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Microbial diversity and ecosystem function

Bland J. Finlay, Stephen C. Maberly and J. Ian Cooper

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The nature and scale of ecosystem functions, such as carbon-fixation and nutrient cycling in a freshwater pond, appear to be governed by complex reciprocal interactions involving physical, chemical and microbiological factors. Moreover, these interactions continuously create new microbial niches that are quickly filled from the resident pool of rare and 'cryptic' (and probably cosmopolitan) microbial species. This could mean that microbial activity and diversity are both a part of, and inseparable from, pond ecosystem function, and that concepts such as 'redundancy' of microbial species, and the 'value' of conserving biodiversity at the microbial level have little meaning.

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A substantial worldwide scientific effort is currently directed at understanding the role of biodiversity in the natural environment. This area of science is, however, not new. Darwin believed that species-rich plant communities were more productive, Elton (1958) advanced the hypothesis that "diversity begets stability" and, from the early 1970's, much theoretical and experimental work has probed the tangled web of biodiversity–stability–productivity relationships, in terrestrial ecosystems in particular. What *is* new is that the questions have become more specific. Specific ecosystem functions such as carbon-fixation and nutrient cycling are identified and quantified, and the relation of these functions to the species richness of natural and manipulated communities is examined in detail. At the heart of all such studies is the desire to discover if it makes any difference how many species are present: perhaps some species are 'redundant', and ecosystems perform just as well with fewer species.

There is now a consensus, drawn largely from work with manipulated terrestrial systems (Naeem et al. 1994, Tilman 1996, Tilman et al. 1996), that increased species-richness brings increased variation in population

abundance of individual species, ecosystem functions that are more stable over time, and productivity that tends to be higher. There is some doubt, however, that this general picture also applies to the real biodiversity of real ecosystems, in which many hundreds of species are involved. Tilman's work with terrestrial plant communities indicates that the biggest gains in stability and productivity come with the first ten species. Additional species do not appear to bring significant additional 'benefits', perhaps because all available functional niches are already filled. This could indicate that natural ecosystems, often containing very large numbers of species, have much greater diversity than is ever likely to be needed to reach peak productivity. Does the apparent surfeit of plant species have any role to play with respect to ecosystem function?

This question is difficult to answer for terrestrial communities of higher plants and animals, and the problem is essentially one of spatial and temporal scale. For example, we may suspect that niche diversification in a forest is more intricate than can easily be observed because of small spatial differences in environmental conditions in the soil or canopy: the 'redundant' species

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may in fact be occupying cryptic niches. In addition, when a species has a relatively long life-span, or can produce long-lived propagules, its maintenance in the community may be supported by environmental conditions of low frequency and short duration; such as rainfall in a desert.

Microbial diversity in aquatic systems

These problems of scale and detection of appropriate environmental conditions are less severe for aquatic systems dominated by microbes. Although it may sometimes be difficult to define the boundaries of what constitutes a microbial species (Colwell et al. 1995, Finlay et al. 1996a), the short generation times of microbes – days or even hours – permit rapid changes in population abundance. Moreover, changes in microbial community structure are often the result of environmental conditions that vary with high amplitude and frequency. In a lake or pond, the spectacular variation in microbial activity and diversity observed during a single summer (e.g. Wetzel 1983, Giller et al. 1994) probably exceeds that of the most dramatic successions of terrestrial plant communities spanning many years. In the course of a few days, the habitat of a microbial community may shift from oxygen supersaturation to anoxia; from an excess of dissolved nutrients to complete nitrogen depletion. New microbial niches will be created, filled and destroyed in rapid succession. By witnessing this relatively rapid succession of microbial species, while recording changes in the accompanying environmental factors, we may quickly gather information concerning the relationship between species-richness and ecosystem function. In addition, although it is likely that much of the microbial diversity in a pond is typically rare or cryptic at any moment in time, the high rate of turnover of microbial species increases the probability that we will occasionally glimpse, and even understand, bursts of activity from these 'redundant' species.

Reciprocal interactions

The one-hectare, productive pond known as 'Priest Pot' (in Cumbria, UK) has been the subject of a considerable research effort over a period of more than 40 yr (e.g. Gorham 1960, Belcher et al. 1966, Goulder 1971, Robinson et al. 1984, Finlay 1985, Berninger et al. 1986, 1993, Davison and Finlay 1986, Stewart and George 1987, Finlay et al. 1988, 1996b, Guhl et al. 1994). Like all such ponds, a great variety of biological and non-biological factors interact with each other to make the pond function in the way it does. A key consideration is that these are invariably *reciprocal* interactions, for this implies that microbial diversity, far

from being something which acts upon, or responds to ecosystem function, may actually be *a part of* ecosystem function. This idea can be explained by closer examination of these reciprocal interactions. Fig. 1 synthesises information abstracted from the large body of published research (> 50 publications) on Priest Pot, within the spatial and temporal framework of events and processes observed in 1996.

Increasing solar radiation in the spring, and the establishment of physical stratification, reduces the rate of oxygen supply to the sediment and eventually produces an anoxic hypolimnion. Aerobic microbes then migrate out of the sediment and into the overlying water, removal of the oxidised sediment–water interface solubilises bound phosphate, and nutrients such as ammonia and CO₂ escape to the water column. The oxic–anoxic boundary eventually stabilises at an intermediate depth, where a dense food web based on microbial micro-aerophiles develops, sustained by the opposing fluxes of light and dissolved oxygen from above, and dissolved CO₂, nitrogen and phosphorus from below. Meanwhile, in the anoxic hypolimnion, a transient niche opens for nitrate respirers. These soon exhaust the nitrate, and sulphate-reducing bacteria grow to replace them. At the same time, fermenting bacteria in the sediment continue to degrade organic matter to CO₂. Syntrophic consortia are established, incorporating H₂-evolving and H₂-consuming bacteria; and anaerobic protozoa (which have now excysted) carry symbiotic bacteria, including methanogens (Fenchel and Finlay 1995). Two important things now happen. First, the metalimnetic community reaches its maximum biomass but continues to intercept most of the available light. Second, in the anoxic hypolimnion, the sulphide produced by sulphate reducers increases in concentration. Thus a niche is created for anaerobic photosynthetic bacteria that use low levels of long-wavelength light, and sulphide as electron donor. These bacteria reach maximum abundance about 90 cm above the sediment, in late August. They produce a thick layer of slow-growing biomass that consumes nutrients, including ammonia that would otherwise pass to the overlying metalimnetic community. So nitrification is depressed, and in the absence of rainfall (as in 1996), the entire aerobic water column becomes depleted in inorganic nitrogen. Nitrogen-fixing bacteria suddenly appear and symbiotic associations between ciliates and chlorellae (the ciliate providing the chlorellae with nitrogen) now dominate the protozoan community (Finlay et al. 1996b).

At this stage of seasonal development, the water column consists of three superimposed 'compartments' (anoxic hypolimnion, micro-aerobic metalimnion, and oxygenated epilimnion), each supporting a characteristic microbial community (Finlay et al. 1988). The species in each compartment change continuously and often dramatically, with respect to both abundance and

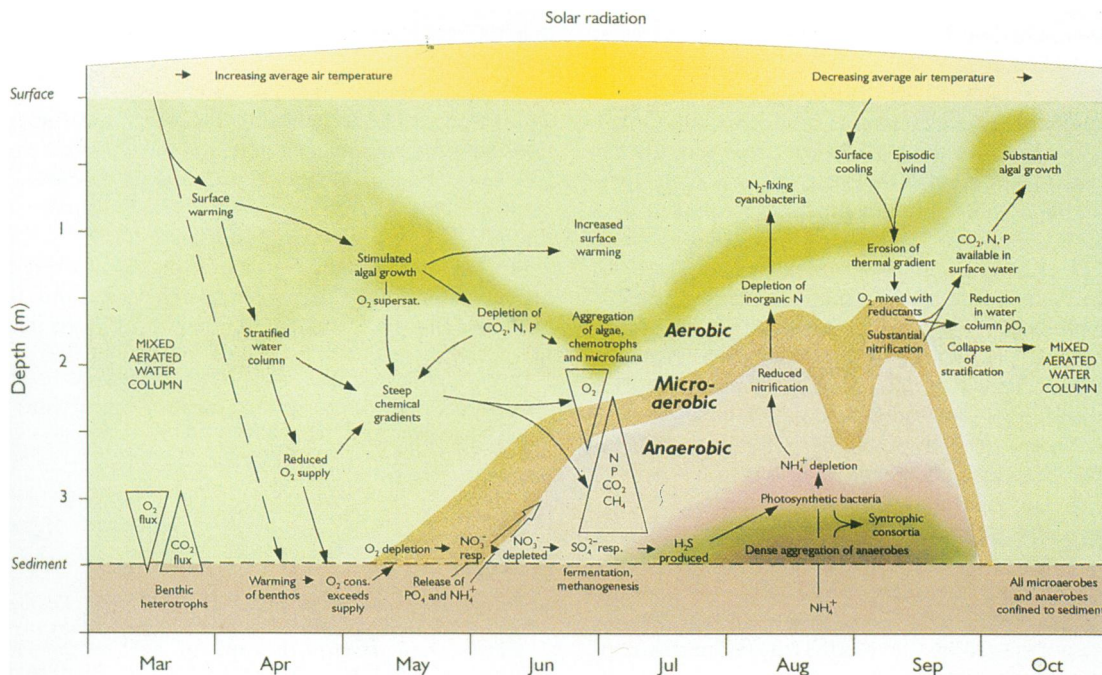


Fig. 1. An illustration of some reciprocal interactions involving physical, chemical and microbiological variables in Priest Pot, based on data obtained in 1996. The water column divides into three superimposed redox 'compartments' (Aerobic, Micro-aerobic and Anaerobic). The illustration of these compartments in the figure does accurately reflect their spatiotemporal distributions in the pond during 1996. Some processes and microbial functional groups have been excluded for simplicity, e.g. the diversity of chemoautotrophs. It is also likely that a variety of other microbial niches are periodically created in the pond although we do not yet have information on the microbes that could, at least in theory, fill them. Examples of the functional types of organisms concerned (most probably bacteria) would include those capable of anaerobic ammonia oxidation (Broda 1977), and ferrous iron oxidation by anoxygenic phototrophs (Widdel et al. 1993).

types of microbes present, but direct interactions (predation, competition) between species in different compartments are relatively rare. This presumably helps to maintain (May 1973) the typically large microbial species diversity that is characteristic of the stratified water column. The separate communities of microbes are, however, flexibly connected by the nutrient cycles. For example, although an aerobic ciliate in the epilimnion cannot feed on the anaerobic bacteria living three metres below, the CO_2 the bacteria produce can eventually be assimilated by the epilimnetic algae on which the ciliate might feed.

By the beginning of September, decreasing solar radiation leads to cooling of surface water and the deep penetration of oxygen. The renewed co-occurrence of O_2 , CO_2 and ammonia, promotes an intense burst of chemotrophic activity whose activity causes a rapid increase in nitrate and a reduction in dissolved O_2 . The return of inorganic nitrogen to the upper water causes a temporary bloom of algae. Stratification then breaks down, and water temperatures slowly fall to winter values. All of the microbial species that appeared during the period of stratification return to the sediment, where they presumably remain viable, as they appear in subsequent years whenever a suitable niche is created.

Thus, Priest Pot provides us with a comprehensible sequence of reciprocal interactions involving physical factors, microbial activity, and water chemistry. These interactions produce a large number of potential niches in space and time which, in conjunction with short microbial generation times, can support high biodiversity. This is apparent from the rapidly growing inventory of microbial 'species' recorded for Priest Pot which currently stands at more than 600. The true microbial diversity will be much higher, as this figure does not include viruses that may be important (Bratbak et al. 1994, Maranger and Bord 1995). These are abundant in the water column of Priest Pot and they comprise a wide variety of morphotypes.

Activity, diversity and function

The net result of all physical-chemical-microbial interactions is the way the ecosystem functions, and as we characterise ecosystem functions as the patterns and scale of mineral cycling and carbon fixation, it is apparent that microbial activity is inseparable from ecosystem function. We may extend this reasoning to claim

that microbial diversity too is inextricably linked to ecosystem function. This requires the proposition that all microbial niches are always filled. This may be so: microbes are inherently fast-growing, extremely abundant, easily dispersed over large distances, and unlikely to become locally extinct (Fenchel 1993). So, all new microbial niches created in Priest Pot are likely to be filled within a short space of time by recruitment from the locally available diversity of rare and dormant microbes (Finlay et al. 1996c, Fenchel et al. 1997). Perhaps it is a general rule that all vacant microbial niches are quickly filled. If new microbial niches are always filled, the number of microbial species *active* at any point in time (i.e. the microbial diversity) depends upon the number of microbial niches available which, as we have seen, depends upon the interaction between microbial activity and the physical–chemical environment. Thus microbial activity and diversity are *both* a part of, and inseparable from, ecosystem function (Fig. 2).

We believe that this study of a small pond illustrates some distinctive general features of microbial diversity that are not shared by the ‘biodiversity’ of macroscopic animals and plants:

(1) Most microbial species are ubiquitous, although many are typically rare or cryptic. As in the case of Priest Pot, many microbes are simply ‘waiting in the wings’ for conditions to change in their favour (e.g. anaerobic photosynthetic, or nitrogen-fixing bacteria). The concept of ‘redundancy’ of microbial species has little meaning.

(2) Microbial diversity in an ecosystem is never so impoverished that the microbial community cannot play its full part in biogeochemical cycling. The species complement of the microbial community quickly adapts,

even to momentous changes in the local environment (e.g. the rapid transition from oxygen supersaturation to anoxia).

(3) Microbial diversity has no discrete ‘role’ to play with respect to ecosystem function. Reciprocal interactions between microbial activity and the physical–chemical environment create a continuous turnover of microbial niches that are always filled, so microbial diversity is a part of ecosystem function.

(4) The undoubtedly legitimate concerns for the loss or extinction of animal and plant species and their habitats cannot be extended to biodiversity at the microbial level.

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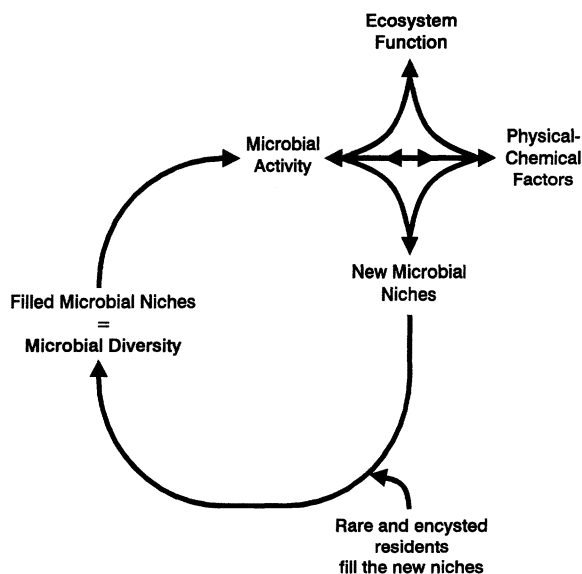


Fig. 2. Microbial diversity is a part of, and inseparable from, ecosystem function.

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