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Microbial services: challenges for microbial ecologists in a changing world

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ABSTRACT: Bacteria, archaea and other microbes have dominated most biogeochemical processes on Earth for >99% of the history of life, but within the past few decades anthropogenic activity has usurped their dominance. Human activity now impacts every ecosystem on the planet, necessitating a new socio-ecological view of ecosystem processes that incorporates human perceptions, responses, activities and ideas into ecology. The concept of ecosystem services is an important link between ecosystem processes and the social sphere. These include the provisioning, regulating, cultural and supporting benefits that ecosystems provide to enhance human well-being. Many ecosystem services are provided by microbes, initiating the concept of microbial services to society — an idea long appreciated by microbial ecologists. Experimental studies of the biodiversity–ecosystem function relationship emphasizing microbial functions are inconclusive, with increasing diversity sometimes being observed to enhance function, while at other times the opposite relationship has been found. A specific function addressing the role of bacteria in helping or hindering carbon storage in the deep ocean in response to iron fertilization is similarly uncertain. Bacteria respond positively to mesoscale iron additions in many cases, but in doing so, may retard carbon storage by decomposing sinking particles. Human exploitation of microbial services to enhance planetary sustainability must be based on focused studies of microbial processes in a human-dominated world.

KEY WORDS: Ecosystem services · Microbial services · Microbial diversity function · Sustainability · Iron fertilization

INTRODUCTION

Earth and its component ecosystems are dominated by 2 vastly different sets of processes. For at least 75% of the 4 billion year history of life, bacteria and archaea controlled elemental cycling, organic matter production and turnover and the planetary climate. In many ways, they still do. Microbes including bacteria, archaea, phytoplankton, protozoans and fungi still catalyze the major transformations of the elements, break down organic matter, and produce and consume oxygen and carbon dioxide (Smil 2003). Around half the global net primary productivity is by unicellular phytoplankton in the sea (Falkowski et al. 2000), and most of the global respiration (terrestrial and marine) is microbial. However, just within the past century (0.00000001% of the history of life), many processes on earth have become dominated by anthropogenic activities. Vitousek et al. (1997) describe the extent of anthropogenic contributions to earth system processes. To name but a few of the examples given by those authors: over 60% of all marine fisheries are fully exploited, overexploited or depleted; over 20% of all bird species on earth have become extinct; and 50% of all accessible surface freshwater is used in human activity. The extent of human perturbation of the chemical composition of the atmosphere is well known: the CO_2 concentration has increased by nearly 40% since 1750. The transformation in the nitrogen cycle is even more striking. Human activity now

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accounts for more than half of all reactive nitrogen entering terrestrial ecosystems — an increase of over 100 % in the global nitrogen cycle. Here, I suggest the importance of recognizing the shared dominance of the planet by the extreme ends of the evolutionary process: microbes and man. Space limits this to a cursory treatment, with most specific examples emphasizing bacteria. I hope the tables and references will spur readers to further investigation.

ECOSYSTEM SERVICES

With every ecosystem on earth influenced by humans (Palmer et al. 2004), it is necessary and inescapable to view human beings and their activities as integral components of ecosystems, not isolated external drivers. Humans act on and are acted upon by ecosystems, forming a complex network of feedback relationships (Fig. 1). In this model of the 'socio-ecological system' are 3 groups of interacting components: (1) climate, influenced by external drivers, biogeochemical processes and human activity; (2) ecosystems as they are typically viewed, with populations, communities and biogeochemical cycles; and (3) the social system, consisting of human communities and cultures, institutions and their actions. The climate box (Box 1) is studied by climatologists and biogeochemists; Box 2 is served by traditional ecology and most of Box 3 by sociology, economics, political science, etc. New studies of socio-ecological systems (e.g. Fig. 1) seek to unify these disciplines in a new field that includes both traditional and human ecology as well as the social sciences and transdisciplinary fields such as adaptive management and ecological economics (Odum 1971).

A key development in socio-ecology has been the conceptualization and assessment of 'ecosystem services' (Table 1), the functions and services supplied by 'natural' ecosystems that benefit human society (Millennium Ecosystem Assessment 2005). The 4 main categories of ecosystem services include (1) Provisioning services: generally durable goods with markets in local to global economies; (2) Regulating services: ecosystem functions essential for maintaining complex human societies on the planet; (3) Cultural services: less tangible services that enhance social institutions and enrich human well-being; and (4) Supporting services: this last category addresses the ecosystem functions that underlie and support the supply of the other services. The ecosystem services concept is important because it articulates in concrete terms the functions of the world's ecosystems as they benefit human society. The concept enables the assessment of their condition and trends in enhancement or degradation, as well as their economic valuation, which is a necessary prerequisite for analysis of the socio-ecological system. There have been several attempts, sometimes controversial, to evaluate ecosystem services in direct monetary terms (Odum 1971, Costanza et al. 1997).

MICROBIAL SERVICES

Even superficial consideration of Fig. 1 and Table 1 will suggest to microbial ecologists what we already

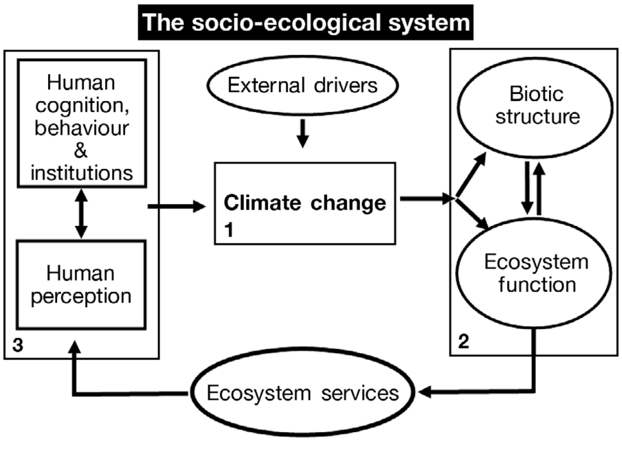

Fig. 1. A new socio-ecological framework providing the basis for exploring research questions about the interplay of human society and the environment. The right-hand side represents the domain of traditional ecological research; the left-hand side (Box 2) represents human dimensions of environmental change; the two are linked by the services provided by ecosystems (Box 3 at bottom), and by disturbances such as climate change influenced or caused by human behavior

Table 1. Ecosystem services: 4 major types and examples

Provisioning services
- Foods (including seafood and game) and spices
- Wood and fiber (animal and vegetable fibers)
- Precursors to pharmaceutical and industrial products
- Fuel (hydropower, biomass fuels)

Regulating services
- Carbon sequestration and climate regulation
- Flood regulation
- Disease regulation
- Waste decomposition and water purification

Cultural services
- Educational
- Recreational experiences (including ecotourism)
- Aesthetic (artistic inspiration)
- Spiritual (sense of place)

Supporting services
- Soil formation
- Nutrient cycling
- Primary production

know about the place of microbes in this scheme: many essential services and functions are carried out by microbes (even though their role is being usurped by humans in some cases). As noted above, microbes carry out most of the essential biogeochemical processes, regulate climate, water quality, atmospheric composition and perform about half the total primary production. Microbes also contribute to other services: domesticated microbes produce food, pharmaceuticals and fuels. Others even contribute to cultural values by forming natural landscape elements with aesthetic and recreational value (e.g. clean water for recreation, colored hotsprings).

This immediately suggests the concept of 'microbial services': the services supplied to humans by different groups of microbes (Table 2). Microbial services are already being exploited for commercial and environmental purposes. For example, microbial supplements are manufactured and sold as soil additives and for environmental cleanup of pollutants, as well as other environmental remediation and ecosystem restoration activities. My argument here is that microbial ecologists can contribute to socio-ecology and efforts toward achieving global sustainability by understanding the characteristics and processes of microbial communities that enable microbial services. Here I expand this argument by describing 2 examples. First I review research on the relationship between microbial (mostly bacterial) biodiversity and their ecological functions. Next I discuss the responses of bacteria and archaea during oceanic iron fertilization, and the (potential) role of marine bacteria in anthropogenic CO_2 sequestration.

Microbial biodiversity–ecosystem function relationships

There is a long list of literature concerning research on the biodiversity–ecosystem function (BEF) relationship that relates species richness and other diversity measures of particular taxa in specific habitats to ecosystem functions such as productivity and grazing (e.g. Loreau et al. 2001). However, there has been little research focusing explicitly on the BEF relationship for the various groups of microbes. This is certainly due in part to the difficulty of defining microbial species and estimating their diversity (Pedros-Alio 2006). New developments in probing community composition suggest a vast untapped wealth of bacterial and archaeal species diversity (Sogin et al. 2006), yet the function of the diversity reservoir is almost entirely unknown. Does microbial diversity enhance ecosystem function? Bell et al. (2005) examined the relationship between community respiration and bacterial species diversity by creating mixtures of up to 72 culturable species in experimental microcosms over a range of species richness (1 to 72 species). They found a significant, positive and decelerating (log-linear) relationship between species richness and respiration rate, with apparent synergisms among different species. The overall positive BEF relationship reflected that found in many studies of higher taxa. However, a more comprehensive review of BEF studies of bacteria and other members of microbial foodwebs shows that no generalization about the size and shape of the microbial diversity–ecosystem function relationships is possible, at least given the few studies reported to date

Table 2. The major groups of microbes and examples of services they provide

Group	Processes	Services (see Table 1)
Heterotrophic bacteria	Organic matter breakdown, mineralization	Decomposition, nutrient recycling, climate regulation, water purification
Heterotrophic bacteria	Extracellular polymer production	Carbon sequestration
Photoautotrophic bacteria	Photosynthesis	Primary production
Chemoautotrophic bacteria	Specific elemental transformations (e.g. sulfate reduction, iron oxidation)	Nutrient recycling, climate regulation, water purification
Unicellular phytoplankton	Photosynthesis	Primary production
Archaea	Specific elemental transformations (e.g. methanogenesis, nitrification)	Nutrient cycling, atmosphere and climate regulation
Protozoans	Consumption and mineralization of other microbes	Decomposition, nutrient cycling, soil formation
Fungi	Organic matter consumption and mineralization	Decomposition, nutrient cycling, soil formation
Fungi (mycorrhizal)	Nutrient recycling	Primary production (indirect)
Viruses	Lysis of hosts	Nutrient cycling

(Table 3). There is no consistent relationship, with about equal (low) numbers of positive, negative or inconclusive responses to increased diversity.

The following generalizations can be made about the state of this research: of the few studies overall, most have used cultured species. Only a few studies examined naturally occurring bacterial plus archaeal diversity and its relationship to *in situ* function (Reinthaler et al. 2006). Most studies are thus highly artificial, which allows isolation of the BEF relationship, but neglects other factors that may affect the relationship and masks the true diversity. Most importantly, few ecosystem processes (functions) have been analyzed. In many cases, the process was selected because it was easy to measure (e.g. bacterial biomass accumulation or production). Bacterial or community respiration is a system-level entity, but is a general consequence of many unrelated microbial taxa acting in concert. As such, it may be difficult to relate to the diversity of organisms actually carrying out the major part of the process. Examination of specific metabolic processes carried out by specific groups like methane oxidizers, nitrifiers or cellulose hydrolyzers may be a more effective approach. Microbial BEF research is a field ripe for progress.

Bacterial roles in the ocean biological pump: the case of iron fertilization

Storage of CO_2 in the deep sea is facilitated by carbon fixation into biomass by phytoplankton, consumption by zooplankton and gravitational sedimentation into the deep ocean: the aggregate process termed the biological pump (Ducklow et al. 2001). Bacteria and protozoans can accelerate carbon sinking and storage by producing extracellular mucins that bind particles into larger aggregates (marine snow) that sink faster, or retard sinking and storage by decomposing the sinking materials. The net effect probably changes according to particular sets of conditions and is not well-understood (Azam & Malfatti 2007). In large regions of the world, ocean primary production and export to depth are limited by micronutrient (iron) limitation (Martin et al. 1991). Several large ecosystem manipulation studies have been performed to examine the potential for artificial iron additions (iron fertilization) to enhance CO_2 storage as a geo-engineering strategy for reducing anthropogenic CO_2 accumulation in the atmosphere (Boyd et al. 2007; Table 4). The studies demonstrate convincingly that iron addition stimulates photosynthesis, macronutrient utilization and CO_2 drawdown. Whether or not carbon export responds as well is less clear (Buesseler & Boyd 2003). If iron addition does not enhance carbon export it cannot be an effective tool for climate change mitigation. Carbon storage via the biological pump is an ecosystem service that potentially has a market through trading of carbon credits. Whether the storage can be verified for trading is still not resolved. The exact role of bacteria and other microbes (their service) is uncertain.

The bacterial response has been studied in some, but not all, mesoscale iron addition experiments (Table 4). Like the BEF relationship, the results vary. The response of bacterial community composition (species composition and richness) is not conclusive, but only very few studies have examined this property. In most

Table 3. Experiments and observations relating microbial diversity and ecosystem function. Diversity is represented as the number of added species. Natural: naturally occurring species diversity in different water samples

Habitat	Diversity	Variable	Relationship	Source
Freshwater	31	Respiration (CO_2)	+	McGrady-Steed et al. (1997)
Freshwater	3	Biomass increase	+	Naeem & Li (1997)
Freshwater	High vs. Low	Productivity	0	Petchey et al. (1999)
Soil	High vs. Low	Respiration (CO_2)	+	Griffiths et al. (2000)
Soil	31	Abundance increase	+	McGrady-Steed & Morin (2000)
Soil	High vs. Low	Respiration (CO_2)	0	Griffiths et al. (2001)
Freshwater	8	Biomass increase	0	Petchey et al. (2002)
Freshwater	6	Biomass increase	–	Gonzalez & Descamps-Julien (2004)
Review	—	Respiration (CO_2)	+	Morin & McGrady-Steed (2004)
Freshwater + litter	8	Cellulose decomposition	+	Wohl et al. (2004)
Tree H_2O	72	Respiration (CO_2)	+	Bell et al. (2005)
Freshwater	4	Biomass increase	+	Steiner et al. (2005)
Freshwater	4	Biomass increase	+	Steiner et al. (2006)
Marine	Natural	Production increase	–	Reinthaler et al. (2005)
Marine	Natural	Respiration increase	–	Reinthaler et al. (2005)
Freshwater	4	Decomposition	0	Jiang (2007)
Freshwater	4	Trophic transfer	0	Jiang (2007)
Freshwater	4	Biovolume increase	+	Jiang (2007)

Table 4. Responses of bacterioplankton assemblages to mesoscale iron fertilization. +: positive response; 0: no response; —: not tested; na: not available

Study	Region/Year	Temp. (°C)	Abund/Prod?	Community shift?	Source
IronEx1	Equatorial Pacific/1993	23	—	—	Martin et al. (1994)
IronEx2	Equatorial Pacific/1995	25	+	—	Cochlan (2001)
SOIREE	Southern Ocean/1999	2	+	—	Hall & Safi (2001)
EisenEx	Southern Ocean/2000	4	+	0	Arrieta et al. (2004)
SEEDS-1	North Pacific/2002	11	0	—	Suzuki et al. (2005)
SOFEX	Southern Ocean/2002	–1	+	+	Oliver et al. (2004), J.L. Oliver et al. (unpubl. data)
SERIES	North Pacific/2002	13	+	+	Boyd et al. (2004), Hale et al. (2006), Agawin et al. (2006)
EIFEX	Southern Ocean/2004	5	na	na	na
SEEDS-2	North Pacific/2004	10	na	na	na
SAGE	Southern Ocean/2004	12	na	na	na
Fee-P	Subtropical Atlantic/2004	21	0	na	Rees et al. (2007)
CROZEX	Southern Ocean/2004-05	2	+	+	Zubkov et al. (2007)

studies, bacterial growth is stimulated following the phytoplankton response, suggesting that bacteria may be carbon- rather than iron-limited (Church et al. 2000). Boyd et al. (2004) calculated that most of the organic matter produced in response to iron addition in the northeast Pacific was consumed by bacteria. If the bacteria are stimulated to decompose organic matter that is produced in response to iron stimulation, their net effect will be to lower the carbon storage efficiency.

The larger issues surrounding the iron fertilization question are too complicated to review in any detail here. However, one further effect is noteworthy. If iron fertilization were effective in stimulating the biological pump, and if it were employed as a long-term, large-scale strategy (this is highly uncertain; see Sarmiento & Orr 1991), the additional input of organic matter would be consumed by heterotrophic microbes, possibly rendering the deep sea hypoxic or anoxic. Fuhrman & Capone (1991) speculated that prolonged iron fertilization could result in large releases of N_2O and methane, 2 powerful greenhouse gases. The net effect would be to enhance, not ameliorate, the anthropogenic greenhouse effect. The complex effects of iron fertilization have not borne out the initial expectations of a greenhouse panacea (Chisholm et al. 2001). As those authors stated (p. 310): "The proponents' claim that fertilization for carbon sequestration would be environmentally benign is inconsistent with almost everything we know about aquatic ecosystems."

When viewed in the context of integrated socio-ecological systems, including human actions and responses such as iron fertilization, the situation originally presented in Fig. 1 is much more complicated (Fig. 2). Iron fertilization provides one example of the interplay of microbial processes and human actions. Microbes and humans together influence climate change via the ecosystem service of carbon storage, but unintended consequences like N_2O production may add other feedbacks to this system. Thus, iron fertilization provides a useful case study of the complex interrelationships and feedback loops that potentially exist among climate change, microbial services and social concerns, perceptions and actions, involving microbial ecologists and the rest of society. The brevity of this article prevents a fuller examination of microbe–human–ecosystem–climate interactions and feedbacks; an enormous topic. I hope it will stimulate new research — or at least second thoughts by interested students.

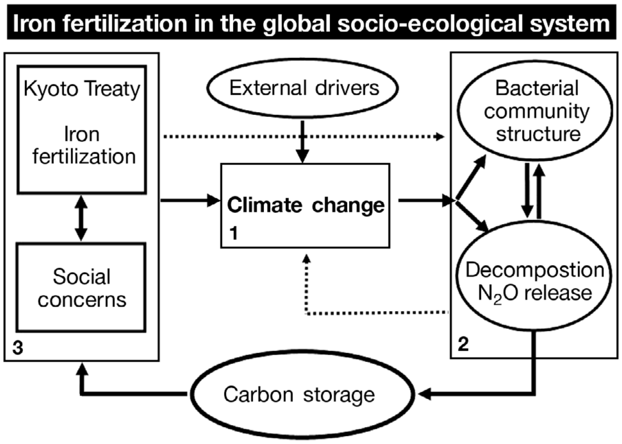

Fig. 2. The same framework as in Fig. 1, specifically showing the relationships in the socio-ecological sphere for purposeful iron fertilization of the ocean ecosystem to mitigate anthropogenic CO_2 accumulation in the atmosphere. Note in both figures that there is no specified starting point for the network of feedback loops in the system

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