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Science **320**, 1039 (2008);

DOI: 10.1126/science.1153475

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57. Supported by NASA and the Agouron Foundation (P.G.F.); the Danish Natural Science Research Council and The Carlsberg Foundation (T.F.); and the Gordon and Betty Moore Foundation, the

Agouron Foundation, NSF, and U.S. Department of Energy (E.F.D.).

10.1126/science.1153213

REVIEW

Microbial Biogeography: From Taxonomy to Traits

Jessica L. Green,^{1*} Brendan J. M. Bohannan,¹ Rachel J. Whitaker²

The biogeographic variation of life has predominantly been studied using taxonomy, but this focus is changing. There is a resurging interest in understanding patterns in the distribution not only of taxa but also of the traits those taxa possess. Patterns of trait variation shed light on fundamental questions in biology, including why organisms live where they do and how they will respond to environmental change. Technological advances such as environmental genomics place microbial ecology in a unique position to move trait-based biogeography forward. We anticipate that as trait-based biogeography continues to evolve, micro- and macroorganisms will be studied in concert, establishing a science that is informed by and relevant to all domains of life.

And so it was indeed: she was now only ten inches high, and her face brightened up at the thought that she was now the right size for going through the little door into that lovely garden.

Lewis Carroll (1865)

Imagine Carl Linnaeus in Alice's shoes, shrinking to only 10 micrometers high. Afforded the opportunity to investigate biological diversity at this spatial scale, would Linnaeus have remained committed to plant exploration, or would he have turned his attention to microbial life? It is not surprising that Linnaeus and his contemporaries founded biogeography—a science that aims to document and understand spatial patterns of biological diversity—by studying organisms visible to the naked eye. Recent advances in our ability to quantify and visualize microbial diversity in natural environments have prompted a new era of microbial exploration, one that builds upon plant and animal biogeography surveys initiated roughly 250 years ago (1). These new explorations have already radically changed thinking in ecology and evolution and upset the hierarchical taxonomic structure that Linnaeus proposed (2). As microbiologists increasingly focus on biogeographical questions, textbook placeholders such as “microbial biogeography is poorly known and rarely discussed” (3) will become obsolete.

A long-held concept in microbial ecology is that microorganisms are dispersed globally and able to proliferate in any habitat with suitable envi-

ronmental conditions. This concept was prompted by Martinus Willem Beijerinck and concisely summarized by Lourens Gerhard Marinus Baas Becking in the widely referenced quote, “everything is everywhere, but the environment selects” (4). Seminal notions of ubiquitous dispersal and environmental determinism are not unique to microbiology. Linnaeus, for example, wrote that “the great Artificer of Nature has provided that every seed shall find its proper soil, and be equally dispersed over the surface of the globe” (1). The development of molecular approaches has allowed a more comprehensive view of microbial diversity than can be developed even with the aided eye, showing that like plant and animal distributions, microbial distributions can be the result of both deterministic (environmental) and stochastic (dispersal) processes [reviewed in (5)].

As with macroorganism biogeography, microbial biogeography initially adopted a taxonomic approach, focusing on sequence signatures to identify groups of microorganisms. These studies revealed classic patterns such as the species-area relationship and isolation by distance (5). Interpreting taxonomic patterns in terms of how they affect the function of a population or community is especially difficult in microorganisms, where a broad range of functional variation may occur among similar organisms (e.g., organisms with the same 16S rRNA sequence).

For macro- and microorganisms alike, there is growing interest in the biogeography of functional traits, characteristics of an organism that are linked with its fitness or performance (6). The study of biogeography includes the study of patterns in space, in time, and along environmental gradients. Such patterns in the distribution of traits can be used to understand complex phenomena, includ-

ing why organisms live where they do, how many taxa can coexist in a place, and how they will respond to environmental change. Although plants have been the focal group in this emerging research area, recent advances in environmental molecular biology such as genomics, proteomics, transcriptomics, and metabolomics place microbial ecology in a unique position to move trait-based biogeography forward.

Trait-Based Biogeography: A Macroorganism Perspective

Trait-based approaches to biogeography have been used since the pioneering work of Andreas F. W. Schimper more than a century ago (7). Although tending to wax and wane in favor over time, there has been a resurgence of interest in trait-based methodologies since the mid-1980s (6, 8). Here, we discuss some examples of plant trait-based research, focusing on applications likely relevant to both plant and microbial ecology.

An emergent theme in trait-based research is the identification of ecological strategies, suites of covarying ecological traits. The study of ecological strategies has been fundamental to the development of plant and animal ecology, and there is growing interest among microbial ecologists as well (9). Examining the slope, intercept, and correlation strength of relationships among traits provides insight into the nature of ecological strategies, including the underlying costs and benefits of different trait combinations. Quantification of trait variation with site properties such as climate, for example, is central to understanding how vegetation properties shift along geographical gradients, and thus for predicting habitat boundaries under changing land-use and warming scenarios. A similar approach has been suggested for microorganisms (9) and could be useful for predicting how microbial properties respond to environmental change.

Figure 1A illustrates how the relationship between two ecologically important plant traits—leaf life span and leaf mass per area—shifts with climate (10). This trait relationship is part of a fundamental ecological strategy known as the “leaf economics spectrum” that ranges from organisms with cheaply constructed, thin, and short-lived leaves to those with costly, thick, and long-lived leaves. The relationship is modulated by site climate, such that organisms at drier sites typically achieve shorter leaf life spans at a given leaf mass per area.

Community “assembly rules” was a concept formulated to understand why organisms live where they do and in what combinations. It has been used to understand how plant and animal communities change through time and to predict

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the response of communities to environmental change. This concept has also grown in popularity among microbial ecologists (11). Weiher and Keddy (12) redefined the assembly-rule paradigm by introducing the idea that traits, not taxon names, are the fundamental units of biodiversity and biogeography. They argued that a trait-based approach would alleviate reliance on “murky taxonomy” and introduced a conceptual model for trait-based community assembly. Organisms with similar traits will share similar niche requirements, which will result in them “sorting” into similar environments. At the same time, environmental sorting is expected to lead to competitive exclusion among organisms with very similar traits. An informative counter-perspective is the neutral theory (13), a community-assembly model that often makes realistic biogeography predictions despite explicitly ignoring trait variation.

Empirical patterns of trait variation across environmental, spatial, and temporal gradients are central to testing hypotheses arising from community assembly models. In a study of spatial variation in traits (Fig. 1B), Swensen and Enquist (14) showed that the mean and variance in community aggregated wood density was negatively correlated with latitude. Their results comply with Weiher and Keddy’s model and suggest that on a global scale, there is strong environmental filtering of wood density values along the latitudinal gradient, whereas on local scales competition becomes increasingly important toward the equator. Shipley and colleagues (15) integrated Weiher and Keddy’s qualitative model with tools borrowed from statistical mechanics to develop a quantitative method for predicting biodiversity patterns across environments. They tested their model using trait variation data collected from abandoned vineyards over successional time (Fig. 1C) and predicted the relative abundance of species at each successional age with great accuracy. Similar questions have been asked using phylogenetic analyses of microbial taxa (16); a focus on traits requires fewer assumptions and more directly addresses microbial properties important to ecosystem function. Such an approach could be valuable for predicting the temporal dynamics of microbial communities and the consequences of environmental change.

Trait-Based Biogeography: A Microbial Perspective

The advancement of environmental molecular biology, in combination with laboratory studies of microbial physiology and metabolism, has provided novel tools for identifying trait patterns in microorganisms on a scale not yet possible for studies of plants and animals. However, we currently know little (relative to our understanding for plants and animals) regarding the distribution of microbial functional traits in nature. Our lack of understanding is due in part to the extraordinary metabolic and physiologic diversity of microbes, our inability to culture many microorganisms, and

the common practice of reducing trait variation (for example, by studying single isolates in culture). The value of studying variation in traits is rapidly becoming apparent to many microbiologists as new patterns of variation are discovered, even within groups once thought to be relatively homogeneous. New tools have become available that allow the study of microbial traits in their natural contexts without necessarily requiring the culturing of the individual organisms.

One of the biggest challenges facing microbiologists interested in functional trait is how to identify them. As for plants and animals, a microbial functional trait is a measurable microbial characteristic that is linked to fitness or performance. Among the many possible types of traits that could fit this definition are those that directly contribute to an organism’s life history (its lifetime pattern of growth, reproduction, and differentiation), traits that mediate the interactions among organisms (e.g., microbial resistance to viruses), and traits that contribute to the storage, transfer, and organization of information (e.g., genome size, content, and mutation rate). The challenge is to determine which characteristics of microorganisms are linked most closely to fitness or performance. To date, this has primarily been accomplished by studying trait variation among cultured isolates.

Microbiologists currently have a detailed understanding of only a small proportion of microbial diversity, primarily those taxa with a long history of laboratory cultivation and study. Microbiologists have comprehensive information on trait variation in the field for only a handful of these, most notably the phototrophs *Prochlorococcus* and *Synechococcus* (17).

For organisms that are not as easy to culture, it is possible from a general understanding of microbial biochemical pathways, energetics, and the mechanisms of metabolic regulation to choose traits that are likely to be linked to fitness. For example, based on decades of research on archaeal isolates, microbiologists have a highly developed understanding of the structure and function of bacteriorhodopsin (a light-sensitive membrane protein capable of generating a proton gradient that can be harvested for energy). This knowledge was used to identify a type of rhodopsin in bacteria—proteorhodopsin—before the existence of any cultured bacterial isolates (18).

Functional traits can also be identified by engineering genetic variation identified from environmental genomic surveys into non-native cultured hosts. Genetic variants of the gene that codes for proteorhodopsin have been inserted into *Escherichia coli*, resulting in a photochemical reac-

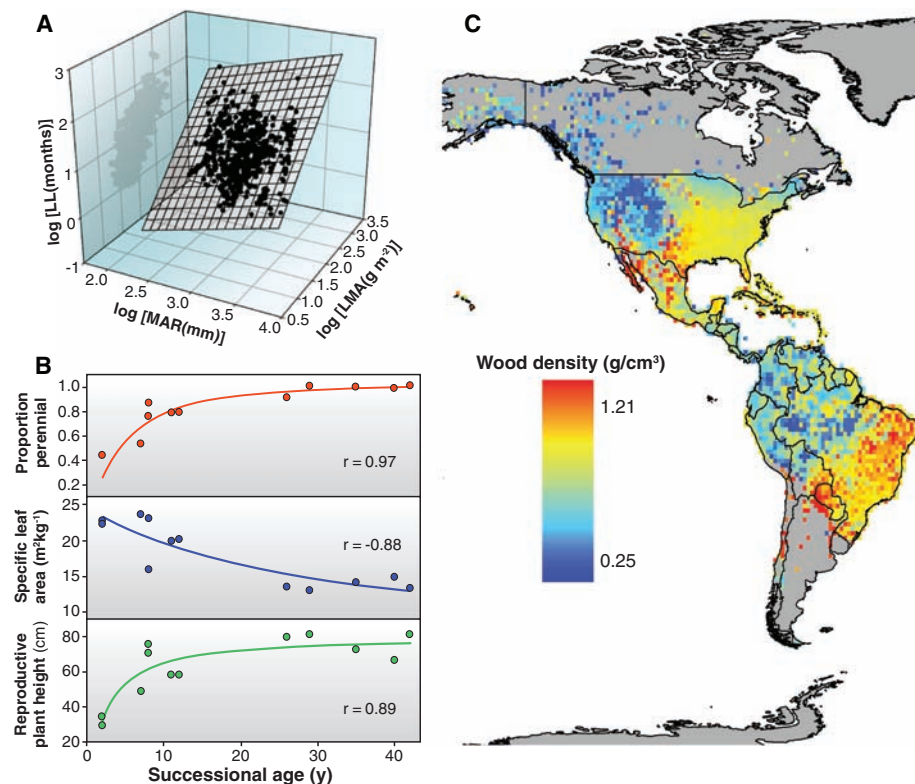


Fig. 1. Examples of trait-based biogeography for macroorganisms. **(A)** Covariation in leaf traits [leaf life span (LL) and leaf mass per area (LMA)] as a function of climate [mean annual rainfall (MAR)]. Data plotted for species sampled worldwide [modified from (10)]. **(B)** Variation in community-aggregated plant traits over successional time. Data sampled from vineyards in France after abandonment [modified from (15)]. **(C)** Variation in community-aggregated wood density with latitude. Data plotted for mean wood density of all species in 1° grid cells [modified from (14)].

tion cycle characteristic of archaeal rhodopsins (18). The presence of proteorhodopsin is now considered a putative functional trait in bacteria, and variants of proteorhodopsin with different spectral properties have been shown to exhibit spatial and temporal patterns in marine environments (19).

Another way to identify putative functional traits from environmental samples is to study relationships among traits. For example, Ram *et al.* (20) used environmental proteomics to identify the prevalence of proteins involved in cobalamin and heme synthesis that are abundantly expressed in combination with cytochrome₅₇₉, a molecule known to be important in iron oxidation in acid mine drainage biofilms. The fact that these two proteins covary with a protein likely linked to fitness suggests that their presence may be a functional trait.

Table 1 illustrates some examples of putative microbial functional traits that have been studied in a biogeographical context. These examples underscore the value of culture-dependent approaches combined with high-throughput technologies that allow for the sampling of genes, proteins, expression patterns, and metabolites in situ. Below we highlight several studies that have revealed patterns of microbial functional trait variation across time, space, and environmental gradients.

Ribosomal Genes and Ecological Succession

One putative functional trait that has been identified for several macro- and microorganisms is ribosomal gene copy number. Ribosomal copy number is one of a suite of life history traits associated with general ecological strategies in bacteria (9), and it may play an important role in microbial community assembly (21). The copy number of ribosomal DNA (rDNA) genes is related to ribosome content and has been linked in microorganisms to maximum growth rate and response time after an increase in resources (21). There also appears to be a competitive cost associated with possessing multiple gene copies under low resource conditions (21), which suggests a life history trade-off.

Shrestha *et al.* (22) tracked microbial ribosomal copy number in a rice paddy soil during succession after flooding. They observed that isolates from early successional soils (after 1 day of flooding) had significantly higher ribosomal gene copy numbers than those from later successional soils (after 70 days of flooding). Isolates from early successional soils also formed colonies on solid media more rapidly than those from late successional soils (Fig. 2A), which suggests a faster response time to an increase in nutrients. Succession is one of several temporal patterns that have been studied extensively in macroorganisms by biogeographers, and patterns in functional traits and ecological strategies have been documented (Fig. 1B).

Ribosomal gene copy number has the potential to have wide-ranging effects on ecosystem function through its effects on cellular stoichiometry and food web interactions (23), and understand-

ing the biogeography of ribosomal gene copy number could be important for predicting the response of ecosystems to environmental change. It is difficult to measure microbial rDNA copy number in situ, and to date most measures have been made on laboratory isolates from environmental samples (22) or microcolonies grown on filters placed in environmental samples (24). Advances in quantitative polymerase chain reaction (qPCR), environmental genomics, and single-cell genomics may soon allow the quantification of ribosomal copy number in situ, on both a community and individual level.

Metabologeography

Metabolomics can be used to characterize microorganisms across space by analysis of the small molecules that are the intermediates and products of metabolism and which leave chemical fingerprints on specific cellular processes. Variation in metabolic profiles not only can be used as an

tabolite assays on environmental samples, and to our knowledge this has not yet been done. However, protein analysis at the community level has been successful for environmental samples (20), and the field of environmental metabolomics is rapidly growing.

Environmental Gradients and Genomics

One approach to studying microbial traits without relying on culture is to make spatially explicit use of sequences from environmental genomics studies. Gene sequences can be used to assign putative physiological traits through sequence similarity to genes of known function by using annotation databases, such as the Kyoto Encyclopedia of Genes and Genomes, Clusters of Orthologous Groups, and SEED subsystems. DeLong *et al.* (26) used this approach to analyze samples of microbial plankton from seven depths in the Pacific Ocean. They prepared community DNA fosmid libraries, end-sequenced ~5000

Table 1. Selected examples of microbial functional traits.

Trait	Potential consequence for fitness or performance	Measure	Example
Gene sequence identity	Protein function	PCR amplification	(19)
Ribosomal copy number	Growth rate, response time	Southern hybridization	(22)
Metabolite content	Survival	Mass spectrometry	(25)
Gene content	Metabolic potential, life history variation	Genomics	(26)
Genome size	Metabolic potential, life history variation	Genomics	(29)
Environmental resistance (antibiotic, viral, radiation, etc.)	Survival	PCR amplification, laboratory screening of isolates	(30)
Transcript abundance	Metabolic switching	Reverse transcription PCR, qPCR	(31)
Mutation rate	Adaptability	Laboratory assays of isolates	(32)
Cell size	Metabolic rate	Flow cytometry	(33)

indirect measure of variation in microbial functional traits but also can indicate interactions among individuals, including cell-cell communication and competition (for example, through antibiotic production).

Rossello-Mora *et al.* (25) sampled isolates of the bacterium *Salinibacter ruber*, from three regions: the Mediterranean, the Peruvian Andes, and the Canary Islands. Genetic methods did not reveal biogeographic patterns among isolates. When high-resolution mass spectrometry was used to identify and quantify metabolites, biogeographic patterns among the isolates were evident (Fig. 2B). Molecules associated with the cell envelope, such as sulfonolipids, left the strongest signature. The differences seen between isolates from different geographic regions were primarily quantitative rather than qualitative, implying that transcriptional and/or posttranscriptional regulation was involved. To make a similar analysis at the community level without culture requires me-

fosmids from each depth, and compared the distribution of genes with depth. From this distribution of genes in space, they were able to identify a number of patterns in putative functional traits (Fig. 2C). As expected, sequences associated with photosynthesis were more common in samples from the photic zone, as were sequences associated with motility. This is consistent with the hypothesis that heterotrophic bacteria in the photic zone may actively compete for resources by swimming from particle to particle. In contrast, sequences associated with surface growth, for example, pilus synthesis, protein export, and polysaccharide and antibiotic synthesis genes, were more prevalent in deeper samples, suggesting an increased importance of a relatively sessile lifestyle at these depths. This approach was able to document, at the community level, patterns in the distribution of single putative functional traits and patterns in suites of covarying traits (e.g., those associated with photosynthesis, motility,

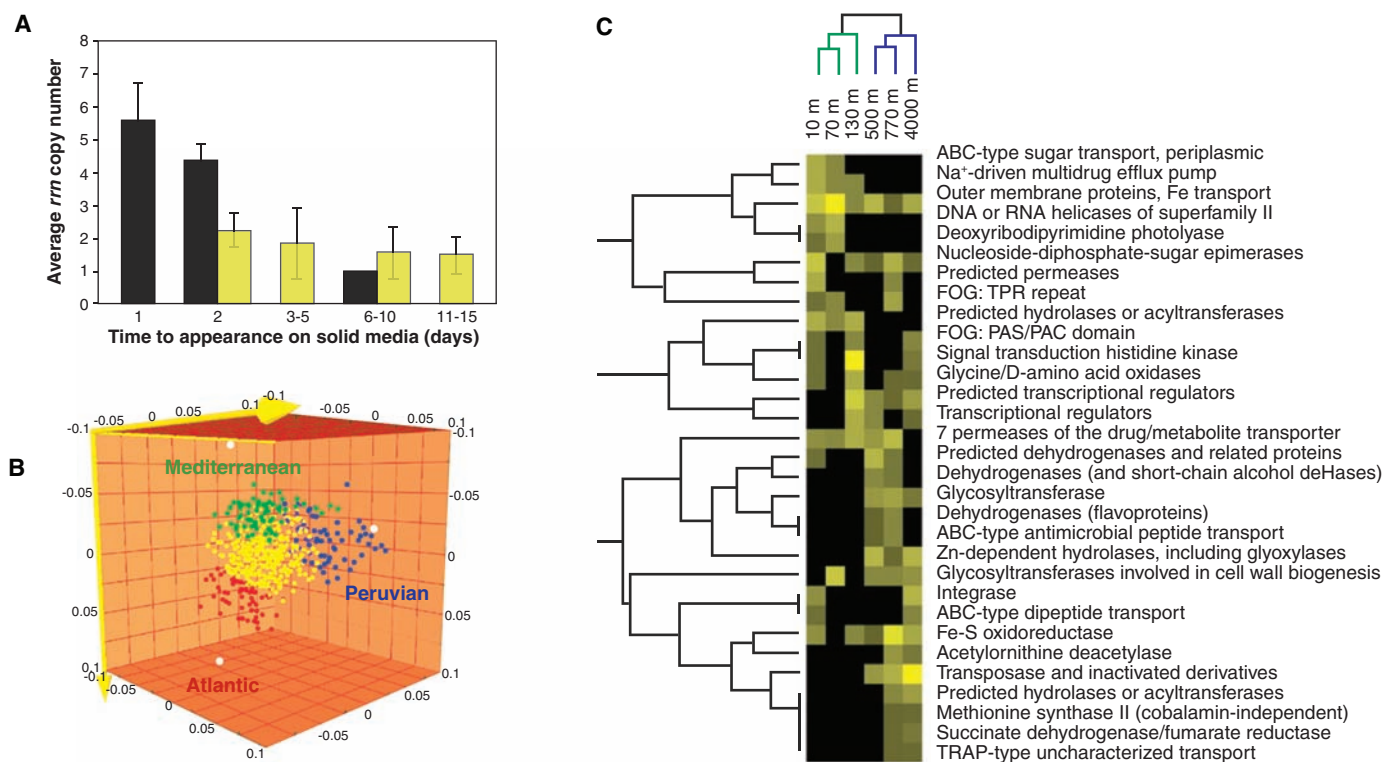


Fig. 2. Examples of microbial trait-based biogeography. **(A)** Mean numbers of rDNA operon copies in early successional (black bars) and late successional (yellow bars) bacterial taxa isolated from rice paddy soil [modified from (22)]. **(B)** Variation in the metabolite composition of *Salinibacter ruber* isolates from different geographic regions. The metabolites having a high cor-

relation with geographic origin are noted with a corresponding color; the nondiscriminating metabolites are represented in yellow [modified from (25)]. **(C)** Variation in the relative abundance of protein categories (inferred via the COG database from environmental DNA sequences) along a depth transect in the Pacific Ocean [modified from (26)].

and surface growth) that may indicate the spatial patterning of ecological strategies.

Outlook

Trait-based approaches to microbial biodiversity and biogeography offer the promise of advancing ecological theory and predicting responses to environmental change. Recent theoretical advances in plant sciences using a trait-based framework have provided a mechanistic basis for quantifying the link between functional trait variation and ecosystem processes (15, 27, 28). A focus on traits that are common to macroorganisms and microorganisms provides a common currency with which to develop and test theory across life's domains. The next step is to revisit these theories in the context of microbial systems.

The historical emphasis on taxonomy-based conservation has been mired in the argument of functional redundancy, which assumes that taxa are functionally interchangeable. This idea has been especially influential in microbial ecology, resulting in the assumptions that neither a loss in microbial taxonomic diversity nor a turnover in microbial community composition will have consequences for microbial-mediated processes, because many different microbial taxa can mediate the same process. In addition, because microorganisms are assumed to evolve rapidly,

microbial taxa distributions have been assumed to be of little value in predicting the response of microbial communities to environmental change. A trait-based approach will recast this debate to better understand the importance of specific suites of microbial functional traits in the environment.

Schimper's seminal text on plant geography (7) is prefaced with the opening statement, "the time is not far distant when all species of plants and their geographical distribution will be known. The objects of geographical botany will not, however, be attained, as is often assumed, but a foundation merely will have been laid on which science can construct a larger edifice. The essential aim of geographical botany will then be an inquiry into the causes of differences existing among the various floras." Building on Linnaeus' taxonomic biogeography, Schimper adopted an ecological approach, summarizing in elaborate detail the form, structure, physiology, and life history of plants around the world. Schimper's vision gives us a universally applicable framework for trait biogeography to which we can now add microorganisms.

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biodiversity in new ways; and N. Swensen and E. Garnier for providing figures. J.L.G., B.J.M.B., and R.J.W. acknowledge the support of the National Science Foundation. J.L.G. also acknowledges support from the Gordon and Betty Moore Foundation.

10.1126/science.1153475

REVIEW

Microbial Ecology of Ocean Biogeochemistry: A Community Perspective

Suzanne L. Strom

The oceans harbor a tremendous diversity of marine microbes. Different functional groups of bacteria, archaea, and protists arise from this diversity to dominate various habitats and drive globally important biogeochemical cycles. Explanations for the distribution of microbial taxa and their associated activity often focus on resource availability and abiotic conditions. However, the continual reshaping of communities by mortality, allelopathy, symbiosis, and other processes shows that community interactions exert strong selective pressure on marine microbes. Deeper exploration of microbial interactions is now possible via molecular prospecting and taxon-specific experimental approaches. A holistic outlook that encompasses the full array of selective pressures on individuals will help elucidate the maintenance of microbial diversity and the regulation of biogeochemical reactions by planktonic communities.

When we try to pick out anything by itself, we find it hitched to everything else in the universe.

John Muir (1911)

Marine microbes are fundamental regulators of biogeochemical cycles [see the accompanying review by Falkowski *et al.* (1)]. While acquiring resources for metabolism and growth, archaea, bacteria, and protists transform C-, N-, P- and S-containing compounds in ways that affect their availability for biological production and their influence on Earth's climate. Questions about the relationships between plankton ecology and these transformations are at the heart of much ocean research and have existed since the investigations of Brandt, Lohmann, and others a century ago [as described in (2)]. Yet, despite a burgeoning toolbox of methods, most research into ocean biogeochemistry and associated microbial ecology is still framed in terms of "bottom-up" considerations (i.e., how do resources and abiotic conditions drive the distribution and function of microbes?). Ecological considerations and recent genomic findings demonstrate that a broader view is necessary. Agents of mortality, including grazers and lytic viruses, must exert strong selective pressure on populations of marine microbes. Additional interactions such as allelopathy and symbiosis also influence community structure and function. Fur-

ther, these processes interact with resource availability in numerous ways so that separate bottom-up versus "top-down" approaches to studying these ecosystems are of limited conceptual or experimental use. Marine microbes are truly hitched to everything else in the ocean universe. Thus, a community perspective is essential for understanding the distribution and function of microorganisms in Earth's oceans. By applying the cornucopia of new ocean research methods to questions of whole-community structure and function, we will gain insights into the regulation of biogeochemical cycling. A community perspective will also aid our understanding of the sources and functions of the vast genomic diversity housed in the oceans' microbes.

The Broader View: Ecological Considerations

Owing to physical and chemical constraints, nearly all primary and most secondary production in the oceans is performed by microbes. Little energy storage or accumulation of structural material is possible in a unicell; hence, in striking contrast to terrestrial ecosystems, almost no marine production accumulates as biomass. Except during bloom events, nearly all marine microbial production "turns over" in days to weeks through various mortality processes (3). In ocean regions remote from land, microbial mortality is mainly due to grazing by protists (4, 5); in other areas, disease, viral lysis, grazing by larger zooplankton, and perhaps microbial senescence can be substantial (6, 7). Cumulative mortality in approximate equivalence with growth leads to a

continual reshaping of the community at a fundamental level and a situation in which avoidance of mortality is tantamount to resource-based growth as a selective pressure on individual microbes (Fig. 1). From these considerations, one would predict that adaptations reducing mortality (e.g., escape behavior, defenses, resistance to infection, camouflage) must constitute a substantial part of the genotypic and phenotypic repertoire of marine microbes.

The Broader View: Genomic Considerations

Sequencing of cultured marine microbes and metagenomic surveys of natural environments are revealing genes related to community interactions. Using shotgun sequencing of fosmid clone termini, DeLong and co-workers (8) assessed the depth distribution of microbial genes in the North Pacific subtropical gyre. Deep-water sequences were enriched in genes for antibiotic synthesis, which are hypothesized to play a role in structuring particle-associated communities. The cyanobacterium *Synechococcus* is a major prokaryotic contributor to ocean primary production, and genomes of several isolates have been sequenced. Both Sargasso Sea and California Current isolates contain several different polysaccharide biosynthesis genes; the authors speculate that these allow changes in cell-surface characteristics, providing camouflage from or resistance to phage or predator attack (9). *Prochlorococcus* is another important genus of photosynthetic prokaryotes, one in which the links between genetics and ecophysiology are particularly well characterized. A survey of *Prochlorococcus* "ecotypes" in the Atlantic Ocean found that environmental gradients in light, temperature, and nutrient availability explained considerably less than half of the variability in spatial distribution for all but one ecotype (10). Unexplained aspects of distribution hinted at important but poorly characterized differences in competitive ability and susceptibility to grazing and viral lysis.

In the following sections, I present examples of how community processes can drive biogeochemical cycling of Si, C, and N, as well as the climatically important gas dimethyl sulfide (DMS). I then outline two research areas in which further investigation promises to elucidate mechanistic links between community ecology and biogeochemistry.

Paradigms Lost

Current paradigms, largely revolving around resource acquisition and abiotic conditions, are often insufficient to explain major patterns of functional group dominance in the sea [see the accompanying

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