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17 Ecosystem Consequences of Microbial Diversity and Community Structure

J. SCHIMEL

17.1 Introduction

Biodiversity has become a major theme in ecological research and environmental policy (Schulze and Mooney 1993). This concern has arisen because people value diversity both for its own sake and because diversity may control important ecosystem services (food, fiber, animal production, tourism). While the first rationale for concern over biodiversity should apply to microbes, they lack charisma. I therefore doubt that arguments about microbial biodiversity for its own sake will carry much weight for most people, and our concerns with the issue will rest primarily on the implications of their diversity for ecosystem function. While several papers have discussed the effect of functional diversity on ecosystem processes (Meyer 1993; Beare et al. 1994), they basically conclude that microbes carry out many processes that are important to ecosystem function and that their interactions are complex. Formulating meaningful conclusions about the importance of diversity within functional groups, however, has been difficult.

The challenge in relating microbial diversity to ecosystem function is fundamentally one of relating the scales of microbial life to the scale of the ecosystem. Studies whose primary focus is at the ecosystem level may range from the landscape scale (to put the system into a larger perspective), to the process scale (to explain why the system behaves the way it does). When we discuss "microbes", however, we are considering organisms whose cells (for bacteria) or individual hyphae (for fungi) are microns in diameter, though individual fungal mycelia can extend over many square meters. At a small enough scale, microbial community structure *must* be a dominant control on ecological processes, but as we move up in scale toward the ecosystem and integrate across many individual communities, the influence of individual community structures decreases. The central question for this chapter can therefore be usefully phrased and diagrammed (Fig. 1):

Is there some minimal scale necessary to adequately explain ecosystem processes at which microbial community structure still has a measurable influence on the nature and rates of those processes?

This approach forces us to first determine whether we can adequately explain the dynamics of ecological processes without specifically considering the

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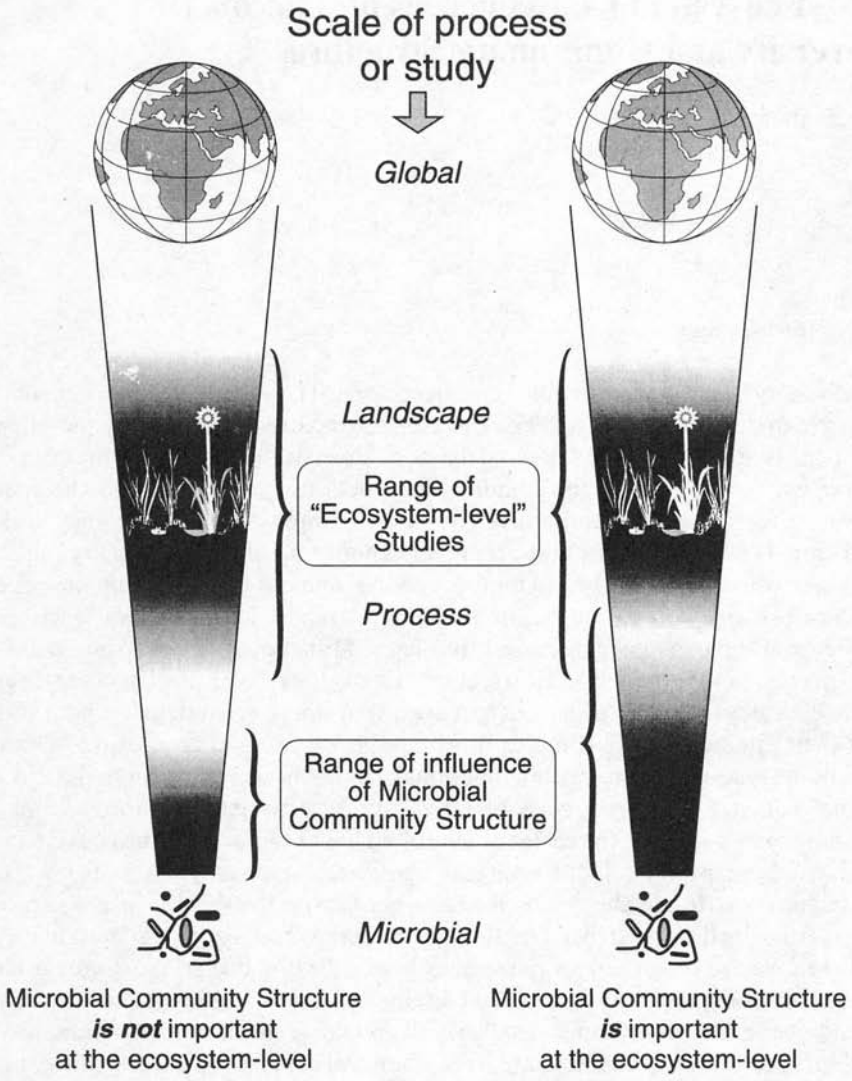

Fig. 1. Framework for deciding which kinds of ecological processes require understanding microbial community structure in order to understand ecosystem-level dynamics

microbial community. Only if this fails, do we need to examine microbial community structure. Thus, initially at least, we avoid difficult issues such as the vast diversity of unculturable organisms in soil. While such issues may be important in *microbial* ecology, their significance to *ecosystem* ecology remains unclear. My objective is to provide a framework for research in this area by identifying the kinds of processes for which microbial diversity and community structure may play a role at the ecosystem level. I will focus on tundra systems,

but many examples will come from other systems because there has been very little appropriate study in the tundra.

17.2 "Broad" Processes

The initial challenge in addressing the importance of microbial diversity comes from ecosystem modeling. Few, if any, ecosystem-level models incorporate the biomass or diversity of microbial populations to drive C and nutrient flows (e.g. Rastetter et al. 1992). Even process-oriented models of decomposition and organic matter dynamics do not include microbial community structure (e.g. Grant et al. 1993), yet, they generally predict carbon, nutrient, and microbial biomass dynamics reasonably well. This poses a challenge to microbial ecologists: Does microbial community structure have *any* system-level consequences in terrestrial ecosystems?

That ecosystem models "work" suggests that large-scale biogeochemical cycling is insensitive to microbial community structure. The next step in determining whether microbial community structure can affect ecosystem level dynamics therefore should be to shift the perspective to the next smaller scale and to examine the more specific processing of substrates during carbon and nutrient turnover in soil. Several studies provide information on this issue.

Sugai and Schimel (1993) tested the hypothesis that as the inputs of carbonhydrates and phenolics in litter varied through succession in the taiga, adaptation of the microbial community to a changing substrate would cause changes in its ability to use these compounds. The primary polymeric material of plant and soil organic matter must be broken down to sugars and simple phenolics by extracellular enzymes before they can be used by microbes, so we therefore tested the ability of different communities to use sugar and phenolic monomers. We collected soils from six sites dominated by tree species ranging from alder to white spruce and assayed their ability to metabolize ^{14}C-labeled model compounds. We measured the conversion of glucose, p-hydroxybenzoic acid, and salicylic acid (o-hydroxybenzoic acid) into CO_2 and microbial biomass over a 48-h period. While each compound was metabolized quite differently from the others, the differences with successional state or season were minimal (Fig. 2). Even the time courses over the 48-h assays were remarkably similar. While the microbial communities presumably varied between the sites, the metabolic pathways and even C-use efficiencies for each substrate were consistent across all of them. At the functional level examined by this experiment, the communities all behaved the same, suggesting limited importance of microbial diversity in controlling metabolism of simple C-compounds. This is not to say that a different process, such as lignin breakdown, would not exhibit functional differences related to microbial population structure.

A second study examined microbial uptake kinetics across a range of tundra soils. Using techniques similar to those of Schimel and Firestone (1989), I measured short-term (6-h) $^{15}NH_4^+$ uptake in soil slurries with different NH_4^+ to

determine the microbial N-uptake kinetics. There was a strong relationship between %N in the soil material and the maximum NH_4^+ uptake rate (Fig. 3). Tussock and intertussock soils showed very similar N-contents and N-assimilation kinetics despite very different chemical and physical composition. Tussock soils consist of dead *Eriophorum vaginatum* roots in a densely tangled mass, while intertussock soil is primarily composed of decomposed mosses. Intertussock soils are wetter and thaw much later in the season than tussocks. Thus, it is likely that the microbial communities would be substantially different, yet their N-assimilation kinetics were remarkably similar.

These studies suggest that for broad-scale processes and for broad physiologies, there is little apparent influence of microbial community structure. The next level to consider is therefore "narrower" processes or physiologies, those carried

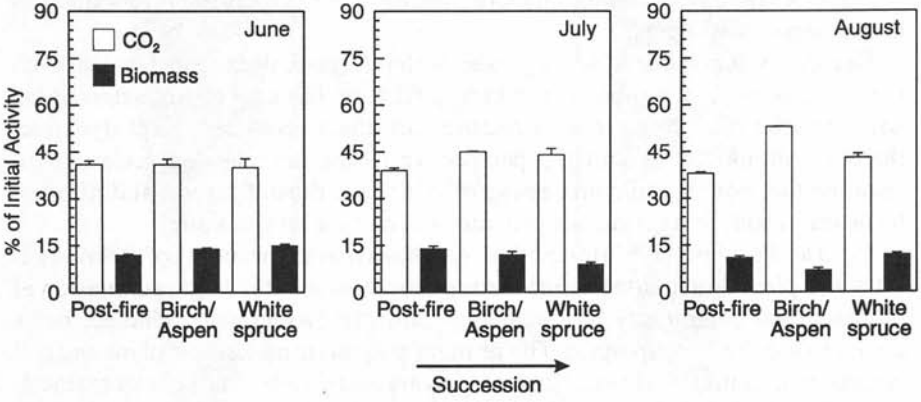

Fig. 2. Metabolism of p-hydroxybenzoic acid in soils from a post-fire secondary succession in the Alaskan taiga. Data represent the % of initial ^{14}C activity found in either CO_2 or K_2SO_4 extractable biomass. (Sugai and Schimel 1993 with permission of Pergamon Press)

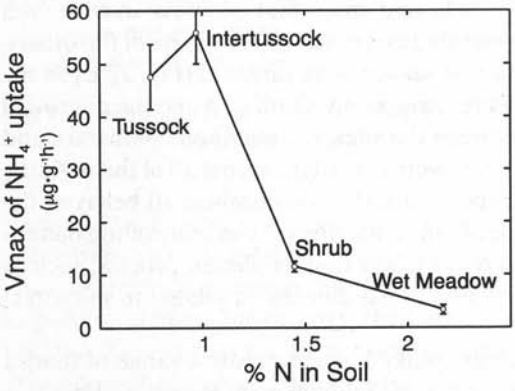

Fig. 3. V_{max} of NH_4^+ uptake by tundra soil in slurry assays

out by restricted groups of microorganisms. I will consider three groups of processes that have broad ecosystem importance, yet may be considered "narrow" and should therefore test whether at this level microbial population structure may have ecosystem-level significance. These are plant-microbe interactions, litter decomposition, and trace gas production.

17.3 "Narrow" Processes

17.3.1 Plant-Microbe Interactions

Plant-microbe interactions occur at different levels ranging from nutrient competition to highly specific symbiotic and pathogenic relationships, which may affect ecosystem structure and function at very large scales.

Mycorrhizae have diverse effects on plants and these effects are sensitive to the specific fungi that form the mycorrhizae (Read 1993). Many of these effects are reviewed in depth in Harley and Smith (1983) and Allen (1992) and so will only be mentioned briefly here. Direct effects that are sensitive to the fungiforming mycorrhizae include: inorganic N uptake (Finlay et al. 1992), organic N use (Abuzinadah and Read 1986), P metabolism (Ho and Zak 1979), pathogen resistance (Azcón-Aguilar and Barea 1992), and drought tolerance (Read 1992). Indirect effects include: the rate of soil organic matter decomposition (Dighton et al. 1987; Haselwandter et al. 1990), altered rhizosphere populations (Azcón Aguilar and Barea 1992), altered soil fauna populations (Fitter and Saunders 1992), and altered mammal diets–many animals eat mycorrhizal fruit bodies (Trappe and Maser 1977). These effects may not only be sensitive to the species of mycorrhizal fungus present but even in some cases to the specific fungal strain (Ho 1987). The fungi infecting the roots of ectomycorrhizal plants also change with both age of the plant and successional time (Dighton and Mason 1985), thus changing the nature of mycorrhizal communities and their effects on system behavior.

Not surprisingly, mycorrhizae affect the dynamics of plant communities. Ectomycorrhizae can enhance the reestablishment of forests after disturbance (Perry et al. 1989). Mycorrhizae also affect plant competition after colonization, though these effects are complex, sometimes favoring one species, while other times alleviating negative interactions between species (Miller and Allen 1992). For example, VA mycorrhizal infection enhances the competitive ability of late-successional grasses over nonmycorrhizal early invaders (Allen and Allen 1984; Miller and Allen 1992). Ectomycorrhizal infection of Douglas fir and Ponderosa pine seedlings, however, removed the mutual growth inhibition between the species that occurred with uninfected plants (Perry et al. 1989); this effect was dependent on the specific infecting fungi.

Many ectomycorrhizae form extensive mycelial mats, which may cover square meters with a single mycelium. Mycelial mats substantially alter the rates of decomposition and nutrient cycling within them. Studies by Griffiths et al. (1990) and Entry et al. (1991) have shown that N and P loss from decomposing litter is

greater in mat than nonmat soil and that nitrate concentrations are significantly lower in the mats as well (Fig. 4). This may result partially from increased nutrient uptake and transfer into the plants but it may also result from specific changes in decomposition as suggested previously (Gadgil and Gadgil 1975). Some saprophytic fungi also produce mycelial mats. The presence or absence of a single species of fungus can therefore significantly alter important nutrient cycling processes.

N fixers probably show less dramatic but similar effects on community dynamics. Different strains of N fixers vary considerably in their abilities to infect roots and to fix N; some strains are highly infectious but are poor N fixers, while other strains are effective N fixers but less efficient at infection. This is true in both the legume-rhizobium (Alexander 1985) and the actinorhizal-Frankia system (Benson and Silvester 1993). The establishment and survival of legumes and actinorhizal plants depend, at least in part, on the availability of appropriate symbionts and on the effective functioning of those symbionts. Thus, establishment of plant communities in primary succession, where N fixing plants are often critical, may be sensitive to the dynamics of N fixer populations (Halvorson et al. 1991).

Microbial pathogens can also spread over wide ranges and dramatically alter ecosystem dynamics. For example, the potato crop of Ireland was nearly wiped out by potato blight during the 19th century and the forests of the eastern USA are still recovering from the introduction of chestnut blight (Stephenson 1986). Under stable, natural conditions without long-range transport of pathogens, plants often coevolve with their pathogens to limit the damage done by them (Burdon 1993). Human transport of novel pathogens into new territory, however, can cause large-scale damage to plant populations sensitive to the new organisms. Additionally, factors such as changing climate, pollution, and UV radiation

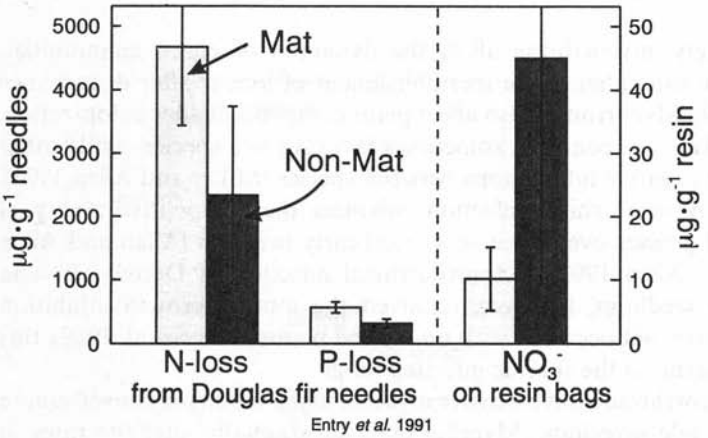

Fig. 4. Effect of *Hysterangium* mats on nutrient loss from decomposing Douglas fir needles and on NO_3^- accumulation on resin bags. Data from Entry et al. (1991)

may stress plant populations sufficiently to allow minor endemic pathogens to become major problems (Nihlgård 1985). Human factors may therefore enhance the importance of microbial pathogens as controls on ecosystem structure at a large scale.

The ecosystem-level impact of specific plant-microbe interactions, both mutualistic and pathogenic, appears to be greatest under conditions of change: plant migration, organism introduction, and environmental stress changing the susceptibility of hosts. Tree-line movement into tundra systems may be the process most sensitive to specific plant-microbe interactions. Tree establishment may rely on the availability of appropriate mycobionts, yet such fungi are unlikely to be found in tundra soils. As many ectomycorrhizal fungi fruit underground, their migration may also be slow and at least partially dependent on the activity of small mammals (Molina et al. 1992). Shifting the balance of woody shrubs in tundra may also be influenced by mycorrhizal interactions, but most of the common tundra shrubs are widely distributed, and so, probably, are their mycobionts. The introduction of novel plant pathogens, I suspect is unlikely in the Arctic. The dominant arctic flora is circumpolar (see chapters by Walker and others, this Vol.) and many species have migrated extensively in post-glacial time (see Murray, this Vol.). Therefore, it seems unlikely a plant would encounter a pathogen that it had not been previously exposed to.

17.3.2 Litter Decomposition

While litter decomposition may not seem to be a "narrow" physiology, litter is relatively chemically and physically homogeneous, composed largely of cellulose, hemicellulose, and lignin in a well-defined physical structure. Leaf litter also falls onto the soil surface where fluctuations of moisture and temperature are the most extreme, and episodic stress may limit microbial populations to those capable of surviving harsh conditions.

The labile components of litter (protein, lipids, etc.) are probably broken down by a wide range of different organisms and processes. The structural materials (cellulose and lignin), however, are broken down by exoenzymes, endo- and exocellulase for cellulose (Ljungdahl and Eriksson 1985) and a small variety of peroxidases for lignin (Gold and Alic 1993). Each of these groups of enzymes is produced by a relatively narrow group of microorganisms, which can therefore act as keystone species in litter decomposition. Cellulase is produced by both bacteria and fungi; in forest systems it is generally assumed that fungi are the more important group (Ljungdahl and Eriksson 1985), but in wet tundra bacteria may be important as well. Lignin is decomposed largely by white rot fungi, though some actinomycetes also have lignolytic activity (Gold and Alic 1993). Because only limited groups of microbes are responsible for litter decomposition, it is possible for large-scale effects to result from differences between litter communities. Several studies illustrate such effects.

First, it has commonly been reported that white rot fungi only produce substantial amounts of lignin-degrading enzymes under N-limiting conditions

(Gold and Alic 1993), suggesting important linkages between wood decomposition and nutrient availability. However, this is based largely on lab studies using *Phanaerochaete chrysosporium*. Other fungi, such as *Dichomitus squalens* and *Bjerkandera* sp., show lignolytic activity at high N concentrations (Périé and Gold 1991; Kaal et al. 1993). Thus, the response of lignin degradation to N availability in the field may depend on the white rot fungi present.

Hunt et al. (1988) examined decomposition of grass and pine litters in prairie, meadow, and forest sites. Over 1 year in the prairie and meadow, grass decomposed rapidly while pine litter showed essentially no mass loss; in the forest site, however, pine litter decomposed as rapidly as the grasses. Since the different decomposition rates of grass in the two sites should have accounted for microclimate effects, the relatively greater decomposition of pine litter in the forest resulted from the presence of a soil community adapted to processing pine litter. The microbial biomass in the pine site was dominated by fungi; the ratio of fungal to bacterial biomass was 8, while in the meadow the ratio was 0.1 (Ingham et al. 1989). Additionally, the fungi were different in the sites (2.5-μm-diameter hyphae in the meadow vs 4 μm in the pine site) and the bacterial communities appear different as well (J. C. Moore, pers. comm.). McClaugherty et al. (1985) found similar results in a litter transplant study: forest litters decomposed better in their native sites than could be predicted by assuming no interaction between litter and system, indicating microbial adaptation to the native litter. These studies illustrate that the specific composition of the microflora can affect litter decomposition in different sites.

The last study is a litter bag experiment at the Bonanza Creek Long Term Ecological Research Site near Fairbanks, Alaska. We collected litter bags monthly over 2 years and subsampled each bag to measure respiration potential (short-term respiration rate after adjusting samples to 15 °C and 50% of water holding capacity). This assay integrates substrate quality and the ability of the microbial community to use the available substrate. The respiration potential dropped from the first year to the second (Fig. 5), reflecting changes in substrate quality and the resulting changes in microbial activity. The response to moisture, however, changed as well. During the first year, there was a strong positive correlation between respiration potential and litter moisture at the time of sampling (before moisture adjustment), but in the second year the correlation became negative. These data therefore indicate that the litter microbial community changed during decomposition, and its response to moisture also changed. Thus, the response of litter decomposition to moisture is sensitive to the composition of the microbial community.

17.3.3 Trace Gases

A third major group of processes that may be sensitive to microbial community structure is the production and consumption of trace gases, particularly CH_4, N_2O, and NO. In tundra, CH_4 is of greatest concern but globally N_2O and NO are also important. Metabolism of these gases is generally carried out by very

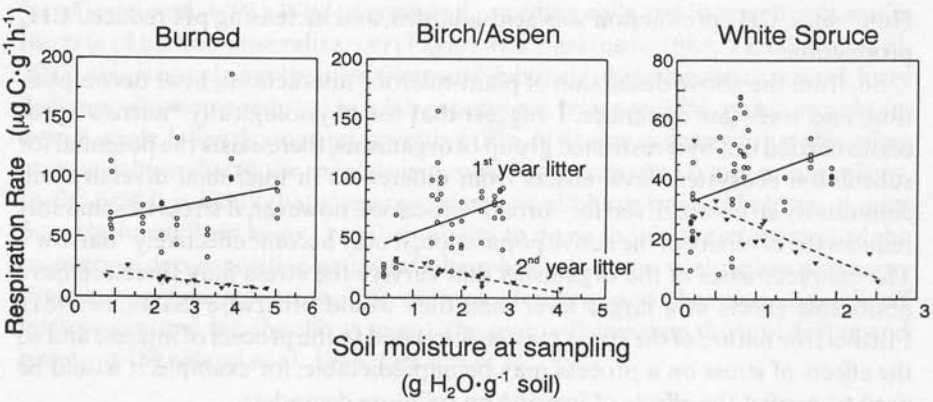

Fig. 5. Respiration potential of decomposing litter over 2 years in the field. o, First- year litter; ▼ Second-year litter

taxonomically restricted groups of bacteria. Methane is produced exclusively by a group of archaebacteria (Jones 1991) while it is oxidized primarily by methanotrophs, a small, distinctive group of bacteria (Lidstrom 1992). Nitrous and nitric oxides can be produced via both nitrification and denitrification (Firestone and Davidson 1989). While denitrification is carried out by a taxonomically diverse group of organisms (Tiedje 1988), it is physiologically narrow with only one or two basic enzyme systems for each step in the pathway (Zumft 1992). Autotrophic NH_4^+ oxidizers, on the other hand, are both taxonomically and physiologically narrow (Bock et al. 1992). We might therefore expect that the specific dynamics of most of these gases should be sensitive to the dynamics of the responsible populations and that these populations may be sensitive to environmental factors.

Even so, it is hard to find examples where the structure of the active community has effects on gas production dynamics, mostly because few appropriate studies have been done. An exception to this is the differential control of N_2O and NO production by nitrifiers and denitrifiers. The active group of organisms in the field strongly affects the rate and controls on gas production (Firestone and Davidson 1989; Schuster and Conrad 1992). Nitrifiers are aerobic autotrophs (Bock et al. 1992), while essentially all soil denitrifiers are heterotrophs that denitrify anaerobically (Zumft 1992). Since the product of nitrification is the substrate for denitrification, however, almost all production of these gases is controlled by nitrification. Thus, changes in the ammonium oxidizer community could affect NO and N_2O production from both nitrification and denitrification.

Few studies have allowed determination of any noticeable effects of microbial community structure on methane dynamics. One study on CH_4 production in peat soils, however, showed that the pH sensitivity of CH_4 production differed among communities (Valentine et al. 1994). In the neutral peats of most of their sites, methanogenesis was acid-sensitive, but in the acid, nutrient-poor "Black

Hole" sites, CH_4 production was acid-adapted, and increasing pH reduced CH_4 production.

So, from the above discussion of plant-microbe interactions, litter decomposition, and trace gas dynamics, I suggest that for physiologically "narrow" processes carried out by a restricted group of organisms, there exists the potential for substantial ecosystem-level effects from differences in microbial diversity and community structure. Even for "broad" processes, however, if stress of some sort reduces the diversity of the active population, it may become effectively "narrow". The characteristics of the organisms that survive the stress may therefore have noticeable effects at a larger level than they would otherwise (Salonius 1981). Further, the nature of the stress may be unrelated to the process of interest and so the effects of stress on a process may be unpredictable; for example, it would be hard to predict the effects of freezing on cellulose degraders.

17.4 Stress

Stress, both chemical and physical, can reduce both microbial biomass and community diversity (Atlas 1984; Domsch 1984). Chemical stress may result naturally from changing inputs of specific plant compounds to the soil or from human pollution. While many plant compounds are microbial substrates, others such as phenolics and terpenoids, may be toxic (Rice 1984; White 1986). The effects of different phenolic acids on soil populations vary with compound, concentration, type of organism, and soil horizon, often stimulating but sometimes inhibiting microbial activity (Blum and Shafer 1988). Of specific relevance to the Arctic, many lichens produce complex phenolics that are strongly antimicrobial (Lawrey 1989). Anthropogenic chemical stresses that have been shown to reduce biomass or alter communities include acidification (Visser and Parkinson 1989), heavy metals (Domsch 1984; Brookes et al. 1986), and organic compounds such as pesticides, oil, or industrial chemicals (Domsch 1984; Leahy and Colwell 1990). Chemical stress can have complex effects on microbial communities. For example, additions of jet fuel to soil increased total populations of bacteria, fungi, and hydrocarbon degraders, but reduced total microbial activity, suggesting that breakdown of native soil organic matter was inhibited (Song and Bartha 1990).

Physical stresses may be more common than chemical stresses and include aggregate disruption by tillage, roots, or microfauna, freezing, drought, and rapid variation in these factors such as drying/rewetting and freeze/thaw events. Drought is a major stress on microbial populations and has different effects on different groups of bacteria and fungi (Harris 1981). The stresses from drought and reduced water potential include direct water stress on the organisms (Harris 1981), reduced substrate diffusion in dry soils (Skopp et al. 1990), and increased microbial demand for C and N (Harris 1981; Schimel et al. 1989).

Despite the range of stress imposed by drought, rewetting may be worse. Drying and rewetting can kill a large part of the microbial biomass and substantially alter the composition of the surviving community (Kieft et al. 1987;

Van Gestel et al. 1991). While drying and rewetting soils and litters often increase the rate of carbon mineralization (Taylor and Parkinson 1988; Van Gestel et al. 1993), this is not always the case. Clein and Schimel (1994) showed that birch litter decomposition was reduced in a lab experiment by up to 25% over 2 months by even a single 1-day drying and rewetting (Fig. 6). It was suggested that this effect may have been due to the reduction in some key group of enzymes or organisms. In the field it is likely that these organisms would have been able to recolonize from the forest floor below, but their ability to do so should therefore control the recovery of decomposition activity. Other physical stresses may be less damaging than drying and rewetting. For example, freezing and thawing also kill off microorganisms, but the effects seem to be generally less than those of drying and rewetting (Skogland et al. 1988; DeLuca et al. 1992).

17.5 Implications for Tundra

Several properties of tundra systems may be particularly sensitive to microbial community structure: plant nitrogen uptake, vegetation response to changing climate, and the effects of arctic pollution. Nutrient supply to plants may be more sensitive to microbial community structure in tundra than in most other systems. Tundra plants often appear to acquire nutrients released by freeze/thaw events or other stresses that kill microbes (Gersper et al. 1980; Schimel et al. 1994). Thus, the specific ability of organisms to survive the stress and the ability of the survivors to grow and compete for the nutrients released may affect nutrient availability to plants. Second, amino acids appear to be an important source of N for many tundra plants (Chapin et al. 1993). Amino acids are excellent microbial substrates as well as breakdown products of polymer metabolism. The release and uptake of different amino acids involve a complex suite of processes,

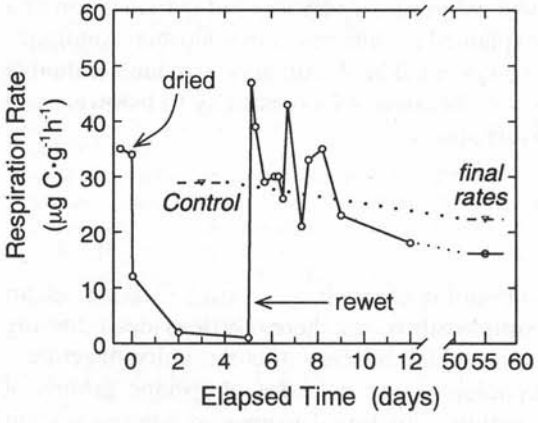

Fig. 6. Effects of drying and rewetting on microbial activity in birch litter

intimately linked to fundamental microbial biochemistry; it therefore may be sensitive to the specific structure of the microbial community. The second area that may be sensitive to the composition of the microbial community is the invasion of shrubs and trees into tundra. As previously discussed, mycorrhizal and rhizosphere populations may control plant community development. Finally, increased pollution in the Arctic could reduce critical microbial populations and thereby alter the dynamics of ecological processes in significant, though possibly unpredictable ways.

17.6 Overall Considerations

It appears that for "narrow" processes or where diversity is reduced by stress, the specific composition of the microbial community may have large-scale effects on ecological processes. This suggests that even for broad processes, the structure of the community may influence process dynamics, but without being able to link a process to different populations under different conditions, we are unable to demonstrate this. For these "broad" processes that involve many organisms, it is easy to see the diversity as redundancy, but each organism may only carry out the process under a specific set of conditions, rather than being truly redundant. Thus, in some cases, redundancy may be more apparent than real. Our inclination to see microbial diversity as redundancy may result in part from our very broad definitions of many microbial functional groups, e.g. denitrifiers. If we used equally broad categories for plants, we might only be able to divide plants into trees, shrubs, forbs, graminoids, and bryophytes.

There are ways in which microbial community structure and diversity have impacts at the ecosystem level, yet we know very little about many of those impacts. Because of this, I have included much speculation in this chapter. Only recently have techniques become available for studying microbial community ecology and linking community studies with process studies. I therefore expect that as such studies develop, we will see progressively more of the variation and surprises in microbial processes explained as differences in microbial communities from site to site and system to system. The Arctic may provide a valuable testing ground for some of these ideas because of its sensitivity to belowground processes and environmental perturbations.

17.7 Conclusions

1. For "broad" processes and physiologies, such as overall C flows in an ecosystem and metabolism of simple substrates, there is little evidence for any ecosystem-scale significance of microbial diversity or community structure.
2. For a range of "narrow" physiologies, the presence of specific groups of microorganisms or differences within a functional group may have significant impacts on process dynamics. Specific plant-microbe interactions are highly

sensitive to the presence of specific microbial species (e.g. pathogens and mycorrhizae), but processes such as litter decomposition and trace gas dynamics are also sensitive to changes in microbial communities.

3. Chemical and physical stresses (pollution, drying-rewetting, etc.) can reduce microbial numbers and diversity to such an extent that the size of specific populations, rather than substrate availability, may become the limiting factor in a range of processes.

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