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Microorganisms and their roles in fundamental biogeochemical cycles

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Biogeochemistry is the discipline that strives to understand intricate processes, often microbially mediated ones, that transform and recycle both organic and inorganic substances in soils, sediments, and waters. These processes, manifestations of diverse and highly evolved cellular mechanisms catalyzed by *Bacteria* and *Archaea,* maintain the biosphere. Progress in biogeochemistry relies upon the underlying science of environmental microbiology. Over the last 2 years, important discoveries have advanced the ecological, physiological, biochemical, and genomic bases for a variety of microbiological processes including anaerobic methane oxidation, photosynthesis, phosphorous uptake, biodegradation of organic pollutants, and numerous aspects of the nitrogen and sulfur cycles. Here recent literature is assessed and placed within a five-stage paradigm for making scientific progress in environmental microbiology, biogeochemistry, and biotechnology.

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Introduction: biogeochemistry is advanced by environmental microbiology and is converging with environmental biotechnology

The term ''biogeochemistry'' was first coined by V. Vernadsky in 1926 (cited in [1]). Explicit in ''biogeochemistry'' is the merging (the linking) of three scientific disciplines: biology, geology, and chemistry. Other prominent authors [2,3] have extended and reinforced the immanent traits, the realities, of how ecosystems function at local and global scales. Multidisciplinary biogeochemical approaches are the way to understand complex processes that occur in forested watersheds, coastal sediments, agriculture fields, grasslands, oceans, other habitats, and the entire biosphere, itself.

The term ''biotechnology'' originated in 1917 when used by a Hungarian engineer, Karl Ereky, in reference to the integration of biological processes to achieve a desired goal [4]. ''Environmental biotechnology'' has recently been defined as ''the integrated use of biochemistry, molecular biology, genetics, microbiology, plant and animal science, and chemical engineering to addresses environmental needs and problems'' [5].

The central thesis of this essay is that ''biogeochemistry'' and ''environmental biotechnology'' are converging disciplines. This is because the mechanistic understanding of relatively simple biological systems that has fostered the creation of biotechnology is being extended to complex naturally occurring microbial communities that dwell in the waters, sediments, and soils. It is these microbial communities that maintain the biosphere through the biogeochemical reactions they catalyze. Modern biogeochemistry, like biotechnology, demands fundamental mechanistic knowledge of the genomic, genetic, enzymatic, biochemical, and physiological bases of a plethora of microbially mediated processes (e.g. ranging from photosynthesis to sulfate reduction to nitrogen fixation). Such knowledge provides a deep level of understanding, which is the gateway to two important goals: (i) wise and efficient management of ecosystems, and (ii) potential exploitation of the process for attaining new or improved services or technologies.

The objective of this review is to begin to substantiate the above-suggested convergence between biotechnology and biogeochemistry by proposing a five-stage paradigm for inquiry and then reviewing key recent advances in the discipline that underlies biogeochemistry: environmental microbiology. The scope of biogeochemistry and environmental microbiology is so broad as to prevent a comprehensive review of these topics. However, key publications from 2009 to 2010, illustrative of how environmental microbiology discoveries are made, will be highlighted.

Biogeochemical processes and how they maintain the biosphere

From a scale of cubic centimeters to one of the entire planet, Earth habitats can be viewed as complex mixtures of reduced and oxidized materials in chemical disequilibrium [5,6]. Ultimately, this disequilibrium is maintained by constant influx of radiant energy from the sun, and constant efflux of heat and reduced materials (e.g. CH_4, H_2S, H_2) from the Earth's core [5]. This disequilibrium has driven life processes and evolution for nearly 4 billion

Box 1 Background definitions, terms, and key tools used in biogeochemistry and environmental microbiology

• A sampling of broadly recognized biogeochemical processes

Nutrient cycle	Process	Operational definition
Carbon	Photosynthesis	Light-driven CO_2 fixation into biomass
	Carbon Respiration	Oxidation of organic C to CO_2
	Methanogenesis	Methane production
	Aerobic methane oxidation	Methane becomes CO_2
	Anaerobic methane oxidation	Methane becomes CO_2
Nitrogen	Nitrogen fixation	N_2 gas becomes ammonia
	Ammonium oxidation	Ammonia becomes nitrite, nitrate
	Anaerobic ammonium oxidation	Nitrite and ammonia become N_2 gas
	Denitrification	Nitrate is used as an electron acceptor and converted to N_2 gas
Sulfur	Sulfur oxidation	Sulfide and sulfur become sulfate
	Sulfate reduction	Sulfate is used as an electron acceptor and converted to sulfur and sulfide
Other elements	Hydrogen oxidation	Hydrogen is oxidized to H^+, electrons reduce other substances
	Uranium reduction	Uranium oxycation is used as an electron acceptor; hence immobilized
	Iron reduction	Ferric ion is used as electron acceptor and converted to Fe^{2+}

• Five key approaches in environmental microbiology ''tool box''

Site geochemistry: Analytical chemistry proves presence of compounds indicative of microbial process (reinforced by flux data and isotopic fractionation patterns).

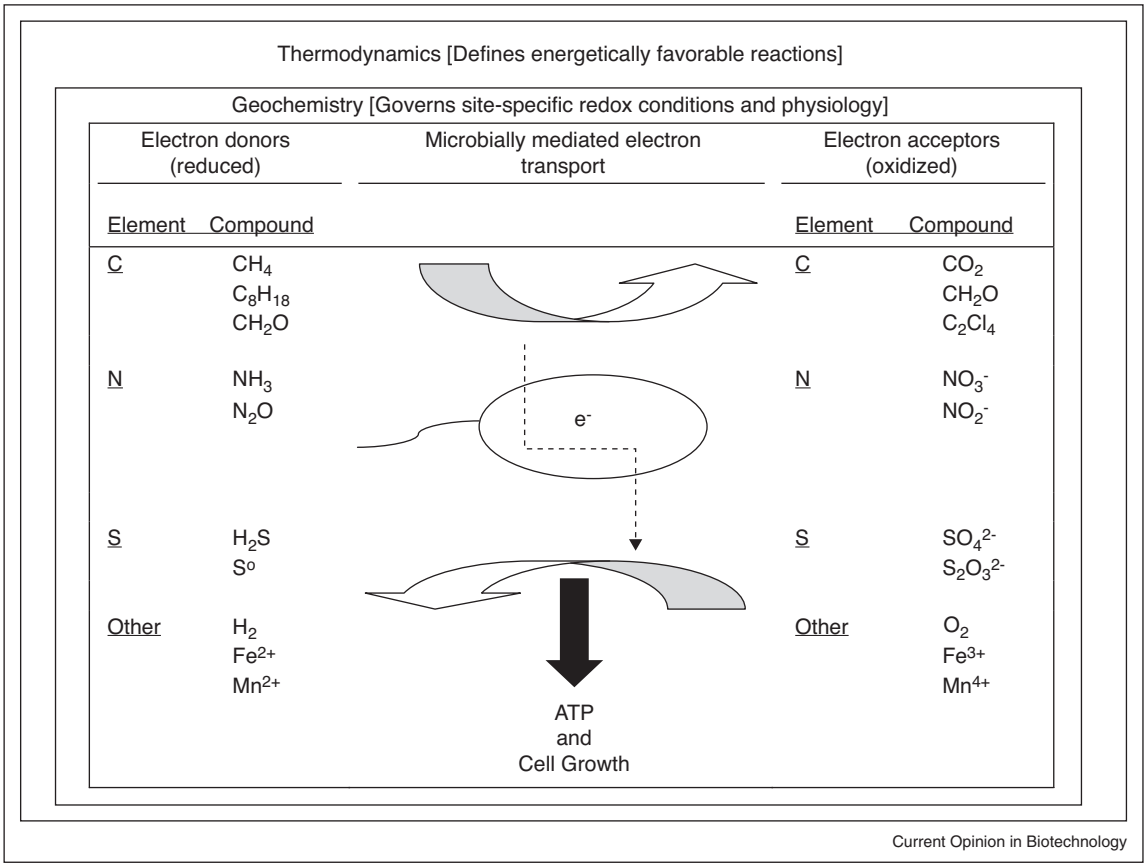
Cultivation: Provision of appropriate nutrients in liquid or solid media allows isolation of microorganisms catalyzing process of interest (e.g. denitrification or benzene biodegradation).

Incubations: Placing environmental samples or pure cultures in sealed, laboratory vessels allows documentation of physiological changes (e.g. methane generation or consumption) effected by microorganisms.

Biomarkers: Extraction and analysis of key cellular constituents. These provide insights into the taxonomic composition and/or functional potential of microorganisms by focusing upon phospholipid fatty acids, DNA, ribosomal RNA, messenger RNA, or proteins followed by GC/MS, LC/MS and/or various molecular biology procedures ranging from small-scale sequencing to high-throughput meta-genomics, meta-transcriptomics, and meta-proteomics.

Microscopy: Allows images of microorganisms and cell associations to be obtained from site samples or laboratory incubations. Depending upon analytical approach and staining targets, information yielded includes enumeration, identity (e.g. via small subunit rRNA FISH probes), localization of biomarkers within cells, and cell-specific substrate incorporation (e.g. via secondary ion mass spectrometry).

Figure 1



Conceptual view of how microorganisms catalyze biogeochemical reactions between electron donors and electron acceptors that occur in habitats such as soil, sediments, and waters. The specific reactions that occur in a given habitat are governed by both local geochemistry and the laws of thermodynamics. Each electron donor ''half reaction'' (upper curved arrow, center) must be coupled to an electron acceptor ''half reaction'' (lower curved arrow, center).

istic bases of the biogeochemical reactions that occur in soils, sediments, and waters. Five major types of analytical, microbiological, and/or molecular tools are routinely used to advance environmental microbiology: site geochemistry, cultivation, incubations, biomarkers, and microscopy (see Box 1, bottom). These tools are applied in varied proportions throughout what are formally proposed here to be the five stages of environmental microbiological inquiry leading to advances in biogeochemistry:

- *Stage 1. Discovery of new microbiological process*. Prove that microorganisms are capable of catalyzing the process of interest. This is achieved via laboratory incubation of environmental samples and/or via chemical or biomarker assays performed on complex, uncharacterized microbial communities accompanied by materials from soils, sediments, or waters.
- *Stage 2. Validation of the discovery by finding representative microbiological agents*. Refine the test system by isolating a single microorganism capable of catalyzing the process or obtaining a simplified, highly enriched consortium of microbial populations exhibiting the process or via a convincing combination of biomarkers and physiological evidence.
- *Stage 3. Characterization of agents and the physiological, biochemical, and/or genomic mechanisms of the biogeochemical process(es) they catalyze*. Use of controlled laboratory incubations, chemical assays, isotopic tracers, biomarkers (see Box 1), and often bioinformatics to define metabolites, metabolic pathways, enzymatic reactions, and the genetic basis of cellular processes.
- *Stage 4. Field verification of ecological relevance of agents and/or their biogeochemical impact*. Apply the tools, insights, biomarker analyses from Stage 3 to real-world field sites where microbiological agents (specific taxa and/or their functional genes) are influencing ecological conditions.
- *Stage 5. Biotechnological innovation and/or improved site management based on understanding biogeochemical process mechanisms*. In some instances microbial-mediated processes can be transplanted from their ecosystem contexts to human-engineered settings for commercial or industrial applications.

The path from initial discovery of microbially mediated biogeochemical processes (Stage 1) through to their biotechnological applications (Stage 5) begins in field study sites where biogeochemical processes are suspected to occur in their native ecological settings. These ecological settings pose many challenges for deciphering and documenting geochemical change within complex environmental matrixes containing thousands of microbial species. Arguably, the most important of these challenges is the difficulty of isolating a single microbial culture (or a defined mixture of cultures) that replicate the biogeochemical process in the laboratory (Stage 2); as new methods and strategies proliferate in the post-genomic era, alternative but equivalent means of attaining Stage 2 are developing. Once a model system has been implemented in laboratory culture, then tools including microscopy, biomarker sequencing (linked to bioinformatic analysis), isotopic tracers, analytical chemistry, and enzymology, can be used to decipher both microbial associations essential for the process and the biochemical mechanisms of the process (Stage 3). Among the key types of information yielded by Stage 3 investigations are proteins, DNA signatures, mRNA signatures, characteristic metabolites, and other biomarkers that can be used in verifying the ecological relevance and geographical prevalence of the process in the original field study site and perhaps in globally distributed analogs of that field study site (Stage 4). A recently successful example of Stage 5 (biotechnological application) is the use of anaerobic ammonium oxidation (anammox) to treat high-ammonia-containing wastewater effluent [7].

A selection of prominent recent environmental microbiology studies

Contributions to the field of environmental microbiology addressing biogeochemistry constantly appear in discipline-specific journals (e.g. *Applied and Environmental Microbiology*, *Environmental Microbiology*, *ISME Journal*, *Geomicrobiology*, *Geobiology*, *FEMS Microbiology Ecology*, *Microbial Ecology*) and in broader, higher-profile journals (*Proceedings of the National Academy of Sciences*, *Science*, and *Nature*). Using the five-stage scheme above, I have classified and grouped studies representative of trends and new developments with broad impact on both biogeochemistry and environmental microbiology (Table 1).

Four entries appear in the initial discovery category (Stage 1) of Table 1. Of these, only Beal *et al.* [8•] (entry #1) conforms perfectly to the classic approach of bringing an environmental sample into the laboratory and applying analytical chemistry procedures to document a previously undescribed physiological process mediated by microorganisms. For decades it has been acknowledged that it is thermodynamically feasible for microorganisms to use methane as an electron donor and both Mn-oxide and Fe-oxide as electron acceptors. Beal *et al.* [8•] were the first to select the right environmental samples, featuring the right native microbial community, incubated under the right conditions, analyzed with the right procedures. Stages 2–5 are sure to gradually unfold in the future for Mn-based and Fe-based oxidation of methane. Entries #2–4 in Table 1 (respectively addressing: linkage between dissimilatory reduction of nitrate to ammonia and the oxidation of both aromatic hydrocarbons and ammonia, polychlorinated biphenyl (PCB) biodegradation, and regulatory small RNAs in biogeochemically active ocean microbial communities) relied on the analysis of either environmental transcripts (mRNA expressed in a field site), or structural genes (DNA), or

Table 1

Survey of recent environmental microbiological studies advancing knowledge of biogeochemistry. The stages of discovery correspond to those described in the text

Stage of inquiry	Entry	Biogeochemical process(es)	Habitat	Key findings	Reference
1. Discovery	1	Mn-dependent and Fe-dependent oxidation of methane (anaerobic)	Ocean sediment	Production of $^{13}CO_2$, from ^{13}C-methane was enhanced by addition of Mn-oxide and Fe-oxide in 4-month laboratory incubations; comparison of clone libraries [16S rRNA and methanogenesis (*mcrA*) genes] gave clues about active populations	[8•]
	2	Linkage between carbon and nitrogen cycles: aromatic hydrocarbon oxidation, dissimilatory reduction of nitrate to ammonia (DNRA) and nitrification	Contaminated groundwater	The pool of mRNA in an aquifer contaminated with aromatic hydrocarbons showed *in situ* expression of aromatic biodegradation and N-cycle-related genes; ammonia was also enriched in the groundwater	[9]
	3	Aromatic hydrocarbon oxidation	Polychlorinated biphenyl-contaminated soil adjacent to tree roots	New genetic diversity as revealed by high throughput (454 Pyro) sequencing of PCR-amplified biphenyl dioxygenase genes; >2600 sequences yielded 25 novel clusters of dioxygenase genes	[10]
	4	Potential regulation of carbon, nitrogen, and phosphorous cycling	Ocean waters	High throughput (454 Pyro) sequence of the mRNA pool gathered from four ocean depths showed sequence of previously unknown small RNAs likely to be important regulatory elements within microbial populations controlling oceanic C-, N-, or P-cycles	[11]
2. Validation	5	P uptake and assimilation	Ocean water	P uptake and assimilation into phytoplankton lipids was measured in samples of both Sargasso Sea (<10 nmol/L P) and the South Pacific (>100 nmol/L P); the phytoplankton synthesize non-phosphorous ''substitute lipids'' when adapting to P scarcity	[12]
	6	Oxidation of sulfur, reduction of nitrate, CO_2 fixation	Anaerobic ocean water	The metagenome of a ubiquitous microbe (SUP05) was assembled — providing a metabolic map of its likely biogeochemical roles in oxygen-depleted marine waters	[13]
	7	Photosynthesis, N_2 fixation, S metabolism, P uptake, arsenic detoxification	*Trichodesmium* (a cyanobacterium) in Ocean water	High throughput (454 pyro) sequencing of the mRNA pool yielded 5711-day and 5385-night mRNA sequences; P-limitation stress was indicated in *Trichodesmium*; the majority of transcripts were from co-occurring microbes: cyanobacteria, heterotrophic bacteria, eukaryotes, and phage	[14]
	8	Nitrogen fixation, transfer of fixed N to associated microbes in consortium that oxidizes methane using sulfate as electron acceptor	Ocean sediment	Microscopic imaging (fluorescent *in situ* hybridization and nanometer secondary-ion mass spectrometry) of incorporated ^{15}N from $^{15}N_2$ into cell biomass and N transfer from one cell type to another	[15•]
	9	Photosynthesis and N_2 fixation in a widely distributed uncultivated marine microbe, UCYN-A	Ocean water	Whole genome sequencing of DNA was completed for 5000 cells from sea water; data showed absence of oxygen-producing photo-system II, a nitrogen fixation pathway, and a small (1.44 Mb) genome lacking many biosynthetic pathways (implying metabolic dependence upon other organisms)	[16]
Mechanism	10	Aerobic oxidation of ammonia to nitrate (nitrification) by a recently isolated ubiquitous member of the marine *Archaea*	Ocean water	Genome sequence of *Nitrosopumilus maritimus* revealed highly copper-dependent systems for ammonia oxidation and electron transport that are distinct from known ammonia oxidizing *Bacteria*	[17]

Table 1 (*Continued*)

Stage of inquiry	Entry	Biogeochemical process(es)	Habitat	Key findings	Reference
	11	Nitrification by *Nitrosopumilus maritimus*	Ocean water	Kinetic and biochemical characterization of *N. maritimus* shows remarkably high specific affinity for ammonium, explaining its likely ecological role as nitrifier in the oligotrophic ocean	[18•]
	12	Oxygen production and nitrite-driven anaerobic methane oxidation	Freshwater soil and sediment	Genomic, transcriptomic and proteomic procedures were used to discover the mechanism by which an enrichment culture carries out nitrite-dependent anaerobic methane oxidation; nitrite reduction pathways were absent; instead, oxygen-dependent methane-oxidation pathways were present; nitrite-dependent oxygen production was documented and a pathway converting NO to O_2 and N_2 was proposed.	[19••]
	13	P uptake as selective pressure in oligotrophic seawater	Ocean water	Completed genomes of two ubiquitous marine photosynthetic bacteria (*Prochlorococcus* and *Pelagibacter*) were used to interpret metagenomic surveys of the Sargasso Sea (P-limited) and the North Pacific; cross-habitat comparison showed P availability to be in the dominant selective pressure causing divergence of pan-oceanic populations	[20•]
Field verification	14	Entire N cycle [ammonia oxidation, nitrate-reduction, anammox, dissimilatory nitrite reduction to ammonia (DNRA)]	Ocean water near Peru	Geochemical and physiological and quantitative determination of both structural genes and their transcripts at three depths in four locations off the Peruvian Coast; findings document a new variant of the N cycle in which DNRA supplies ammonium to the anammox portion of the cycle	[21••]
	15	Denitrification versus anammox	Arabian Sea	Measurements included geochemical depth profiles, physiological rates of anammox versus denitrification, and quantification of genes indicative of anammox and denitrification; in seven of eight experiments denitrification was responsible for 87–99% of total N_2 production	[22]
	16	Aerobic ammonia oxidation (Nitrification)	Ocean water (Southern Californian Bight)	Long-term monitoring (2003–2006) of three depths was completed for geochemical and microbial-community profiles and for copies of genes indicative of *Archaea* and ammonia oxidation genes; trends show population dynamics and decoupling of ammonia and nitrite oxidation	[23]
	17	Biodegradation of aromatic hydrocarbons	Contaminated groundwater	Sixteen-year record shows diminishing concentrations of aromatic contaminants; community 16S rRNA fingerprints show dynamic system; small subunit rRNA sequences indicated an extensive microbial food chain, including eukaryotes	[24•]
	18	Flow of electric current	Anaerobic marine sediments	Geochemical profiles in Danish harbor sediments and time-series responses of O_2 and H_2S during oxic-anoxic cycles were measured; the rapid system responses could not be explained by chemical diffusion; instead extracellular conductivity (perhaps via microbial nanowires) were evoked	[25]
	19	Sulfide oxidation linked to nitrate reduction	Anaerobic marine waters off coastal western Africa	A 7,000 km^2 area of the African shelf was detoxified of its sulfidic waters by a bloom of sulfide oxidizing bacteria; data gathered included geochemical profiles, stoichiometric modeling, physiological incubations, sequencing of 16S rRNA and sulfide oxidizing genes, and microscopic enumeration of sulfide-oxidizing bacteria	[26••]

Table 1 (*Continued*)

Stage of inquiry	Entry	Biogeochemical process(es)	Habitat	Key findings	Reference
	20	Iron and sulfate reduction, acetate oxidation, methanogenesis	Oceanic subsurface sediments	The International Ocean Drilling Program produced vertical geochemical profiles and sediment samples analyzed by microscopy, 16S rRNA community gene profiles, physiological incubations, and quantitative PCR of genes indicative of *Archaea, Bacteria, Geobacter*, dissimilatory sulfite reductase and methanogenesis	[27]
Biotechnology innovation	21	Generation of electric current	Various habitats, including sediments and bioreactors	Promising technologies rely upon innate adaptations (nanowires, extracellular electron carriers, etc.) by anaerobic bacteria for transferring electrons to surfaces of insoluble electron acceptors; engineered microbial fuel cells are under development	[28]
	22	Anaerobic ammonium oxidation (Anammox)	Various freshwater and other sediments and bioreactors	The ability of microorganisms to use ammonium as electron donor and nitrite as electron acceptor to produce N_2 has led to commercial reactors that economically treat high-strength industrial ammonium waste waters	[29]

both to gain insight into the metabolic functioning of naturally occurring microbial communities.

Regarding the second stage of biogeochemical inquiry in Table 1, entries #5–9 validate, confirm, or extend information about previously reported processes. Pertinent to the P cycle, entry #5 used biochemical characterization procedures to show the photosynthetic (phytoplankton) portion of oceanic microbial communities is capable of adapting to extreme P scarcity by substituting non-P-containing lipids in cellular membranes. Entry #6 used bioinformatic analysis of environmental DNA (metagenomics) to assemble evidence about the probable physiological role of an uncultivated marine microorganism previously show to flourish in oxygen-depleted zones of the ocean. Entry #7 analyzed environmental mRNA (metatranscriptomics) extracted from the raft-forming cyanobacterium, *Trichodesmium*, harvested from Pacific surface waters: insights into the *in situ* physiological status and nutrient stresses of the associated community (from viruses to eukaryotes) were revealed. High-resolution mass spectrometric (nanoSIMS) imaging of the composition of individual bacterial cells (entry #8) allowed Dekas *et al.* [15•] to prove that one member of a consortium of microbial types known to anaerobically oxidize methane also fixed $^{15}N_2$ into its cell biomass and then shared that fixed nitrogen with another member of the consortium. Finally, analysis of a completed 1.44 Mb genomic sequence of a widespread uncultured photosynthetic marine cyanobacterium revealed its likely physiological niche, which includes the absence of O_2 generation and nutritional dependence upon neighboring cells in its community (entry #9, Table 1).

Research advancing the mechanistic details of microbially mediated biogeochemical reactions addressed the cycling of N, O, C, and P (entries #10–13, Table 1). Long-standing questions about the biogeochemical role of broadly disseminated *Archaea* in the world's oceans were addressed by entries #10 and #11: analysis of the genome of *Nitrosopumilus maritimus* revealed a novel aerobic ammonium oxidation mechanism, while kinetic and biochemical measurements on *N. maritimus* proved its ability to successfully take up and oxidize ammonia at the low concentrations that prevail in ocean waters. Entry #12 provides a remarkable example of how bioinformatic interpretation of nucleic acid and proteome data from a mixed-enrichment culture (that anaerobically oxidizes methane using nitrite/nitrate as the electron acceptor) can lead to the discovery of a previously unrecognized enzymatic process: the conversion of NO to N_2 and O_2. Entry #13 of Table 1 reports the use of comparative genomics and DNA sequence analysis from microbial communities in low-P and high-P areas of the world oceans: Coleman and Chisholm [20•] showed that P availability is the predominant driving force for genomic divergence of *Prochlorococcus* and *Pelagibacter* populations dwelling in the Sargasso Sea and North Pacific.

The field verification section (Stage 4) in Table 1 features three studies addressing the N cycle. Entry #14 presents comprehensive, nearly revolutionary assembly of geochemical, physiological, and nucleic acid (both DNA and mRNA) assays establishing dissimilatory nitrate reduction to ammonia (DNRA) and anammox as essential links in nitrogen cycle off the Peruvian Coast. Ward *et al.* [22] (entry #15) showed the predominant pathways of electron flow in the oxygen-depleted zone of the Arabian Sea is denitrification (not anammox). Beman *et al.* [23] (entry #16) used long-term monitoring of geochemistry and the composition and abundance of ammonia oxi-

dation genes to establish a link between *Archaea* and nitrification. Yagi *et al*. [24•] (entry #17) provided a 16-year record of contaminant-loss data and linked this biodegradation process to dynamic microbial communities that included an extensive food chain involving protozoan predation. Entry #18 [25] raises the possibility that recent reports of extracellular electron transfer by anaerobic bacteria may have broad-scale ecological significance. Entries #19 [26••] and #20 [27] of Table 1 bring extensive teams together to examine site-specific microbial processes: these were, respectively, nitrate-based oxidation of a potentially toxic plume of hydrogen sulfide off the west coast of Africa and anaerobic populations dwelling in deep oceanic sediment and their potential metabolic activity.

The final section of Table 1 (Stage 5, entries #21 and #22) provides two examples of biotechnological innovations directly related to microbially mediated biogeochemical processes: microbial fuel cells and anammox.

Conclusions

The goal of this article was not to comprehensively review all of the biogeochemistry and related environmental microbiology literature that has emerged in the past 2 years. Instead, the goal was to establish a framework for understanding the intricate relationships between environmental microbiology, biogeochemistry, and biotechnology. A five-stage structure for achieving scientific progress in biogeochemistry was described and then selected recent influential reports were placed in the framework.

Where is the field going? Several dominant trends are apparent:

1. Methodologies in analytical chemistry, microscopic imaging, and high-throughput analysis of microbial biomarkers (metagenomics, metatranscriptomics, metaproteomics) will continue to gain sophistication.
2. As these methodologies are increasingly applied to complex microbial communities in real-world field sites, clear patterns in the data will likely emerge.
3. The patterns in the data can serve as foundations for hypotheses about relationships between geochemical settings, expressed genes catalyzing particular physiological processes, and the identity of key catalytic microbial populations.
4. Progress is likely to continue for procedures that isolate (via cultivation, cell sorting, or other techniques) individual microorganisms and/or consortia capable of catalyzing biogeochemical processes.
5. Information resulting from points #3 and #4 will increasingly converge, thereby strengthening mechanistic understanding of biogeochemical reactions. This should facilitate improved approaches to ecosystem management and the development of new biotechnologies.

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