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Linking species richness, biodiversity and ecosystem function in soil systems

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Summary

Soils are the central organizing entities in terrestrial ecosystems and possess extremely diverse prokaryotic and eukaryotic biota. They are physically and chemically complex, with micro- and macro-aggregates embedded within a solid, liquid and gaseous matrix that is continually changing in response to natural and human-induced perturbations. Recent advances in molecular techniques in systematics have provided opportunities for the study of biodiversity and biocomplexity of soil biota. A symposium and workshop on soil biogeochemistry and biodiversity International Symposium on Impacts of Soil Biodiversity on Biogeochemical Processes in Ecosystems, Taiwan Forestry Research Institute, Taipei, Taiwan April 18-24, 2004. Convened an international array of participants working in biomes on virtually every continent on the planet (ranging from polar to tropical regions). This special issue reports on the theoretical bases and applications of molecular methods for the measurement of soil biodiversity.

Themes addressed include a melding of classical taxonomic investigations with biochemical fingerprinting and molecular probing of organism identities. Several papers highlight new advances in identifications of prokaryotic and eukaryotic organisms. Examples include new developments in "fingerprinting" of microbes active in "mycorrhizospheres" using immunocapture and other innovative techniques. Developments in the study of impacts of invasive plant and animal species on ecosystem function and subsequent microbial community composition and function have been very great in the last 2-3 years. Soils are major repositories of legacies, including fine and coarse woody debris and other organic products, which have feedbacks on soil diversity. The ways in which species diversity and function of microbial and faunal communities interact and their importance to ecosystem function are examined in biological and biochemical detail. This paper provides an overview of soil biodiversity and its feedbacks on soil biogeochemical processes in ecosystems.

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Introduction: the nature and extent of biodiversity

In the last several years, there has been a surge of interest in soils as reservoirs of biodiversity. It is important to define biodiversity, which is an inclusive concept. Biodiversity is concerned with the functional attributes of ecosystems, e.g., decomposition and nutrient cycling, in addition to numbers of species of all the biota present. This differentiates it from the concept of species diversity, which is concerned with the identity and distribution of species in a given habitat or region (Coleman, 2001; Wardle, 2002). Prokaryotes constitute two of the three principal biological Domains, Bacteria and Archaea. The third Domain Eucarya consists of protists, fungi, plants and animals (Fig. 1; Pace, 1999). All three Domains are well represented within terrestrial ecosystems, and soils may contain some of the last great "unknowns" of many of these biota. In addition to well-studied fauna such as ants (Hölldobler and Wilson, 1990), the soil ecosystem contains many less studied as well as more numerous mesofauna, such as microarthropods (Behan-Pelletier and Newton, 1999) and nematodes (Ettema and Yeates, 2003), that interact with elements of the microbiota such as mycorrhiza in a variety of different types of symbioses (Wall and Moore, 1999). In addition, while much has been learned in the last decade about prokaryotic genetic diversity in soils, much more remains to be learned about these organisms (Hugenholtz et al., 1998).

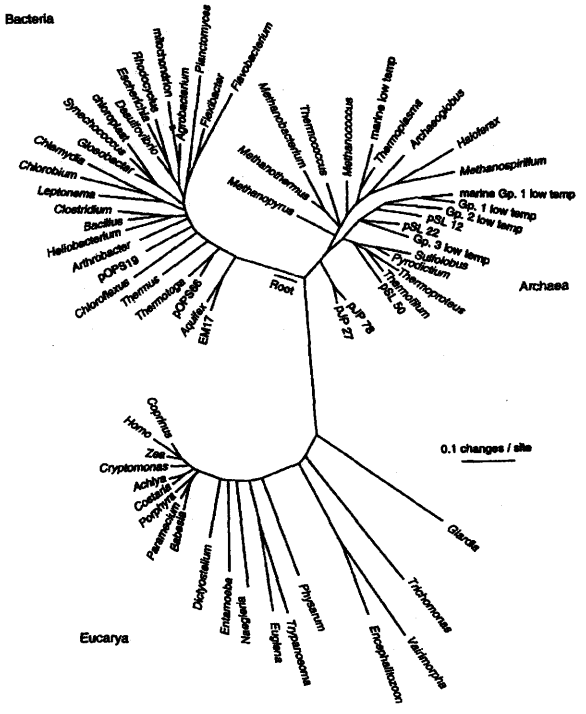

Figure 1. Phylogenetic tree showing the three Domains of life: Archaea, Bacteria, and Eucarya (Pace, 1999).

Biodiversity of prokaryotes

In order to understand the consequences of biodiversity, we must first estimate its extent. Bacteria are probably the most speciose array of organisms on earth (Tiedje et al., 2001; Torsvik and Øvreås, 2002). In addition, they are undoubtedly the most numerous organisms on earth, and have been estimated to number from 4 to 6×10^{30} cells, with a sizable proportion, about 92%, being in the subsurface, which includes the earth's mantle to 4 km. in depth (Whitman et al., 1998). Numbers of bacteria in soils of all biomes were estimated to be 2.5×10^{29} cells, with desert (Negev) soil numbers being similar to those in cultivated soils (Fliessbach et al., 1994). The foregoing counts translate into 2×10^{9} cells g^{-1} in the top meter, and 1×10^{8} cells g^{-1} in the 1–8 m soil depth, with numbers in forest soils being markedly lower (Whitman et al., 1998). At this level of abundance, the amount of cellular nitrogen and phosphorus in soil prokaryotes is comparable to that found in terrestrial plants, which illustrates the importance of the these organisms to biochemical processes in soil.

Historically, the diversity of prokaryotes had been greatly underestimated because identification relied on culturing and the laborious nutritional, chemotaxonomic and morphological characterization of isolates. The development of molecular tools and implementation of signature DNA sequences has greatly facilitated the identification of novel taxa. Currently, hundreds of novel isolates are identified yearly. Importantly, it has also been possible to examine the signature sequences in DNA extracted directly from the environment. Thus, it was realized that probably less than 5% of the prokaryotic phylotypes known to exist have actually been cultured (Joseph et al., 2003; Hugenholtz et al., 1998; Fig. 2). Currently, we believe that there are at least 53 bacterial phyla on earth based upon signature sequences encountered in DNA extracted directly from the environment. Of these, representatives of only 27 phyla have been cultivated and described in pure culture. Most of these phyla are represented by only a few isolates and some with only one described species. Only five

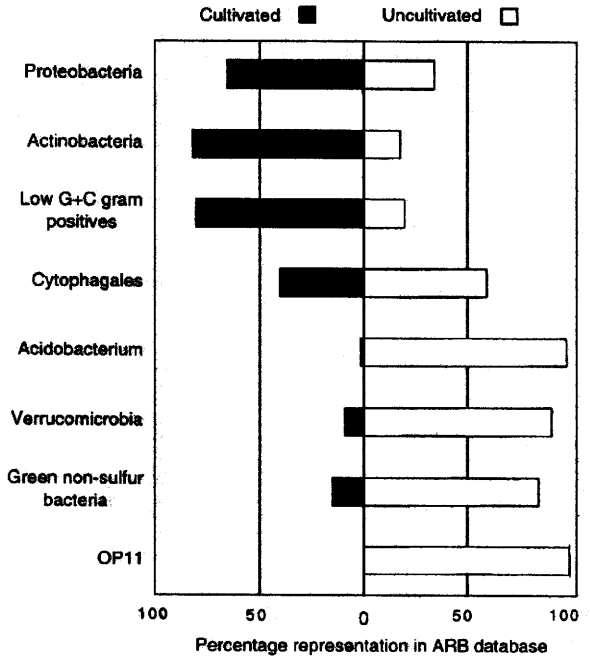

Figure 2. Percentage cultivated (<5% of total phylotypes) and uncultivated groups in selected cosmopolitan bacterial divisions of 16S rRNA sequences (from Hugenholtz et al., 1998). Many of these groups are abundant members of the soil microbial community.

phyla – Actinobacteria, Bacteroidetes, Cyanobacteria, Firmicutes, and Proteobacteria – represent 95% of all cultivated and published species (Fig. 3; Keller and Zengler, 2004).

Signature sequences have also provided strikingly different pictures for the distribution of specific groups of prokaryotes than previously believed based upon culture work. For instance, Archaea were previously considered to be limited to extreme environments, including deep-sea trenches and vents and hot springs, or unusual life styles, such as methanogenesis. Recently, they have also been found to be numerous in other habitats, including fresh water lakes and forest and agricultural soils (Bintrim et al., 1997; Jurgens et al., 1997; Nicol et al., 2003). In one agricultural soil, archaeal rRNA represented 1–2% of the total community rRNA (Buckley et al., 1998). Presumably, the relative amount of rRNA is proportional to the cellular abundance. Based upon these and similar studies, it is now believed that the diversity of Archaea in temperate environments is probably higher than that in extreme environments (Dawson et al., 2000).

Even though signature DNA sequences allow us to infer the extent of biodiversity in prokaryotes, signature sequences provide limited insights into the phenotypic and functional properties of these organisms. To fully understand the incredibly wide phenetic diversity of prokaryotes and their roles in soil, it is still necessary to isolate pure cultures and determine the properties of the organisms. Yet the total number of prokaryotic taxa on earth is still unknown. A recent survey of the sequence databases found evidence for greater than 3.5×10^4 taxa, defined quite broadly as all organisms with >97% rRNA sequence similarity, in current sequence databases (Schloss and Handelsman, 2004). Importantly, collector curves are still increasing rapidly, and it is not possible to estimate an asymptote or predict a maximum value. By another estimate, a ton of soil may contain 4×10^6 taxa (Curtis et al., 2002). In contrast to the number believed to exist, the number of described species is less than 10^4. Generally, members of prokaryotic species contain >99.8% rRNA sequence similarity, so the number of described 'taxa' at the lower level of sequence similarity is much less (Keswani and Whitman, 2001). Clearly, only a small proportion of the prokaryotes in nature have been investigated.

Even though the isolation of undescribed prokaryotes is a tremendous challenge, the description of novel prokaryotes has increased greatly in the past decade. Numerous accounts of their growth and nutritional properties, physiology, morphology and phylogeny are published yearly. The descriptions are summarized and reviewed periodically in Bergey's Manual of Systematic Bacteriology (at http://www.cme.msu.edu/bergeys/) and The Prokaryotes: An Evolving Electronic Resource for the Microbiological Community (Springer-Verlag at http://link.springer-ny.com/link/service/books/10125/). A further reason for great optimism is the recent progress in isolation of representatives of many of the poorly described phyla from soil (Joseph et al., 2003; Stevenson et al., 2004). Many of these organisms proved to be slowly growing oligotrophs, which may explain the failure of previous investigators to isolate them. For more information on soil prokaryote interactions in soils and rhizospheres, see the review by Kent and Triplett (2002).

Methods to study prokaryotic diversity

A method often used to analyze bacterial populations is to amplify DNA extracted from environmental samples by the polymerase chain reaction (PCR), using primers universal to the 16S rRNA genes of bacteria and archaea (Lane, 1991;

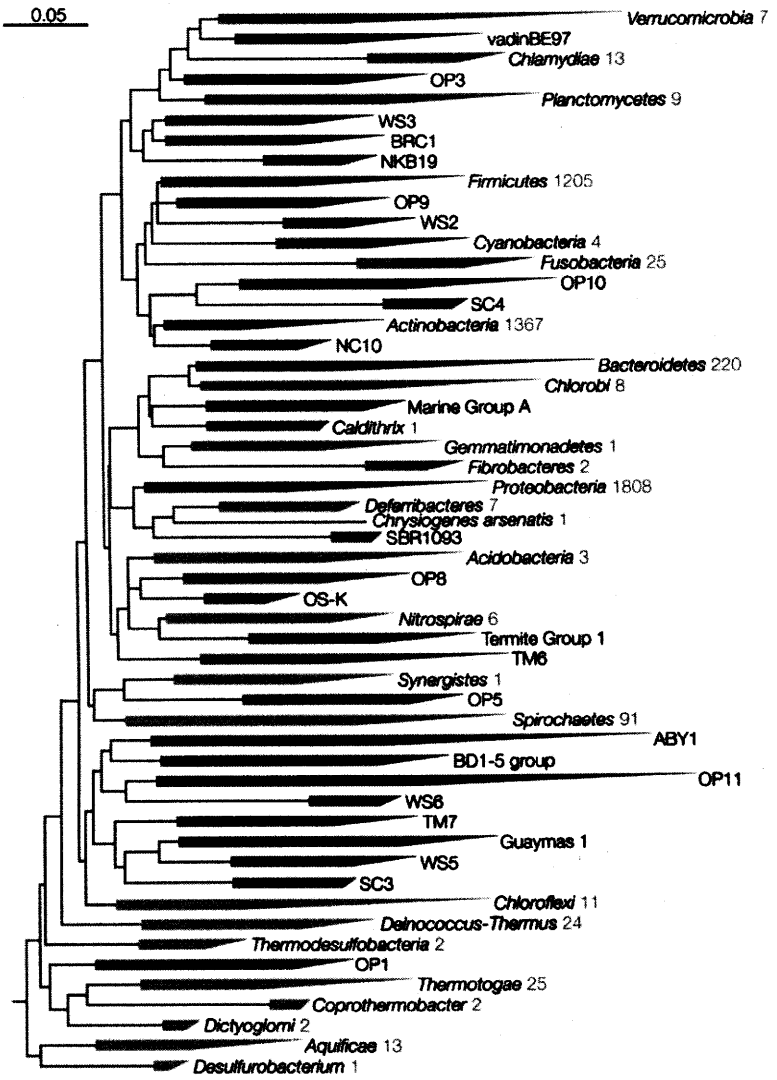

Figure 3. Reconstructed phylogenetic tree of the domain Bacteria based upon the sequences of the small subunit 16S rRNA gene. Prokaryotic branches labeled with numbers or other informal designations represent phyla where a representative organism has never been isolated. Scale bar corresponds to 0.05 changes per nucleotide position (from Keller and Zengler, 2004).

Prosser, 2002). Either DNA or RNA can be extracted from soils, but a majority of the studies have been based on DNA extraction, which is easier to accomplish efficiently due to the higher lability and turnover of RNA (Keller and Zengler, 2004). Ribosomal RNA content in active cells is higher than in inactive ones, thus rRNA-based analyses are a better approach for characterizing active microbial populations in soils (Ogram and Sharma, 2002). Techniques are now available to analyze microbial community structure and function by analyzing microbial rRNA and mRNA, respectively (Keller and Zengler, 2004). Both types of RNA can be extracted from soils and converted to cDNA (complementary DNA) by the enzyme reverse transcriptase for subsequent PCR amplification. Standard PCR analyses using "universal primers" for rRNA genes are not quantitative but do provide very useful qualitative information on dominant microbial populations. As long as suitable primers are available, it is possible to quantify microbial rRNA and mRNA using quantitative or "real time" PCR. These latter approaches provide an important means for linking soil microbial community structure and function. Over the past two decades, numerous methods, including rRNA gene sequencing, fluorescence in situ hybridization (FISH), denaturing gradient gel electrophoresis (DGGE), metagenomic libraries

(Rondon et al., 2000), restriction-fragment length polymorphism and terminal-fragment length polymorphism (T-RFLP) have been developed to measure and collate microbial diversity (Keller and Zengler, 2004).

A large proportion of soil ecology studies have focused on processes occurring in the O and upper A horizons because so much of the short-term dynamics occur there. With tools of microbial community analysis, Fierer et al. (2003) used phospholipid fatty acid (PLFA) analysis to examine the vertical distribution of specific microbial groups and their diversity in two soil profiles down to a depth of 2 m. The number of different types of PLFAs decreased by ca. one-third from the soil surface down to 2 m. Changes in certain ratios of fatty acid precursors and ratios of total saturated/total monounsaturated fatty acids increased with soil depth, indicating that microbes in the lower horizons were more carbon limited. Interestingly, approximately 35% of the total amount of microbial biomass was found in soil below a depth of 25 cm. Gram positive bacteria and actinomycetes tended to increase in relative abundance with depth, whereas Gram-negative bacteria, fungi and protozoa were highest at the soil surface. Treonis et al. (2004) combined microbial community PLFA analyses with an in situ stable isotope $^{13}CO_2$ labelling approach to identify microbial groups actively involved in assimilation of root-derived C in grassland soils (Fig. 4). Four and 8 d after label application, several biomarkers specific for fungi and gram-negative bacteria showed the most ^{13}C enrichment and rapid turnover rates, suggesting that these microorganisms were assimilating recently-photosynthesized root inputs to soils.

The distribution and abundance of microorganisms is so patchy that it is very difficult to determine their mean abundances with accuracy without dealing with a very high variance about that mean, when viewed on a macro-scale. Part of this variation is due to the close correlation of microbial populations with "patches" of organic matter. There are aggregations of microbes around living roots (rhizosphere) and mycorrhiza (Garbaye, 1991; Lynch, 1990), the walls of the biopores from dead roots, around fecal pellets and other patches of organic matter (Foster, 1994) and in pore necks between aggregates and particles (Fig. 5) (Foster and Dormaar, 1991). In addition, microorganisms concentrate in the mucus secretions which line the burrows of earthworms (the "drilosphere", as

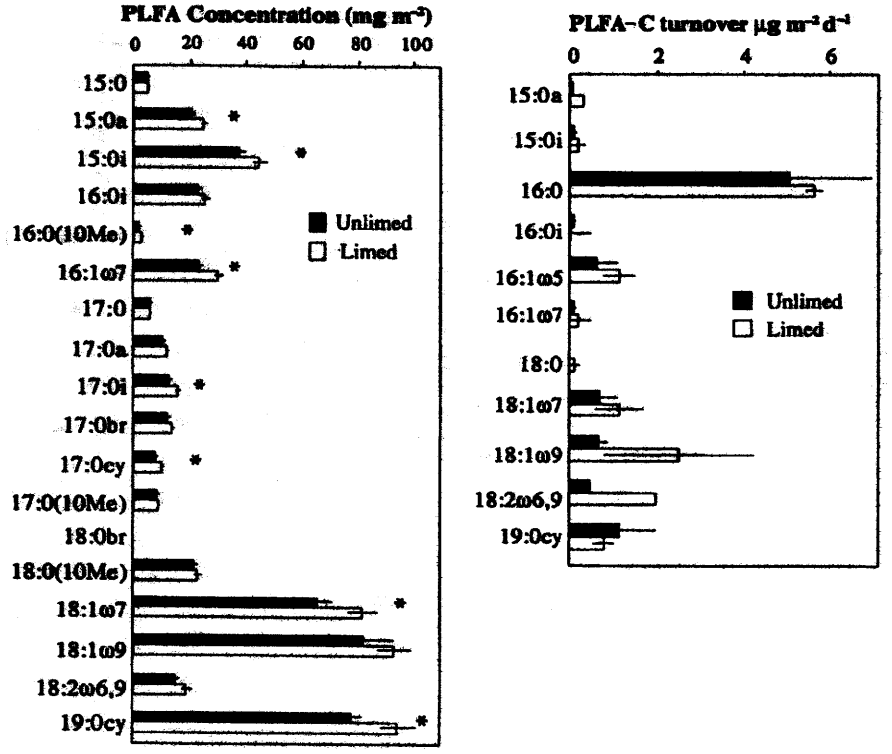

Figure 4. ^{13}C-labelled PLFA-C turnover measurements in soil. An example linking microbial structure and activity. Left side: PLFA Concentrations; Right side: PLFA-C turnover rates (Treonis et al., 2004).

Figure 5. (1) an amoeba probing a soil aggregate containing cell wall remnants (CWR) and a microcolony of bacteria (B) P, pseudopodium; R, root; S, soil minerals, bar, 1μm. (2) An amoeba with an elongated pseudopodium reaching into a soil pore. (3) An amoeba with partly digested bacteria in food vacuoles; (4) A pseudopodium associated with a Gram-positive microorganism (from Foster and Dormaar, 1991).

defined by Bouché (1975) and reviewed by Lee (1985)).

The field of mycorrhizosphere research (Andrade et al., 1998) has taken a quantum leap forward with elegant microscopic methods in conjunction with molecular tools to pinpoint organisms that are co-associates. Artursson and Jansson (2003) used the thymidine analog bromodeoxyuridine (BrdU) to identify active bacteria associated with arbuscular mycorrhizal (AM) hyphae. After adding BrdU to the soil and incubating for 2 days, DNA was extracted, and the newly synthesized DNA was isolated by immunocapture of the BrdU-containing DNA. The active bacteria in the community were identified by 16S rRNA gene PCR amplification and DNA sequence analysis. Based on gene sequence information, a selective medium was used to isolate the corresponding active bacteria. *Bacillus cereus* strain VA1, one of the bacteria identified by the BrdU method, was isolated from the soil and tagged with green fluorescent protein. Using confocal microscopy, this bacterium was shown to clearly attach to AM hyphae (Fig. 6). This study by Artursson and Jansson (2003) is a pioneering attempt, using molecular and traditional approaches to isolate, identify and visualize a specific bacterium that is active in fallow soil and associates with AM hyphae.

Figure 6. Immunofluorescent-labeled *Bacillus cereus* associated with an arbuscular mycorrhiza in an undisturbed fallow field near Uppsala, Sweden. (Artursson and Jansson, 2003). See text for details.

Table 1. Comparison of the numbers of known and estimated total species globally of selected groups or organisms. Modified from Hawksworth (1991)

Group	Known species	Estimated total species	Percentage known
Vascular plants	220 000	270 000	81
Bryophytes	17 000	25 000	68
Algae	40 000	60 000	67
Fungi	69 000	1 500 000	5
Bacteria	3000	unknown	unknown
Viruses	5000	130 000	4

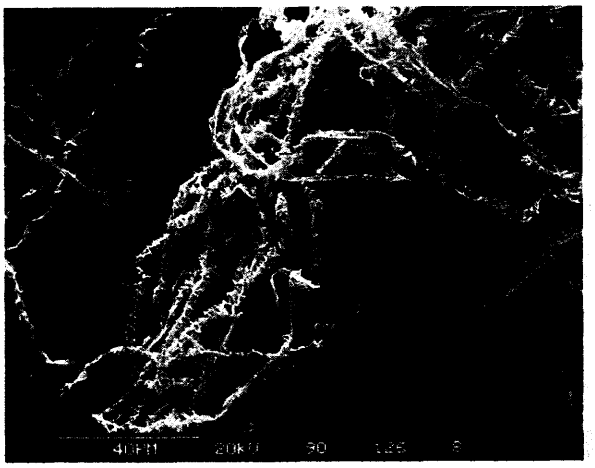

Figure 7. Fungal hyphae, showing Ca oxalate crystals on their surface (SEM courtesy of V.V.S.R. Gupta, pers. comm.).

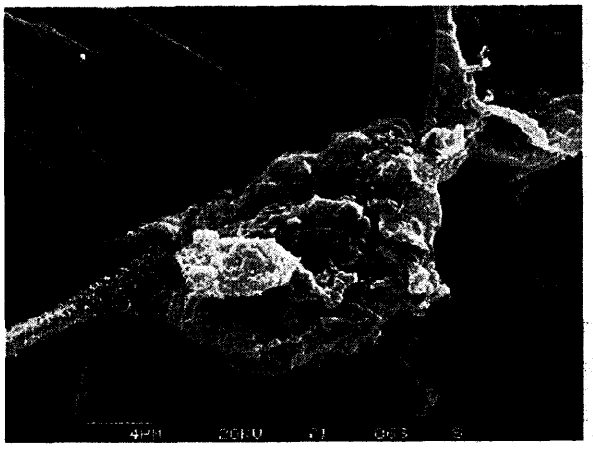

Figure 8. Mycophagous amoeba, ingesting fungal hyphal material. (SEM courtesy of V.V.S.R. Gupta, pers. comm.).

Fungal biodiversity

Another principal "player" in the decomposition process is the fungi, whose diversity has only recently become appreciated. There are currently 70 thousand species of fungi described (Table 1; Hawksworth, 1991). By assuming that a constant ratio of fungal species exists to those plant species already known, Hawksworth (2001) calculated that there may be a total of 1.5 million species of fungi described when this mammoth classification task is completed.

The roles of fungi at micro-scales are also of interest to soil ecologists. In elegant SEM studies, Ca oxalate crystals were shown to accumulate on hyphae (Fig. 7) and mycophagous amoebae shown to ingest fungal material (Fig. 8).

Spatial distribution of the biodiversity of soil fauna

In soil biodiversity studies it is essential to know not only which species are present, but also where the species occur in relation to one another. Do species occur together at every microsite, or do they occur individually in separate sites? This aspect of species distribution has an important bearing on competition and other interactions, with functional consequences for the ecosystem. Ettema and Yeates (2003) measured patterns of small (cm) and intermediate (m) scales in nematode communities in forest and pasture ecosystems of a similar soil type in New Zealand. Forestland was assumed to have greater variation

in vegetation and hence belowground inputs on small and intermediate scales when compared to the pasture. Thus, they hypothesized that nematode genera would be more strongly aggregated (occurring in "hot spots") in the mixed forest than in the ryegrass/white clover pasture. Applying a geostatistical method for sampling optimization called spatial simulated annealing, they sampled along 40 m transects for the m scale, with distance classes of 3 m, reflecting the scale of tree spacing. The cm scale transect was one-tenth of the large scale, or 4 m. The total number of nematodes per soil core volume was more than five times higher in the pasture (2800 nematodes $\pm$ 1234) than in the forest (430 $\pm$ 252), but the average number of genera in the forest cores (23.7 $\pm$ 3.3) was higher than in the pasture cores (19.1 $\pm$ 2.5). Also, many more nematode genera occurred in total in the forest (53) than in the pasture (37). Dissimilarity analysis showed that generic turnover i.e., rate of change in genera, was significantly greater in the forest than in the pasture, both at the small and intermediate scales (Fig. 9; Ettema and Yeates, 2003). Increasing distance in the forest led to increasing dissimilarity between communities, and no plateau was reached. Thus, it is possible that there is additional species turnover on scales larger than those explicitly sampled. The amount of work required for larger scale studies would be much greater, and should be kept in mind when considering work on spatial scales even with soil fauna of relatively small size.

What is the implication of the apparent "excess" of species diversity of soil microflora and fauna, where many species exist at a very low frequency and in an inactive state? If considerable species richness and accompanying large genetic pools are maintained in soils, what are the impacts on the evolution of new taxa? What are the implications for ecosystem function? Does it imply that some of the organisms are somehow vestigial remnants or relics of bygone conditions (Coleman et al., 1994)? What are the functional roles of such hidden or apparently cryptic organisms? Are they performing some essential, but unknown functions, perhaps at microsites, e.g., microaggregates (Jastrow et al., 1998) that we don't usually observe or study? Or are they functionally redundant, brought together by chance in a competitive environment and coexisting for a relatively short time period? One approach that promises to address these questions uses reporter genes linked to promoters in order to measure in situ expression of specific enzymes related to defined processes (Wilson et al., 1994).

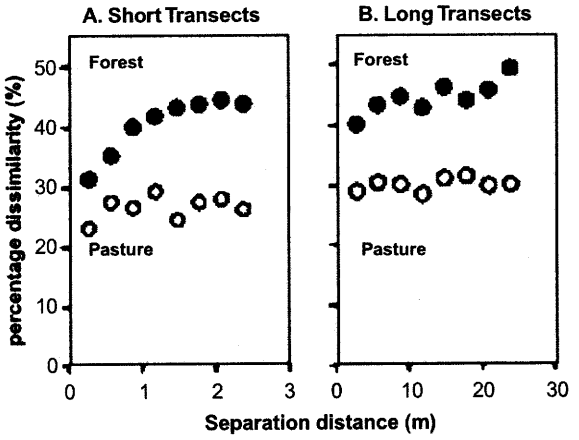

Figure 9. Mean dissimilarity (%) as a function of separation distance of soil nematodes in New Zealand forest (closed symbols) and pasture (open symbols) soils. Each point is an average of $p = 35-42$ observation pairs. Short transect = 0–3 m., Long transect = 0–30 m. (Ettema and Yeates, 2003).

Biodiversity in soils and impacts on ecosystem function

More than 20 studies of the empirical evidence of relationships between ecosystem processes and different components of plant diversity (species richness, functional richness and functional composition) were followed in natural and synthetically assembled groups of grassland species worldwide (Diaz and Cabido, 2001). The linkages are neither simple nor universal, but some significant trends are found. The range and more particularly the functional traits of plants, (e.g., whether they harbor nitrogen-fixing symbionts, warm-season grasses or rosette forbs) are generally strong drivers of ecosystem processes. These studies combined simplified microcosms and natural field sites, so extrapolation from them is limited. However, it is noteworthy that most of the studies showed that species richness and functional composition had positive effects on aboveground biomass.

Numbers of species above ground and below ground may be correlated when taxa in both habitats respond similarly to the same or correlated environmental driving variables, in particular across large gradients of disturbance, climate, soil conditions, or geographic area. However, differentiating between simple correlation and causation is problematic. High diversity in plant species can result in high diversity of litter quality or types of litter entering the belowground system. This

resource heterogeneity can lead to a greater diversity of decomposers and detritivores (Hooper et al., 2000). In contrast, a high diversity of resources and species in soil could feed back to a high diversity aboveground, where certain species or functional groups are closely linked to groups below ground. For example, van der Heijden et al. (1998) found a positive correlation between the diversity of endomycorrhizal species and plant diversity, perhaps because different species of fungi infect different species of plants to different degrees, although alternative explanations have been offered (Wardle et al., 1999). Interestingly, Hartnett and Wilson (1999) and Smith et al. (1999) working in a Kansas tallgrass prairie showed that the presence of mycorrhiza promoted obligately mycorrhizal C_4 grasses, resulting in competitive exclusion of facultatively mycorrhizal C_3 species, reducing overall plant species diversity. A similar mechanism seems to operate in tropical rainforests, in which ectomycorrhizal tree species competitively exclude arbuscular mycorrhizal species (Connell and Lowman, 1989, cited in Wardle, 2002). It should be noted that this pattern is not consistent at the level of functional types of mycorrhiza: low-diversity AM can be associated with high diversity of plants, and high-diversity ECM communities can be associated with low diversity of plants (Allen et al., 1995).

What are the linkages between biodiversity and ecosystem function? It should be possible to look for natural "experiments", such as regions with low species richness, e.g., on an island, versus sites at similar latitudes that are on continents. Under such conditions, all of the major abiotic factors should be reasonably similar, allowing study of the impacts of species richness of key indicator microflora or fauna on ecosystem processes of interest, e.g., rates of decomposition or nutrient cycling. Such experiments are certainly possible, and might yield some surprising results.

In an extensive experiment carried out under field conditions, Porazinska et al. (2003) tested aboveground–belowground diversity relationships in a naturally developed tallgrass prairie ecosystem by comparing soil biota and soil processes occurring in homogeneous and heterogeneous C_3 and C_4 plant combinations. Some bacterial and nematode groups were affected by plant characteristics specific to a given plant species, but no uniform patterns emerged. Interestingly, invasive and native plants were quite similar with respect to the measured soil variables (e.g., phospholipid fatty acids, protozoa, and nematode functional groups).

Heterogeneity of carbon substrates and effects on soil biodiversity

Does diversity change occur during decomposition of organic substrates? Dilly et al. (2004) measured changes in 16S rRNA gene sequences of the prokaryotic community during litter decomposition in soil in central Germany, using (DGGE). They compared decomposition of wheat and rye litters in agricultural fields over a 180 day time interval. They found that microbial diversity increased during the course of litter decomposition, with more refractory wheat straw enabling development of microbial communities with greater diversity than in the more readily decomposable rye litter (Table 2; Dilly et al., 2004).

A stepwise process for the ways in which increased heterogeneity of carbon (C) substrates from aboveground will positively influence belowground diversity is as follows (Fig. 10; Hooper et al., 2000): (1) diversity of primary producers leads to diversity of C inputs belowground; (2) carbon resource heterogeneity leads to diversity of herbivores and detritivores; and (3) diversity of detritivores or belowground herbivores leads to diversity of organisms at higher trophic levels in belowground food webs. The critical points are the nature and extent of trophic interactions (Hooper et al., 2000). There are three general categories of interactions by which organisms in one compartment can affect biodiversity in another one: (1) obligate, selective interactions (one-to-one

Table 2. Bacterial diversity as indicated by the number of DNA bands and Shannon–Weaver (S–W) diversity index of 16S rRNA gene sequences during rye and wheat litter decomposition in agricultural soils in central (51°N) Germany (Dilly et al., 2004). Values are means for two replicates. Std. deviations were generally <4% for the number of DNA bands, and <1% for the diversity index

Material	Day	No. of DNA Bands	S–W diversity index
Rye	0	27.5	2.77
	18	36.5	3.09
	58	40.0	3.19
	118	37.0	3.21
	180	39.0	3.34
Wheat	0	35.5	3.01
	18	39.5	3.01
	58	44.5	3.30
	118	52.0	3.61
	180	49.0	3.50

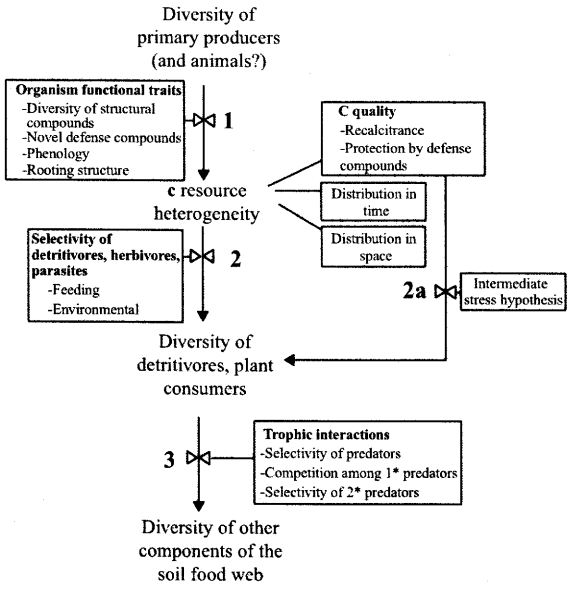

Figure 10. Diversity of terrestrial ecosystem components as a function of resource heterogeneity and trophic interactions (Hooper et al., 2000).

linkage) through mutualism, for example; (2) one-to-many species linkages, via keystones and dominants, and (3) causal richness, or many-to-many linkages. The nature and extent of these interactions varies a great deal depending on the systems studied and the spatial scales at which the mechanisms are being considered.

Is our knowledge of the species richness in soils sufficient to make educated guesses about the total extent of organisms or the number of endangered species (Hawksworth, 1991, 2001; Coleman et al., 1994, Coleman, 2001)? Some organisms, such as the fungus- and litter-consuming microarthropods, are very speciose. For example, there are up to 170 species in one order of mites, the Oribatida, in the forest floor of one watershed in western North Carolina. This number exceeds that of some tropical forest Oribatids (Noti et al., 2003). A SEM close-up shows the chelicerae and other mouthparts making Oribatids efficient fungal feeders (Fig. 11). In a 3-year field study, Hansen (2000) measured a decline in species richness of Oribatids as she decreased litter species richness in experimental (1 m^2) enclosures from seven to one species of deciduous tree litter (Fig. 12; Hansen, 2000). This decline was attributed to the lower physical and chemical diversity of available microhabitats, which is in accord with the mechanisms suggested earlier by Anderson (1975). Somewhat surprisingly, the species richness of Oribatids occurring in litter bags in the forest floor of a pitch pine-oak xeric watershed at Coweeta LTER in western North

Figure 11. SEM of Oribatid mite from a forest floor, showing chelicerae used for feeding on fungi and other substrates (Valerie Behan-Pelletier, pers. comm.).

Carolina (Lamoncha and Crossley, 1998) is nearly half as large (78) as that in the watershed only 3 km distant, used for the mixed deciduous litter experiments of Hansen (2000). We suggest that this high oribatid species richness in the oligospecific leaf litter of a forest floor might be a strong indication of the species richness of the decomposer fungal community, which could be a primary causal factor of fungivorous mite species richness. But see Maraun et al. (2003) for comments on the paucity of evidence for fungal diversity effects on microarthropod diversity; most microarthropods appear to be generalist feeders, although they seem to prefer dark Dematiaceous fungi. Analytical tools to examine the species richness of decomposer fungi are now at hand that should provide an answer to this apparent conundrum.

Only 30–35% of the Oribatids in North America have been adequately described (Behan-Pelletier and Bissett, 1993) despite many studies carried out over the last 20–30 years. Thus, there may be more than 80 thousand undescribed species of oribatid mites yet to be discovered (Table 3). Particularly in many tropical regions, Oribatids and other small arthropods are poorly described in both soil and tree canopy environments (Behan-Pelletier and Newton, 1999, Nadkarni et al., 2002). This difficulty is compounded by our very incomplete knowledge of the identities of the immature stages of soil fauna, particularly the mites and Diptera. The application of molecular techniques may solve this problem by more effectively identifying all life stages of the soil fauna (Behan-Pelletier and Newton, 1999; Coleman, 1994; Freckman, 1994). We concur with Behan-Pelletier and Bissett (1993): "Advances in systematics and ecology must progress in tandem: systematics providing both the basis and predictions for ecological studies, and

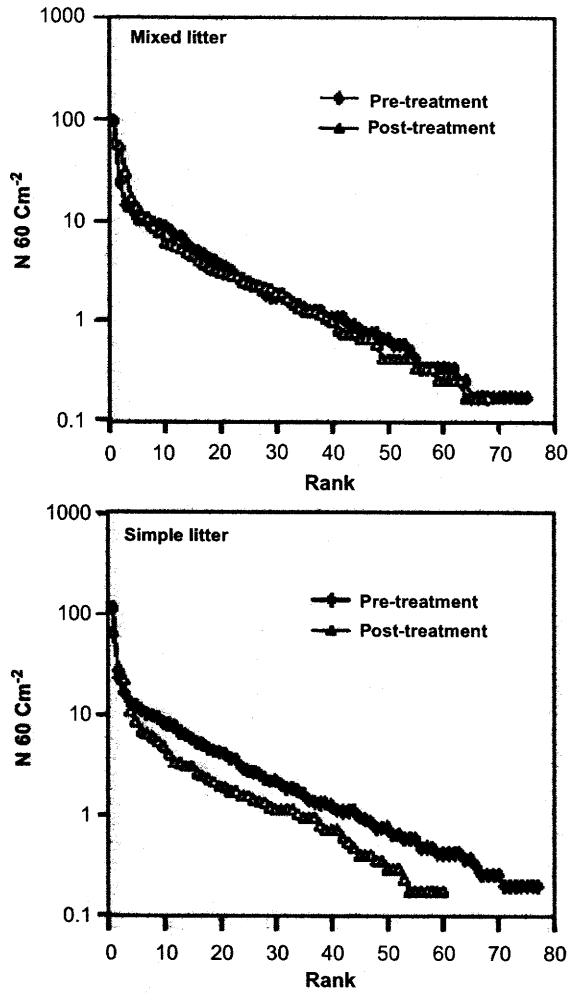

Figure 12. Average rank vs. abundance curves for the oribatid assemblages pretreatment and 3 years post-treatment in simple and mixed litter plots at Coweeta LTER site, western North Carolina. Species were ranked according to their mean abundance in each of the five litter types. Data shown are the abundance at each rank averaged among the three simple litters and between the two mixed litters. Assemblages in simple litters underwent a broad-based decline in both average abundance of many species and in total richness, while in the mixed litter the relative abundance structure of the assemblages remained intact (Hansen, 2000).

ecology providing information on community structure and explanations for recent evolution and adaptation."

Legacies in soils (organisms and substrates)

Soils are rife with historical signs and legacies, as has been made evident by studies using soil thin sections, showing mite fecal pellets in the soil

Table 3. Species richness of key soil eukaryotes. Modified from Coleman (2001)

Taxonomic group	Spp. Described	Spp. Estimated
Protozoa	40 000	200 000
Fungi	70 000	1 500 000
Nematodes	5000	20 000
Collembola	6500	15 000
Acari	20 000	80 000
Isoptera	2600	10 000
Earthworms	3700	8000

Figure 13. Soil thin section (5-cm depth), showing microarthropod feces associated with sorghum litter breakdown in a Georgia piedmont agroecosystem, Griffin, GA (L.T. West, pers. comm.).

profile that persist for years (Fig. 13). Radiotracer and stable isotope studies have also demonstrated legacies in soil profiles (Stout et al., 1981; Nadelhoffer et al., 1985, Gaudinski et al., 2000). Recent studies of coarse (dia. >10 cm) and fine (dia 1–10 cm) woody debris have proved informative about distribution and diversity of fungi. In broad-leaf forests in southern Sweden, the numbers of species per unit wood volume and per forest area were significantly higher for fine than for coarse woody debris for both ascomycetes and basidiomycetes (Figs. 14 and 15; Nordén et al., 2004). When the number of species was plotted against the number of published records, coarse woody debris was more species rich than fine woody debris for a given number of basidiomycete records. Of the ascomycetes, 75% were found exclusively on fine woody debris (vs. only 30% for basidiomycetes). Nordén et al. (2004) conclude that fine woody debris is important for diversity of wood-inhabiting fungi, particularly ascomycetes, in northern broad-leaved forests. However, coarse woody debris must also be provided to insure the occurrence of many basidiomycete species. It will be worthwhile to compare these results with those in the future from temperate and tropical forested sites.

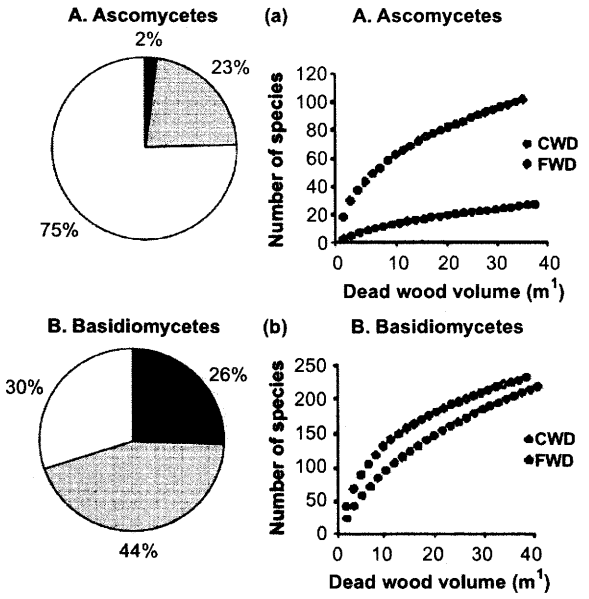

Figure 14. The proportion of species found exclusively on Coarse woody debris (>10 cm dia, CWD) (black) and Fine Woody Debris (1–10 cm dia., FWD) (white) or on both for (A) ascomycetes, and (B) basidiomycetes [Left side].; The average species accumulation curves showing species density as mean number of species plotted against mean cumulative dead wood volume for (A) ascomycetes and (B) basidiomycetes (Nordén et al., 2004).

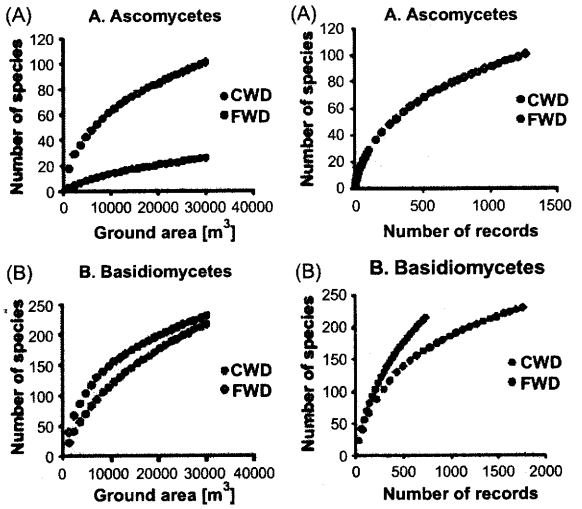

Figure 15. Average species accumulation curves showing species density as mean number of species plotted against cumulative forest ground area for (A) ascomycetes, (B) basidiomycetes on CWD and FWD (the dots represent sites) [left side]; Average species accumulation curve showing species richness as mean number of species plotted against number of records on CWD and FWD for (A) ascomycetes and (B) basidiomycetes (the dots represent sites) [right side]. Curves were constructed through random resampling. Note greater accumulation of Basidiomycetes on CWD than on FWD (Nordén et al., 2004).

There is a strong interaction between ecosystem function, organismal abundance and diversity and the nature of humus forms in soil. Ponge (2003) compared more than 20 ecosystem attributes and the nature of the processes and organisms occurring in mull, moder and mor soils (Table 4; Ponge, 2003). This table is a useful means of comparing many soil attributes across a broad range of physical, chemical and biological traits. It shows a marked gradient from high (mull) to low (mor) biodiversity and rapid to slow and very slow rates of humification. Not surprisingly, a key determinant of litter decomposability, phenolic content, varied inversely with litter decomposability across the same sequence of three humus types. Of course, we have yet to see how well these generalizations hold up when including a detailed analysis of the microbial communities in all three humus types.

Impacts of species richness on ecosystem function

Recent studies of Wall and colleagues in the McMurdo Dry Valleys of Antarctica offer some insights into the impacts of species richness. The dry valley ecosystems contain only three species of nematode: one bacterial feeder, one microbial feeder, and one omnivore-predator. They are present in very low numbers (2–5 kg^{-1} soil; Wall and Virginia, 1999). These systems have very low precipitation (~10 cm rainfall equivalent y^{-1}) and make the usually-harsh climate of the Chihuahuan desert of New Mexico seem like an oasis, with the nematodes represented by seven plant parasites, 10 genera of microbivores, two omnivore genera and three genera of predators (Fig. 16; Wall and Virginia, 1999). The latter system contains numerous vascular plants, with considerable organic inputs both above- and belowground. In the McMurdo Dry Valleys, the sources of organic matter are restricted to allochthonous inputs from algae in nearby lakes or streams and small amounts of indigenous soil algae and cyanobacteria. Although depauperate in species, nematode distributions are markedly different spatially and highly correlated with differences in tolerances to desiccation and salinity, with the omnivore-predator and bacterivore species being more water-requiring and concentrating in stream beds. The microbivorous (bacteria and yeast spp.) endemic species

Table 4. Humus types and ecosystem properties (Ponge, 2003)

	MULL	MODER	MOR
Ecosystems	Grasslands, deciduous woodlands with rich herb layer, Mediterr. scrublands	Deciduous and conif. woodlands with poor herb layer	Heathlands, conif. woodlands, sphagnumbogs, alpine meadows
Biodiversity	High	Medium	Low
Productivity	High	Medium	Low
Litter horizons	OL, OF	OL, OF OH	OL, OM
Soil type	Brown soils	Grey-brown podzolic	Podzols
Litter phenolic content	Poor	Medium	High
Humification	Rapid	Slow	Very slow
Humified O.M.	organo-mineral aggregs. with clay-humus complexes	Holorganic fecal pellets	Slow oxidation of plant debris
Exchange sites	Mineral	Organic (rich)	Organic (poor)
Mineral weath.	High	Medium	Poor
Min. buffer type	Carbonate range	Silicate range	Fe/Al range
Fire impact	Low (except Medit.)	Medium	High
Regen. trees	Easy (permanent)	Poor (cyclic processes)	None (fire needed)
Dom. mycorrhiz.	AM	ECM	Ericoid, arbutoid
Mycorrhiz. partners	Zygomycetes	Basidiomycetes	Ascomycetes
Nitrogen forms	Protein, NH_4^+, NO_3^-	Protein, NH_4^+,	Protein
Nutrient avail. to plants	Direct (absorb. Hairs)	Indirect, via extramatrical mycel	Poor
Nutr. use effic.	Low	Medium	High
Fauna	Megafauna, macrofauna, Mesofauna, microfauna	Macrofauna (poor), mesofauna (rich), microfauna	Mesofauna (poor) Microfauna (poor)
Dominant fauna in biomass	Earthworms	Enchytraeids	None
Dom. microb. grp.	Bacteria	Fungi	None
Affinities w. pollut. condition	Low	Medium	High

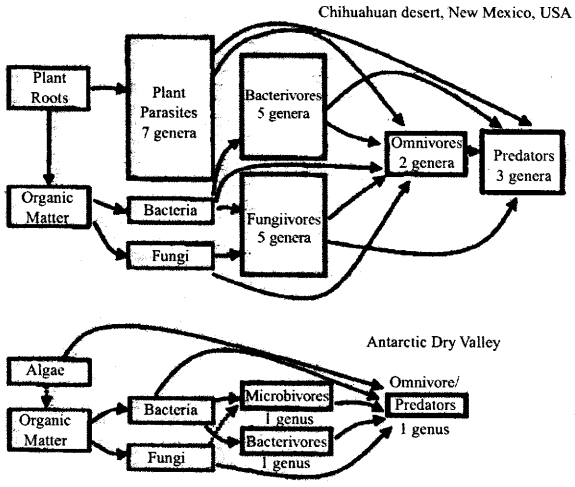

Figure 16. Detrital food webs: complex in the Chihuahuan desert; very simple in Taylor Dry Valley, Antarctica, with only three spp. of microbivorous nematodes (Wall and Virginia, 1999).

Scottnema lindsayae are restricted to the drier uplands (Treonis et al., 1999). Although complicated in terms of life-history details, the fact that the number of species is so small makes it likely that a fuller understanding of microbial and faunal interactions related to diversity is possible.

The role of redundant species and the functional roles played by them is crucial to understanding the interplays between biodiversity and ecosystem function. Without detailed knowledge of the biology of species involved, it can be difficult to decide how many functional types are present in a system or determine the functional roles of individual species (Bolger, 2001). Pathogen protection benefits of arbuscular mycorrhizas may be as significant as the nutritional benefits to many plants growing in temperate ecosystems (Newsham et al., 1995; cited in Bolger, 2001).

Models, microcosms and soil biodiversity

Hunt and Wall (2002) modeled the effects of loss of soil biodiversity, viewed from a functional group perspective, on ecosystem function. They constructed a model for carbon and nitrogen transfers among plants and functional groups of microbes

and fauna. They used 15 functional groups of microbes and soil fauna, comprised of: bacteria, saprophytic and mycorrhizal fungi, root-feeding, bacteria-feeding, fungal-feeding, omnivorous and predaceous nematodes, flagellates and amoebae, collembola, r- and k-selected fungal-feeding mites, nematophagous and predaceous mites (Fig. 17, Hunt et al., 1987). The 15 functional groups were deleted one at a time and the model was run to steady state. Only six of the 15 deletions led to as much as a 15% change in abundance of a remaining group, and only deletions of bacteria and saprophytic fungi led to extinctions of other groups. By this analysis, no single faunal group had a significant effect on subsequent ecosystem behavior. However, the authors caution that, despite numerous compensatory mechanisms that occurred, it is premature to assume that the system is inherently stable even with the loss of several faunal groups. In fact, earlier analyses of similar food webs by Moore et al. (1993) and Moore and de Ruiter (2000) showed that loss of top predators had much greater impacts on lower trophic levels than their low biomasses might indicate.

Another approach to microcosm studies was taken by the group working in the Ecotron facility at Silwood Park, UK Constructing analogs of a temperate, acidic, sheep-grazed grassland in northern Britain, Bradford et al. (2002) established terrestrial microcosms of graded complexity, with soil, plants and microorganisms, and then assemblages of microfauna, micro- and mesofauna, and then micro-, meso- and macrofauna. Thus, soil community composition was manipulated through assemblages of different animal body sizes. This functional group approach provided a range of metabolic rates, generation times, population densities and food size. The microcosms were maintained in the Ecotron for a period of 8.5 months. Bradford et al. (2002) found significant increases in decomposition rate in the most complex faunal treatment, but both mycorrhizal colonization and root biomass were less abundant in the macrofauna treatments. Interestingly plant growth was not enhanced in these treatments, despite higher nutrient (N and P) availability. Contrary to initial hypotheses, neither aboveground NPP (plant biomass) nor net ecosystem production (net CO_2 uptake) were enhanced in the most complex microcosms because positive and negative faunal-mediated effects canceled each other out. Bradford et al. suggested that respiration was most likely buffered by the combined stimulatory effect of both mesofauna and macrofauna on microbes,

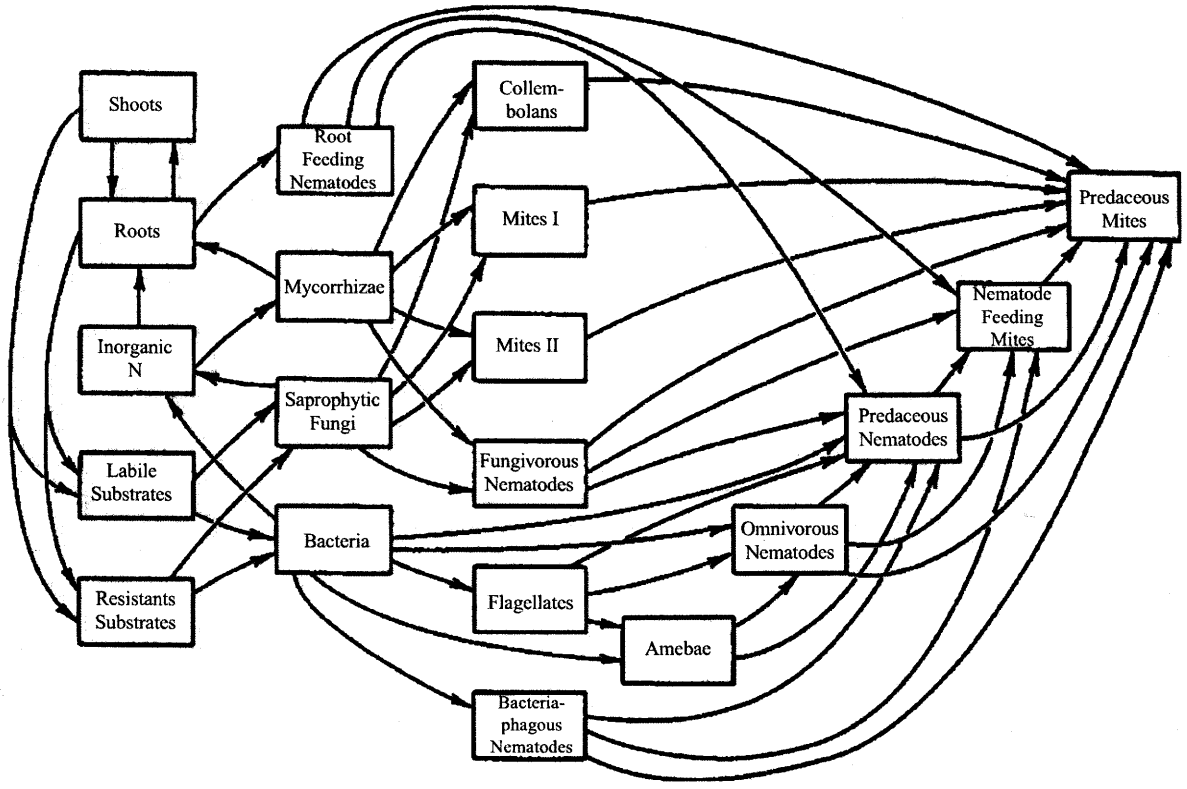

Figure 17. Shortgrass prairie detrital food web, showing high redundancy. See text for details (Hunt et al., 1987).

which served to maintain microbial activity at a level equivalent to that in the microfauna and mesofauna communities. This study has been considered a benchmark in large-scale microcosm studies, but as Bradford et al. (2002) note, it is not a substitute of longer-term in situ field studies.

In an extensive comparison of seven food webs of native and agricultural soils, de Ruiter et al. (1998) modeled energetics and stability, evaluating the roles of various groups of organisms and their interactions in energy flow and community stability. They measured feeding rates, interaction strengths, and impacts of the interactions on food web stability (%), arranged according to trophic position in a total of seven belowground food webs. The food webs simulated those found in the Central Plains of Colorado, two tillage manipulations at Lovinkhoeve in the Netherlands, two tillage manipulations at Horseshoe Bend, Athens, GA, and no fertilizer and fertilizer additions at Kjettslinge in southern Sweden. de Ruiter et al. (1998) found that only a fraction of the species manipulations had a strong effect on food web structure. Also there was no correlation between the impacts on stability and feeding rates. Thus, some interactions representing a relatively low rate of flow of materials can have a large impact on stability, and interactions having a high rate of material flow can have a small impact on stability. For instance, the higher-level predatory mites and nematodes had an impact far out of proportion to their biomass, and the contrary was true of the high biomass organisms, namely bacteria and fungi. de Ruiter et al. (1998) urge that future research be focused on the energetic properties of the organisms forming the basis of the patterning of interaction strengths. This is a big order and one that will require innovative experiments under both laboratory and field conditions. These studies should help to provide further insights into the nature of biodiversity and ecosystem function in soils.

Experimental additions and deletions in soil biodiversity studies

Additional studies of biotic roles of soil fauna and bacteria and fungi have been approached in two ways. One approach is by gamma irradiating sieved soils and inoculating them with suspensions of full-strength, 10^2, 10^4 and 10^6-fold dilutions of soil organisms (Griffiths et al., 2001). The other approach subjects soils to chloroform fumigation prior to incubation (Griffiths et al., 2000) and following the subsequent changes in functional variables, e.g., ammonium, nitrate, and soil respiration, in relation to microbial biomass and diversity, as measured by DNA patterns on DGGE. Results were divergent in the two studies, with the chloroform fumigation simplification of community biomass and species diversity having a direct impact on the functional stability, as measured by the physiological response variables. In contrast, although there were progressive declines in biodiversity of the soil microbial and protozoan populations, there were no consistent changes in functional parameters. Some functions showed no trend (thymidine and leucine incorporation, nitrate accumulation, respiratory growth response). Others showed a gradual increase with increasing dilution (substrate induced respiration). Some declined only at the highest dilution treatment (short-term respiration from added grass, potential nitrification rate, and community level physiological profile), while others varied even more idiosyncratically. At no stage were any of the physiological functions eliminated completely. The final commentary on this by Griffiths et al. (2001) concludes that within any realistic range of changes in biodiversity likely to be experienced by soils, there will be no direct effect on any soil functional parameters measured. Other authors, e.g., Wardle et al. (1999) suggested that it is possible to overcome selective species effects by (a) measuring the effects of all species in monoculture and (b) by species removal experiments. Neither of these approaches is feasible with current technology, so this problem awaits the attention of a future generation of soil ecologists.

Problems yet remaining in soil biodiversity studies

An alternative to the above functional approaches is taken by André et al. (2002), who note that most investigators use inadequate sampling designs or sample too shallowly in the soil profile to get a complete sample of microarthropods for testing the models noted above. In an extensive survey of the worldwide literature on microarthropods, they claim that on average, at most 10% of the soil microarthropod populations have been explored and 10% of the species described, due to the use of inefficient extraction procedures. Indeed, Walter and Proctor (2000) suggest that perhaps only 5% of the species of mites worldwide are described so far. André et al. (2002) make the very valid point that ecologists need to be aware of the numerous pitfalls and possible flaws inherent in

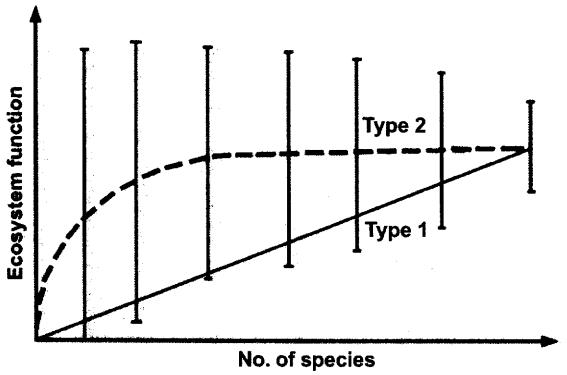

Figure 18. Species richness and ecosystem function (Type 1 = all species unique in function; Type 2 = some species redundant) (Bengtsson, 1998).

many extraction procedures; i.e., none of them is 100% efficient.

Some quantifiable relationship needs to be elucidated between ecosystem function and diversity. Two curves of ecosystem function are given for increasing numbers of species (Fig. 18; Bengtsson, 1998). Type 1, a continually ascending curve, represents the hypothesis that all species are important for ecosystem function. Type 2, initially convex and then flat, represents the species redundancy hypothesis. Bengtsson (1998) notes that it is more informative to consider specific functions in ecosystems, namely decomposition, nutrient mineralization or primary production, focusing on quantifiable phenomena. Bengtsson (1998) argues strongly that diversity does *not* play a role in ecosystem function. He asserts that: "correlations between diversity and ecosystem functions – which may very well exist – will be mainly non-causal correlations only." As we are trying to show in this chapter, the truth may well lie in some mid-point between these extremes. The fact that certain functions may be linked to just a few genera or species, e.g., autotrophic and heterotrophic nitrifiers, means that this might well be a "pressure point," for concern about long-term ecosystem function. The "natural insurance capital" concept of Folke et al. (1996; see Bolger, 2001) suggests that it is essential to retain the maximum species richness possible to ensure that complete ecosystem services exist as human needs or environmental changes occur.

Why is soil diversity so high?

The high species and functional diversity in soils is well appreciated (e.g., Anderson, 1975, 2000), but its root causes remain unknown. As noted by Wardle (2002), the belowground environment provides numerous niche axes in the Hutchinson (1957) hyperspace, concerning numerous microhabitats, microclimatic properties, soil chemical properties, and phenologies of the organisms themselves. When one adds in the fact that many of the organisms may exist in quiescent or dormant stages (Coleman, 2001), there is considerable niche space for the impressive belowground species diversity.

When considering the diverse array of many kingdoms in all three domains of the biota, there are ample causative factors for the impressively large biodiversity observed in soils. These factors encompass many physically distinct microhabitats, organismal phenologies, numerous legacy effects, including stabilizing effects of SOM, and facilitation effects from many mutualistic interactions. Thus, the time seems ripe for major advances in this exciting and fast-changing field of study.

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