool is constantly recycled. All organisms need nitrogen to grow, but only a few can use the gaseous form of nitrogen (dinitrogen or  $\text{N}_2$ ) that is in the atmosphere. Certain microorganisms "fix" atmospheric nitrogen into a form that other organisms can use, and increasing  $\text{CO}_2$  concentrations may lead to higher rates of nitrogen fixation by some microbes. Influxes of fixed nitrogen from human activities accelerate production and emission of oxidized nitrogen gases that add dramatically to the greenhouse gas budget.

This report explores how shifts in Earth's climate affect microbial ecosystems and the biogeochemical cycles they mediate, and what feedbacks might be expected from these changing microbial ecosystems that accelerate or mitigate climate change.

## Terrestrial Polar Regions

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### What are the effects of climate change on the terrestrial polar regions?

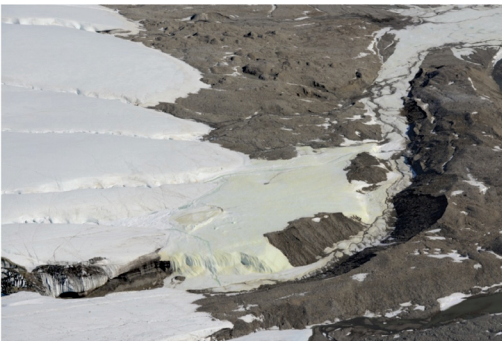
The terrestrial polar regions are experiencing drastic melting of glaciers, sea ice, and **permafrost** (frozen soil) along with shifts in precipitation. The rate of environmental change in polar regions, in particular, has been very high and clearly evident in our lifetimes. As access to stored nutrients in the previously frozen soils increases, shifts in vegetation are predicted to occur. Terrestrial polar areas may see an increase in shrubs and woody plants or even conversion to

forest. Satellite data indicate that the “greening” of the Arctic—increased plant cover linked to longer growing seasons and changes in soil composition—has been happening for at least the past 60 years. This phenomenon is leading to changes in **albedo**, a measure of the reflectivity of the Earth’s surface, which affects what can grow in the environment. In the atmosphere, microbes can serve as particulates which spur the formation of ice crystals in clouds, which influences where and how rain and snow fall. Along with increasing precipitation, ice in clouds changes the albedo, reflecting more heat and serving as negative feedback to climate change.

New vegetation also introduces the possibility of fire, a natural part of every ecosystem. For example, in the Alaskan tundra, it is predicted that the annual area consumed by fire will double by the end of the century, consuming millions of hectares per year (Hu et al. 2015). At the microbial scale, increased fires will affect soil moisture and access to carbon (Taş et al. 2014).

A research site at Borup Fiord Pass glacier, 81°N 81°W, Ellesmere Island, Nunavut, Canada. The image on the left is from 2014 and on the right, 2016. As viewed, the research site is vanishing due to melting, with an ~100-m retreat of the glacial toe. *Images courtesy of John Spear and Steve Grasby.*

As the permafrost in the polar regions melts, changes in the movement and distribution of water are occurring, producing dried and fractured soils in some areas and creating new wetlands or lakes in others. Organic carbon previously sequestered in polar soils can move into aquatic systems and from there to larger rivers and eventually to the ocean.





## Priority Areas for Future Study

### Terrestrial Polar Regions

Participants identified the following priority areas for future study:

- Large-scale field studies and experiments—examining the response of microbes to shifts in temperature and the movement and distribution of water.
- Linkages between biogeochemical cycles—learning more about how carbon, nitrogen, and other element cycles are related and interconnected.
- Plant-microbe interactions—understanding the interplay between microbes and plants during climate-driven vegetation shifts.

## What are the interactions between climate change and microbial ecosystems in terrestrial polar regions?

Warming and thawing of permafrost allow microbes to access and decompose previously frozen organic matter, liberating large amounts of carbon that is currently locked away in soils. Because warming soils also result in increased microbial activities, organic matter will be converted by microbes to carbon dioxide (Schuur et al. 2015) or methane (McCalley et al. 2014). These greenhouse gases can then be released in greater quantities into the atmosphere, where they affect Earth's temperature.

Methane is made by members of the domain Archaea (the other two domains of life being Bacteria and Eucarya), but we still have not identified all the important players in the methane cycle (Vanwonterghem et al. 2016; Nobu et al. 2016). Due to the number of environments where methane-producing organisms are found, their ability to decompose previously frozen organic matter in a warming world may greatly increase the amount of methane produced (Bridgham et al. 2013; Yvon-Durocher et al. 2014). The ratio of carbon dioxide to methane produced is also important, since methane traps heat much more effectively than carbon dioxide yet has a shorter persistence time in the atmosphere. In response to higher methane production, a different group of microorganisms that are able to consume methane (the methanotrophs) may increase and potentially mitigate effects on climate change.

All of the changes in the polar soil environment—warming, melting, thawing, drying, and plant community shifts—are expected to drive changes in the composition and diversity of the microbial communities (Jansson and Tas 2014). As new plant species establish themselves, microbial communities associated with plant roots and surrounding soils will shift in response. These microbes may, in turn, feed back to further alter vegetation through their interactions with specific plant species. For example, rates of microbial nitrogen fixation in terrestrial polar regions are predicted to be a key factor in determining which plants are successful in a warming environment (Bordeleau and Prévost 1994).

# Soil, Agriculture, and Freshwater

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## What are the effects of climate change on soil, agriculture, and freshwater environments?

As in polar environments, the effects of climate change on soils, lakes, rivers, and agricultural systems broadly include warming temperatures from elevated greenhouse gases, as well as changes in the movement and distribution of water. Precipitation changes are particularly important in these systems, affecting the pattern and amount of water inputs. The frequency of extreme precipitation events, which are particularly damaging to soils because they promote erosion and change biogeochemical properties, is increasing (see <http://www.globalchange.gov/browse/multimedia/observed-us-trend-heavy-precipitation>). In addition, lakes are predicted to experience increases in stratification (layering) due to temperature increases in surface waters, which inhibits mixing of nutrients through the water column. Sea level rise associated with climate warming is predicted to affect soils and freshwater environments. Groundwater is expected to increase in salinity due to changes in precipitation, evaporation, and saltwater intrusion along coastlines globally.



Urban heat island effect above San Jose, California. The marine layer is clearly burned off above the downtown area and still visible everywhere else. *Image courtesy of John Spear.*

Land use changes are second only to fossil fuels in shaping climate change, via their effects on plant cover and biogeochemical cycles, surface albedo (reflectivity), and local climate, and have affected tropical regions and coastal habitats most strongly. Increases in urbanization cause increased surface runoff and affect local precipitation and temperature through the creation of urban heat islands. Land use shifts linked to agricultural practices result in loss of forest cover (affecting CO<sub>2</sub> exchange with the atmosphere and nitrogen cycling), soil nutrients, and compaction of soils (Loveland et al. 2012). Conventional row crop food production where soil is tilled (plowed or overturned) results in erosion and pollution runoff (Lal et al. 2004) and can change local precipitation patterns, temperature, and near surface moisture—all of which affect ecosystem carbon balance. The use of nitrogen fertilizers to promote crop growth and increase productivity has substantially altered the global nitrogen cycle as well.



As some areas warm, farmers may have to switch to different crops, varieties, and management practices (e.g., timing of planting, irrigation). In some regions, climate change may allow for a longer growing period (or even two crop rotations per year), while in others, drought or salinization may mean row crop cultivation is no longer possible (see <http://www.nytimes.com/interactive/2016/10/24/world/asia/living-in-chinas-expanding-deserts.html> on desertification in China).

## **What are the interactions between climate change and microbial ecosystems in soil, agriculture, and freshwater environments?**

### **Soil**

Plants and microorganisms are tightly coupled in soil environments. The Free-Air CO<sub>2</sub> Enrichment (FACE) experiments found that while the effects of elevated carbon dioxide on soil microbial communities and plant growth were varied, increased CO<sub>2</sub> is expected to lead to an increase in the plant root exudates that support microbial growth. However, we have no comprehensive knowledge of the microbiomes (the complete set of microbes in an environment) associated with plants and how these interactions will be affected by climate change.

Coffee leaf rust, caused by a fungus, at a farm in Cauca, southwestern Colombia. This image is from the Two Degrees Up series of case studies on the effect of climate change on agriculture. Image courtesy of Neil Palmer (CIAT).



Regarding precipitation, microbes are resilient to usual drying and rewetting of soils, but their ability to respond to the larger fluctuations anticipated with climate change is not well understood. In addition, drought and fire can cause weathering of soil and minerals, which further changes the processes and linkages between plants and microbes.

Drought, elevated CO<sub>2</sub>, and/or nitrogen deposition are also likely to

affect soil processes by affecting soil food webs and the interactions between microbial communities and protists, viruses, and nematodes that forage on microorganisms. Changes in precipitation can impact soil structure, water content, and plant-microbe interactions, all of which can influence the abundance of soil inhabitants and change how soil food webs operate (Lindberg and Bengtsson 2005; Ilieva-Makulec and De Boeck 2013; Perdue and Crossley 1989; Kardol et al. 2011). The structure and interactions within soil food webs are known to regulate carbon and nitrogen flux in soils, impacting stabilization of soil organic matter (Fox et al. 2006). Plants that are associated with certain types of fungi (called arbuscular mycorrhizae) are known to be more drought tolerant (Augé 2001). Protozoa, nematodes, and other soil organisms require water films or relatively high moisture content to be active (Kremer 2012), so prolonged drought periods could lead to elimination of key soil functional groups that may alter overall soil function. Soil moisture has a profound effect on the spread and viability of phages (Zablocki et al. 2016), which are viruses that infect as many as 40% of all bacterial cells, particularly in soil surrounding plant roots. By disrupting soil food webs and microbial interactions, changes associated with climate change may lead to more viral and fungal diseases and more vectors moving pathogens within ecosystems.

## Agriculture

Microbes in agriculture systems can serve as **symbionts**, including microbes that fix nitrogen gas to supply plant nutrients, as well as the fungi that establish relationships with plant roots (called mycorrhizae),

and can enhance drought tolerance of plants. The need to increase food and textile fiber production for Earth's growing populations in the face of an unpredictable global climate highlights the need to better understand how soil microorganisms could influence food security and nutrition, as well as the supply of plant-based products used for energy and industry. This includes the possibility of using microbes as a probiotic in agriculture to mitigate the effects of

A satellite image from NOAA shows an aerial view of Lake Erie's massive 2011 algal bloom. *Image courtesy of NASA's Earth Observatory.*



## Priority Areas for Future Study

### Soil, Agriculture, and Freshwater

Participants identified the following priority areas for future study:

- Understanding interactions between the physical and biological properties of soil—the hydrological cycle, microbial responses to water potential, microbial interactions with metabolites in soil.
- Baseline measurements of the microbial communities in present-day environments, as well as in archived soils, to look for markers of past climate changes.
- Characterizing the total microbiome associated with plant species used in agriculture and occurring in natural ecosystems, including the microbial traits important in establishing a plant community and benefitting plant host fitness.

climate change and promote plant growth under new conditions. Current usage of nitrogen fertilizers substantially increases the greenhouse gas burden through microbial activities and is not a sustainable practice for increasing the food supply. Different agricultural practices (for example, no-till versus till) impact microbial nutrient cycling in soils, resulting in cropping systems that are either more or less resilient to climate change variables (Gelfand et al. 2011; Levine et al. 2011).

#### Freshwater

Heavy precipitation due to climate change can impact nutrient delivery and microbial productivity in freshwater systems. Nutrients typically accumulate in soil over a period of time, especially with fertilizer application. During heavy rain events, these nutrients are flushed out of the soil and carried in the rainwater to freshwater systems like lakes (a process called eutrophication when the nutrient concentrations are unnaturally high). When microorganisms make use of this influx of nutrients and rapidly multiply, some can dominate the ecosystem and form “blooms.” Dinoflagellates and cyanobacteria are microbes that commonly form such blooms. The toxins secreted by high concentrations of algae and bacteria can make water unsafe for both humans and fish. As patterns of precipitation and temperature shift due to climate change, the conditions that support harmful algal blooms may increase in frequency and duration (Wells et al. 2015; Glibert et al. 2014). Extreme weather events might also impact recreational water security (e.g., more interactions with harmful toxins in recreational lakes) and wastewater security (e.g., more frequent overflow of untreated sewage and release of harmful microbes into the environment).

## What are the effects of climate change on the oceans?

The increasing concentration of greenhouse gases in the atmosphere is causing Earth's oceans to warm and their pH to decrease. Physical changes resulting from surface warming, acidification, and increased ocean stratification (layering) are altering the distribution of nutrients and oxygen in the oceans. This affects overall ocean productivity, nitrogen inputs into and losses from the ocean, and ocean biogeochemistry in general. In recent geologic history, the Earth has experienced only small ranges of variability in many ocean properties. Disruption of these ranges as a consequence of climate change will have large impacts on the balanced dynamics of a healthy ocean. For example, disruptions are predicted to bring about changes in the microbial species that dominate the ocean and the biogeochemical cycles they mediate, which will likely have both positive and negative feedbacks on Earth's climate system.

Higher concentrations of atmospheric CO<sub>2</sub> will impact photosynthetic organisms, the foundation of oceanic food webs. Higher concentrations of atmospheric CO<sub>2</sub> cause more CO<sub>2</sub> to be absorbed into the ocean, and this affects the carbonate chemistry of the ocean, the 'natural buffer' of the Earth, resulting in a lower oceanic pH (acidification). Higher inorganic carbon concentrations increase the availability of CO<sub>2</sub> for photosynthesis, but the associated acidification affects the ability of some phytoplankton and other calcareous organisms to deposit their calcium carbonate shells. Changes in the ocean's carbonate chemistry will likely exert selective pressure on photosynthetic organisms.

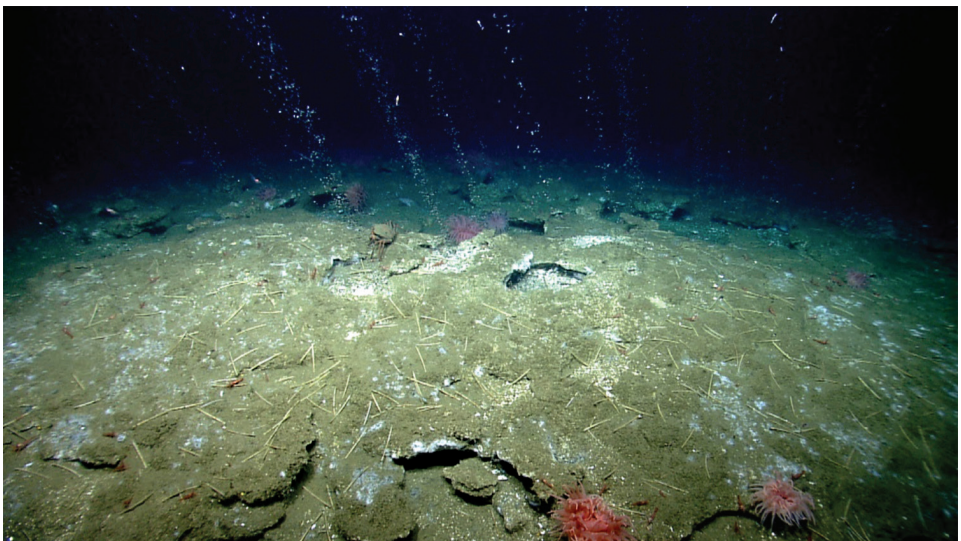
Oxygen minimum zones (OMZs) naturally occur beneath the productive, well-lit surface layer in the ocean where respiration (oxygen consumption) exceeds photosynthesis (oxygen production). In OMZs, oxygen saturation is at its lowest, and this selects for microbial communities whose functions are different from those in oxygenated surface waters. In certain oceanic realms, high surface productivity, combined

Large methane bubbles seeping from the bottom of the ocean and 'leaking' out of the continents (Schwartz et al. 2016) contribute to atmosphere pools and cause effects such as climate warming. Shown here is methane bubbling from the seafloor at an about 425-meter depth off the Virginia coast, USA. *Image courtesy of NOAA Okeanos Explorer Program, 2013 ROV Shakedown and Field Trials in the U.S. Atlantic Canyons, <http://oceanexplorer.noaa.gov/okeanos/explorations/ex1304/background/coldseeps/media/bubbles.html>.*

with ocean circulation and poor ventilation, creates oxygen-deficient zones (ODZs) where oxygen is entirely absent. These regions harbor microbial communities with unique functions and are major areas of nitrogen loss from the oceans.

Oxygen-depleted or -devoid "dead zones" also occur in coastal systems and estuaries where high nutrient loads contribute to excess algal production (eutrophication). When the algal blooms die and sink to the bottom, microbial decomposers increase their activity and consume any available oxygen as they decompose the algae, over time depleting the oxygen. These eutrophication-driven dead zones have insufficient oxygen to support healthy ecosystems and fisheries.

Whether oxygen-depleted zones expand or contract with climate change is still unclear. While coastal dead zones are likely to expand as a result of continued nutrient inputs from human activities (Diaz and Rosenberg 2008), changes in oceanic productivity and circulation may expand or contract oceanic OMZs and ODZs (Deutsch et al. 2014; Ulloa et al. 2012). Shifts in wind patterns due to climate change may also affect microbial productivity in the oceans. These are expected to occur as temperature differ-





ences between the equator and the poles decrease, affecting the heat balance of the planet. Changes in wind patterns will influence surface ocean circulation, delivery of terrestrial dust and nutrients across the ocean, and will likely result in shifts in microbial communities and their biogeography, with the potential to alter ocean productivity and food webs. Terrestrial dust and sediment are major sources of iron in marine systems. Iron is an essential trace element for microbes, and so changes in dust delivery will affect marine microbial communities. Interactions between dust transported by the atmosphere and ocean microbes have impacted Earth's climate across geologic times scales (Jickells et al. 2005; Jickells and Moore 2015). Notably, in recent years, scientists have found evidence of rapid changes, such as enhanced iron-rich dust and sediment input to the oceans from melting glaciers (Prospero et al. 2012) and from expanding desert sources (Mahowald et al. 2010). These increases in dust deposition result in increases in ocean productivity.

## **What are the interactions between climate change and microbial ecosystems in the oceans?**

The ocean ecosystem is characterized by dynamic interactions among organisms and between organisms and their environment. Ocean microbes are responsible for mediating the cycling of critical elements such as carbon, nitrogen, and phosphorus and for exchanging materials with the atmosphere and terrestrial ecosystems. Our current understand-

ing of microbes in the ocean is built on several decades of intensive study examining their growth and responses to individual stressors; with climate change, microbial communities are being exposed to multiple stressors simultaneously. Temperature increases, ocean

Surveying the bleaching at Heron Island (in the southern Great Barrier Reef) during February 2016. Image courtesy XL Catlin Seaview Survey/Underwater.





## Priority Areas for Future Study

### Oceans

Participants identified the following priority areas for future study:

- **Changes and variability in the biogeochemical cycling of major and micronutrient elements such as nitrogen, phosphorus, and iron that could lead to alteration in ecosystem services provided by microorganisms.**
- **Effects of climate on microbial interactions with macroorganisms.**
- **Baseline measurements for both coastal and open oceans using remote-sensing methods, long-term observations, and retrospective data for ocean ecosystems.**
- **Effects of multiple stressors acting simultaneously on ocean ecosystems (e.g., temperature, stratification, and ocean acidification).**

acidification, and changes in nutrient availability and ocean circulation are occurring at the same time, and the combined effects of these stressors may interact to produce unexpected responses and feedbacks. Recent genomic advances may allow us to gain new, more detailed insight into how organisms are responding to multistressors.

An excellent example are coral reef ecosystems that offer an important model for studying effects of climate change on microbial function, serving as a prime example of the intricate interactions that occur between marine microorganisms and animals. Corals harbor photosynthetic unicellular algae as symbionts inside their cells that both provide food to the animal and contribute energy for the production of its calcium carbonate skeleton. Corals also host diverse communities of bacteria in the mucus layer on their surface. The relationship between corals and their associated microbes (together called a holobiont) is affected by warming and acidification of the ocean. Higher carbon dioxide concentrations can stimulate symbiont photosynthetic rates and reduce calcification rates. The stress of higher temperatures causes the symbiotic algae to leave the coral tissues, resulting in corals that are “bleached.” Acidification affects the corals directly by dissolving and preventing them from making and maintaining their calcium carbonate skeletons and indirectly by affecting the ability of their symbiotic algae to photosynthesize. The microbial communities in coral holobiont are a biological buffer between corals and seawater, and a healthy community can ward off opportunistic pathogens that otherwise would infect the coral. Changes in temperature are affecting the composition and function of the coral holobiont (Hass et al. 2016).

The oceans’ large and mostly remote environment makes comprehensive sampling of ocean microbial communities and their activities nearly impossible. At the most basic level, it is unclear whether our current understanding of microbes and microbial processes in the oceans represents baseline measurements of an unperturbed system or a survey of microbial processes that have already begun to be changed by climate shifts.

# Microbiomes of the Earth

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## What is a “microbiome”?

‘Microbiome’ is a relatively new term for an old concept—an ecological community of microorganisms from the three domains of life that share an environment. The new term emerged among scientists about 15 years ago, coined by researchers studying the roles of microbial communities in human and animal health. Yet the importance of networks of microbial cells acting and interacting in virtually all habitats of the Earth had been increasingly recognized for decades, with a heightening of this recognition occurring in the 1970s when new scientific methods first showed that microbe numbers were being underestimated by 1,000- to 100,000-fold. Microbiomes are now known to be critical components of the human gut and skin, trees and crop plants and the soils they grow in, the surface and deep oceans, the air inside our homes, and habitats extending well below the Earth’s surface. Indeed, “nearly every habitat and organism hosts a diverse constellation of microbiomes” (Alivisatos et al. 2015).

## How is climate change expected to affect microbiomes?

Scientists are still taking inventories of microbiomes, learning about the cells, what’s inside them (their genes, proteins, metabolites), and how microbes influence each other and their habitat or host. As the climate warms over the next decades, one area of intense research is biodiversity: an accounting of the variety of microorganisms and their ecological roles in ecosystems. Scientists are asking how the taxonomic, functional, and genetic variety of microbiomes is likely to change as the climate shifts and what roles microbes will play in mitigating or exacerbating the consequences.

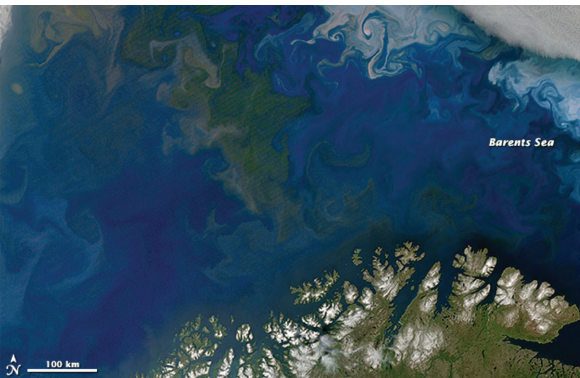
Environmental conditions are known to be key determinants of microbiome composition in aquatic habitats (Carpenter et al. 2007), soils (Castro et al. 2010), oceans (Sunagawa et al. 2015), and many other ecosystems. Yet teasing out changes in microbial diversity

due to short-term events versus those arising from climate change is challenging for scientists. For example, was a recent collapse in bacterial diversity observed in a high-nutrient lake in Wisconsin due to drought conditions or indicative of a long-term trend (Katherine McMahon, unpublished work)? Were changes in the abundance of tick-borne microbial pathogens in squirrels and mice in Yosemite National Park associated with specific events or attributable to temperature changes occurring over decades (Stephenson et al. 2016)? The answers to these questions are critical for understanding the extent to which climate change will affect processes ranging from the functioning of Earth's carbon cycle to the distribution of microbial pathogens and transmission of human diseases.

## Can microbiomes adapt to climate change?

In the face of a changing environment, microbes can adapt either by altering their physiology or by changes in their genomes. The former is more rapid and can be temporary (an acclimation response), while the latter represents a permanent change in hard-wired capabilities of the cell (an evolutionary response). For example, marine phytoplankton exhibit shifts in cell size and nitrogen content when experiencing higher CO<sub>2</sub> concentrations in seawater, and these shifts can be traced both to evolutionary response mechanisms (Collins et al. 2014) and to changes in how their genes are expressed (Benner et al. 2013, Walworth et al. 2016). Soil microbes decrease their respiration rates in response to high temperatures (Bradford et al. 2008) and become more tolerant of changes in precipitation patterns (Evens and Wallenstein 2012). Because microbes have the potential to evolve on time scales of just months or years, they are particularly informative about how more slowly evolving organisms might respond to climate change.

Phytoplankton blooms in the Barents Sea off the coast of Norway and Russia, shown in natural color from NASA's Aqua satellite on July 10, 2014. The type and distribution of phytoplankton can be estimated from these remote-sensed images, with green areas indicative of diatom blooms and white regions revealing coccolithophores. *Image courtesy NASA's Earth Observatory.*



Examples of genetic adaptations that could occur in response to climate change include the acquisition or modification of genes helpful for survival under conditions of drought or high temperature (Wallenstein and Hall 2012) or changes in regulation of genes involved in cell wall calcification or CO<sub>2</sub> acquisition (Collins et al. 2014).

To what extent can microbiomes mitigate climate change? Their key roles in CO<sub>2</sub> and methane consumption and release, their mediation of nitrogen fixation, their interactions with plant and animal hosts, and their ability to quickly acclimate and evolve all suggest that microbes are the 'first responders' to Earth's changing climate.

## Cross-Cutting Theme

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### Role of Observational Data and Experiments

Environmental observations, experiments, and modeling are three interwoven approaches that will help us better understand the interactions between climate change and microbial ecosystems. Baseline observational data (e.g., ecology, taxonomy, physiology) from microbial communities in existing ecosystems are needed in order to track future changes. Experiments provide information on the microbial response to known variables relevant to climate change; those that consider pulsed and extreme events are especially valuable, as are large-scale field experiments that encompass longer periods of time in dynamic environments. Modeling is important to better understand and integrate observational and experimental data, and particular efforts are needed in the modeling of Arctic and Antarctic systems.

Long-term research programs established for agriculture (USDA program) and ecology (the National Science Foundation's Long-Term Ecological Research program and the Department of Energy's programs Next-Generation Ecosystem Experiments [NGEE] Arctic and Spruce and Peatland Responses Under Climatic and Environmental Change [SPRUCE]) have been investing in ecosystem dynamics for several decades and are now providing invaluable data on how critical ecosystems are changing. The growing field of geobiology is similarly adding key observations, in this case about subsurface ecosystems. Additional efforts to understand the effects of climate change on the foundational properties of microbial communities in all types of ecosystems are needed.

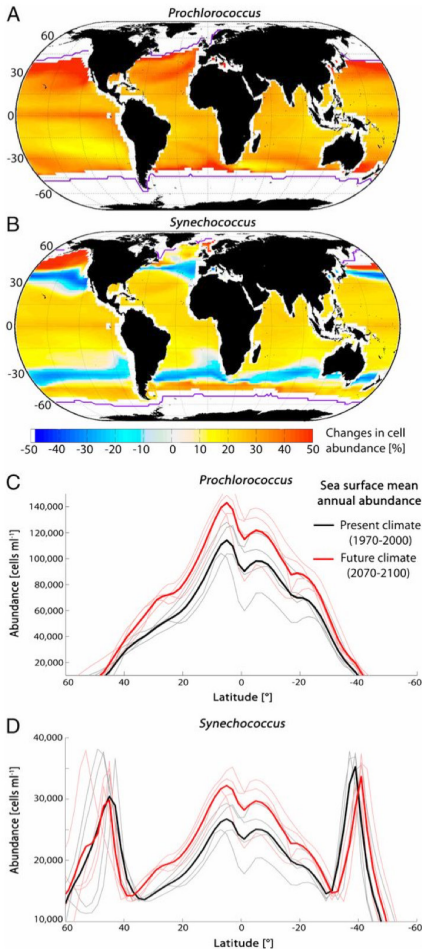
## Cross-Cutting Theme

# Incorporating Microbial Processes into Models to Make Predictions

Historically, earth system models used to examine the causes and effects of climate change have not taken microbial processes into account, even though microbes mediate key steps in all biogeochemical cycles. Through new studies, scientists are learning more about how microorganisms respond to changes in the environment but are still challenged

by the difficulty of building models that can encompass the impact of very-small-scale variations in microbial community structure and function on large-scale (global) biogeochemical cycling.

Nonetheless, models are already helping us to understand microbial roles in a future Earth. For the oceans, earth system models incorporate a simplistic representation of photosynthetic microbial communities. Models are being developed that include microbial information to predict the rates and proportions of greenhouse gas emissions into the atmosphere (Xu et al. 2015). In addition, smaller-scale models are being used to understand, and sometimes predict, how pathogens move within and between environments. While uncertainty is often an inherent property of natural ecosystems, the more we learn from observations and experiments, the better we can build mechanistic models and make predictions to guide decision making. Because microorganisms acclimate and evolve at the highest rate of all organisms, modelers can use them as sentinels for the onset of biological change.



Example of modeling: change in global abundance and distribution of the marine cyanobacteria *Prochlorococcus* and *Synechococcus* projected for the year 2100. From P. Flombaum et al., *Proc Natl Acad Sci U S A* 110:9824-9829, 2013. Credit: Hansen et al. 2010.

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