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Abstract

In the Anthropocene, in which we now live, climate change is impacting most life on Earth. Microorganisms support the existence of all higher trophic life forms. To understand how humans and other life forms on Earth (including those we are yet to discover) can withstand anthropogenic climate change, it is vital to incorporate knowledge of the microbial unseen majority. We must learn not just how microorganisms affect climate change (including production and consumption of greenhouse gases) but also how they will be affected by climate change and other human activities. This Consensus Statement documents the central role and global importance of microorganisms in climate change biology. It also puts humanity on notice that the impact of climate change will depend heavily on responses of microorganisms, which are essential for achieving an environmentally sustainable future. The microbial majority with which we share Earth often goes unnoticed despite underlying major biogeochemical cycles and food webs, thereby taking a key role in climate change. This Consensus Statement highlights the importance of climate change microbiology and issues a call to action for all microbiologists.

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Scientists' warning to humanity: microorganisms and climate change

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Abstract | In the Anthropocene, in which we now live, climate change is impacting most life on Earth. Microorganisms support the existence of all higher trophic life forms. To understand how humans and other life forms on Earth (including those we are yet to discover) can withstand anthropogenic climate change, it is vital to incorporate knowledge of the microbial 'unseen majority'. We must learn not just how microorganisms affect climate change (including production and consumption of greenhouse gases) but also how they will be affected by climate change and other human activities. This Consensus Statement documents the central role and global importance of microorganisms in climate change biology. It also puts humanity on notice that the impact of climate change will depend heavily on responses of microorganisms, which are essential for achieving an environmentally sustainable future.

Habitats
Environments in which an organism normally lives; for example, lake, forest, sediment and polar environments represent distinct types of habitats.

Ecosystem
The interacting community of organisms and non-living components such as minerals, nutrients, water, weather and topographic features present in a specific environment.

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Human activities and their effects on the climate and environment cause unprecedented animal and plant extinctions, cause loss in biodiversity[1–4] and endanger animal and plant life on Earth[5]. Losses of species, communities and habitats are comparatively well researched, documented and publicized[6]. By contrast, microorganisms are generally not discussed in the context of climate change (particularly the effect of climate change on microorganisms). While invisible to the naked eye and thus somewhat intangible[7], the abundance (~10^{30} total bacteria and archaea)[8] and diversity of microorganisms underlie their role in maintaining a healthy global ecosystem: simply put, the microbial world constitutes the life support system of the biosphere. Although human effects on microorganisms are less obvious and certainly less characterized, a major concern is that changes in microbial biodiversity and activities will affect the resilience of all other organisms and hence their ability to respond to climate change[9].

Microorganisms have key roles in carbon and nutrient cycling, animal (including human) and plant health, agriculture and the global food web. Microorganisms live in all environments on Earth that are occupied by macroscopic organisms, and they are the sole life forms in other environments, such as the deep subsurface and 'extreme' environments. Microorganisms date back to the origin of life on Earth at least 3.8 billion years ago, and they will likely exist well beyond any future extinction events.

Although microorganisms are crucial in regulating climate change, they are rarely the focus of climate change studies and are not considered in policy development. Their immense diversity and varied responses to environmental change make determining their role in the ecosystem challenging. In this Consensus Statement, we illustrate the links between microorganisms, macroscopic organisms and climate change, and put humanity on notice that the microscopic majority can no longer be the unseen elephant in the room. Unless we appreciate the importance of microbial processes, we fundamentally limit our understanding of Earth's biosphere and response to climate change and thus jeopardize efforts to create an environmentally sustainable future[6] (BOX 1).

Scope of the Consensus Statement

In this Consensus Statement, we address the effects of microorganisms on climate change, including microbial climate-active processes and their drivers. We also address the effects of climate change on microorganisms,

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focusing on the influences of climate change on microbial community composition and function, physiological responses and evolutionary adaptation. Although we focus on microorganism–climate connections, human activities with a less direct but possibly synergistic effect, such as via local pollution or eutrophication, are also addressed.

For the purpose of this Consensus Statement, we define 'microorganism' as any microscopic organism or virus not visible to the naked eye (smaller than 50 μm) that can exist in a unicellular, multicellular (for example, differentiating species), aggregate (for example, biofilm) or viral form. In addition to microscopic bacteria, archaea, eukaryotes and viruses, we discuss certain macroscopic unicellular eukaryotes (for example, larger marine phytoplankton) and wood-decomposing fungi. Our intent is not to exhaustively cover all environments nor all anthropogenic influences but to provide examples from major global biomes (marine and terrestrial) that highlight the effects of climate change on microbial processes and the consequences. We also highlight agriculture and infectious diseases and the role of microorganisms in climate change mitigation. Our Consensus Statement alerts microbiologists and non-microbiologists to address the roles of microorganisms in accelerating or mitigating the impacts of anthropogenic climate change (BOX 1).

Marine biome

Marine biomes cover ~70% of Earth's surface and range from coastal estuaries, mangroves and coral reefs to the open oceans (FIG. 1). Phototrophic microorganisms use the sun's energy in the top 200 m of the water column, whereas marine life in deeper zones uses organic and inorganic chemicals for energy[10]. In addition to sunlight, the availability of other energy forms and water temperature (ranging from approximately −2 °C in ice-covered seas to more than 100 °C in hydrothermal vents)

Food web
Interconnecting components describing the trophic (feeding) interactions in an ecosystem, often consisting of multiple food chains; for example, marine microbial primary producers and heterotrophic remineralizers through to the highest trophic predators or trees as primary producers, herbivores and microbial nitrogen fixers and remineralizers.

Subsurface
The area below Earth's surface, with subsurface ecosystems extending down for several kilometres and including terrestrial deep aquifer, hydrocarbon and mine systems, and marine sediments and the ocean crust.

Eutrophication
Increased input of minerals and nutrients to an aquatic system; typically nitrogen and phosphorus input from fertilizers, sewage and detergents.

Phytoplankton
Single-celled, chlorophyll-containing microorganisms (eukaryotes and bacteria) that grow photosynthetically and drift relatively passively with the current in oceans or lakes.

Biomes
Systems containing multiple ecosystems that have common physical properties (such as climate and geology); here 'biome' is used to refer to all terrestrial environments (continents) and all marine environments (seas and oceans).

Phototrophic
Using sunlight to generate energy for growth.

Water column
The water layer in a lake or ocean.

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Box 1 | **Scientists' warning**

The Alliance of World Scientists and the Scientists' Warning movement was established to alert humanity to the impacts of human activities on global climate and the environment. In 1992, 1,700 scientists signed the first warning, raising awareness that human impact puts the future of the living world at serious risk[267]. In 2017, 25 years later, the second warning was issued in a publication signed by more than 15,000 scientists[5]. The movement has continued to grow, with more than 21,000 scientists endorsing the warning. At the heart of the warning is a call for governments and institutions to shift policy away from economic growth and towards a conservation economy that will stop environmental destruction and enable human activities to achieve a sustainable future[268]. Linked to the second warning is a series of articles that will focus on specific topics, the first of which describes the importance of conserving wetlands[269]. A film, The Second Warning, also aims to document scientists' advocacy for humanity to replace 'business as usual' and take action to achieve the survival of all species by averting the continuing environmental and climate change crisis.

Complementing the goals of the Alliance of World Scientists are the United Nations Sustainable Development Goals, which were formulated to realize dignity, peace and prosperity for people and the planet, now and into the future[6]. The goals are framed around environmental, economic and social needs, and address sustainability through the elimination of poverty, development of safe cities and educated populations, implementation of renewables (energy generation and consumption) and urgent action on climate change involving equitable use of aquatic and terrestrial systems to achieve a healthy, less polluted biosphere. The goals recognize that responsible management of finite natural resources is required for the development of resilient, sustainable societies.

Our Consensus Statement represents a warning to humanity from the perspective of microbiology. As a microbiologists' warning, the intent is to raise awareness of the microbial world and make a call to action for microbiologists to become increasingly engaged in and for microbial research to become increasingly integrated into the frameworks for addressing climate change and accomplishing the United Nations Sustainable Development Goals (BOX 2). It builds on previous science and policy efforts to call attention to the role of microorganisms in climate change[7,126,270–272] and their broad relevance to society[7]. Microbiologists are able to endorse the microbiologists' warning by becoming a signatory.

influence the composition of marine communities[11]. Rising temperatures not only affect biological processes but also reduce water density and thereby stratification and circulation, which affect organismal dispersal and nutrient transport. Precipitation, salinity and winds also affect stratification, mixing and circulation. Nutrient inputs from air, river and estuarine flows also affect microbial community composition and function, and climate change affects all these physical factors.

The overall relevance of microorganisms to ocean ecosystems can be appreciated from their number and biomass in the water column and subsurface: the total number of cells is more than 10^{29} (REFS[8,12–16]) and the Census of Marine Life estimates that 90% of marine biomass is microbial. Beyond their sheer numbers, marine microorganisms fulfil key ecosystem functions. By fixing carbon and nitrogen, and remineralizing organic matter, marine microorganisms form the basis of ocean food webs and thus global carbon and nutrient cycles[13]. The sinking, deposition and burial of fixed carbon in particulate organic matter to marine sediments is a key, long-term mechanism for sequestering CO_2 from the atmosphere. Therefore, the balance between regeneration of CO_2 and nutrients via remineralization versus burial in the seabed determines the effect on climate change.

In addition to getting warmer (from increased atmospheric CO_2 concentrations enhancing the greenhouse effect), oceans have acidified by ~0.1 pH units since pre-industrial times, with further reductions of 0.3–0.4 units predicted by the end of the century[17–19]. Given the unprecedented rate of pH change[19–21], there is a need to rapidly learn how marine life will respond[22]. The impact of elevated greenhouse gas concentrations on ocean temperature, acidification, stratification, mixing, thermohaline circulation, nutrient supply, irradiation and extreme weather events affects the marine microbiota in ways that have substantial environmental consequences, including major shifts in productivity, marine food webs, carbon export and burial in the seabed[19,23–29].

Microorganisms affect climate change. Marine phytoplankton perform half of the global photosynthetic CO_2 fixation (net global primary production of ~50 Pg C per year) and half of the oxygen production despite amounting to only ~1% of global plant biomass[30]. In comparison with terrestrial plants, marine phytoplankton are distributed over a larger surface area, are exposed to less seasonal variation and have markedly faster turnover rates than trees (days versus decades)[30]. Therefore, phytoplankton respond rapidly on a global scale to climate variations. These characteristics are important when one is evaluating the contributions of phytoplankton to carbon fixation and forecasting how this production may change in response to perturbations. Predicting the effects of climate change on primary productivity is complicated by phytoplankton bloom cycles that are affected by both bottom-up control (for example, availability of essential nutrients and vertical mixing) and top-down control (for example, grazing and viruses)[27,30–34]. Increases in solar radiation, temperature and freshwater inputs to surface waters strengthen ocean stratification and consequently reduce transport of nutrients from deep water to surface waters, which reduces primary productivity[30,34,35]. Conversely, rising CO_2 levels can increase phytoplankton primary production, but only when nutrients are not limiting[36–38].

Some studies indicate that overall global oceanic phytoplankton density has decreased in the past century[39], but these conclusions have been questioned because of the limited availability of long-term phytoplankton data, methodological differences in data generation and the large annual and decadal variability in phytoplankton production[40–43]. Moreover, other studies suggest a global increase in oceanic phytoplankton production[44] and changes in specific regions or specific phytoplankton groups[45,46]. The global sea ice (Sea Ice Index) is declining, leading to higher light penetration and potentially more primary production[47]; however, there are conflicting predictions for the effects of variable mixing patterns and changes in nutrient supply and for productivity trends in polar zones[34]. This highlights the need to collect long-term data on phytoplankton production and microbial community composition. Long-term data are needed to reliably predict how microbial functions and feedback mechanisms will respond to climate change, yet only very few such datasets exist (for example, the Hawaii Ocean Time-series and the Bermuda Atlantic Time-series Study)[48–50]. In this context, the Global Ocean Sampling Expedition[51], transects of the Southern

Stratification
Water layers forming due to a difference in the density of water between the surface and deeper waters; stratification is increasing owing to warming of surface waters and freshwater input from precipitation and ice melting.

Remineralizing
Converting organic matter back into its constituent inorganic components; remineralization by marine and terrestrial heterotrophs involves respiration that releases CO_2 to the atmosphere.

Sediments
Material that has precipitated through the water column and settled on the bottom of a lake or ocean.

Primary production
Production of biomass by phototrophic organisms, such as phytoplankton or plants.

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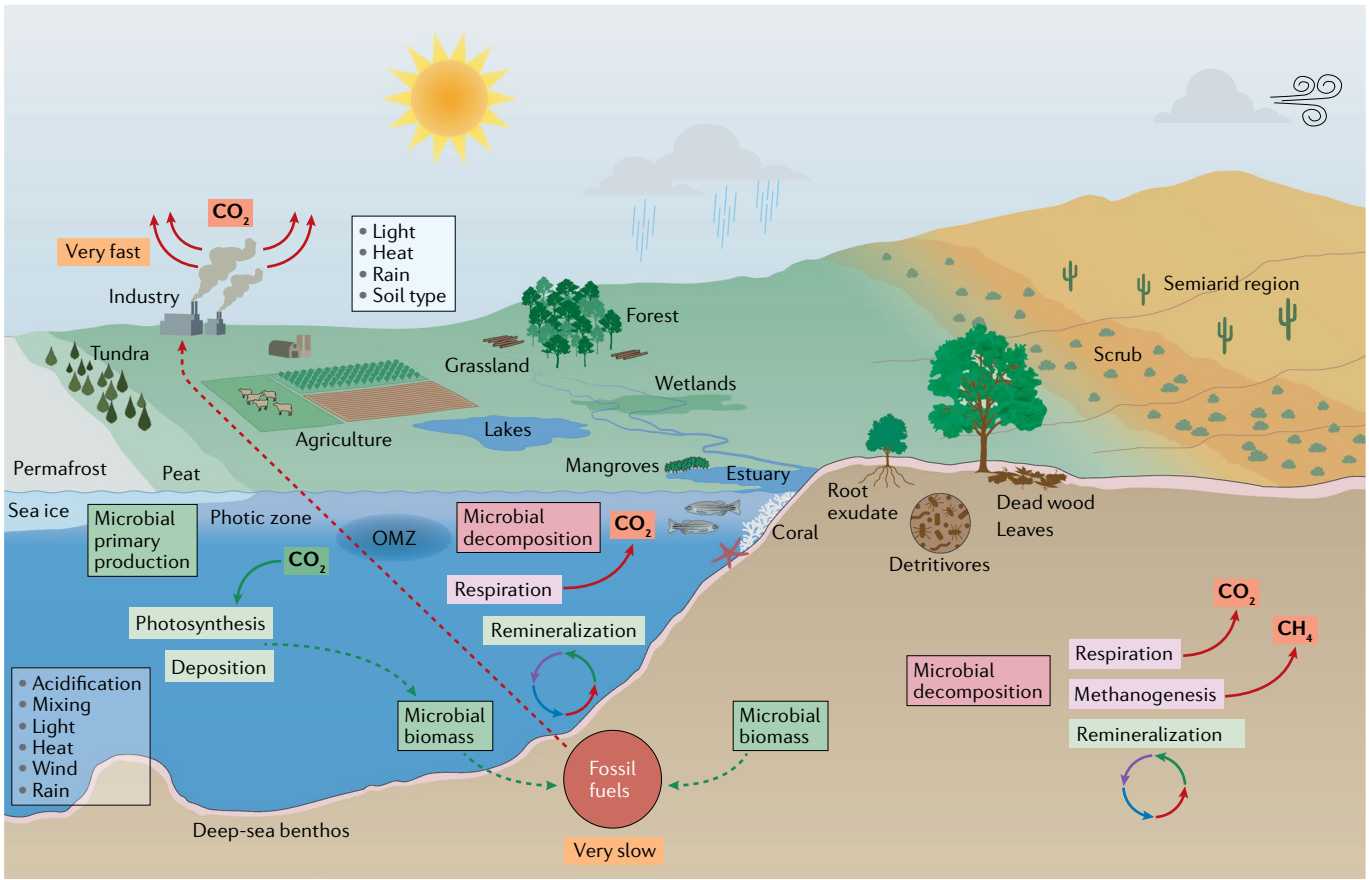


Fig. 1 | **Microorganisms and climate change in marine and terrestrial biomes.** In marine environments, microbial primary production contributes substantially to CO_2 sequestration. Marine microorganisms also recycle nutrients for use in the marine food web and in the process release CO_2 to the atmosphere. In a broad range of terrestrial environments, microorganisms are the key decomposers of organic matter and release nutrients in the soil for plant growth as well as CO_2 and CH_4 into the atmosphere. Microbial biomass and other organic matter (remnants of plants and animals) are converted to fossil fuels over millions of years. By contrast, burning of fossil fuels liberates greenhouse gases in a small fraction of that time. As a result, the carbon cycle is extremely out of balance, and atmospheric CO_2 levels will continue to rise as long as fossil fuels continue to be burnt. The many effects of human activities, including agriculture, industry, transport, population growth and human consumption, combined with local environmental factors, including soil type and light, greatly influence the complex network of microbial interactions that occur with other microorganisms, plants and animals. These interactions dictate how microorganisms respond to and affect climate change (for example, through greenhouse gas emissions) and how climate change (for example, higher CO_2 levels, warming, and precipitation changes) in turn affect microbial responses. OMZ, oxygen minimum zone.

Bloom
The growth to high concentration certain types of microorganisms, such as phytoplankton; typically in the form of a boom and bust cycle which consists of the rapid cell division of phytoplankton followed by growth of, for example, a virus that lyses the cells and causes the collapse of the bloom.

Diatoms
A class (Bacillariophyceae) of single-celled algae that have a silica-containing skeleton.

Respiration
Heterotrophic respiration by microorganisms and autotrophic respiration by plants generate CO_2, and photosynthetic respiration by plants, microalgae and cyanobacteria fixes CO_2 and generates O_2.

Methanogens
Anaerobic members of the Archaea that generate methane by methanogenesis. They reduce carbon dioxide, acetic acid or various one-carbon compounds, such as methylamines or methanol, to generate energy for growth.

Ocean[52,53], and the Tara Oceans Consortium[11,54–59] provide metagenome data that are a valuable baseline of marine microorganisms.

Diatoms perform 25–45% of total primary production in the oceans[60–62], owing to their prevalence in open-ocean regions when total phytoplankton biomass is maximal[63]. Diatoms have relatively high sinking speeds compared with other phytoplankton groups, and they account for ~40% of particulate carbon export to depth[62,64]. Physically driven seasonal enrichments in surface nutrients favour diatom blooms. Anthropogenic climate change will directly affect these seasonal cycles, changing the timing of blooms and diminishing their biomass, which will reduce primary production and CO_2 uptake[65]. Remote sensing data suggest a global decline of diatoms between 1998 and 2012, particularly in the North Pacific, which is associated with shallowing of the surface mixed layer and lower nutrient concentrations[46].

In addition to the contribution of marine phytoplankton to CO_2 sequestration[30,66–68], chemolithoautotrophic archaea and bacteria fix CO_2 under dark conditions in deep ocean waters[69] and at the surface during polar winter[70]. Marine bacteria and archaea also contribute substantially to surface ocean respiration and cycling of many elements[18]. Seafloor methanogens and methanotrophs are important producers and consumers of CH_4, but their influence on the atmospheric flux of this greenhouse gas is uncertain[71]. Marine viruses, bacteriovorous bacteria and eukaryotic grazers are also important components of microbial food webs; for example, marine viruses influence how effectively carbon is sequestered and deposited into the deep ocean[57]. Climate change affects predator–prey interactions, including virus–host interactions, and thereby global biogeochemical cycles[72].

Oxygen minimum zones (OMZs) have expanded in the past 50 years as a result of ocean warming, which

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reduces oxygen solubility[73–75]. OMZs are global sinks for reactive nitrogen, and microbial production of N_2 and N_2O accounts for ~25–50% of nitrogen loss from the ocean to the atmosphere. Furthermore, OMZs are the largest pelagic methane reservoirs in the ocean and contribute substantially to open ocean methane cycling. The observed and predicted future expansion of OMZs may therefore considerably affect ocean nutrient and greenhouse gas budgets, and the distributions of oxygen-dependent organisms[73–75].

The top 50 cm of deep-sea sediments contains $\sim 1 \times 10^{29}$ microorganisms[8,16], and the total abundances of archaea and bacteria in these sediments increase with latitude (from 34° N to 79° N) with specific taxa (such as Marine Group I Thaumarchaeota) contributing disproportionately to the increase[76]. Benthic microorganisms show biogeographic patterns and respond to variations in the quantity and quality of the particulate matter sinking to the seafloor[77]. As a result, climate change is expected to particularly affect the functional processes that deep-sea benthic archaea perform (such as ammonia oxidation) and associated biogeochemical cycles[76].

Aerosols affect cloud formation, thereby influencing sunlight irradiation and precipitation, but the extent to which and the manner in which they influence climate remains uncertain[78]. Marine aerosols consist of a complex mixture of sea salt, non-sea-salt sulfate and organic molecules and can function as nuclei for cloud condensation, influencing the radiation balance and, hence, climate[79,80]. For example, biogenic aerosols in remote marine environments (for example, the Southern Ocean) can increase the number and size of cloud droplets, having similar effects on climate as aerosols in highly polluted regions[80–83]. Specifically, phytoplankton emit dimethylsulfide, and its derivate sulfate promotes cloud condensation[79,84]. Understanding the ways in which marine phytoplankton contribute to aerosols will allow better predictions of how changing ocean conditions will affect clouds and feed back on climate[84]. In addition, the atmosphere itself contains ~10^{22} microbial cells, and determining the ability of atmospheric microorganisms to grow and form aggregates will be valuable for assessing their influence on climate[8].

Vegetated coastal habitats are important for carbon sequestration, determined by the full trophic spectrum from predators to herbivores, to plants and their associated microbial communities[85]. Human activity, including anthropogenic climate change, has reduced these habitats over the past 50 years by 25–50%, and the abundance of marine predators has dropped by up to 90%[85–87]. Given such extensive perturbation, the effects on microbial communities need to be evaluated because microbial activity determines how much carbon is remineralized and released as CO_2 and CH_4.

Climate change affects microorganisms. Climate change perturbs interactions between species and forces species to adapt, migrate and be replaced by others or go extinct[28,88]. Ocean warming, acidification, eutrophication and overuse (for example, fishing, tourism) together cause the decline of coral reefs and may cause ecosystems shifts towards macroalgae[89–93] and benthic cyanobacterial mats[94,95]. The capacity for corals to adapt to climate change is strongly influenced by the responses of their associated microorganisms, including microalgal symbionts and bacteria[96–98]. The hundreds to thousands of microbial species that live on corals are crucial for host health, for example by recycling the waste products, by provisioning essential nutrients and vitamins and by assisting the immune system to fight pathogens[99]. However, environmental perturbation or coral bleaching can change the coral microbiome rapidly. Such shifts undoubtedly influence the ecological functions and stability of the coral–microorganism system, potentially affecting the capacity and pace at which corals adapt to climate change, and the relationships between corals and other components of the reef ecosystem[99,100].

Generally, microorganisms can disperse more easily than macroscopic organisms. Nevertheless, biogeographic distinctions occur for many microbial species, with dispersal, lifestyle (for example, host association) and environmental factors strongly influencing community composition and function[54,101–103]. Ocean currents and thermal and latitudinal gradients are particularly important for marine communities[104,105]. If movement to more favourable environments is impossible, evolutionary change may be the only survival mechanism[88]. Microorganisms, such as bacteria, archaea and microalgae, with large population sizes and rapid asexual generation times have high adaptive potential[22]. Relatively few studies have examined evolutionary adaptation to ocean acidification or other climate change-relevant environmental variables[22,28]. Similarly, there is limited understanding of the molecular mechanisms of physiological responses and the implications of those responses for biogeochemical cycles[18].

However, several studies have demonstrated effects of elevated CO_2 levels on individual phytoplankton species, which may disrupt broader ecosystem-level processes. A field experiment demonstrated that increasing CO_2 levels provide a selective advantage to a toxic microalga, *Vicicitus globosus*, leading to disruption of organic matter transfer across trophic levels[106]. The marine cyanobacterial genus *Trichodesmium* responds to long-term (4.5-year) exposure to elevated CO_2 levels with irreversible genetic changes that increase nitrogen fixation and growth[107]. For the photosynthetic green alga *Ostreococcus tauri*, elevated CO_2 levels increase growth, cell size and carbon-to-nitrogen ratios[108]. Higher CO_2 levels also affect the population structure of *O. tauri*, with changes in ecotypes and niche occupation, thereby affecting the broader food webs and biogeochemical cycles[108]. Rather than producing larger cells, the calcifying phytoplankton species *Emiliania huxleyi* responds to the combined effects of elevated temperature and elevated CO_2 levels (and associated acidification) by producing smaller cells that contain less carbon[109]. However, for this species, overall production rates do not change as a result of evolutionary adaptation to higher CO_2 levels[109]. Responses to CO_2 levels differ between communities (for example, between Arctic phytoplankton and Antarctic phytoplankton[110]). A mesocosm study identified variable changes in the diversity of viruses that infect *E. huxleyi* when it is growing under elevated

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CO_2 levels, and noted the need to determine whether elevated CO_2 levels directly affected viruses, hosts or the interactions between them[111]. These examples illustrate the need to improve our understanding of evolutionary processes and incorporate that knowledge into predictions of the effects of climate change.

Ocean acidification presents marine microorganisms with pH conditions well outside their recent historical range, which affects their intracellular pH homeostasis[18,112]. Species that are less adept at regulating internal pH will be more affected, and factors such as organism size, aggregation state, metabolic activity and growth rate influence the capacity for regulation[112].

Lower pH causes bacteria and archaea to change gene expression in ways that support cell maintenance rather than growth[18]. In mesocosms with low phytoplankton biomass, bacteria committed more resources to pH homeostasis than bacteria in nutrient-enriched mesocosms with high phytoplankton biomass. Consequently, ocean acidification is predicted to alter the microbial food web via changes in cellular growth efficiency, carbon cycling and energy fluxes, with the biggest effects expected in the oligotrophic regions, which include most of the ocean[18]. Experimental comparisons of *Synechococcus* sp. growth under both present and predicted future pH concentrations showed effects not only on the cyanobacteria but also on the cyanophage viruses that infect them[113].

Environmental temperature and latitude correlate with the diversity, distribution and/or temperature optimum (T_{opt}) of certain marine taxa, with models predicting that rising temperatures will cause a poleward shift of cold-adapted communities[52,114–118]. However, T_{opt} of phytoplankton from polar and temperate waters was found to be substantially higher than environmental temperatures, and an eco-evolutionary model predicted that T_{opt} for tropical phytoplankton would be substantially higher than observed experimental values[116]. Understanding how well microorganisms are adapted to environmental temperature and predicting how they will respond to warming requires assessments of more than T_{opt}, which is generally a poor indicator of physiological and ecological adaptation of microorganisms from cold environments[119].

Many environmental and physiological factors influence the responses and overall competitiveness of microorganisms in their native environment. For example, elevated temperatures increase protein synthesis in eukaryotic phytoplankton while reducing cellular ribosome concentration[120]. As the biomass of eukaryotic phytoplankton is ~1 Gt C (REF.[13]) and ribosomes are phosphate rich, climate change-driven alteration of their nitrogen-to-phosphate ratio will affect resource allocation in the global ocean[120]. Ocean warming is thought to favour smaller plankton types over larger ones, changing biogeochemical fluxes such as particle export[121]. Increased ocean temperatures, acidification and decreased nutrient supplies are projected to increase the extracellular release of dissolved organic matter from phytoplankton, with changes in the microbial loop possibly causing increased microbial production at the expense of higher trophic levels[122]. Warming can also alleviate iron limitation of nitrogen-fixing cyanobacteria, with potentially profound implications for new nitrogen supplied to food webs of the future warming oceans[123]. Careful attention needs to be paid to how to quantify and interpret responses of environmental microorganisms to ecosystem changes and stresses linked to climate change[124,125]. Key questions thus remain about the functional consequences of community shifts, such as changes in carbon remineralization versus carbon sequestration, and nutrient cycling.

Terrestrial biome

There is ~100-fold more terrestrial biomass than marine biomass, and terrestrial plants account for a large proportion of Earth's total biomass[15]. Terrestrial plants perform roughly half of net global primary production[30,67]. Soils store ~2,000 billion tonnes of organic carbon, which is more than the combined pool of carbon in the atmosphere and vegetation[126]. The total number of microorganisms in terrestrial environments is ~10^{29}, similar to the total number in marine environments[8]. Soil microorganisms regulate the amount of organic carbon stored in soil and released back to the atmosphere, and indirectly influence carbon storage in plants and soils through provision of macronutrients that regulate productivity (nitrogen and phosphorus)[126,127]. Plants provide a substantial amount of carbon to their mycorrhizal fungal symbionts, and in many ecosystems, mycorrhizal fungi are responsible for substantial amounts of nitrogen and phosphorus acquisition by plants[128].

Plants remove CO_2 from the atmosphere through photosynthesis and create organic matter that fuels terrestrial ecosystems. Conversely, autotrophic respiration by plants (60 Pg C per year) and heterotrophic respiration by microorganisms (60 Pg C per year) release CO_2 back into the atmosphere[126,129]. Temperature influences the balance between these opposing processes and thus the capacity of the terrestrial biosphere to capture and store anthropogenic carbon emissions (currently, storing approximately one quarter of emissions) (FIG. 1). Warming is expected to accelerate carbon release into the atmosphere[129].

Forests cover ~30% of the land surface, contain ~45% of terrestrial carbon, make up ~50% of terrestrial primary production and sequester up to 25% of anthropogenic CO_2 (REFS[130,131]). Grasslands cover ~29% of the terrestrial surface[132]. Non-forested, arid and semiarid regions (47%) are important for the carbon budget and respond differently to anthropogenic climate change than forested regions[132,133]. Lakes make up ~4% of the non-glaciated land area[134], and shallow lakes emit substantial amounts of CH_4 (REFS[135,136]). Peat (decomposed plant litter) covers ~3% of the land surface and, due to plant productivity exceeding decomposition, intact peatlands function as a global carbon sink and contain ~30% of global soil carbon[137,138]. In permafrost, the accumulation of carbon in organic matter (remnants of plants, animals and microorganisms) far exceeds the respiratory losses, creating the largest terrestrial carbon sink[139–141]. Climate warming of 1.5–2 °C (relative to the global mean surface temperature in 1850–1900) is predicted to reduce permafrost by 28–53% (compared with levels in

Growth efficiency
A measure of how effectively microorganisms convert organic matter into biomass, with lower efficiency meaning more carbon is released to the atmosphere.

Oligotrophic
Conditions low in nutrients or nutrient flux, particularly of carbon, nitrogen or phosphorus, thereby limiting the concentration of cells the system supports; the bulk of the ocean is oligotrophic, apart from the coast and upwelling sites.

Cyanobacteria
Oxygen-producing photosynthetic bacteria that use sunlight as an energy source.

Microbial loop
The microbial component of a food web; for example, organic matter in marine microorganisms is released due to cell death and predation by grazers and viruses and used as nutrients for growth of cells that then feed higher trophic level organisms.

Photosynthesis
The conversion of sunlight into energy used to produce ATP and the subsequent fixing (conversion) of CO_2 into organic matter; the process is photoautotrophic.

Autotrophic
Able to grow on carbon dioxide as the sole source of carbon.

Heterotrophic
Using organic compounds as nutrients to produce energy for growth.

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1960–1990)[142], thereby making large carbon reservoirs available for microbial respiration and greenhouse gas emissions.

Evaluations of the top 10 cm of soil[143] and whole-soil profiles to 100 cm deep, which contain older stocks of carbon[144], demonstrate that warming increases carbon loss to the atmosphere. Explaining differences in carbon loss between different soil sites will require a greater range of predictive variables (in addition to soil organic matter content, temperature, precipitation, pH and clay content)[145,146]. Nevertheless, predictions from global assessments of responses to warming indicate that terrestrial carbon loss under warming is causing a positive feedback that will accelerate the rate of climate change[143], particularly in cold and temperate soils, which store much of the global soil carbon[147].

Microorganisms affect climate change. Higher CO_2 levels in the atmosphere increase primary productivity and thus forest leaf and root litter[148–150], which leads to higher carbon emissions due to microbial degradation[151]. Higher temperatures promote higher rates of terrestrial organic matter decomposition[152]. The effect of temperature is not just a kinetic effect on microbial reaction rates but results from plant inputs stimulating microbial growth[152–154].

Several local environmental factors (such as microbial community composition, density of dead wood, nitrogen availability and moisture) influence rates of microbial activity (for example, fungal colonization of wood) necessitating Earth system model predictions of soil carbon losses through climate warming to incorporate local controls on ecosystem processes[155]. In this regard, plant nutrient availability affects the net carbon balance in forests, with nutrient-poor forests releasing more carbon than nutrient-rich forests[156]. Microbial respiration may be lower in nutrient-rich forests as plants provide less carbon (for example, as root exudates) to rhizosphere microorganisms[157].

Plants release ~50% of fixed carbon into the soil, which is available for microbial growth[158–160]. In addition to microorganisms using exudates as an energy source, exudates can disrupt mineral–organic associations, liberating organic compounds from minerals that are used for microbial respiration, thereby increasing carbon release[159]. The relevance of these plant–mineral interactions illustrates the importance of biotic–abiotic interactions, in addition to biotic interactions (plant–microorganism) when one is evaluating the influence of climate change[159]. Thermodynamic models that incorporate the interactions of microorganisms and secreted enzymes with organic matter and minerals have been used to predict soil carbon–climate feedbacks in response to increasing temperature; one study predicted more variable but weaker soil carbon–climate feedbacks from a thermodynamic model than from static models[160].

The availability of soil organic matter for microbial degradation versus long-term storage depends on many environmental factors, including the soil mineral characteristics, acidity and redox state; water availability; climate; and the types of microorganisms present in the soil[161]. The nature of the organic matter, in particular substrate complexity, affects microbial decomposition. Furthermore, the microbial capacity to access organic matter differs between soil types (for example, with different clay content)[162]. If access is taken into account, increasing atmospheric CO_2 levels are predicted to allow greater microbial decomposition and less soil retention of organic carbon[162].

Elevated CO_2 concentrations enhance competition for nitrogen between plants and microorganisms[163]. Herbivores (invertebrates and mammals) affect the amount of organic matter that is returned to soil and thereby microbial biomass and activity[164]. For example, grasshoppers diminish plant biomass and plant nitrogen demand, thereby increasing microbial activity[163]. Climate change can reduce herbivory, resulting in overall alterations to global nitrogen and carbon cycles that reduce terrestrial carbon sequestration[163]. Detritivores (for example, earthworms) influence greenhouse gas emissions by indirectly affecting plants (for example, by increasing soil fertility) and soil microorganisms[165]. Earthworms modify soils through feeding, burrowing and deposition of waste products. The anaerobic gut environment of earthworms harbours microorganisms that perform denitrification and produce N_2O. Earthworms enhance soil fertility, and their presence can result in net greenhouse gas emissions[165], although the combined effects of increased temperature and decreased rainfall on detritivore feeding and microbial respiration may reduce emissions[166].

In peatlands, decay-resistant litter (for example, antimicrobial phenolics and polysaccharides of *Sphagnum* mosses) inhibits microbial decomposition, and water saturation restricts oxygen exchange and promotes the growth of anaerobes and release of CO_2 and CH_4 (REFS[137,167]). Increased temperature and reduced soil water content caused by climate change promote the growth of vascular plants (ericaceous shrubs) but reduce the productivity of peat moss. Changes in plant litter composition and associated microbial processes (for example, reduced immobilization of nitrogen and enhanced heterotrophic respiration) are switching peatlands from carbon sinks to carbon sources[137].

Melting and degradation of permafrost allows microbial decomposition of previously frozen carbon, releasing CO_2 and CH_4 (REFS[139–141,168,169]). Coastal permafrost erosion will lead to the mobilization of large quantities of carbon to the ocean, with potentially large CO_2 emissions occurring through increased microbial remineralization[170], causing a positive feedback loop that accelerates climate change[139–141,168–171]. Melting of permafrost leads to increases in water-saturated soils[172], which promotes anaerobic CH_4 production by methanogens and CO_2 production by a range of microorganisms. Production is slow compared with metabolism in drained aerobic soils, which release CO_2 rather than CH_4. However, a 7-year laboratory study of CO_2 and CH_4 production found that once methanogen communities became active in thawing permafrost, equal amounts of CO_2 and CH_4 were formed under anoxic conditions, and it was predicted that by the end of the century, carbon emissions from anoxic environments will drive climate

Earth system model
A simulation of Earth's physical (including climate), chemical and biological processes that integrates interactions of the biosphere with the atmosphere, ocean, land and ice.

Rhizosphere
The soil zone that surrounds and is influenced by the roots of plants.

Detritivores
Organisms that grow by decomposing detritus (animal and plant organic matter).

Denitrification
The process of converting oxidized forms of nitrogen such as nitrate (NO_3) or nitrite (NO_2) into more reduced forms, including nitrous oxide (N_2O) and nitrogen gas (N_2).

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change to a greater extent than emissions from oxic environments[172].

A 15-year mesocosm study that simulated freshwater lake environments determined that the combined effects of eutrophication and warming can lead to large increases in CH_4 ebullition (bubbles from accumulated gas)[135]. As small lakes are susceptible to eutrophication and tend to be located in climate-sensitive regions, the role of lake microorganisms in contributing to global greenhouse gas emissions needs to be evaluated[135,136].

Climate change affects microorganisms. Shifts in climate can influence the structure and diversity of microbial communities directly (for example, seasonality and temperature) or indirectly (for example, plant composition, plant litter and root exudates). Soil microbial diversity influences plant diversity and is important for ecosystem functions, including carbon cycling[173,174].

Both short-term laboratory warming and long-term (more than 50 years) natural geothermal warming initially increased the growth and respiration of soil microorganisms, leading to net CO_2 release and subsequent depletion of substrates, causing a decrease in biomass and reduced microbial activity[175]. This implies that microbial communities do not readily adapt to higher temperatures, and the resulting effects on reaction rates and substrate depletion reduce overall carbon loss[175]. By contrast, a 10-year study found that soil communities adapted to increased temperature by changing composition and patterns of substrate use, leading to less carbon loss than would have occurred without adaptation[176]. Substantial changes in bacterial and fungal communities were also found in forest soils with a more than 20 °C average annual temperature range[177], and in response to warming across a 9-year study of tall-grass prairie soils[178].

Two studies assessed the effects of elevated temperatures on microbial respiration rates and mechanisms and outcomes of adaptation[179,180]. The studies examined a wide range of environmental temperatures (−2 to 28 °C), dryland soils (110 samples) and boreal, temperate and tropical soils (22 samples), and evaluated how communities respond to three different temperatures (~10–30 °C). Thermal adaptation was linked to biophysical characteristics of cell membranes and enzymes (reflecting activity-stability trade-offs[180]) and the genomic potential of microorganisms (with warmer environments having microbial communities with more diverse lifestyles[179]). Respiration rates per unit biomass were lower in soils from higher-temperature environments, indicating that thermal adaptation of microbial communities may lessen positive climate feedbacks. However, as respiration depends on multiple interrelated factors (not just on one variable, such as temperature), such mechanistic insights into microbial physiology need to be represented in biogeochemical models of possible positive climate feedbacks.

Microbial growth responses to temperature change are complex and varied[181]. Microbial growth efficiency is a measure of how effectively microorganisms convert organic matter into biomass, with lower efficiency meaning more carbon is released to the atmosphere[182,183]. A 1-week laboratory study found that increasing temperature led to increases in microbial turnover but no change in microbial growth efficiency, and predicted that warming would promote carbon accumulation in soil[183]. A field study spanning 18 years found microbial efficiency was reduced at higher soil temperature, with decomposition of recalcitrant, complex substrates increasing by the end of the period along with a net loss of soil carbon[182].

Similarly, in a 26-year forest-soil warming study, temporal variation occurred in organic matter decomposition and CO_2 release[184], leading to changes in microbial community composition and carbon use efficiency, reduced microbial biomass and reduced microbially accessible carbon[184]. Overall, the study predicted anthropogenic climate change to cause long-term, increasing and sustained carbon release[184]. Similar predictions arise from Earth system models that simulate microbial physiological responses[185] or incorporate the effects of freezing and thawing of cold-climate soils[186].

Climate change directly and indirectly influences microbial communities and their functions through several interrelated factors, such as temperature, precipitation, soil properties and plant input. As soil microorganisms in deserts are carbon limited, increased carbon input from plants promotes transformation of nitrogenous compounds, microbial biomass, diversity (for example, of fungi), enzymatic activity and use of recalcitrant organic matter[133]. Although these changes may enhance respiration and net loss of carbon from soil, the specific characteristics of arid and semiarid regions may mean they could function as carbon sinks[133]. However, a study of 19 temperate grassland sites found that seasonal differences in rainfall constrain biomass accumulation[132]. To better understand aboveground plant-biomass responses to CO_2 levels and seasonal precipitation, we also need improved knowledge of microbial community responses and functions.

Metagenome data, including metagenome-assembled genomes, provide knowledge of key microbial groups that metabolize organic matter and release CO_2 and CH_4 and link these groups to the biogeochemistry occurring in thawing permafrost[187–191]. Tundra microbial communities change in the soil layer of permafrost after warming[192]. Within 1.5 years of warming, the functional potential of the microbial communities changed markedly, with an increasing abundance of genes involved in aerobic and anaerobic carbon decomposition and nutrient cycling. Although microbial metabolism stimulates primary productivity by plants, the balance between microbial respiration and primary productivity results in a net release of carbon to the atmosphere[192]. When forests expand into warming regions of tundra, plant growth can produce a net loss of carbon, possibly as a result of root exudates stimulating microbial decomposition of native soil carbon[153,193]. Although there are reports of carbon accumulating owing to warming (for example, REF.[183]), most studies describe microbial community responses that result in carbon loss.

Rapid warming of the Antarctic Peninsula and associated islands resulted in range expansion of Antarctic hair grass (*Deschampsia antarctica*), as it outcompetes

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other indigenous species (for example, the moss *Sanionia uncinata*) through the superior capacity of its roots to acquire peptides and thus nitrogen[194]. The ability of the grass to be competitive depends on microbial digestion of extracellular proteins and generation of amino acids, nitrate and ammonium[194]. As warmer soils in this region harbour greater fungal diversity, climate change is predicted to cause changes in the fungal communities that will affect nutrient cycling and primary productivity[195]. Cyanobacterial diversity and toxin production within benthic mats from both the Antarctic Peninsula and the Arctic increased during 6 months of exposure to high growth temperatures[196]. A shift to toxin-producing species or increased toxin production by existing species could affect polar freshwater lakes, where cyanobacteria are often the dominant benthic primary producers[196].

Climate change is likely to increase the frequency, intensity and duration of cyanobacterial blooms in many eutrophic lakes, reservoirs and estuaries[197,198]. Bloom-forming cyanobacteria produce a variety of neurotoxins, hepatotoxins and dermatoxins, which can be fatal to birds and mammals (including waterfowl, cattle and dogs) and threaten the use of waters for recreation, drinking water production, agricultural irrigation and fisheries[198]. Toxic cyanobacteria have caused major water quality problems, for example in Lake Taihu (China), Lake Erie (USA), Lake Okeechobee (USA), Lake Victoria (Africa) and the Baltic Sea[198–200].

Climate change favours cyanobacterial blooms both directly and indirectly[198]. Many bloom-forming cyanobacteria can grow at relatively high temperatures[201]. Increased thermal stratification of lakes and reservoirs enables buoyant cyanobacteria to float upwards and form dense surface blooms, which gives them better access to light and hence a selective advantage over nonbuoyant phytoplankton organisms[202,203]. Protracted droughts during summer increase water residence times in reservoirs, rivers and estuaries, and these stagnant warm waters can provide ideal conditions for cyanobacterial bloom development[204].

The capacity of the harmful cyanobacterial genus *Microcystis* to adapt to elevated CO_2 levels was demonstrated in both laboratory and field experiments[205]. *Microcystis* spp. take up CO_2 and HCO_3^- and accumulate inorganic carbon in carboxysomes, and strain competitiveness was found to depend on the concentration of inorganic carbon. As a result, climate change and increased CO_2 levels are expected to affect the strain composition of cyanobacterial blooms[205].

Agriculture

According to the World Bank (World Bank data on agricultural land), nearly 40% of the terrestrial environment is devoted to agriculture. This proportion is predicted to increase, leading to substantial changes in soil cycling of carbon, nitrogen and phosphorus, among other nutrients. Furthermore, these changes are associated with a marked loss of biodiversity[206], including of microorganisms[207]. There is increasing interest in using plant-associated and animal-associated microorganisms to increase agricultural sustainability and mitigate the effects of climate change on food production, but doing so requires a better understanding of how climate change will affect microorganisms.

Microorganisms affect climate change. Methanogens produce methane in natural and artificial anaerobic environments (sediments, water-saturated soils such as rice paddies, gastrointestinal tracts of animals (particularly ruminants), wastewater facilities and biogas facilities), in addition to the anthropogenic methane production associated with fossil fuels[208] (FIG. 2). The main sinks for CH_4 are atmospheric oxidation and microbial oxidation in soils, sediments and water[208]. Atmospheric CH_4 levels have risen sharply in recent years (2014–2017) but the reasons are unclear so far, although they involve increased emissions from methanogens and/or fossil fuel industries and/or reduced atmospheric CH_4 oxidation, thereby posing a major threat to controlling climate warming[209].

Rice feeds half of the global population[210], and rice paddies contribute ~20% of agricultural CH_4 emissions despite covering only ~10% of arable land. Anthropogenic climate change is predicted to double CH_4 emissions from rice production by the end of the century[210]. Ruminant animals are the largest single source of anthropogenic CH_4 emissions, with a 19–48 times larger carbon footprint for ruminant meat production than plant-based high-protein foods[211]. Even the production of meat from non-ruminant animals (such as pigs, poultry and fish) produces 3–10 times more CH_4 than high-protein plant foods[211].

The combustion of fossil fuels and the use of fertilizers has greatly increased the environmental availability of nitrogen, perturbing global biogeochemical processes and threatening ecosystem sustainability[212,213]. Agriculture is the largest emitter of the potent greenhouse gas N_2O, which is released by microbial oxidation and reduction of nitrogen[214]. The enzyme N_2O reductase in rhizobacteria (in root nodules) and other soil microorganisms can also convert N_2O to N_2 (not a greenhouse gas). Climate change perturbs the rate at which microbial nitrogen transformations occur (decomposition, mineralization, nitrification, denitrification and fixation) and release N_2O (REF.[213]). There is an urgent need to learn about the effects of climate change and other human activities on microbial transformations of nitrogen compounds.

Climate change affects microorganisms. Crop farming ranges from extensively managed (small inputs of labour, fertilizer and capital) to intensively managed (large inputs). Increasing temperature and drought strongly affect the ability to grow crops[215]. Fungal-based soil food webs are common in extensively managed farming (for example, grasslands) and are better able to adapt to drought than bacterial-based food webs, which are common in intensive systems (for example, wheat)[216,217]. A global assessment of topsoil found that soil fungi and bacteria occupy specific niches and respond differently to precipitation and soil pH, indicating that climate change would have differential impacts on their abundance, diversity and functions[218]. Aridity, which is predicted to increase owing to climate change,

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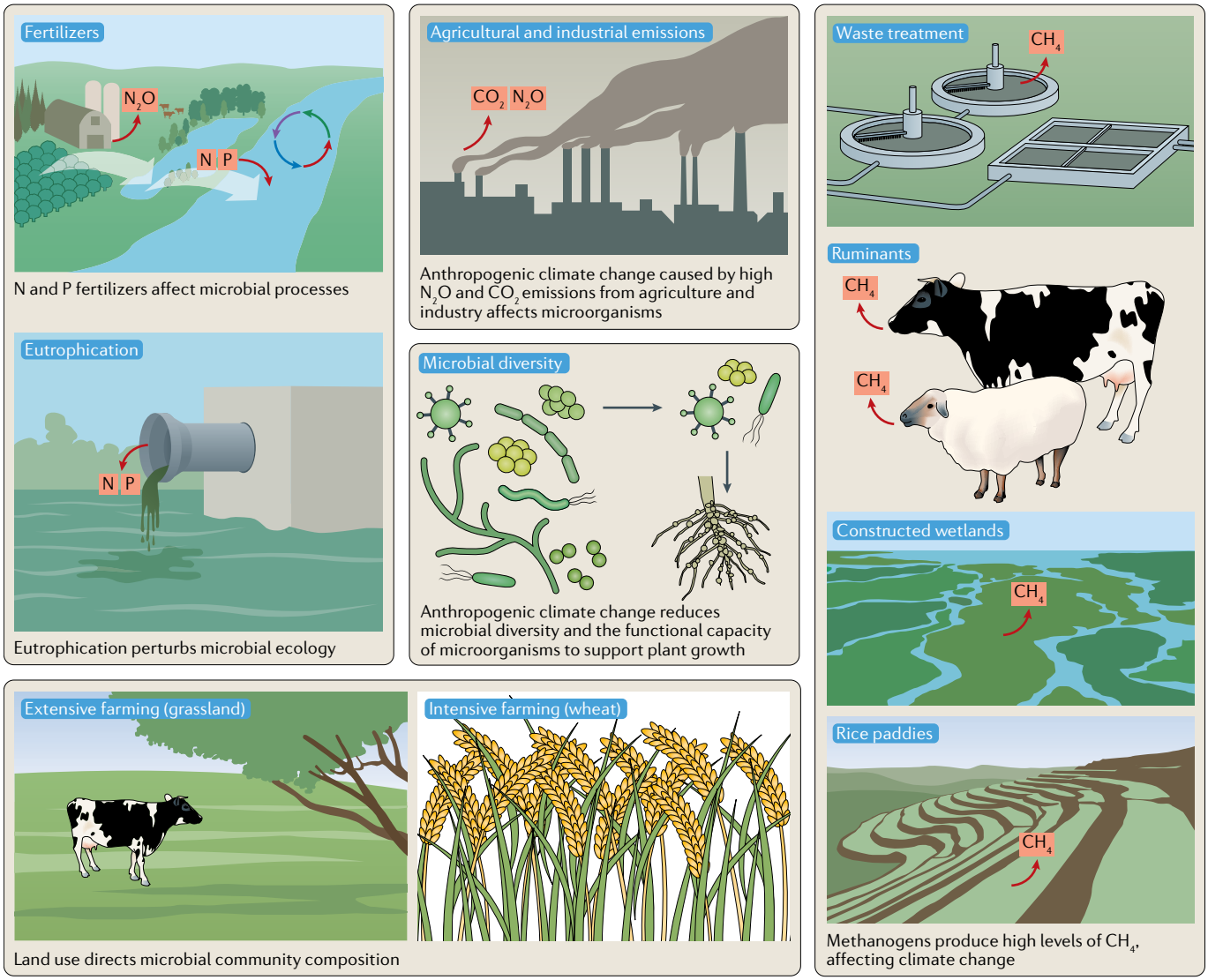


Fig. 2 | **Agriculture and other human activities that affect microorganisms.** Agricultural practices influence microbial communities in specific ways. Land usage (for example, plant type) and sources of pollution (for example, fertilizers) perturb microbial community composition and function, thereby altering natural cycles of carbon, nitrogen and phosphorus transformations. Methanogens produce substantial quantities of methane directly from ruminant animals (for example, cattle, sheep and goats) and saturated soils with anaerobic conditions (for example, rice paddies and constructed wetlands). Human activities that cause a reduction in microbial diversity also reduce the capacity for microorganisms to support plant growth.

reduces bacterial and fungal diversity and abundance in global drylands[219]. Reducing soil microbial diversity reduces the overall functional potential of microbial communities, thereby limiting their capacity to support plant growth[173].

The combined effects of climate change and eutrophication caused by fertilizers can have major, potentially unpredictable effects on microbial competitiveness. For example, nutrient enrichment typically favours harmful algal blooms, but a different outcome was observed in the relatively deep Lake Zurich[220]. Reducing phosphorus inputs from fertilizers reduced eukaryotic phytoplankton blooms but increased the nitrogen-to-phosphorus ratio and thus the non-nitrogen-fixing cyanobacterium *Planktothrix rubescens* became dominant[220]. In the absence of effective predation, annual mixing has an important role in controlling cyanobacterial populations. However, warming increased thermal stratification and reduced mixing, thereby facilitating the persistence of the toxic cyanobacteria[220].

Infectious diseases

Climate change affects the occurrence and spread of diseases in marine and terrestrial biota[221] (FIG. 3), depending on diverse socioeconomic, environmental and host–pathogen-specific factors[222]. Understanding the spread of disease and designing effective control strategies requires knowledge of the ecology of pathogens, their vectors and their hosts, and the influence of dispersal and environmental factors[223] (TABLE 1). For example, there is a strong link between increasing sea surface temperatures and coral disease and, although

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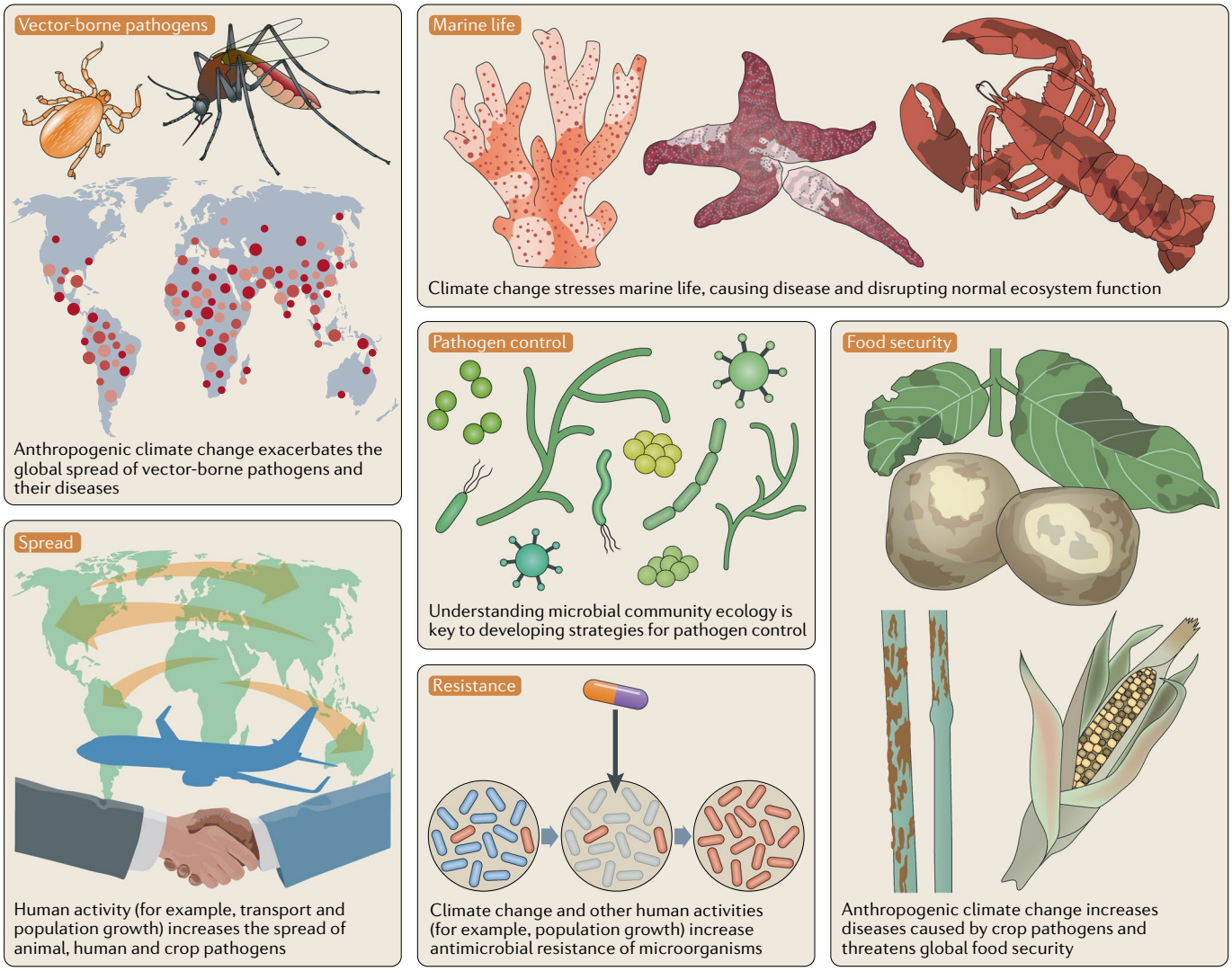


Fig. 3 | **Climate change exacerbates the impact of pathogens.** Anthropogenic climate change stresses native life, thereby enabling pathogens to increasingly cause disease. The impact on aquaculture, food-producing animals and crops threatens global food supply. Human activities, such as population growth and transport, combined with climate change increase antibiotic resistance of pathogens and the spread of waterborne and vector-borne pathogens, thereby increasing diseases of humans, other animals and plants.

the disease mechanisms are not absolutely clear for all the different syndromes, associations with microbial pathogens exist[224–226]. Peaks in disease prevalence coincide with periodicities in the El Niño Southern Oscillation (ENSO)[227]. In particular, in some coral species, ocean warming can alter the coral microbiome, disrupting the host–symbiont equilibrium, shifting defensive mechanisms and nutrient cycling pathways that may contribute to bleaching and disease[99]. Ocean acidification may also directly cause tissue damage in organisms such as fish, potentially contributing to a weakened immune system that creates opportunities for bacterial invasion[228].

Sea star species declined by 80–100% along an ~3000 km section of the North American west coast, with peak declines occurring during anomalous increases in sea surface temperatures[229]. As sea stars are important predators of sea urchins, loss of predation can cause a trophic cascade that affects kelp forests and associated marine biodiversity[229,230]. Given the effects of ocean warming on pathogen impacts, temperature monitoring systems have been developed for a wide range of marine organisms, including corals, sponges, oysters, lobsters and other crustaceans, sea stars, fish and sea grasses[231].

Forest die-off caused by drought and heat stress can be exacerbated by pathogens[232]. For crops, a variety of interacting factors are important when one is considering response to pathogens, including CO_2 levels, climatic changes, plant health and species-specific plant–pathogen interactions[233]. A broad range of microorganisms cause plant diseases (fungi, bacteria, viruses, viroids and oomycetes) and can, therefore, affect crop production, cause famines (for example, the oomycete *Phytophthora infestans* caused the Irish potato famine) and threaten food security[233]. An assessment of more than 600 crop pests (nematodes and insects) and pathogens since 1960 found an expansion towards the poles

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Table 1 | **Transmission response of pathogens to climatic and environmental factors**

Example pathogens or diseases	Climatic and environmental factors	Transmission parameters
Vector-borne		
West Nile virus	Precipitation, relative humidity, temperature, El Niño Southern Oscillation	Vector abundance, longevity and biting rate, pathogen replication rate in vector[273–276]
Malaria		
Dengue fever		
Lyme disease		
Waterborne		
Cholera	Temperature, precipitation variability, salinity, El Niño Southern Oscillation	Pathogen survival, pathogen replication in environment, pathogen transport[244,277–279]
Non-cholera *Vibrio* spp.		
Cryptosporidium spp.		
Rotavirus		
Airborne		
Influenza	Relative humidity, temperature, wind	Pathogen survival, pathogen and/or host dispersal[280–284]
Hantavirus		
Coccidioidomycosis		
Foodborne		
Salmonella spp.	Temperature, precipitation	Pathogen replication, human behaviour[239,240]
Campylobacter spp.		

that is attributable to climate change[233]. The spread of pathogens and the emergence of disease are facilitated by transport and introduction of species and are influenced by effects of weather on dispersal and environmental conditions for growth[233].

Climate change can increase the disease risk by altering host and parasite acclimation[234]. For ectotherms (such as amphibians), temperature can increase susceptibility to infection, possibly through perturbation of immune responses[234,235]. Monthly and daily unpredictable environmental temperature fluctuations increase the susceptibility of the Cuban tree frog to the pathogenic chytrid fungus *Batrachochytrium dendrobatidis*. The effect of increasing temperature on infection contrasts with decreased growth capacity of the fungus in pure culture, illustrating the importance of assessing host–pathogen responses (rather than extrapolating from growth rate studies of isolated microorganisms) when evaluating the relevance of climate change[234].

Climate change is predicted to increase the rate of antibiotic resistance of some human pathogens[236]. Data from 2013–2015 suggest that an increase of the daily minimum temperature by 10 °C (which is conceivable for some parts of the USA by the end of the century) will lead to an increase in antibiotic resistance rates of *Escherichia coli*, *Klebsiella pneumoniae* and *Staphylococcus aureus* by 2–4% (up to 10% for certain antibiotics)[236]. Potential underlying mechanisms include elevated temperatures facilitating horizontal gene transfer of mobile genetic elements of resistance, and increased pathogen growth rates promoting environmental persistence, carriage and transmission[236]. Population growth, which amplifies climate change, is also an important factor in contributing to the development of resistance[236].

Vector-borne, foodborne, airborne, waterborne and other environmental pathogens may be particularly susceptible to the effects of climate change[237–240] (TABLE 1). For vector-borne diseases, climate change will affect the distribution of vectors and hence the range over which diseases are transmitted, as well as the efficiency with which vectors transmit pathogens. Efficiency depends on the time between a vector feeding on an infected host and the vector becoming infectious itself. At warmer temperatures, this time can be reduced substantially, providing more opportunity for transmission within the vector's lifespan. Certain vector-borne diseases, such as bluetongue, an economically important viral disease of livestock, have already emerged in Europe in response to climate change, and larger, more frequent outbreaks are predicted to occur in the future[241]. For certain waterborne infections by pathogenic *Vibrio* spp., poleward spread correlates with increasing global temperature and lower salinity of aquatic environments in coastal regions (such as estuaries) caused by increased precipitation[242]. These changed conditions can promote the growth of *Vibrio* spp. in the environment[242]. Increasing sea surface temperatures also correlate with increases in *Vibrio cholerae* infections in Bangladesh[243], infections with several human-pathogenic *Vibrio* spp. in the Baltic Sea region[242] and the abundance of *Vibrio* spp. (including human pathogens) in the North Atlantic and North Sea[244].

Malaria and dengue fever are two vector-borne diseases that are known to be highly sensitive to climate conditions, and thus their spatial distributions are expected to shift in response to climate change[4,141,245]. Climate change can facilitate the spread of vector-borne pathogens by prolonging the transmission season, increasing the rate of replication of pathogens in the vector and increasing the number and geographic range of mosquitoes. This is especially the case for *Aedes aegypti*, the major vector of dengue, Zika, chikungunya and yellow fever viruses, which is currently limited to tropical and subtropical regions because it cannot survive cold winters. In combination with other mosquito-borne diseases (such as West Nile fever and Japanese encephalitis) and tick-borne diseases (such as Lyme disease), millions of people are predicted to be newly at risk under climate change[4,238,246–249].

Many infectious diseases, including several vector-borne and waterborne diseases, are strongly influenced by climate variability caused by large-scale climate phenomena such as the ENSO, which disrupts normal rainfall patterns and changes temperatures in about two thirds of the globe every few years. Associations with ENSO have been reported for malaria, dengue fever, Zika virus disease, cholera, plague, African horse sickness and many other important human and animal diseases[250–254].

Adaptation of species to their local environment has been studied less in microorganisms than in animals (including humans) and plants, although the mechanisms and consequences of adaptation have been studied in natural and experimental microbial populations[255]. Viral, bacterial and fungal pathogens of plants and animals (such as crops, humans and livestock) adapt to abiotic and biotic factors (such as temperature, pesticides,

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interactions between microorganisms and host resistance) in ways that affect ecosystem function, human health and food security[255]. The cyclic feedback between microbial response and human activity is well illustrated by the adaptation patterns of pathogenic agricultural fungi[256]. Because agricultural ecosystems have common global features (for example, irrigation, fertilizer use and plant cultivars) and human travel and transport of plant material readily disperse crop pathogens, 'agro-adapted' pathogens have a higher potential to cause epidemics and pose a greater threat to crop production than naturally occurring strains[256]. The ability of fungal pathogens to expand their range and invade new habitats by evolving to tolerate higher temperatures compounds the threat fungal pathogens pose to both natural and agricultural ecosystems[257].

Microbial mitigation of climate change

An improved understanding of microbial interactions would help underpin the design of measures to mitigate and control climate change and its effects (see also REF.[7]). For example, understanding how mosquitoes respond to the bacterium *Wolbachia* (a common symbiont of arthropods) has resulted in a reduction of the transmission of Zika, dengue and chikungunya viruses through the introduction of *Wolbachia* into populations of *A. aegypti* mosquitoes and releasing them into the environment[258]. In agriculture, progress in understanding the ecophysiology of microorganisms that reduce N_2O to harmless N_2 provides options for mitigating emissions[214,259]. The use of bacterial strains with higher N_2O reductase activity has lowered N_2O emissions from soybean, and both natural and genetically modified strains with higher N_2O reductase activity provide avenues for mitigating N_2O emissions[214]. Manipulating the rumen microbiota[260] and breeding programmes that target host genetic factors that change microbial community responses[261] are possibilities for reducing methane emission from cattle. In this latter case, the aim would be to produce cattle lines that sustain microbial communities producing less methane without affecting the health and productivity of the animals[261]. Fungal proteins can replace meat, lowering dietary carbon footprints[262].

Biochar is an example of an agricultural solution for broadly and indirectly mitigating microbial effects of climate change. Biochar is produced from thermochemical conversion of biomass under oxygen limitation and improves the stabilization and accumulation of organic matter in iron-rich soils[263]. Biochar improves organic matter retention by reducing microbial mineralization and reducing the effect of root exudates on releasing organic material from minerals, thereby promoting growth of grasses and reducing the release of carbon[263].

A potentially large-scale approach to mitigation is the use of constructed wetlands to generate cellulosic biofuel using waste nitrogen from wastewater treatment; if all waste in China were used, it could supply the equivalent of 7% of China's gasoline consumption[264]. Such major developments of constructed wetlands would require the characterization and optimization of their core microbial consortia to manage their emissions of greenhouse gases and optimize environmental benefits[265].

Microbial biotechnology can provide solutions for sustainable development[266], including in the provision (for example, of food) and regulation (for example, of disease or of emissions and capture of greenhouse gases) of ecosystem services for humans, animals and plants. Microbial technologies provide practical solutions (chemicals, materials, energy and remediation) for achieving many of the 17 United Nations Sustainable Development Goals, addressing poverty, hunger, health, clean water, clean energy, economic growth, industry innovation, sustainable cities, responsible consumption, climate action, life below water, and life on land[6] (BOX 1). Galvanizing support for such actions will undoubtedly be facilitated by improving public understanding of the key roles of microorganisms in global warming, that is, through attainment of microbiology literacy in society[7].

Conclusion

Microorganisms make a major contribution to carbon sequestration, particularly marine phytoplankton, which fix as much net CO_2 as terrestrial plants. For this reason, environmental changes that affect marine microbial photosynthesis and subsequent storage of fixed carbon in deep waters are of major importance for the global carbon cycle. Microorganisms also contribute substantially to greenhouse gas emissions via heterotrophic respiration (CO_2), methanogenesis (CH_4) and denitrification (N_2O).

Many factors influence the balance of microbial greenhouse gas capture versus emission, including the biome, the local environment, food web interactions and responses, and particularly anthropogenic climate change and other human activities (FIGS 1–3).

Human activity that directly affects microorganisms includes greenhouse gas emissions (particularly CO_2, CH_4 and N_2O), pollution (particularly eutrophication), agriculture (particularly land usage) and population growth, which positively feeds back on climate change, pollution, agricultural practice and the spread of disease. Human activity that alters the ratio of carbon uptake relative to release will drive positive feedbacks and accelerate the rate of climate change. By contrast, microorganisms also offer important opportunities for remedying human-caused problems through improved agricultural outcomes, production of biofuels and remediation of pollution.

Addressing specific issues involving microorganisms will require targeted laboratory studies of model microorganisms (BOX 2). Laboratory probing of microbial responses should assess environmentally relevant conditions, adopt a 'microbcentric' view of environmental stressors and be followed up by field tests. Mesocosm and in situ field experiments are particularly important for gaining insight into community-level responses to real environmental conditions. Effective experimental design requires informed decision-making, involving knowledge from multiple disciplines specific to marine (for example, physical oceanography) and terrestrial (for example, geochemistry) biomes.

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Box 2 | **A call to action**

The microbiologists' warning calls for:

- Greater recognition that all multicellular organisms, including humans, rely on microorganisms for their health and functioning; microbial life is the support system of the biosphere.
- The inclusion of microorganisms in mainstream climate change research, particularly research addressing carbon and nitrogen fluxes.
- Experimental design that accounts for environmental variables and stresses (biotic and abiotic) that are relevant to the microbial ecosystem and climate change responses.
- Investigation of the physiological, community and evolutionary microbial responses and feedbacks to climate change.
- A focus on microbial feedback mechanisms in the monitoring of greenhouse gas fluxes from marine and terrestrial biomes and agricultural, industrial, waste and health sectors and investment in long-term monitoring.
- Incorporation of microbial processes into ecosystem and Earth system models to improve predictions under climate change scenarios.
- The development of innovative microbial technologies to minimize and mitigate climate change impacts, reduce pollution and eliminate reliance on fossil fuels.
- The introduction of teaching of personally, societally, environmentally and sustainability relevant aspects of microbiology in school curricula, with subsequent upscaling of microbiology education at tertiary levels, to achieve a more educated public and appropriately trained scientists and workforce.
- Explicit consideration of microorganisms for the development of policy and management decisions.
- A recognition that all key biosphere processes rely on microorganisms and are greatly affected by human behaviour, necessitating integration of microbiology in the management and advancement of the United Nations Sustainable Development Goals.

Forcings
Climate (or radiative) forcings are factors (for example, anthropogenic greenhouse gases, surface reflectivity (albedo), aerosols) other than the climate system itself (for example, oceans, land surface, cryosphere, biosphere and atmosphere) that cause climate change. Positive forcing occurs when more energy from sunlight is absorbed by Earth than is radiated back into space.

To understand how microbial diversity and activity that govern small-scale interactions translate to large system fluxes, it will be important to scale findings from individuals to communities and to whole ecosystems. Earth system modellers need to include microbial contributions that account for physiological and adaptive (evolutionary) responses to biotic (including other microorganisms, plants and organic matter substrates) and abiotic (including mineral surfaces, ocean physics and chemistry) forcings.

We must improve our quantitative understanding of the global marine and soil microbiome. To understand biogeochemical cycling and climate change feedbacks at any location around the world, we need quantitative information about the organisms that drive elemental cycling (including humans, plants and microorganisms), and the environmental conditions (including climate, soil physiochemical characteristics, topography, ocean temperature, light and mixing) that regulate the activity of those organisms. The framework for quantitative models exists, but to a large extent these models lack mechanistic details of marine and terrestrial microorganisms. The reason for this omission has less to do with how to construct such a model mathematically but instead stems from the paucity of physiological and evolutionary data allowing robust predictions of microbial responses to environmental change. A focused investment into expanding this mechanistic knowledge represents a critical path towards generating the global models essential for benchmarking, scaling and parameterizing Earth system model predictions of current and future climate.

Extant life has evolved over billions of years to generate vast biodiversity, and microbial biodiversity is practically limitless compared with macroscopic life. Biodiversity of macroscopic organisms is rapidly declining because of human activity, suggesting that the biodiversity of host-specific microorganisms of animal and plant species will also decrease. However, compared with macroscopic organisms, we know far less about the connections between microorganisms and anthropogenic climate change. We can recognize the effects of microorganisms on climate change and climate change on microorganisms, but what we have learned is incomplete, complex and challenging to interpret. It is therefore not surprising that challenges exist for defining causes and effects of anthropogenic climate change on biological systems. Nevertheless, there is no doubt that human activity is causing climate change, and this is perturbing normal ecosystem function around the globe (BOX 1). Across marine and terrestrial biomes, microbially driven greenhouse gas emissions are increasing and positively feeding back on climate change. Irrespective of the fine details, the microbial compass points to the need to act (BOX 2). Ignorance of the role of, effects on and feedback response of microbial communities to climate change can lead to our own peril. An immediate, sustained and concerted effort is required to explicitly include microorganisms in research, technology development, and policy and management decisions. Microorganisms not only contribute to the rate of climate change but can also contribute immensely to its effective mitigation and our adaptation tools.

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Author contributions

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Competing interests

The authors declare no competing interests.

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