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PERSPECTIVE

Soil Microbial Communities and Restoration Ecology: Facilitators or Followers?

Jim Harris

Microorganisms have critical roles in the functioning of soil in nutrient cycling, structural formation, and plant interactions, both positive and negative. These roles are important in reestablishing function and biodiversity in ecosystem restoration. Measurement of the community indicates the status of the system in relation to restoration targets and the effectiveness of management interventions, and manipulation of the community shows promise in the enhancement of the rate of recovery of degraded systems.

Soil microbes ranging from free-living bacteria to single fungi covering several square kilometers are a vastly diverse group in terms of taxonomy, structure, and function. We know the biology of few species directly because most soil microbes are currently impossible to cultivate (less than 1% grow readily on agar plates), and we instead rely on indirect means of analyses, principally biochemical markers, and measurements of the whole, or selected parts, of the communities' metabolic activities. Does the soil microbial community merely reflect what is happening in the rest of the ecosystem, or could it be a key player in facilitating restoration objectives? We do know that microorganisms are essential to soil function, particularly in organic matter decomposition and nutrient cycling, and therefore in regulating plant productivity and community dynamics (1, 2) and in soil structural generation (3). Hence, their study could be an essential part of any program aimed at the restoration of an ecosystem. However, soil microbes have only recently become a focus for restoration ecology, and research on the interactions between microorganisms and plants in both undisturbed and degraded ecosystems has begun to yield interesting results (4).

Recently, microbes have been investigated in two ways in relation to restoration: first to indicate the state of the ecosystem in reference to "target" sites or conditions, and second as a

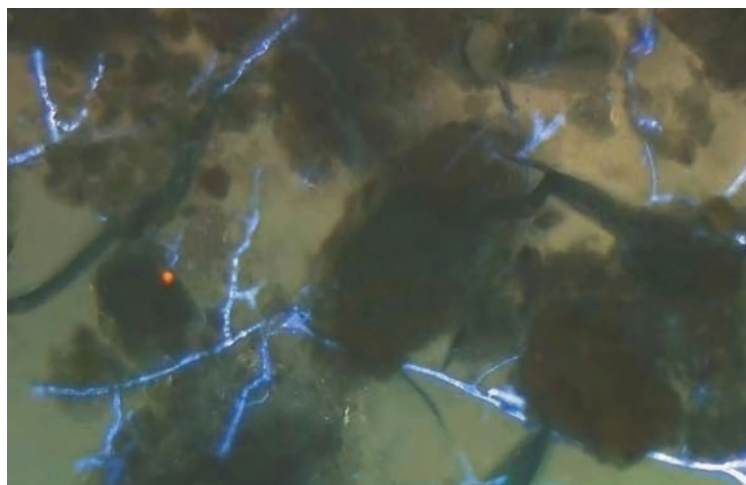


Fig. 1. Fungal hyphae ramify through soil, enmeshing and binding soil particles tighter so as to stabilize structure, accelerate decomposition, and affect plant diversity. [Image courtesy of K. Ritz, National Soil Resources Institute, Cranfield University]

system component to be manipulated so as to enhance the speed with which the system can be moved along to the desired state by overcoming "biotic barriers," either the absence of desirable components (such as mutualists) or the presence of undesirables (such as invasive plants) (5). We can distinguish between studies carried out on restoration sites to elucidate mechanisms and those on "natural" sites, which have implications for restoration practice. Sometimes the division

between the two is not clear cut; how might we classify an investigation in which the site of interest is field-abandoned for many years and now being "restored" to species-rich grassland? Restoration purists may regard this as reversing the wrong way down a successional gradient, away from a climax endpoint of mature forest in temperate ecosystems (of, for example, northern Europe), but the restoration of species-rich grassland is a common target for many conservation bodies.

There has been a long history of using analysis of the soil microbial community to indicate the condition of soil-based ecosystems. Work in this area provides clear evidence that as intensive use of sites is deliberately decreased in order to achieve a more natural state, there is an increase in the ratio of fungal to bacterial biomass (6) as more-complex organic material enters the soil matrix in these systems and physical perturbations decrease. The ratio increases further with scrub and forest development, which is consistent with the observation of a shift of resource and energy flows from root to fungal "energy channels" (7) as systems move from early to later successional stages. This work suggests that the microbial community "follows" and is dependent on what is going on in the above-ground community and can indicate the impact of restoration-management practices (8).

More difficult to assess is the role the microbial community plays in facilitating the establishment of plant communities at various successional stages and the possibilities for manipulation of the soil microbial community to "enhance" the rate at which a mature, stable ecosystem is established. In recent years, there has been an increasing focus on restoring ecosystem function, with associated flows of ecosystem goods and services, rather than "putting things back the way they were"—particularly in regard to shifting of species ranges caused by climate change and local extinction of key species. We are attempting to hit a moving target in this rapidly changing biophysical environment. Species assemblages that would have been found at a particular geographical location in the past may be impossible to reestablish under a changed climatic regime

Department of Natural Resources, Cranfield University, Cranfield, Bedfordshire MK43 0AL, UK.

and where key historical species components have become locally or totally extinct (9).

It has long been thought that one preeminent group of microorganisms, the mycorrhizae, could demonstrably improve the establishment, survival, and success of target plant species. In mycorrhizal relationships, which occur in most plant groups, fungal hyphae either penetrate or (in tree species) form sheaths around plant roots, then ramify out into the soil's mineral matrix. The fungi gain ready access to photosynthate; the plants gain access to mineral nutrients and protection from pathogens and drought; and thus both gain a competitive advantage. The links between mycorrhizae, plant diversity and productivity, and system heterogeneity are well established (10), and it follows that establishing a mycorrhizal community in an appropriate configuration is a prerequisite for establishing a target plant assemblage (11). In the restoration of extensively disturbed areas, such as large-scale mining, mycorrhizae offer a potentially low-cost means of establishing plant communities. The proximity of the restoration site to established mycorrhizal networks and propagule sources is an important factor in establishing new mycorrhizal relationships in restored systems (12). There are numerous cases in which the addition of mycorrhizae symbiont propagules has improved establishment, particularly in desert ecosystems (13). However, more recent work suggests that this effect may be more hit and miss than was previously thought (14) because of the complexity of plant-mycorrhizal symbioses, the multiplicity of plant-fungal specificity at different growth stages of the plant, and the prevailing soil/hydrological conditions (15). Although preinoculation of plants with mycobiont may help increase mycorrhizal diversity in soils with impoverished mycorrhizal communities, this approach appears to decrease mycorrhizal diversity when used in mature ecosystems (16). There is another dimension to these interactions, that of the role of bacteria that appear to help the formation of the mycorrhizal relationship (17), adding another layer of complexity to what we need to know before we can carry out manipulations with sufficient confidence that they will result in the desired ecosystem outcome. Fungi have a more general role to play in stabilizing soil structure by enmeshing and linking mineral particles in their hyphae; bacteria produce gums and mucilages that act as adhesives (Fig. 1).

Restoration sites using raw materials excavated by mining provide close if not precise analogies of those conditions occurring in systems that result from volcanic eruptions and the retreat of glaciers. Even here, past observations that autotrophs are the first to establish are being

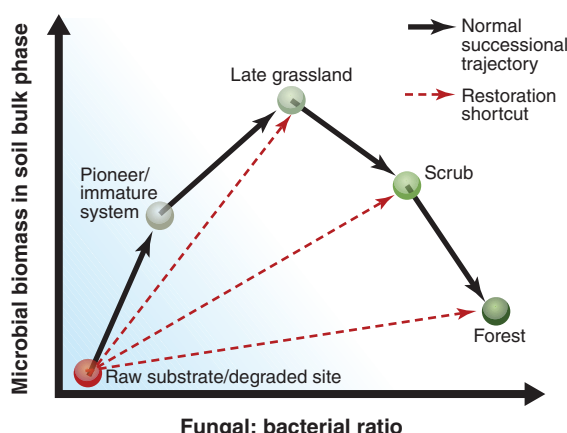


Fig. 2. As ecosystems mature, there is a switch in dominance from bacterial to fungal biomass; total microbial biomass in bulk (non-rhizosphere) soil peaks around midsuccession because this is the period in which root exudates in this phase peak. As fungal symbionts begin to dominate the rhizosphere, fewer plant exudates diffuse into the soil bulk phase. The aim of restoration to mature forest systems is to shortcut this trajectory by means of establishing fungal dominance at an early stage.

challenged; heterotrophic organisms arriving with organic matter may be a prerequisite for the establishment of later successional species (18). If this is the case, then accelerating succession by means of organic amendment may be an essential, not merely desirable, intervention on former mining sites. Such raw substrates offer a rich opportunity to explore the subtle interactions between above- and below-ground components in developing ecosystems without the constraints encountered in fragile or rare ecosystems. It is possible to manipulate carbon:nitrogen ratios so as to favor particular microbial groups capable of reducing the prevalence of invasive plants in abandoned fields; activated carbon added to soil has been shown to have the potential for reducing allelopathic compound concentrations produced by invasive plant species, reducing their competitiveness and thus lengthening the time available for the establishment of pathogens specific to invasive plants (19). The diversity of the bacterial community in general, and the nitrogen-fixing guild in particular, has been found to be positively correlated with the development of spatial heterogeneity and niche diversification in alpine grasslands (20).

Is it possible to shortcut succession in order to achieve desired ecosystem target states, or do ecosystems have to go through all successional stages (Fig. 2)? Accelerated succession may not always be possible, or at least easy to achieve. Kardol *et al.* (21) have observed that introducing soil or turves from target ecosystems with a high fungal content from a species-rich grassland site did not result in the establishment of the target-plant assemblages in the receptor site; it would appear that the mismatch in abiotic conditions between donor and receptor sites overwhelmed any biotic influence.

The investigation of soil microbial communities in systems undergoing restoration is providing fruitful insights into how “pristine” ecosystems work as well as the restored areas. Measurements of the size, composition, and activity of the soil microbial community accurately describe the status of restored systems in relation to target sites or systems, particularly when presented together in the form of two- or three-dimensional scatterplots (8), and work on this aspect of restoration ecology continues to be refined and extended. More work is needed to elucidate the role of microbes in generating soil structure in perturbed systems and their potential for enhancing the rate at which this proceeds. It is not yet clear that manipulation of microbial components of the soil subsystem can be guaranteed to effect enhanced ecosystem succession and function except in certain cases. There is a need for a more complete assessment of the role of all of the soil biological community and its interaction with the above-ground components and the mineral-organic matrix in the context of reversing ecosystem degradation, and there are clear signs that the research community is taking up this challenge.

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