

Beyond boxes and arrows: Putting the 'bio' into biogeochemistry



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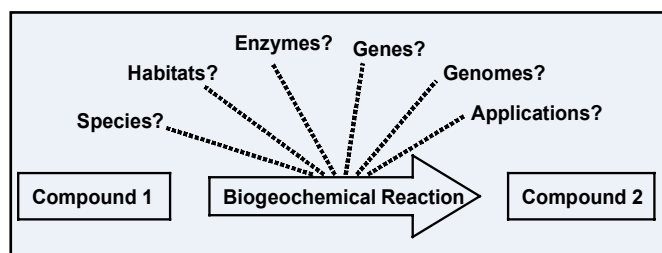
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The Gaia hypothesis proposes that the earth can be viewed as a single living entity¹. While this idea remains controversial, there is no doubt that the biotic and abiotic components of the earth are intimately linked in complex webs of chemical reactions collectively described as biogeochemistry^{2,3}. Microbes are the catalysts of most such reactions, but despite their importance, there is a tendency to oversimplify microbial contributions using boxes (compounds) and arrows (reactions) (Fig 1). In this brief review, I will highlight recent research that looks beyond the boxes and arrows to the microbes themselves, and describe some examples where the activities of biogeochemical microbes and enzymes have been harnessed for environmental benefits.

New ways of capturing energy

Microbial energy capture is the driving force for most biogeochemistry, and new ways for microbes to extract energy from their environment are constantly being discovered. An excellent example is the unexpected discovery of the light-harvesting pigment proteorhodopsin in BAC clones derived from marine bacteria⁴. This finding indicated that aerobic anoxygenic photosynthesis was occurring in the oceans, thus challenging the traditional assumption that *Cyanobacteria* are the main oceanic phototrophs, and transforming our understanding of marine ecosystem energetics. Subsequent studies using both metagenomic and genome sequencing approaches have revealed that proteorhodopsin-containing bacteria are

Figure 1. A lot of interesting biology is hidden in the arrows representing biogeochemical reactions.



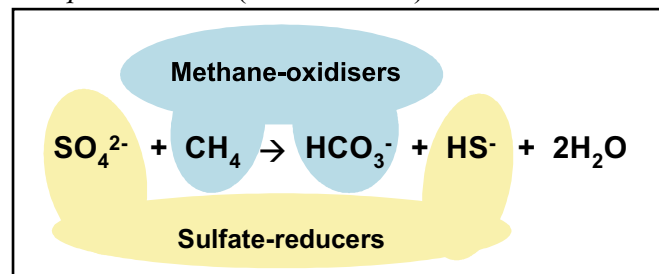
widespread and diverse, including *Gamma*proteobacteria⁵, *Alphaproteobacteria*⁶ and *Flavobacteria*⁷.

Greenhouse gases and the carbon cycle

Concern over global warming due to anthropogenic emissions of CO₂ has reinvigorated research into the carbon cycle. Some of the most exciting (and controversial) experiments in this area have involved fertilising large ocean areas with iron^{8,9}, with the aim of converting CO₂ into biomass that can sink into sediments. Although there are serious challenges in using such geoengineering approaches for mitigating greenhouse gas emissions, these experiments have been valuable in confirming the crucial role of iron in controlling phytoplankton growth, and have revealed specific microbial community shifts in response to iron fertilisation, e.g. a transition from pinnate to centric diatoms¹⁰.

Research into anaerobic methane oxidation represents another important frontier in studies on the carbon cycle. This reaction (Figure 2) was once thought impossible, but now appears to be of global significance. While first reported in 1980¹¹, it was not until twenty years later that anaerobic methane oxidation was associated with specific microbes¹², namely a symbiotic association of methane-oxidising *Archaea* and sulfate-reducing *Deltaproteobacteria*. Sulfate-linked methane oxidation provides a crucial link between the carbon and sulfur cycles in anaerobic environments. The initial reaction is catalysed by a variant of the terminal methanogenic enzyme (methyl coenzyme M reductase)¹³, in a fine illustration of the way in which evolution can co-opt existing structures for new functions.

Figure 2. Anaerobic methane oxidation requires the combined activities of *Euryarchaeota* (methane oxidizers) and *Deltaproteobacteria* (sulfate reducers).



Accumulation and excretion of phosphorous

Phosphorous (P) is required by all organisms as a nutrient, but in excess, this element can be a problematic water pollutant. One strategy for minimising P pollution has been to encourage the growth of P-accumulating bacteria in wastewater systems. Such bacteria have proven recalcitrant to culturing, but the use of molecular methods such as full-cycle 16S rRNA analysis¹⁴ and MAR-FISH¹⁵ have indicated that both *Betaproteobacteria* and *Actinobacteria* are involved. The retrieval of a near-

complete genomic sequence from '*Candidatus Accumulibacter phosphatis*' (*Betaproteobacteria*)¹⁶ has given several surprising insights into these bacteria, including the likely presence of an anaerobic TCA cycle. Another approach to minimising P pollution is to target phosphate excretion from livestock. One recent innovation is the genetic engineering of animals with microbial phytase¹⁷, an enzyme that converts organic P (phytate) to inorganic P. Phytase increases the nutritional value of animal feeds, eliminating the need to supplement diets with phosphate and thus reducing P excretion.

Ammonium oxidisers are exceedingly diverse

The bacteria of the nitrogen cycle catalyse some unique reactions not seen in eukaryotes, and have been an especially rich source of recent microbiological breakthroughs. Anaerobic ammonium oxidation (Anammox) involves *Planctomycetes* with several unusual properties including ladderane lipids (Figure 3) and intracellular compartments¹⁸. Despite the importance of Anammox to the N cycle, it was only in 2006 that details of the genetics involved became available, thanks to genome reconstruction from enrichment DNA¹⁹. On the aerobic side of the nitrogen cycle, the last few years have seen the emerging recognition of mesophilic *Archaea* as key players in nitrification (ammonia oxidation) in both marine²⁰⁻²² and terrestrial²³ environments – these findings have revolutionised our understanding of the biology and ecology of the Crenarchaeota.

Figure 3 Methyl 8-(5)-ladderane-octanoate, a cyclobutane ladderane lipid from the anammoxosome.



Marine sulfur oxidisers and symbionts

The sulfur cycle involves many unique microorganisms, but perhaps the most spectacular is *Thiomargarita namibiensis*, which holds the current record as the largest known bacterium (cells up to 0.5 mm diameter)²⁴. The large cell size is due to central vacuoles containing up to 0.8 M nitrate, which is used by the cells as an electron acceptor to oxidise sulfide and elemental sulfur. Recent work suggests that such giant sulfur bacteria are involved in the formation of phosphorite (phosphate rock) deposits²⁵, suggesting they occupy a special position at the intersection of the sulfur, nitrogen and phosphorous cycles. Another important niche for sulfide/sulfur-oxidising bacteria is as symbionts in hydrothermal vent invertebrates²⁶. Despite the unculturability of such symbionts, they can be studied by methods such as proteomics, which has recently led to the discovery of two separate CO₂ fixation pathways in the symbiont of the tubeworm *Riftia pachyptila*²⁷.

Conclusions

While space constraints have not permitted discussion of a larger slice of microbial and biochemical diversity (e.g. the many fascinating redox transformations of metals²⁸), I hope I have communicated a sense of the importance and excitement of research in biogeochemistry. Elucidating the identities and

functions of microbes involved in elemental cycles is critical if we are to effectively manage the earth's ecosystems in the face of environmental challenges such as global warming, pollution, and loss of biodiversity.

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