Microbial Biodiversity☆

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Glossary

Archaea One of the two entirely microbial domains of single-celled organisms, evolutionarily distinct from bacteria. Many archaeal characteristics are more similar to eukaryotes than bacteria.

Bacteria An entirely microbial domain of single-celled organisms, evolutionarily distinct from Archaea.

Eukarya A primarily microbial domain of organisms having a membrane-enclosed nucleus and other organelles; includes animals, plants, fungi, and protists.

Fungi Nonphototrophic, heterotrophic eukaryotic microorganisms that contain rigid cell walls; includes mushrooms, molds, and the fungal part of lichens.

Metagenomics The genomic analysis of microorganisms by direct extraction and cloning of community deoxy ribonucleic acid (DNA) from an environmental sample.

Microorganism Single-celled organisms that can only be observed with a microscope, including bacteria, archaea, small eukaryotes, and viruses.

Operational taxonomic unit (OTU) A group of organisms regarded as being distinct from other groups, based on any clearly defined variables.

Polymerase chain reaction (PCR) A method for copying DNA sequences by repeated cycles of synthesis using specific primers and DNA polymerase.

Virus A genetic element containing either DNA or ribonucleic acid (RNA) that replicates in cells but is characterized by having an extracellular state.

Introduction

Although it might not be immediately obvious, our world is a microbial one. Biodiversity is usually discussed in terms of large organisms, but no organisms are more ubiquitous, abundant, or diverse than microorganisms. Microorganisms were the first cellular life forms and were active more than 3 billion years before the appearance of macroorganisms. The metabolic activities that they carried out during this time were critical for creating the conditions for the evolution of multicellular forms. The universal tree of life (**Fig. 1**; Ciccarelli *et al.*, 2006) emphasizes this point. Multicellular Eukarya (Metazoa, some Fungi, Plantae) are crown groups compared with most microbial Eukarya (eg, Chromalveolata and Diplomonadida), Bacteria, and Archaea. Microbes force us to stretch our imagination about the limits of metabolic lifestyles, the geography of life, and the roles that organisms play in our lives.

Before the development of molecular methods, it was particularly challenging to understand the evolutionary relationships between organisms. It was generally accepted that there were two basic kinds of organisms, prokaryotes and eukaryotes, distinguished by the absence or presence of a membrane-bound nucleus. In the mid-1970s, Woese and colleagues assembled the universal tree of life based on sequence information of small-subunit ribosomal RNA (SSU rRNA). This breakthrough revealed that life consisted of two very distinct microbial domains, the Bacteria and Archaea, which appear to have diverged very early on in evolutionary history, and a third mostly microbial domain, Eukarya, the exact origins of which remain obscure. Archaea and Bacteria share similar morphological characteristics but Archaea possess several cellular and genetic characteristics that are more similar to eukaryotes, and these organisms tend to be more abundant under extreme environments. As a consequence, Bacteria and Archaea often perform quite different functional roles. For example, photosynthesis is performed by Bacteria, spread across five different clades, and is not found within the Archaea kingdom; while methanogenesis is restricted to Archaea. Due to the ubiquity of functional roles, it is no surprise that members of these two domains occupy all habitats on Earth.

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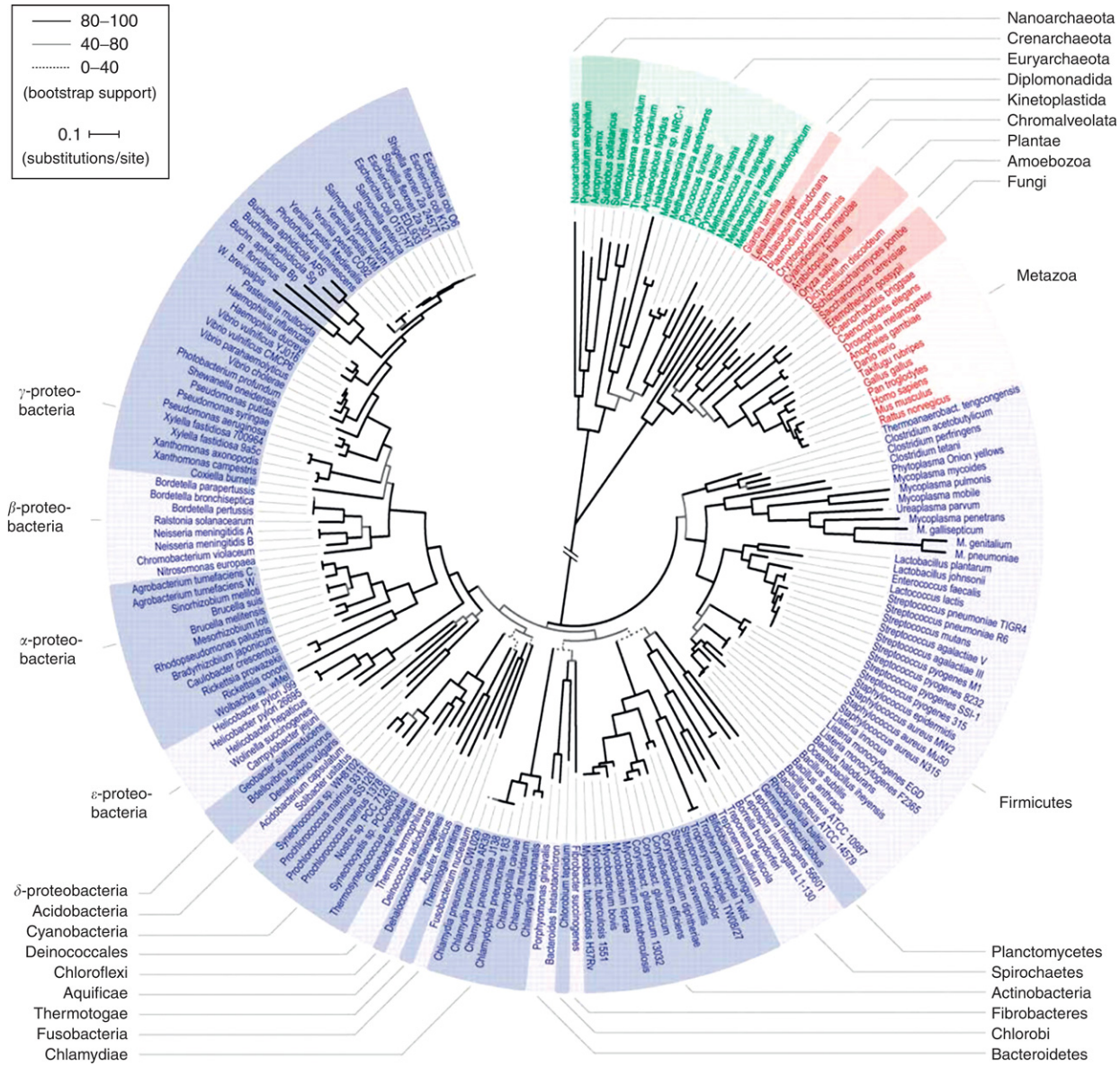

Fig. 1 A phylogeny of some fully sequenced organisms showing the relationship between the three Domains. Green section, Archaea; red, Eukaryota; blue, Bacteria. Labels and color shadings indicate various subdivisions. The branch separating Eukaryota and Archaea from Bacteria in this unrooted tree has been shortened for display purposes. Reproduced from Ciccarelli, F.D., Doerks, T., von Mering, C., *et al.*, 2006. Toward automatic reconstruction of a highly resolved tree of life. Science 311, 1283–1287, with permission from AAAS.

Characterizing Microbial Diversity

Although delineating species can be challenging for some macroorganisms, defining a microbial species is particularly challenging, in part because of their genetics. For sexual organisms, a species is usually defined as a group of potentially interbreeding organisms. But many microorganisms, bacteria in particular, are asexual. Supplementary, further complications arise due to the ability by microorganisms to transfer genes between organisms outside of sexual reproduction in a process known as horizontal gene transfer. Further, microorganisms are too small to define simply by morphological characteristics, as is usually done by plant and animal taxonomists. Thus, in stark contrast to diversity surveys of large organisms, these microorganisms often focus on variation in their DNA rather than in their phenotype. For instance, bacterial species are defined as a group of strains that share at least 70% cross hybridization (DDH: DNA–DNA hybridization). In practice, this requires the melting the genomic DNA of two bacteria and measuring the rate at which they reanneal, a rate determined in part by the similarity of the organisms' genomes.

However, the use of DDH is difficult to implement and inapplicable for environmental studies, as many "named" species have large variations in their phenotype. Instead, researchers use genetic markers to characterize microbial community composition and define an operational taxonomic unit (OTU). For instance, in studies that sequence the 16S ribosomal DNA (rDNA) of bacteria, a common OTU definition is a group of sequences that are similar by 97%. This definition is based on the rough relationship between 16S rDNA similarity and the 70% genomic similarity definition. Once microbial species, or other taxonomic units, are defined, then the diversity of a microbial community can be measured. In its simplest form, community diversity is the richness (total number of OTUs) and evenness (relative abundance of the OTUs) in a defined area. A full description of microbial diversity, however, includes variation at many levels of biological organization from the alleles at a particular genetic locus to differences in communities among habitats.

Culture Techniques

Throughout most of the 20th century, microbiologists used culturing techniques to characterize the composition of microbial communities. Traditionally, these techniques involve trying to grow microorganisms from environmental samples on artificial media and mimicking natural environmental conditions, such as temperature and light, in a laboratory setting. These traditional cultivation techniques tend to select for fast-growing taxa, and therefore grossly underestimate actual diversity. The techniques are thought to capture generally less than 1% of all bacterial species and therefore provide a biased view of microbial community composition in most environments. In the early 20th century, however, promising new cultivation techniques were developed to overcome these deficiencies. For instance, researchers used small diffusion chambers to grow bacterial colonies in a more natural environment and resource regimen. Others have used high-throughput methods to culture novel strains of oceanic bacteria in a low-nutrient media. These newer techniques have allowed microbial biologists to study the ecophysiological properties of organisms that had been previously inaccessible.

Genetic Methodologies

The development of culture-independent methods, based on the genetic characterization of microbial communities, has allowed the detection of nonculturable species and a more detailed description of microbial communities. Because rDNA molecules are found in all organisms and are probably rarely horizontally transferred, they have become a standard phylogenetic marker of microorganisms. Pace *et al.* (1986) built on this idea and used the polymerase chain reaction (PCR) to amplify rDNA genes from community DNA in environmental samples. After PCR, the products can then be further assayed to characterize the diversity of the community using the rDNA genes. Current open-access databases such as GenBank, Ribosomal Database Project (RDP), and SILVA contain thousands of rDNA gene sequences.

Numerous methods can be used to characterize the diversity of PCR-amplified fragments. DNA sequencing provides the most detailed information, but can be expensive. Fingerprinting methods provide an alternative for characterizing microbial community composition. For instance, terminal restriction fragment length polymorphism (T-RFLP), a modification of the conventional RFLP approach, allows the characterization of a community by analyzing the size polymorphisms of PCR-amplified genes that have been cut at precise sequence locations by restriction enzymes. The resulting fragments are separated by gel electrophoresis and produce a banding pattern that can be used as a fingerprint for comparing community composition among samples.

As DNA sequencing has become faster and cheaper, the field of metagenomics has emerged. Metagenomics uses the DNA sequences of fragments of DNA obtained from a natural microbial community to describe the collective diversity of microbial genomes. Shotgun sequencing breaks up an organism's or a community's DNA into a myriad of short fragments that are individually sequenced. These fragments are then computationally ordered based on overlaps in the genetic code and reassembled into larger genomic fragments. For instance, Venter *et al.* (2004) applied this approach to an open ocean environment in the Sargasso Sea. This pilot project detected 150 new species of bacteria and more than 1.2 million new genes. Screening of metagenomic soil libraries has already led to the identification of various novel biomolecules including enzymes and antibiotics. Use of metagenomes enables analysis of a broader array of the true microbial diversity, specifically capture of uncultivated microbes, and provides insight into the functional capabilities within a community context. More recently, advances in computational methods have allowed for the extension of culture-independent approaches to monitor microbial diversity at a higher resolution. Specifically, developments of metagenomic methods are being implemented to reconstruct microbial genomes from environmental samples to provide thorough analysis on functional and evolutionary potential. An alternative approach allows the insertion of large continuous sequences of DNA to be incorporated into bacteria to form artificial chromosomes (BACs), which are then sequenced. This latter approach is much more labor-intensive and time consuming, but allows one to see how genes are organized within microbes, which is important information if one is interested in understanding their evolutionary history.

What Is Microbial Diversity?

The immense diversity, small size, and clonal nature of most microorganisms explain why quantifying the biodiversity of microorganisms is fundamentally different from quantifying that of macroorganisms. Microorganisms are so abundant and diverse that only a minute fraction of their diversity has been described (**Table 1**; Martiny and Field, 2005). Currently, it is infeasible to completely quantify the microbial diversity in even a gram of soil or a liter of seawater. However, a number of studies have tried to estimate microbial diversity globally or within particular habitat types.

Bacterial and Archaeal Diversity

The sheer abundance of bacteria makes estimating the number of bacterial taxa difficult. It has been calculated that there are more bacteria on Earth than there are stars in the universe and that most microbial communities harbor 10^{10}–10^{17} bacterial cells that compose greater than 107 different taxonomic groups and innumerable functional groups. The magnitude of bacterial diversity is still a matter of debate and perhaps even beyond practical calculation. Dykhuizen (1998) has speculated that there could be 10 billion species of bacteria on Earth. It has only recently been demonstrated that different habitats harbor different amounts of prokaryotic diversity (**Fig. 2**). For instance, Torsvik *et al.* (2002) used DNA–DNA reassociation methods to quantify the total genomic diversity in different communities. They estimate that a few grams of soil or sediment contain thousands of bacterial and archaeal "species." In comparison, aquatic environments appear to support fewer bacterial taxa (Torsvik *et al.*, 2002).

Because of their high taxonomic and evolutionary diversity, bacteria are incredibly functionally diverse. Bacteria have a striking variety of modes of energy conversion, many unique metabolic pathways, and can utilize a wide range of substrates. Bacteria can oxidize and reduce inorganic sulfur and can assimilate atmospheric nitrogen. Many bacteria have an anaerobic energy metabolism

Table 1 Comparison of the total number of species currently described and the number of species predicted to exist. The term "species" is used loosely as it must be defined differently across taxa

Group	*Number of "species"*		
	Described	*Estimated*	*Described (%)*
Eukaryotes	1.8×10^6	12×10^6	15.0
Fungi	$7.2–10 \times 10^4$	1.5×10^6	5.3
Archaea	217		
Bacteria	5007	$4.5–1000 \times 10^6$	0.1
Viruses	4000	1.0×10^8	0.004

Source: Modified from Martiny, J.B.H., Field, D., 2005. Ecological perspectives on the sequenced genome collection. Ecology Letters 8, 1334–1335.

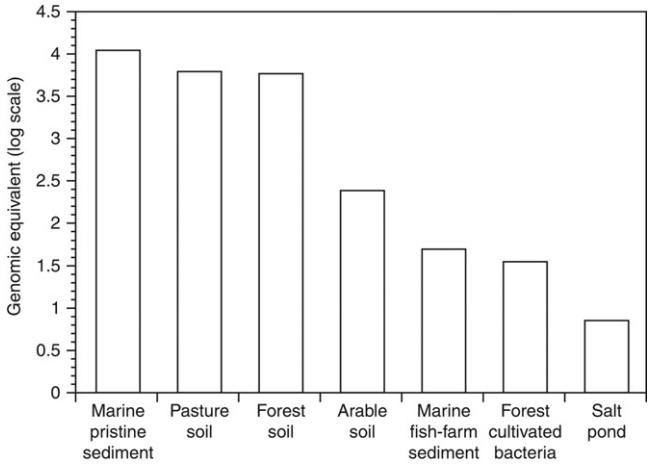

Fig. 2 Prokaryotic diversity (genome equivalents) estimated from the reassociation rate of DNA isolated from various habitats. Estimates for pasture soil and arable soil are averages.

and are often the only organisms living in anoxic environments. Bacteria can even degrade xenobiotic compounds, such as herbicides and pesticides, which are toxic to other organisms.

Because archaea require particular effort to culture, the diversity of this group is historically less well understood than bacteria. Molecular phylogenetic surveys, more commonly applied to the study of bacterial communities, are now more frequently being used to characterize the genetic diversity and ecological significance of archaea in a variety of environments including hot springs, deep-sea hydrothermal vents, and coastal waters. A couple hundred archaeal "species" have been described compared with approximately 5000 bacterial "species," and we lack estimates of how diverse these prokaryotes might be.

Archaea have typically been found living at physical or chemical extremes such as high temperature, high salinity, or strictly anaerobic environments and are immensely physiologically and metabolically diverse. Methanogenic archaea, which occupy anaerobic habitats such as sediments, marshes, and hydrothermal vents, produce methane as a by-product of their metabolism, a process restricted to this domain. Recently, archaea have been found in more benign marine, freshwater, and soil environments. For example, it has generally been assumed that specialist bacteria, which convert ammonia into nitrate, a key step in nitrification, are the main ammonia oxidizers in soil. However, it has been recently suggested that archaea may be the most abundant ammonia oxidizers in both pristine and agricultural soils.

Microbial Eukaryotic Diversity

Molecular methodologies that have revolutionized the understanding of bacterial and archaeal diversity have only recently been adapted to study eukaryotic diversity. Perhaps not surprisingly, molecular surveys suggest that morphological characteristics may conceal a large amount of eukaryotic diversity. For example, Slapeta *et al.* (2005) analyzed the rDNA genes of protists in two ponds and found high within-morphotype diversity. In addition, they detected a number of sequences very divergent from known protist species, implying that the description of global protist diversity is far from complete. Others argue that while local microbial eukaryotic diversity is high, global diversity may be relatively low. They document that many free-living protists (as defined by morphology) are cosmopolitan and suggest that nearly all free-living ciliates have already been discovered.

Like protists, fungal species have been traditionally defined morphologically. Hawksworth (1991) suggests that there are at least 1.5 million fungal species globally. Somewhere between 72,000 and 100,000 fungal species have been described, suggesting that as little as 5% of fungal diversity has been discovered. Moreover, with the application of genetic methods such as those applied to bacteria and archaea, estimates of global fungal diversity will likely increase substantially. For example, scientists surveyed the genetic diversity of fungi in the roots of one grass species and found 49 different fungal OTUs, only seven of which were similar to known DNA sequences, and only 6% of which have known ecological roles.

Viral Diversity

Given the remarkable diversity of Bacteria, Archaea, and Microbial eukaryotes, it is perhaps not surprising that the viruses that infect them appear to be similarly abundant and diverse. Viral abundance is estimated to be of the order of 10^{31}, the majority of which infect bacteria and archaea. One kilogram of marine sediment may harbor a million different viral genotypes, and 200 L of seawater contain more than 5000 viral genotypes. In general, viral abundance is well correlated with bacterial abundance, and in fact, bacteriophages are estimated to infect and kill between 4 and 50% of bacteria produced daily in aquatic environments. How, or even whether, viral diversity varies by habitat type is unclear. Researchers have reviewed the extent and distribution of viral diversity in marine habitats and proposed that viruses are highly diverse on a local scale but that this diversity does not vary much over space. In other words, local viral diversity may be representative of global viral diversity.

Maintenance of Microbial Diversity

Ecologists have long been motivated to understand the factors that influence the extraordinary diversity of life on Earth. However, despite the extent of microbial diversity, most of what we know about the maintenance of diversity is based on studies of plants and animals. For example, Hutchinson (1961) observed two species of water-bugs in a homogenous aquatic environment and wondered how they could coexist if they both use similar nutrient resources; the same is true about the thousands of microbial taxa that coexist in all habitats. Although a synthetic view of microbial diversity might not be possible, it is useful to consider whether universal patterns and processes govern the diversity of all organisms, large and small.

From an evolutionary perspective, high microbial diversity is created because the rate of diversification exceeds the rate of extinction. If laboratory studies are indicative, the potential for rapid diversification seems greater in microorganisms than macroorganisms. Bacteria and Archaea, in particular, have several traits that make rapid speciation likely. Because they exist in large populations and have rapid growth rates, they have the capacity to accumulate large numbers of novel mutations, which can generate substantial genetic variation. They can also readily take up DNA and get rid of extraneous DNA. Gene transfer and

recombination may also accelerate diversification further. Less is known about the extinction rates of microbes relative to larger organisms; however, many researchers have posited that extinction rates of microbial taxa may be low because many microorganisms have large population sizes and have an ability to survive in a range of environments and tolerate harsh conditions.

From an ecological perspective, once this diversity is created, the question remains how this incredible evolutionary diversity coexists in contemporary communities. Some have reviewed ecological factors, known to be of importance to plant and animal communities, which may also influence the diversity of microorganisms. Below, the authors discuss four of these factors (environmental heterogeneity, disturbance, productivity, and dispersal), and review recent studies that test whether these factors are important for environmental microbial communities.

Environmental Heterogeneity

Among large organisms, species diversity increases with the heterogeneity of habitat types available. For instance, bird species diversity increases with foliage height diversity and mite diversity increases with the number of habitat types in soil subhorizons. Both laboratory and field studies support the hypothesis that increased environmental heterogeneity also increases bacterial diversity. For example, spatial isolation in the soil matrix, created by low moisture content, plays an important role in determining community composition. Zhou *et al.* (2002) observed that soils saturated with water had fewer bacterial taxa and a less even distribution of taxa than patchy, unsaturated soils. Additionally, researchers found that bacterial diversity increased significantly by adding flow heterogeneity in stream mesocosms. Treves *et al.* (2003) examined the competitive dynamics of two species growing on a single resource in a uniform sand matrix under varied moisture content. One species dominated the community under saturated conditions, which were also highly connected, suggesting that these conditions allow competitive interactions to structure the community. As moisture content and connectivity decreased, the less-competitive species became established in the community. Finally, another study similarly found that litter bags with a mixture of species litter contained a more diverse bacterial and fungal community that litter bags with only a single type of species.

Disturbance

Most communities are subject to different types of disturbances that vary in both frequency and intensity. Events that disrupt the physical environment or alter resource and substrate availability are known to influence plant and animal community diversity. Across a wide range of taxa, including corals, butterflies, plankton, and tropical trees, diversity peaks at intermediate intensities or frequencies of small-scale disturbances. For example, algal diversity on intertidal boulders is highest when waves overturn the boulders, exposing new substrate for colonization.

It is difficult to test whether the intermediate disturbance hypothesis explains patterns of microbial diversity in the wild because disturbance is typically confounded with other factors such as plant cover or soil structure. Field and laboratory studies that have examined the relationship between disturbance and bacterial diversity have generally found that the intermediate disturbance hypothesis holds. For example, Bruce *et al.* (1995) examined the diversity of mercury-resistance genes in sediment-associated bacteria at sites with varying levels of mercury contamination. Consistent with predictions of the intermediate disturbance hypothesis, sites exposed to intermediate levels of mercury had the highest genetic diversity and both pristine and heavily contaminated sites had low diversity. However, other studies have found that disturbance events always result in decreased diversity. For example, Walsh *et al.* (2005) compared archaeal 16S rRNA gene diversity along a salinity gradient prone to high-salinity fluctuations. Heavy-rainfall events impose local high mortality of haloarchaea, and this disturbance regime appears to promote archaeal diversity. Similarly, another study found that the richness of bacterial communities decreased when exposed to low and high doses of the pollutant pentachlorophenol (PCP). Thus, the effect of a disturbance on a microbial community's diversity appears dependent on the type of disturbance as well as the original microbial community.

Productivity

Productivity, the rate at which energy flows through an ecosystem, has long been considered a primary determinant of both plant and animal diversity. A current ecological paradigm is that peak diversity occurs at intermediate levels of productivity, even though this relationship appears to be scale-dependent.

A number of studies consider the relationship between primary productivity and microbial diversity. Productivity appears to be related to microbial diversity; in some instances, these patterns resemble those of plants and animals. For example, Kassen *et al.* (2000) grew cultures of the bacterium *Pseudomonas fluorescens* over a wide range of nutrient concentrations and found that diversity peaked at intermediate productivities. However, another study surveyed two lagoons with different levels of primary productivity and found a greater number of unique bacterial rRNA gene sequences in the more productive lagoon, suggesting that bacterial taxonomic richness increases with productivity. Finally, Horner-Devine *et al.* (2003) estimated bacterial taxonomic richness along

a primary productivity gradient in freshwater mesocosms. Although overall bacterial richness was not significantly related to productivity, productivity did influence the richness of separate taxonomic groups. For example, some bacterial groups exhibited a significant hump-shaped relationship with productivity while other groups, such as the α-Proteobacteria, exhibited a U-shaped relationship with primary productivity. Thus, the relationship between ecosystem productivity and microbial diversity appears to be complex and may vary widely across environments.

Dispersal

The small size and high abundance of microorganisms have led microbiologists to generalize that microbial dispersal rates to new habitats is very high, overwhelming spatial differences in taxon abundance. For example, Schauer *et al.* (2010) examined the bacterial communities in three oceanic basins of the eastern South Atlantic Ocean that were all separated by the Walvis Ridge, a large physical barrier. They found the microbial communities were highly conserved across sites, suggesting a high dispersal capability, despite the physical barrier. However, debate over this view still exists, as other studies demonstrate large biogeographic differences among microbial communities. This evidence suggests that microbial diversity might be influenced by dispersal and isolation patterns. Based on this theory, it has been argued that local bacterial community composition is in part a product of stochastic dispersal events, rather than solely niche differentiation among taxa. The importance of dispersal relative to other factors influencing microbial diversity requires further investigation.

Importance for Ecosystems

Microorganisms are the drivers of key ecosystem processes, including decomposition, nutrient mineralization, and trace gas emission and consumption. Microorganisms are intimately involved in critical pathways of biogeochemical cycles and are the major pathways by which some elemental forms are regenerated to be used by other organisms.

For instance, microbes have a central role in almost all aspects of the nitrogen cycle. Nitrogen fixation is the process by which atmospheric nitrogen is converted into ammonia, which is quickly ionized to ammonium, a form of nitrogen usable by plants. This process, carried out by nitrogen-fixing bacteria, is essential for maintaining soil fertility and agricultural productivity.

If an entire functional group, such as the nitrogen-fixing bacteria, were removed from an ecosystem, the resulting changes would dramatically alter resource supply, processing rates, and plant productivity. However, below this broad functional group classification, it remains unclear whether microbial diversity matters for ecosystem processes. Recently, numerous studies have highlighted the incredible "microdiversity" of bacteria in some habitats. For example, Acinas *et al.* (2004) sampled 16S rDNA sequences from a coastal bacterioplankton community. They found 516 unique sequences, 50% of which fell into clusters containing less than 1% sequence divergence. Thus, one current avenue of research is to understand whether this type of fine-scale diversity or other levels of diversity have consequences for ecosystem processes.

Microorganisms and Global Change

The composition of microbial communities is known to vary with land-use type, temperature, agricultural growing practices, nutrient status, pollutants, and other environmental variables associated with global change. Additionally, there is some evidence that certain properties associated with entire microbial communities can be altered by global changes, such as total microbial biomass, rates of respiration, and biogeochemical transformations. Little is known, however, how anthropogenic impacts associated with global change will impact microbial communities, and how those changes will ultimately affect ecosystem functioning.

Several studies have examined the links between microbial composition and terrestrial ecosystem functioning and support the hypothesis that global changes will have important consequences for microbially mediated ecosystem processes. Horz *et al.* (2004) considered the impact of multiple global changes on the community composition of ammonia-oxidizing bacteria (AOB) in a California grassland. The authors observed changes in the community structure and abundance of free-living soil bacteria to simultaneous increases in atmospheric CO_2, precipitation, temperature, and nitrogen deposition. The response of AOB was similar to the observed plant responses: Composition and abundance was altered by nitrogen, total abundance decreased in response to elevated CO_2, and both strongly interacted with temperature and precipitation. In contrast, methane-oxidizing bacteria showed a unique response to increased precipitation and temperature; the relative abundance of common methanotroph clades increased in response to both variables, while novel clades had varied responses. Two of the novel clades did not respond to these environmental changes, while one novel clade increased in relative abundance to increased temperature and precipitation.

Further, studies of feedbacks between microbial and plant communities illustrate the potentially unpredictable nature of ecosystem responses to global change. In a 1-year factorial field experiment, researchers tested the influence of decreased plant diversity, elevated CO_2 levels, and increased nitrogen deposition on the severity of disease caused by fungal pathogens in a diverse grassland community. All three treatments substantially increased disease severity in the plant community. Because pathogen

loads also affect grassland ecosystem processes, this result suggests a route in which microbes respond to climate change and simultaneously feedback and affect climate change as well. Mychorrizal fungi may also serve as a feedback to the climate system under increased atmospheric CO_2, because they sequester increased amounts of carbon in living, dead, and residual hyphal biomass. In contrast, nitrogen deposition may increase turnover rates of fungal tissue and negate CO_2 effects on fungal biomass.

In marine systems, examination of the impact of global change on microbial communities has only recently begun. Global change is anticipated to impact the physical marine environment in a variety of ways, including temperature increases, shifts in wind and radiation regimes, changes in the frequency of episodic extreme events (such as storms), and acidification. These changes will likely deeply affect the structure and functioning of marine ecosystems, including marine microbial food webs. Recent evidence suggests that global changes, including rising water temperatures, will have dramatic affects on marine microbial systems. For example, Hoppe *et al.* (2008) conducted a mesocosm experiment to examine the effects temperature increases would have on marine microbial communities. When seawater was warmed by 2, 4, and 6°C, the authors reported an acceleration of bacterial degradation of organic matter derived from a phytoplankton spring bloom, as well as increased respiration rates. Similarly, others incubated samples in microcosms at different temperatures over short periods of time (24–48 h), and measured the different variables of interest throughout a seasonal cycle in a coastal Mediterranean site. In this study, the warmed samples had on average 20% higher total bacterial carbon demand than unwarmed samples, suggesting a positive feedback loop between warming of coastal waters and CO_2 production.

Overall, predicting the impact of future global change on ecosystems will require a much greater understanding of the response of microorganisms to a variety of environmental variables. Additional research needs to be conducted in both terrestrial and marine ecosystems. Finally, linking the marine and terrestrial components together will require knowledge of the feedbacks that microorganisms will have back on their environment.

Microbial Diseases

The relationship between emerging microbial diseases and global change is a topic of great concern. Many pathogens of terrestrial and marine taxa are sensitive to temperature, rainfall, and humidity. Therefore, global change has the potential to alter the risk of disease through changes in pathogen development and survival rates, disease transmission, and host susceptibility.

So far, evidence suggests that global change will influence a variety of plant, wildlife, and human diseases. For example, several plant diseases are more severe after mild winters or during warmer temperatures, which implies that directional climate warming will alter plant disease severity through longer growing seasons and accelerated pathogen development. Additionally, Kushmaro *et al.* (1998) showed that the bacterium *Vibrio shiloi*, a marine pathogen that infects and causes the bleaching of the coral *Oculina patagonica*, grows well at temperatures close to or exceeding probable host optima.

Research suggests that the most severe and least predictable disease outbreaks might occur if global change alters host or pathogen geographic ranges, resulting in the convergence of formerly separated species and populations. Vector-borne diseases are likely to be the strongest candidates for altered abundance and geographic range shifts because rising temperatures seem to affect vector distribution, parasite development, and transmission rates. Vector-borne diseases of livestock, particularly African horse sickness and bluetongue viruses, recently expanded their ranges. Additionally, vector-borne human pathogens such as malaria, African trypanosomiasis, Lyme disease, tick-borne encephalitis, yellow fever, and dengue have increased in incidence or geographic range in recent decades. Most of these diseases have expanded into regions of higher latitude, in each case accompanied by apparent expansion in the ranges of mosquito, tick, and midge vectors. Research to determine whether these expansions are due primarily to global change or other anthropogenic factors is still ongoing, as well as predicting future distributional changes in disease prevalence.

Although associations between climate and disease do not necessarily imply causation, results from correlational studies and short-term experiments help scientists separate the effects of climate and other components of global change. Overall, further research must be done to improve the ability to predict impacts of global change on microbial diseases.

Human Microbiome

Microorganisms exist in all habitats on Earth, and the human body is no exception. The term "human microbiome" refers to the aggregation of microorganisms in and on the human body. Microbial cells are estimated to outnumber human cells by 10:1, and much new research is dedicated to characterizing and identifying these microorganisms that, similar to free-living microbes, have not been previously cultured or isolated. Many studies use molecular tools, such as metagenomics, to identify the thousands of microbial taxa associated with the human microbiome. These co-existing microbes carry out numerous metabolic reactions essential for human health. For example, gut microbes enable absorption of otherwise indigestible carbohydrates and provide protection from invasion of foreign, potentially pathogenic microbes.

Analysis of microbial communities across the human body demonstrates that microbial composition varies by body location. Further, these body site differences are stronger than variation between human individuals (**Fig. 3**). Thus, microbes form

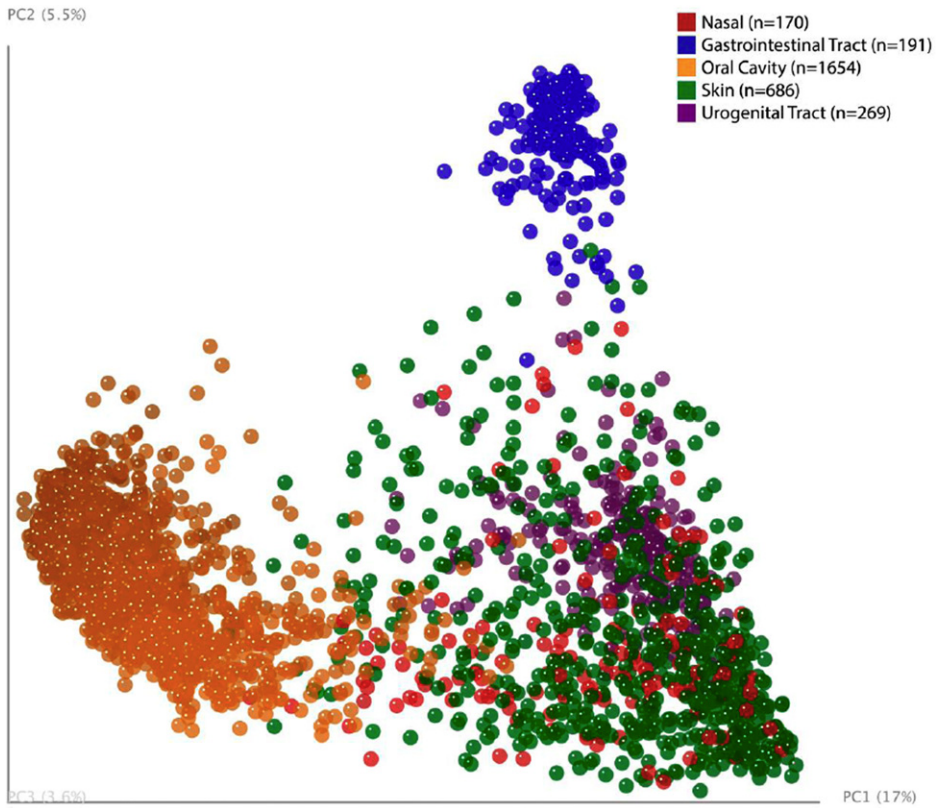

Fig. 3 An unweighted UniFrac principal component analysis showing the human microbiome diversity of over 300 sampled individuals. Colors indicate the source (body site) of sampling from each individual. Points closer to one another indicate microbial communities that are more similar in composition. Reproduced from publically available data produced by the Human Microbiome Project Consortium, 2012. Structure, function, and diversity of the healthy human microbiome. Nature 486 (2012), 207–214.

distinctive communities based on the host-specific microhabitat dictated by the anatomical location. However, at a given anatomical site, differences in the microbial community vary in functional types and abundances from person to person and remain relatively stable over time (Human Microbiome Project Consortium, 2012). Therefore, an individual's body site and microbial makeup can be useful indicators with how variations may be associated with various diseases. For example, Cho and Blaser (2012) documented that a reduced ratio of the phyla Bacteroidetes with respect to Firmicutes has been linked to obesity, while larger cell numbers of the family Enterobacteriaceae are associated with Inflammatory Bowel Disease.

Thus far, most human microbiome analyses have been based on observational data, revealing correlations between microbial composition to host phenotype. However, research integrating multiple techniques such as metabolomics and proteomics may help illuminate the mechanistic interactions that define the microbiome and its function in the regulation of health and progression of diseases.

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