# Microbial Ecology on Land and Sea [and Discussion]

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# Microbial ecology on land and sea

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## SUMMARY

The paper reviews the fundamental ways in which microbes and microbial communities differ between terrestrial and aquatic habitats. It concludes that the fundamental principles and problems of microbial ecology on land and sea are similar. These include the basis in microbial physiology, the diversity in microbial metabolism and the fact that microbes perform key roles in element cycling within the biosphere and in carbon cycling in almost all ecosystems. Finally, the paper proposes that one of the major future roles of microbial ecology will be to achieve a more profound understanding of microbial diversity in nature.

## 1. INTRODUCTION

Microbial ecology has a divided past. In its present form it has drawn inspiration and is composed of elements of different research traditions including general microbiology and microbial physiology, various aspects of applied microbiology, agricultural research, biogeochemistry, limnology and biological oceanography. The bacterial transformation of nitrogen compounds had already been discovered around the turn of the century, and this resulted in research on the role of microbes in soil fertility. Aquatic microorganisms had, of course, been studied from a variety of view points for a long time, but (excepting unicellular phytoplankton) the quantitative role of microbes in the transfer of materials and energy in the sea was appreciated much later (especially during the past 2–3 decades). The origin of microbial ecology as a unified research field can perhaps be traced to Brock's (1966) publication although many principles were established earlier.

The purpose of this paper is to compare properties of microbes and of microbial communities on land and in the sea. It is also the intention to highlight some general principles and concepts of microbial ecology and thus to 'generalize across marine and terrestrial ecology'.

In the past, the term 'microorganism' has been defined in different ways. Traditionally, microorganisms include the prokaryotes and usually some groups of small eukaryotes (often exclusively the fungi or some groups of fungi, but not, for example, protozoa). In the context of this paper, I consider as microorganisms the prokaryotes and the unicellular eukaryotes (protozoa, phototrophic eukaryotes, water moulds and myxomycetes), but not the true fungi (ascomycetes, basidiomycetes).

## 2. MARINE VERSUS TERRESTRIAL MICROBIAL ECOLOGY

### (*a*) *Characteristics of terrestrial microbes*

In a certain sense, terrestrial microbes do not exist as water is an absolute requirement for active microbial life. 'Terrestrial' microbes are therefore really aquatic forms which have adapted to live in the thin films of water which may cover surfaces of plants and litter, or in the water which fills the pores in soils. At least from the view point of a marine biologist, microbes on land represent a special and limited group of organisms which are adapted to an extreme environment. A general comparison between aquatic and terrestrial microbes will therefore seem one-sided, focusing on the peculiarities of the latter. Different types of terrestrial habitats harbour different microbial biota, although compared to the great diversity of marine microbial habitats, and among their inhabitants, terrestrial microbes seem in many respects to share similar adaptations, and in many respects they can be treated as a special group.

Figure 1 is a schematic representation of soil which consists of a matrix of mineral particles, organic debris and interstitia filled with water or air. The water, which provides the habitats for the microbes, is held by capillary forces which can be measured as a head or pressure. The capillary diameter is inversely proportional to the head. By plotting the head against the water content of a soil sample, and because the largest pores tend to empty first, the sizes of water-filled pores can be estimated (Darbyshire 1976; Griffin & Luard 1979; Nedwell & Gray 1987; for further references see Fenchel 1987). When the pore diameter or water film is less than about 1 μm bacterial motility is not possible and the progeny of a cell will be trapped by surface tension. A water layer of around 3 μm is the ultimate lower limit for protozoan (small amoebae) activity while the small ciliate *Colpoda steini* requires a water film measuring at least 30 μm. At ordinary temperatures, a typical soil at field capacity (the water content which can be held against gravity, corresponding to 30–50%) satifies this requirement. But if the water content is lowered to about 20% by evaporation, only active bacterial life is possible. At the wilting point (about 1 kPa) water-filled pores measure only about 0.3 μm in diameter and this excludes microbial activity.

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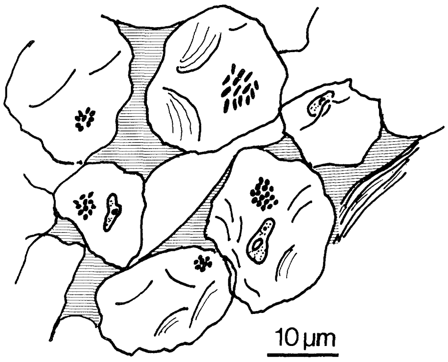

Figure 1. A schematic representation of soil with mineral and organic particles, water-filled pores and microbes.

These conditions of life explain a number of adaptations which are common to many or all soil microbes. Many species are small relative to their aquatic relatives; this is clearly the case for unicellular eukaryotes (Fenchel 1987; Foissner 1987) but this has also been claimed in the case of bacteria (Nedwell & Gray 1987). Apparently, all terrestrial unicellular eukaryotes and many prokaryotes have resting stages (cysts, endospores or other types of spores) which are resistant to desiccation. Many soil microbes have polymorphic life cycles which are adaptations to habitats which are extremely heterogeneous in time and space. These life cycles, which include a desiccation-resistant stage and mechanisms for the dispersal of this stage, exemplify a remarkable convergence between entirely unrelated groups (figure 2). Many protists (e.g. the amoeba-flagellates *Tetramitus* and *Naegleria*) have amoeboid as well as flagellated stages, the latter being induced by an increased water content (rains). The ciliated protozoa belonging to the genus *Colpoda* produce, in addition to (desiccation resistant) resting cysts, reproductive cysts (within which the cell undergoes multiple fissions). In this way the trophic stage can fully utilize the brief episodes of mass occurrence of bacteria following rainfall. In many forms, resting cysts are formed spontaneously (and not necessarily in response to desiccation) and in some forms only a certain fraction of the resting cysts excyst during each rainfall. These traits represent a sort of bet hedging in response to the unpredictability of the duration of moist periods. Finally, many terrestrial microbes tend to develop a mycelium-like or filamentous morphology (e.g. the bacterium *Actinomyces*, myxomycetes and the amoeba *Leptomyxa*).

Among the eukaryotic microorganisms the testate amoebae and the ciliates are represented by almost exclusively terrestrial species (or genera) and many species occur only in particular habitats (soils, litter, mosses, etc.). Other groups (flagellates, naked amoebae) form biota in terrestrial habitats which are quantitatively important, but the existence of exclusively terrestrial forms has been documented more rarely (for references, see Foissner 1987). A few eukaryote groups (e.g. the slime moulds) occur exclusively in terrestrial habitats, whereas other protistan groups (heliozoans, foraminifera, radiolaria, choanoflagellates, dinoflagellates) are totally absent.

Our knowledge of the diversity of terrestrial protists is probably still incomplete. During recent years the application of direct observation (rather than dilution cultures) has greatly increased the number of known terrestrial ciliates (Foissner 1987). Even so, it seems that the number of aquatic protist species by far outnumbers terrestrial forms. In addition to the fact that a number of species-rich groups are absent in terrestrial habitats, the number of terrestrial ciliate species for example constitutes only about 5% of all known ciliate species. In the case of the prokaryotes, similar questions are more difficult to answer. Some prokaryotes, like the streptomycetes and the fruiting myxobacteria are definitely terrestrial forms. The bacterial biota of soils are also characterized by the relative high frequency of certain types (such as spore

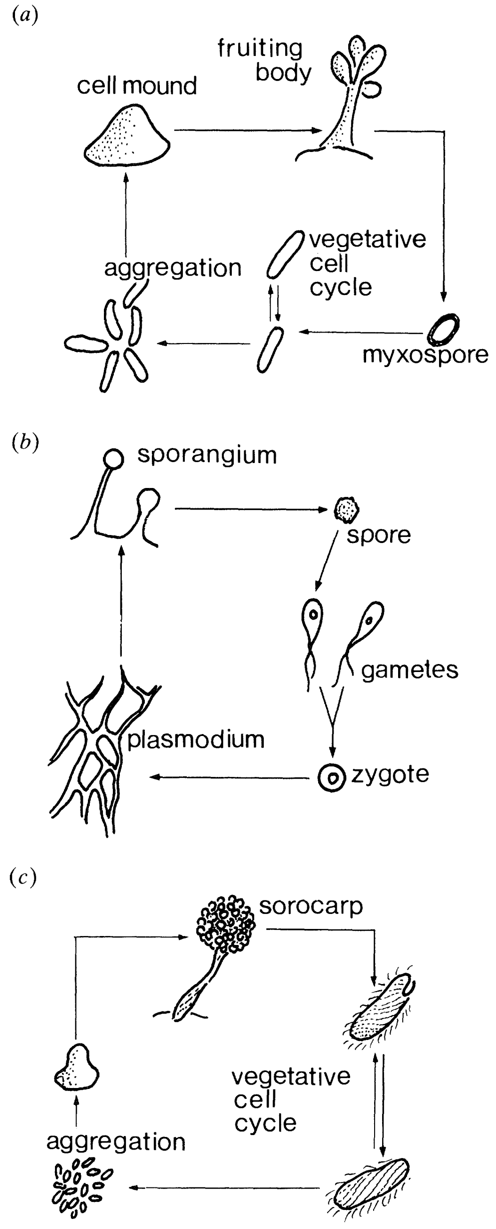

Figure 2. The convergent life cycles of unrelated terrestrial microbes. (*a*) A fruiting myxobacterium (Eubacteria); (*b*) a myxomycete; and (*c*) the ciliate *Sorogena*.

forming Gram + rods), but other types of bacteria are probably of ubiquitous occurrence. The question of bacterial diversity will be discussed further below.

### (*b*) ***Microbial community structure on land and sea***

Among the major types of aquatic biota, plankton organisms have no counterpart on land. The principal characteristics of the pelagic habitat are turbulent mixing and a relatively high transparency to light, allowing for phototrophy at considerable depths. Turbulent diffusion is anisotropic and is significantly greater in the horizontal than in the vertical direction. On a horizontal scale, plankton organisms are apparently mixed randomly and ecological events (blooms of microalgae, successional stages in the microbial communities) are correlated at length scales measured in kilometres (Okubo 1980). On a vertical axis, however, clear zonation patterns are evident on a smaller scale. Light is attenuated with depth, plankton organisms (including many protists) show geotactic or phototactic behaviour and wind-induced turbulent mixing is reduced with depth. The mixed layer ususally extends down to a pycnocline which is maintained by thermal stratification. Microbial communities therefore display vertical zonation patterns on a smaller scale (metres), and sometimes (in particular in the pycnocline) vertical heterogeneity may be apparent on a decimetre scale (Bjørnsen & Nielsen 1991).

However, heterogeneity also occurs on a very small scale in marine plankton. One important example is provided by symbiotic consortia, typically between phagotrophic and photoautotrophic protists (Taylor 1982). Another example of planktonic heterogeneity at the microscopical level is 'marine snow', namely, micro- to centimetre sized suspended aggregates consisting of diatom frustules, fecal pellets and other detrital matter, and held together by mucus which is partly produced by microbes. These particles are colonized by microbial communities including bacteria and various types of protists (Silver *et al.* 1984; Davoll & Silver 1986).

The microbial communities of marine sediments and terrestrial soils are more similar. In both cases the microbial community is found in a matrix of mineral and organic particles and their energy flow is primarily driven by allochthonous organic material and to some degree by photosynthesis in the surface layers. The distinctive difference between these two types of habitats is due to the magnitudes of diffusion coefficients of solutes in water as compared to gases (the latter being about $10^4$ times higher) and the low solubility of $O_2$ in water.

The typical vertical zonation pattern of different chemical species in a shallow water marine sediment is shown in figure 3. The fundamental reason for this pattern is the vertical zonation of microbial processes, because different potential electron acceptors (for mineralizing organic material or for oxidizing reduced endproducts of anaerobic metabolism) are exhausted at different depths. Oxygen represents the energetically most favourable electron acceptor for respiration and it is depleted first by aerobic microorganisms.

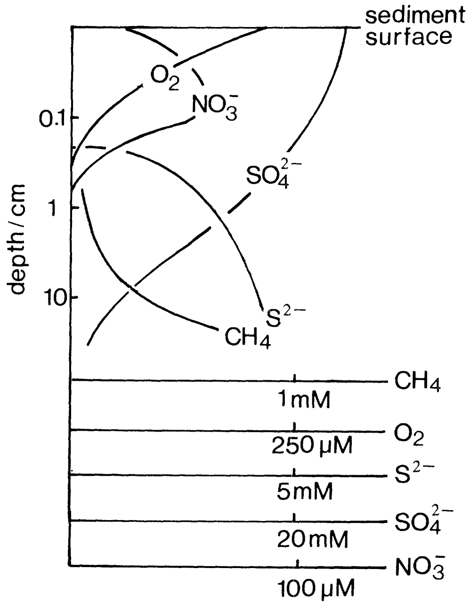

Figure 3. The zonation and approximate concentrations of different chemical species in a marine shallow-water sediment.

Assuming no oxygenic photosynthesis in the surface sediments, the depth at which $O_2$ is depleted is given by $2DC_o\phi/J$, where $D$ is the diffusion constant, $C_o$ the oxygen concentration at the surface, $\phi$ is the porosity of the sediment and $J$ is the oxygen flux (the depth integrated $O_2$-consumption in the surface layer). This depth is typically 1–2 mm, but it extends a few millimetres further down if oxygen is produced photosynthetically in the surface layer. When oxygen is depleted, nitrate becomes the electron acceptor of choice (but this process generally plays a quantitatively modest role). Below this, a zone of sulphate reduction (leading to sulphide as the principle endproduct) is found and at even greater depths $CO_2$ serves as an electron acceptor for methanogenic bacteria. The concentration profiles of the species other than $O_2$ are somewhat more complicated in that they are both consumed and produced at different levels in the sediment, but they can also be explained by diffusion equations and rates of production and consumption (Fenchel & Blackburn 1979; Revsbech & Jørgensen 1986). Notwithstanding that this presentation is simplified insofar as other electron donors or acceptors (especially Fe and Mn) play a role, and because horizontal heterogeneity (such as worm burrows) and mixing by animals may disturb the idealized picture, it does correctly describe microbial communities in sediments as an orderly vertical zonation of different types of organisms and microbial processes.

This is all quite different in ordinary soils with an air phase, so that oxygen can diffuse throughout the soil, which is essentially an aerobic habitat. However, the crumb structure of soil allows for anaerobic conditions within the core. The minimum radius required of an (oxygen consuming) sphere to become anaerobic at its centre is given by $(6C_oD/R)^{1/2}$, where

$R$ is the $O_2$-consumption per unit volume. In practice, this means that water-saturated soil particles with a typical microbial $O_2$-uptake, and exceeding a few millimetres in diameter, will have an anaerobic centre. Important anaerobic processes (sulphate reduction, denitrification, methanogenesis) occur in soils, but they take place in small isolated niches within an aerobic matrix (Nedwell & Gray 1987).

A final difference between terrestrial and marine microbial communities concerns the substrates of bacteria (and thus the base for microbial food chains). In marine environments, the single most important substrate is provided by the excretion of low-molecular mass organic compounds from unicellular algae (especially in plankton; see Azam & Cho 1987) although, of course, various polymers deriving from microalgae, macroalgae and animals also play a substantial role (detrital matter derived from seagrasses resembles terrestrial substrates). On land, primary production is dominated by vascular plants. Soil bacteria also use root excretions for substrates (see Clarholm 1985), but the bulk of organic input consists of structural (cellulose, hemicelluloses, lignin) and secondary plant products (e.g. phenols, tannins) which are almost unique to vascular plants and thus to terrestrial habitats. These compounds are mineralized by bacteria with special hydrolytic capabilities (and by the higher fungi, which are absent in the sea, but are of paramount importance in aerobic mineralization of soil organic matter). A final aspect is the extremely high carbon to nitrogen (and phosphorus) ratios of terrestrial organic substrates which results in patterns of mineral cycling which differ quantitatively from those in the sea.

## 3. GENERALIZING ACROSS MARINE AND TERRESTRIAL MICROBIAL COMMUNITIES

Although terrestrial and marine microbial communities do show distinct differences, as exemplified above, contemporary microbial ecology is a unified field of research. Its most important results, principles, concepts and challenges are common to terrestrial and aquatic studies; these will be the topic of this last section.

Perhaps the most important unifying basis for microbial ecology is microbial physiology. Thus precise knowledge of bioenergetics, growth yields and rates as a function of external factors have formed the basis for a more profound understanding of interactions between species (competition, syntrophy, predation), and experimental systems provide ecological insight. In this way a firm basis for understanding the distribution and abundance of microorganisms in nature has been obtained which is unparalleled in 'macroecology'. Examples of this sort of approach are chemostat studies (e.g. Veldkamp & Jannasch 1972) and studies of the distribution of microorganisms in chemical gradients (e.g. Wimpenny 1981).

Taken as a whole, the prokaryotes represent a metabolic diversity which is unchallenged by eukaryotes. Only prokaryotes are capable of degrading a large number of natural polymers as well as xenobiotic compounds. It is also important that most of the key processes in biogeochemical cycling (the nitrogen, sulphur and carbon cycles, the reduction and oxidation of many metals) are exclusively carried out by more or less specialized bacteria. The nitrogen cycle may be taken as an example. In nature, nitrogen occurs in five different oxidation states. Green plants are capable of assimilatory reduction of nitrate to ammonia (the oxidation state in organic compounds). All other key processes (fixation of $N_2$, denitrification replenishing $N_2$ to the atmosphere, dissimilatory reduction of different oxidized N-compounds and nitrification) are exclusively microbial processes. Although the quantitative importance of various microbial processes may be different in the sea and on land they are qualitatively similar and they are carried out by similar organisms.

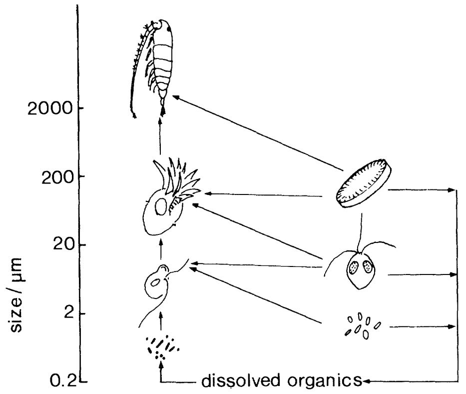

Figure 4. The 'microbial loop' in marine plankton. Pro- and eukaryotic phototrophic organisms serve as food for phagotrophic plankters, but these also excrete low-molecular mass organic compounds which serve as substrate for bacteria which enter the phagotrophic food chain. Redrawn from Fenchel (1988).

Another unifying concept (and result) of microbial ecology is what is referred to as the 'microbial loop'. Although this term has so far been used only in the context of (espcially marine) plankton (see Fenchel 1988) the phenomenon it describes was known much earlier from terrestrial environments. It describes the fact that a substantial (and often the greatest) part of the primary production is not consumed by herbivores, but is degraded by bacteria (and fungi on land) which again form the basis for food chains in which phagotrophic protists predominate at the lowest levels (figure 4).

The underlying reasons for this are several: only the smallest organisms (namely bacteria) can efficiently utilize dilute organic solutes which are excreted by algae or roots, and only bacteria are capable of hydrolysing many plant polymers. Secondly, because these compounds are poor in nitrogen, the decomposing organisms must be capable of assimilating inorganic nitrogen compounds from their surroundings. In some environments, it is also important that only bacteria (and some of their protist grazers) can live in anaerobic habitats. The central role of protozoa as grazers of bacteria is explained by the fact that efficiency in particle capture is optimized by a given size ratio between predator and prey (Fenchel 1984).

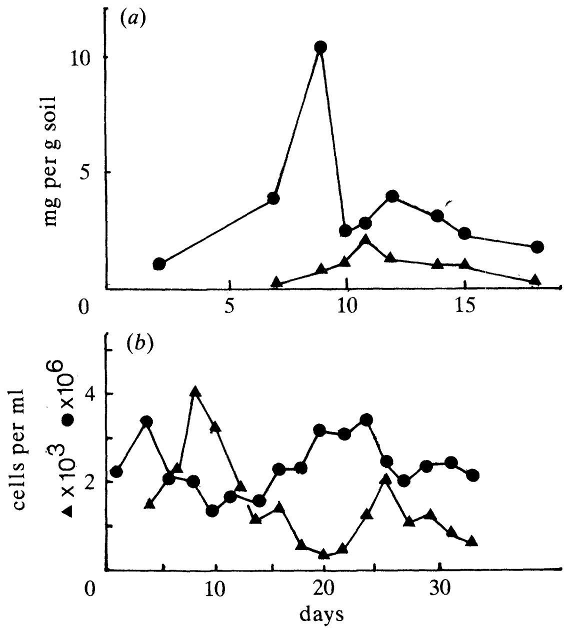

Figure 5. Coupled population oscillations of bacteria (circles) and of their protozoan predators (triangles) in a soil (*a*) and in marine plankton (*b*). In the soil the protozoa were predominantly small amoebae and in the plankton heterotrophic flagellates. In the soil the successional events were triggered by rainfall and in the plankton, by blooms of microalgae. (*a*) is based on data in Clarholm (1981) and (*b*) on data in Fenchel (1982).

Figure 5 shows the similarity in the predator-prey oscillations of bacteria and bacterivorous protozoa in a soil and in marine plankton, respectively.

The last question to be discussed here, which is an important challenge for microbial ecology, is to obtain an understanding of microbial diversity in nature. In the context of eukaryote microbes, our knowledge is probably still incomplete, but this can probably be improved through traditional concepts and methods. With respect to prokaryotes, however, special problems occur. Bacteria have traditionally, but to a small extent, been classified and identified on the basis of morphological traits. More commonly, various biochemical traits have been used, and in particular, properties which ecologists would consider as niche parameters (the ability to grow on particular substrates and under particular environmental conditions). On this basis about 4000 species have so far been named.

Although horizontal transfer of genes occurs among bacteria, it is not possible to apply a 'biological species concept' in bacteria. Recently, sequencing of rRNA genes has provided fundamental insight into the phylogeny of the prokaryotes. These techniques have also been applied for assessing microbial diversity in nature (for references, see Pedrós-Alió 1993). The results of these endeavours have largely been taken to mean that natural environments harbour a substantial diversity of bacteria and that many new species (since in some cases similar rRNA sequences could not be identified in available libraries) remain to be discovered. Recently, however, Rehnstam *et al.* (1993) have provided evidence that the bacterial biota of marine plankton is at any time dominated by one or a few species which are known and culturable.

Several concepts need to be developed and several problems need to be solved before the question of bacterial diversity can be addressed in a meaningful way beyond that of classical bacteriological methods. There are as yet no criteria by which differences in nucleotide sequences can be calibrated with the current species concept of bacteriologists except by taking the extreme (and useless) stand that every adopted mutation represents a new species. Furthermore, it is likely that almost any known type of bacterium will be present in almost any habitat although the cells may be metabolically inactive and there may be only very few cells present. The reason for this is the huge population densities achieved by bacteria wherever they are successful combined with a high potential for dispersal. A more profound understanding of prokaryote diversity in nature which extends beyond the different types of metabolic processes on the one hand and beyond that of classical bacteriology on the other will be an important goal for microbial ecology in the coming years.

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### *Discussion*

M. Whitfield (*Marine Biological Association, Plymouth, U.K.*). In his lecture Dr Fenchel did not mention the role of symbiotic bacteria in structuring ecosystems and enabling higher organisms to inhabit a wider range of ecological niches. Could he comment on the relative importance of such symbiosis (both intracellular and extracellular) in terrestrial and marine ecosystems?

T. Fenchel. A complete answer to this question could easily fill another paper. Microbial ecto- and endosymbionts occur, of course, both in aquatic and terrestrial organisms. I can briefly make two generalizations.

1. Phototrophic symbionts are very important among aquatic organisms (e.g. in many protozoa, coelenterates, turbellaria and molluscs), but (with the exception of lichens) it is a very rare phenomenon on land. One contributing explanation may be that terrestrial animals are generally not transparent to light.
2. Vascular (terrestrial) plants consist mainly of structural carbohydrates (cellulose, xylan, etc.) and lignin. Animals seem not to be able to utilize these compounds directly. Instead many herbivores utilize symbiotic anaerobic fermenting microbes for the degradation of cellulose and other carbohydrates into volatile fatty acids which constitute the carbon and energy source of the host. This is best known from termites and ruminants, but it is found in many other groups of terrestrial arthropods and vertebrates. This type of symbiosis is rare in the sea, where vasular plants play a small role.

P. Meadows (*University of Glasgow, U.K.*). Dr Fenchel makes a clear distinction between the structure of marine sediments and terrestrial soils. While I would agree with most of the points he makes, I have sometimes found it difficult to distinguish the microbial communities on a near-shore marine sand grain from those on a typical terrestrial soil grain, at least at a scanning electron microscope level. This immediately makes me wonder about different scales of spatial and temporal heterogeneity in the two environments. Has anyone compared microscale spatial and temporal variability in microbial community structure between terrestrial soils and marine sediments using exactly the same experimental protocols and techniques? To be really meaningful as a comparison, very careful cross calibration would be required, unless the work was conducted by the same person with the same equipment. If this work has been done what sort of parameters have been measured, what is their accuracy, and at what scales have the parameters been measured?

T. Fenchel. I agree that the ‘aufwuchs’ on marine sand grains can show a considerable patchiness and heterogeneity (as you have previously shown). What I particularly wanted to stress, is that the presence of an air phase in soils makes a difference. In aquatic sediments there is a characteristic vertical zonation which results from different electron acceptors being used sequentially: near the surface $O_2$ is depleted, then $NO_3^-$, etc. In soils, oxygen can diffuse much more rapidly in the air phase and we therefore see small anaerobic microhabitats in the form of water-logged soil particles which are imbedded in an aerobic matrix. I think this is well documented through recent work with microelectrodes for sensing various chemical species. Such electrodes have a spatial resolution of $\approx 100\ \mu\text{m}$, a limit basically determined by diffusion.

J. Huisman (*Department of Plant Biology, University of Groningen, The Netherlands*). Dr Fenchel indicated that the outcome of competition in the chemostat is related to the substrate availability. In this context it is perhaps noteworthy and rather counterintuitive that the outcome of competition for a single substrate is independent of the substrate concentration supplied from the stock vessel into the culture vessel.

T. Fenchel. I am sorry if I have been misunderstood; I do not, in any way, want to dissent from classical chemostat theory. However, the equilibrium substrate concentration in a chemostat is independent of the substrate concentration in the reservoir, and depends only on the dilution rate, the Monod constant and the maximum growth rate constant. The outcome of a competition experiment between two bacteria using the same substrate depends on the dilution rate and the parameters $\mu_m$ and $K_s$, but not on reservoir substrate concentration (which will, however, determine the equilibrium population size).