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Review

From peds to paradoxes: Linkages between soil biota and their influences on ecological processes

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Abstract

Soils and their biota have been studied by a variety of observational and experimental methods that have allowed biologists to infer their structural and functional interactions. Viewing progress made over the last 10 years, it is apparent that an increasing diversity of analytical and chemical methods are providing much more detailed information about feeding preferences and niche overlaps of speciose groups such as oribatid mites.

Other topics in which considerable progress has been made include new advances in knowledge of root and mycorrhiza production and turnover and their impacts on soil ecosystems; soil biota, exudations and secretions and soil aggregation phenomena; the biology of invasive species in soils; soil biodiversity, legacies and linkages to soil processes; and soil biodiversity and ecosystem functional responses. Throughout the review I suggest ways for new progress to be made in future research.

Keywords: Foodwebs; Biodiversity; Microbes and fauna; Decomposition; Nutrient cycling; Niche dimensions

1. Introduction

> The ecological concept is, I think, translatable into common speech.... The sequence of stages in the transmission of food is a food chain.... The chains are not only food chains, they are chains of dependency for a maze of services, competitions, piracies, and cooperations. This maze is complex; no living man (or woman) can blueprint the biotic organization of a single acre, yet the organization is clearly there, else the member species would disappear. They do not disappear (Leopold, 1999).

A paper entitled "Through a Ped Darkly: an ecological assessment of root-soil-microbial-faunal interactions" became widely known, probably due to its eye-catching title, referring to the ped, or pedon (the smallest sampling unit of a soil with the nature of its horizons and range of its properties identified, varying in size from 1 to 10 m^2) and cited frequently by colleagues in the soil ecology world. The paper introduced the major topics of a British Ecological Society meeting ("Ecological Interactions in Soil") in April 1984 at the University of York. It mentioned the international nature of our work; soil development, and gave overviews of "the root as primary producer, interactions with soil microbes, effects of grazing animals, interactions in soil and ecosystem function, and system-level manipulation of soil organisms" (Coleman, 1985). The paper was optimistic about future developments.

One generation ago, soil ecology was considered to be rather esoteric, yet important to practitioners of conservation tillage and other more environmentally friendly managements. It would have been difficult then to imagine a feature issue of Science (11 June 2004) with the theme: "Soils, the Final Frontier." The articles in Science emphasized the emerging concept of soils as being central organizing centers for terrestrial ecosystems (Coleman et al., 1998). Additional issues of Science have featured the Mars explorers and their findings. As noted in the Preface to Coleman et al. (2004), "In the midst of the wonder and awe surrounding the pictures that have been transmitted

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across 100 million miles to Earth during 2004 from the two Mars rovers, it is important to point out a basic fallacy in the discussions over the findings on the surface of Mars. The engineers and physical scientists in charge of the study persist in calling the Mars surface material "soil". …Organisms are one of the five major soil-forming factors, and life itself characterizes a true soil. Anything found on the surface of Mars—barring totally unexpected news to the contrary—is no doubt complex and interesting, but it is essentially weathered parent material, not soil. Arthur C. Clarke came closer with the title of his science fiction novel *Sands of Mars*". Unfortunately, we know only a bit more about soils on the little-studied planet Earth as well.

2. Historical perspective

Where has ecology progressed in the 22 years since "Through a Ped Darkly?" Is there any light in the ped yet, and if so, what have we learned? Have new areas opened up to us that we never imagined back then? What still eludes us? Where are we headed now? What exciting new avenues of research could help to turn up the lights in the ped? I address some of these questions later on, but present first a short overview of four decades of soil ecology.

2.1. Historical roots

My introduction to Soil Ecology was during 10 eventful Postdoctoral months during 1964–1965 with Amyan Macfadyen at the University College of Swansea, in South Wales, UK.

Our food web research entailed getting intact soil cores γ-irradiated at an Atomic Energy Research Centre facility in Wantage, Berkshire. After sterilization with between 2.5 and 5 MegaGrays (MGy) of γ-radiation from an industrial ^{60}Co source, replicate cores (5 cm dia, 10 cm deep) were inoculated with one of three species of litter fungi, and after a few days' incubation at room temperature, replaced back in the field (grazing land dominated by bracken, *Pteridium aquilinum*, and grass, *Nardus stricta*). We found that certain mites and Collembola, as inferred by their recolonization patterns over several weeks, exhibit significant feeding preferences for fungi in the field (Coleman and Macfadyen, 1966). That was novel then; many prior preference studies had been conducted only in the laboratory.

In subsequent research at the Savannah River Ecology Laboratory we used γ-emitting radioisotopes (e.g., ^{65}Zn) to tag soil fungi in the field, measuring radioactivity in individual fungal-feeding and predatory mites during several weeks to delineate fungal food webs (Fig. 1, Coleman and McGinnis, 1970). Later on in Colorado, we worked from the bottom up, starting with single species and then multiple species of microbes, fauna and plants growing in gnotobiotic (e.g., known biology) microcosms. One of the principal findings of this research was the marked impacts that population interactions (predator–prey, and extensive omnivory) have on nutrient cycling in soils, enhancing nitrogen and phosphorus mineralization and subsequent plant nutrient uptake (Coleman et al., 1983; Ingham et al., 1985). This research convinced many soil scientists that interactions of all biota in the food web have a significant effect on nutrient availability in the soil solution (Fig. 2, Wardle, 2002; Wardle et al., 2004).

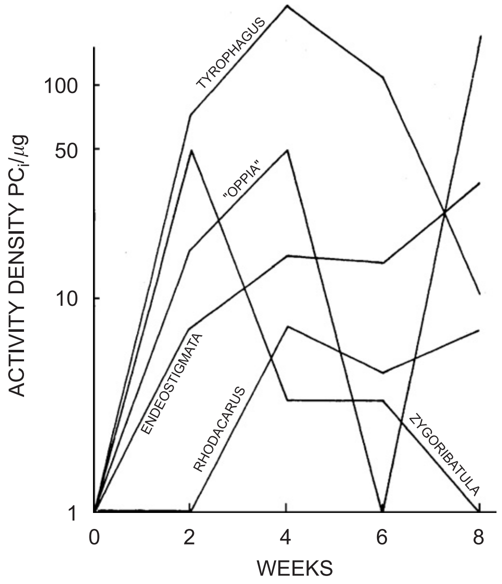

Fig. 1. An early soil fungal foodweb, delineated using ^{65}Zn-labelled soil fungi (*Geotrichum* sp.). Predatory mite activity arose later in the experiment, in accord with expectations (Coleman and McGinnis, 1970).

Detrital food webs are quite complex in hot deserts, such as the Chihuahuan desert, with up to 22 genera of nematodes at several trophic levels. In the cold dry Taylor Valley of Antarctica, only three genera of nematodes are present (Fig. 3); perhaps the food web interactions will be more readily understood in those simpler systems. In a more general sense, trophic interactions are concerned with current energy flow; the physical modifications made by "ecosystem engineers", such as earthworms, ants and termites, set the conditions for existence of the soil biotic community over the long run (Fig. 4, Anderson, 2000; Scheu and Setälä, 2002).

2.2. Activities in the 1980s and onward

In the 1980s, we moved from the laboratory into the field, first in Colorado and Wyoming and later in Georgia, using a wide range of biocides to manipulate entire feeding guilds and trophic groups to follow organic matter dynamics (summarized in Ingham et al., 1986; Beare et al., 1992). We found that with suppression of the fungal pathway, more activity would proceed in the bacterial one, and vice versa. Throughout much of this work, we relied on measurements of microbial biomass carbon, nitrogen, and phosphorus, to determine the extent of nutrient availability enhanced by faunal feeding on the microbes. Although this provided some information, it avoided the overall question, what microbes are present in the soil and on earth (Fig. 5,

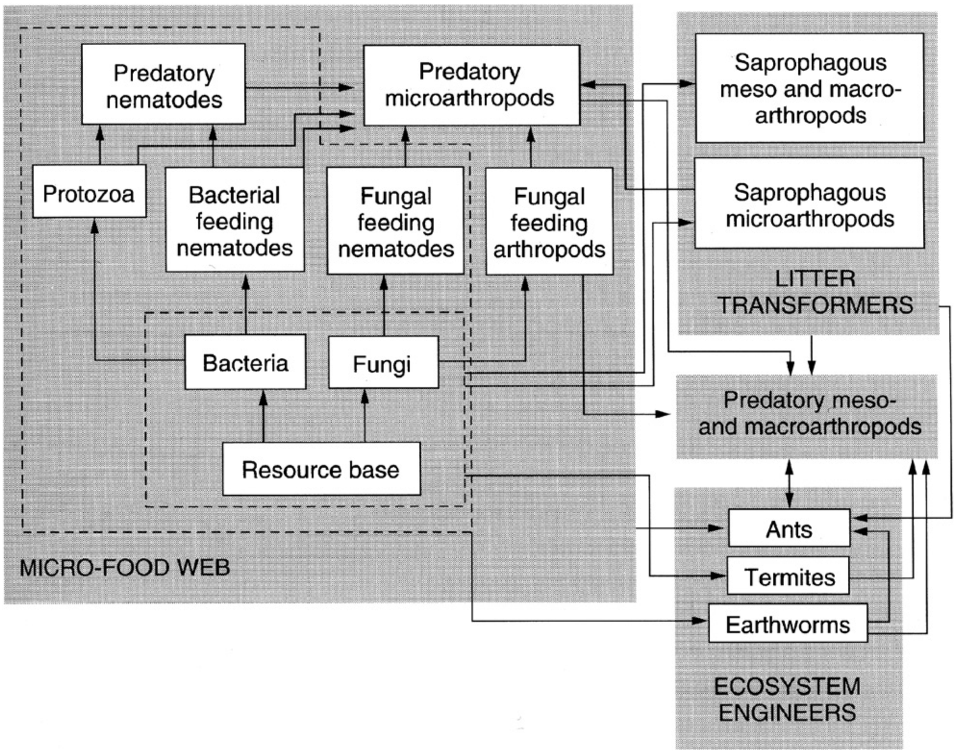

Fig. 2. Organization of the soil food web into three categories—ecosystem engineers, litter transformers and micro-food webs (after Wardle, 2002; Lavelle et al., 1995).

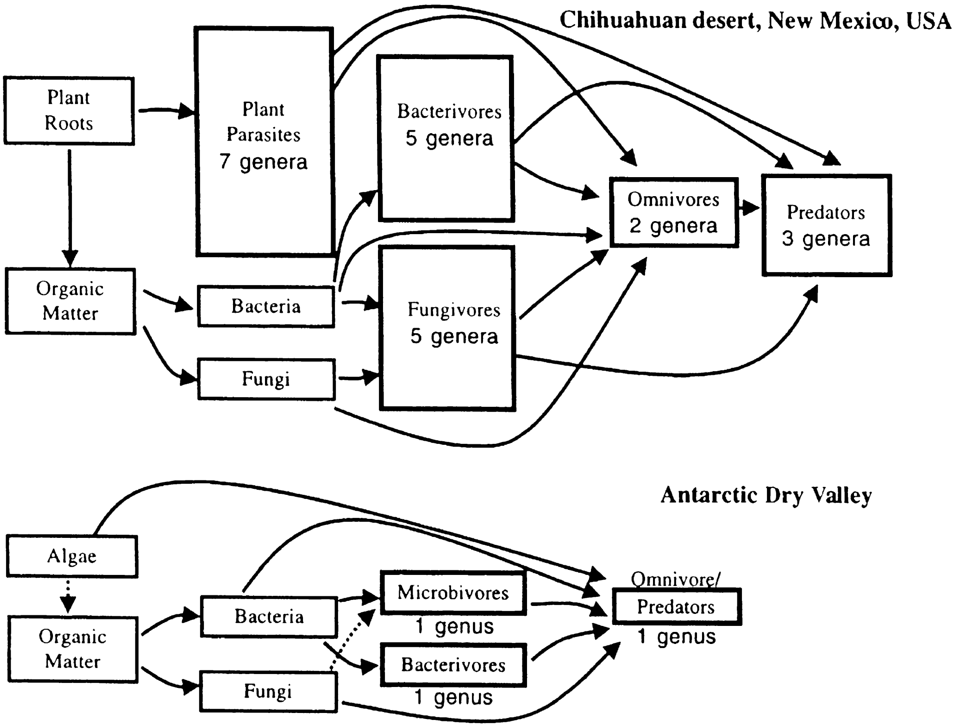

Fig. 3. Detrital food webs: complex in the Chihuahuan desert; very simple in Taylor Dry Valley, Antarctica, with only 3 spp. of microbivorous nematodes (Wall and Virginia, 1999).

Whitman et al., 1998)? Which microbes are culturable or not (many are not yet culturable, Fig. 6) and which ones are actively involved in our soil food webs? That has awaited the slow but steady rise of molecular microbial ecology, using probes, following 16S rRNA genes, enabling one to make soil libraries. For further comments on

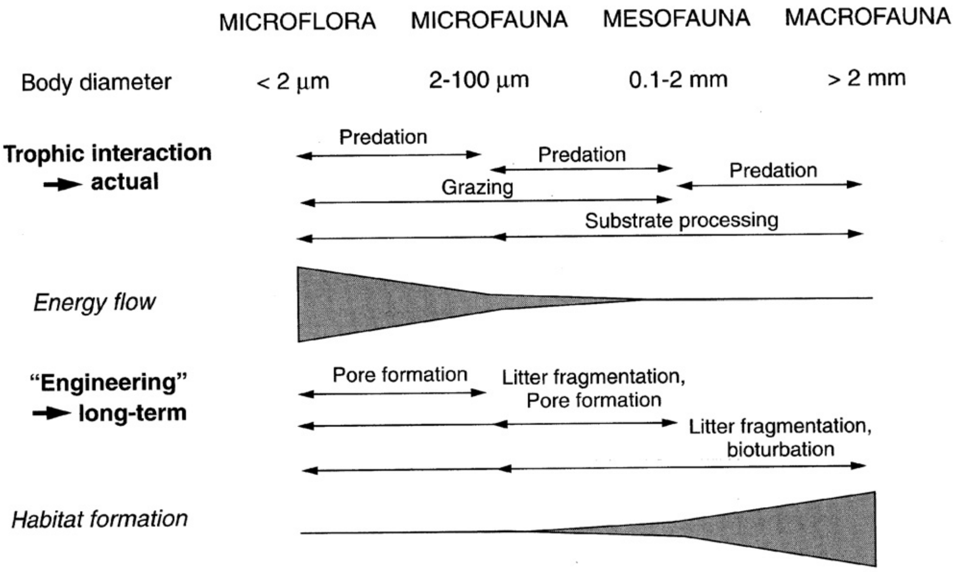

Fig. 4. Size-dependent interactions among soil organisms. Trophic interactions and interactions caused by "engineering" are separated; both are indicated by arrows. Both function at different scales: trophic interactions drive the current energy flow, engineering sets the conditions for the existence of the soil biota community over the long term (Scheu and Setälä, 2002).

microbial aspects of soil diversity, see Coleman and Whitman (2005).

3. Recent developments in soil ecology

Concerning "what exciting new avenues of research could help to turn up the lights in the ped" (J. D. Jastrow, pers. commun.), impressive progress has been made using scanning electron microscopy (SEM), looking at the micro-world of microbial-faunal interactions, such as fungi and calcium oxalate crystal formation, which is important for calcium accumulators such as oribatid mites, gastropods and millipedes, and the activities of mycophagous amoebae feeding on soil fungi, a trophic role often underestimated in soils (Gupta and Yeates, 1997) (see SEM pictures in Coleman et al., 2004).

3.1. New analytical tools

The development of nano-scale secondary ion mass spectrometry (NanoSIMS) in combination with high-resolution microscopy has enabled researchers to determine nutrient uptake at nano-scales and then to scale up to the level of soil aggregates to assess the uptake and turnover of C, N, P and other key nutrients in intriguing ways (Herrmann et al., 2007).

Ecologists now have the tools available, preferably in collaboration with molecular biologists, to determine most of the species or operational taxonomic units (OTU's, defined as the DNA sequences being compared in molecular terms) in soils. Hence we are now ready to address an intriguing theme: by what mechanisms can so many species of microbes, fungi and fauna in soils coexist, seemingly in the same space? We know that many soil organisms can survive in space and time by undergoing estivation, suspended activity, etc., by numerous mechanisms. Among the tens of thousands of organisms seemingly coexisting in soils, who feeds upon whom, and who benefits whom? How are microbial species defined? The standard approach, namely $>97\%$ DNA similarity, is very conservative. If this metric were applied to mammals, chimpanzees and humans would be considered identical (W.B. Whitman, pers. commun.).

4. Coexistence of species in soils

Hutchinson, in an insightful paper (1961) asked how it was possible for so many species of plankton to coexist in water columns. Hence "the paradox of the plankton." Soil ecologists have commented upon similar phenomena in soils, some early researchers being most notably Macfadyen (1962) and Anderson (1975), who coined the phrase: "the enigma of soil animal species diversity." The planktonic and paradoxical analogy for soils is appropriate, considering that much of the active surfaces of soils are water films, with the micro- and meso-fauna in soils analogized as being terrestrial plankton (Francé, 1921).

4.1. Microhabitat diversity

In soils, one might expect an even greater opportunity for niche separation to occur as a function of the nature of the habitat (e.g., texture as an array of sand, silt and clay-sized particles, and structure as an array of micro- and macro-aggregates and pore necks), all of which would provide a widely varying physical environment (Elliott et al., 1980; Ettema, 1998). This environment is characterized

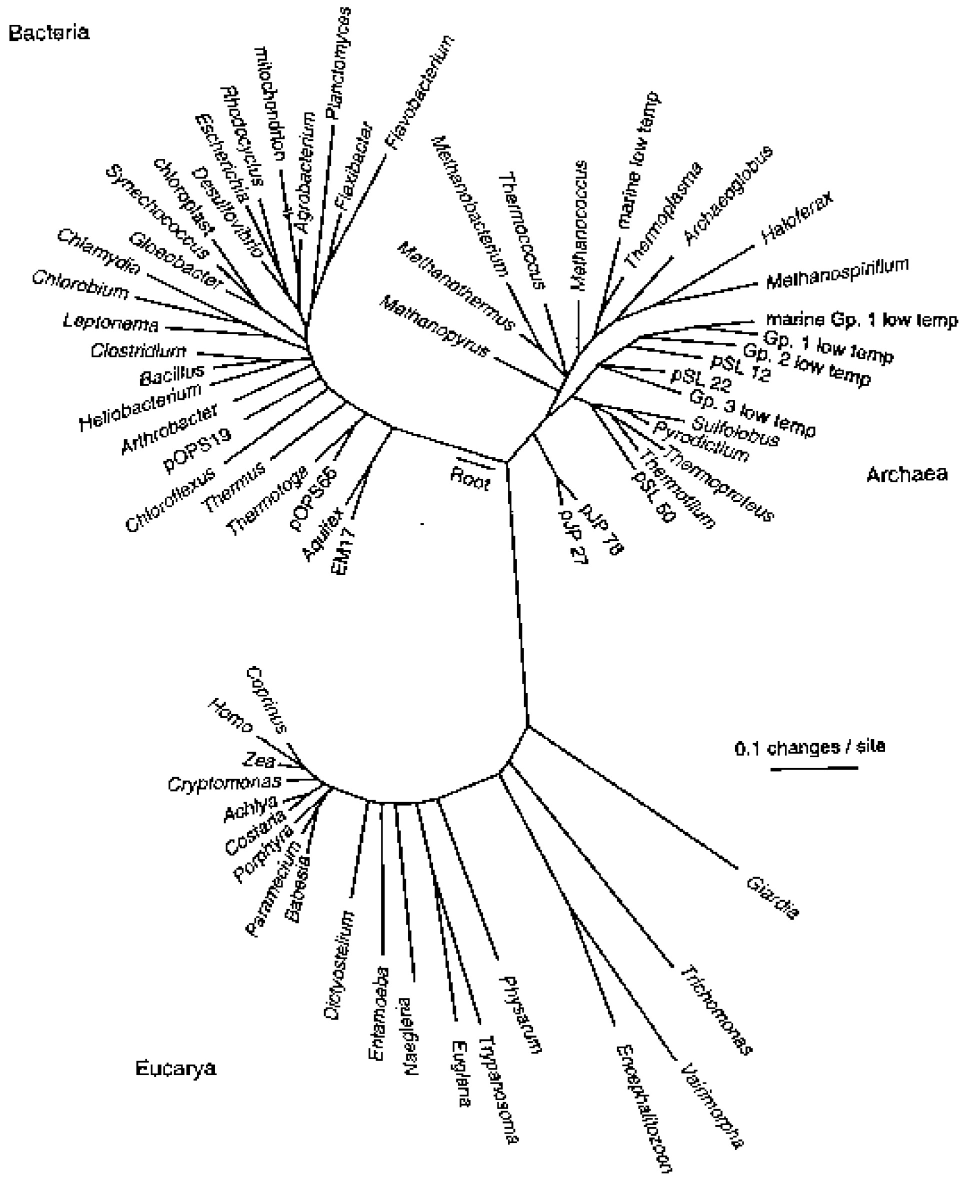

Fig. 5. Phylogenetic tree showing the three Domains of life: Archaea, Bacteria and Eucarya (Pace, 1999).

by the extent to which substrates are actively or passively stabilized against degradation by a variety of physico-chemical methods, and whether there is partial or absolute refuge (e.g., pore necks) from decomposer microbes or fauna (Ekschmitt et al., 2005). Superimposed on this is the considerable niche partitioning among organisms that occupy this environment (Wardle, 2002). Examples of these include phenological differentiation of activities over time, varying distributions by depth, microclimatic properties in the soil layers, and soil chemical properties. An additional key consideration is the fact that a majority of soil microbes (and often fauna as well) is usually dormant, inactive for various time periods (Jenkinson and Ladd, 1981; Coleman et al., 2004).

In the next few paragraphs, I consider the patterns of biodiversity of some microarthropods, the Oribatid mites, the most diverse small arthropod group in forest litter and soil, as an example of how niche differentiation may evolve in soils and is being studied currently.

4.2. Oribatid mite feeding guilds

Oribatid mites are very speciose, numbering 20,000 known species, with perhaps 60,000 yet to be described (Table 1, Coleman, 2001). A widespread assumption in the soil ecology literature (Maraun et al., 2003; Coleman et al., 2004) has been that oribatids feed upon fungi of decomposing leaf and root litter, hence may have narrow niche overlaps in food items they consume. Recent studies in Europe have demonstrated a somewhat wider range of food items in oribatid diets that have been measured by stable isotope ratios ($^{15}N/^{14}N$) (Schneider et al., 2004). A total of four feeding guilds among 36 species/taxa were differentiated, ranging from phycophages/fungivores, with

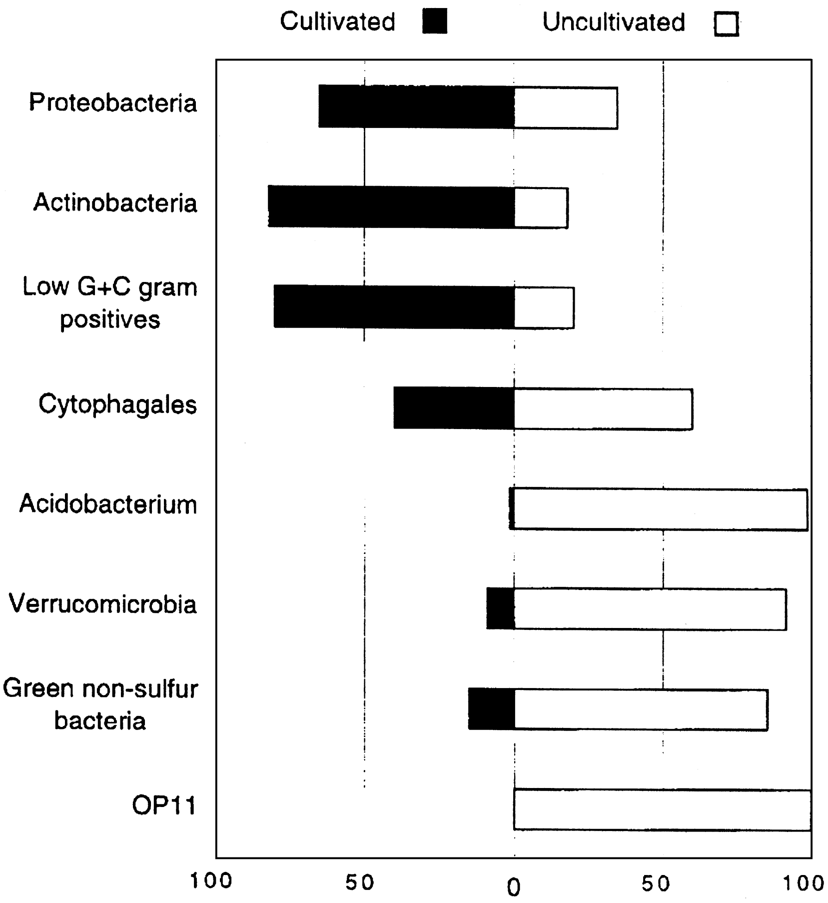

Fig. 6. Percentage cultivated ($<5\%$ of total phylotypes) and uncultivated groups in selected cosmopolitan bacterial divisions of 16S rRNA sequences (from Hugenholtz et al., 1998). Many of these groups are abundant members of the soil microbial community.

δ^{15}N of -4.5, to primary decomposers, feeding on litter (δ^{15}N of -4 to -3), secondary decomposers, feeding on fungi and litter (δ^{15}N of 0–1), and carnivores/scavengers/omnivores, with δ^{15}N of $+3-4$ (Table 2, Schneider et al., 2004).

Expanding the sampling universe from soil to tree bark, Erdmann et al. (2007) measured the natural variation in stable isotope ratios (δ^{15}N, δ^{13}C) of bark and covering vegetation (bryophytes, lichens, algae and fungi) on four common tree species (oak, *Quercus robur*; beech, *Fagus sylvatica*; spruce, *Picea abies* and pine, *Pinus silvestris*). The stable isotope ratios of the respective oribatid mite species on bark of the four tree species were very similar, indicating that the corticolous food sources were also similar. The isotope ratios spanned about 13 δ units for ^{15}N and ca. 7 δ units for ^{13}C, exhibiting a range of about three trophic levels. This is further evidence of the wide ranges of food items that enable oribatids to coexist, given the wide niche breadths of the food sources they consume.

4.3. *High species richness of temperate forest oribatids*

In other parts of the world, in temperate deciduous and tropical forests, Oribatids are more speciose than in Germany. One notable example of high temperate zone oribatid diversity is that up to 170 species occur in just a few hundred square meters of the forest floor of a mesic, mixed deciduous forest watershed in western North Carolina (Hansen, 2000a, b). This species richness, or α-diversity (the diversity within a given site), 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. 7). In a 3-year field study, Hansen (2000a, b) measured a decline in species richness of oribatids as she decreased litter species richness in experimental ($1\,m^2$) enclosures from five down to one species of deciduous tree litter (Fig. 8, Hansen, 2000a). The decline in oribatid species richness was

Table 1
Species richness of key soil groups of eukaryotes (from Coleman, 2001)

Taxon. group	Spp. descr.	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
Oligochaeta	3650	8000

Table 2
(from Schneider et al., 2004)

Oribatid mite taxa	Feeding guild	Food materials
Amerus troisil *Hypochthonius rufulus* Oppiidae/ Suctobelbidae *Nothrus silvestris* Galumnidae	Carnivores/ scavengers/omnivores	Living and dead animals (nematodes, collembolans) and fungi
Eniochthonius minutissimus Damaeidae Oribatulidae/ Scheloribatidae Chamobatidae *Nanhermannia coronata* *Cepheus dentatus* *Malaconothrus* spp. *Eupelops plicatus* *Carabodes femoralis* *Nanhermannia nana*	Secondary decomposers	Predominantly fungi, in part litter
Ptyctima *Adoristes* spp. *Oribatella* spp. *Euzetes globules* *Liacarus* spp. *Tectocepheus* spp. *Nothrus palustris* *Platynothrus peltifer* *Carabodes marginatus* *Achipteria coleoptrata*	Primary decomposers	Predominantly litter
Carabodes labyrinthicus	Phycophages/ fungivores	Lichens and algae

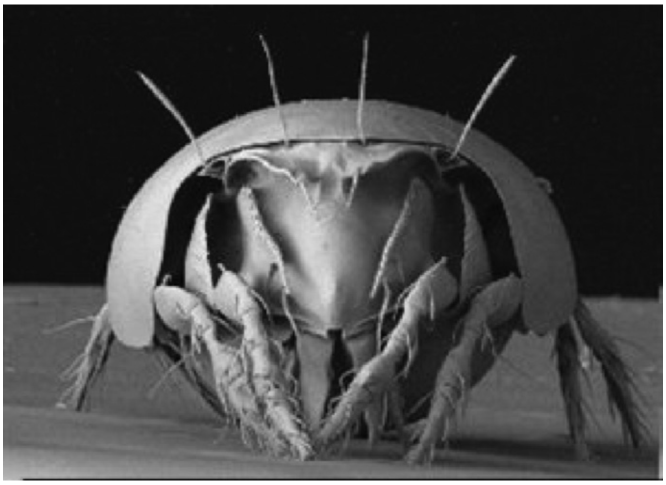

Fig. 7. SEM of Oribatid mite from a forest floor, showing chelicerae used for feeding on fungi and other substrates (Valerie Behan-Pelletier, pers. commun.).

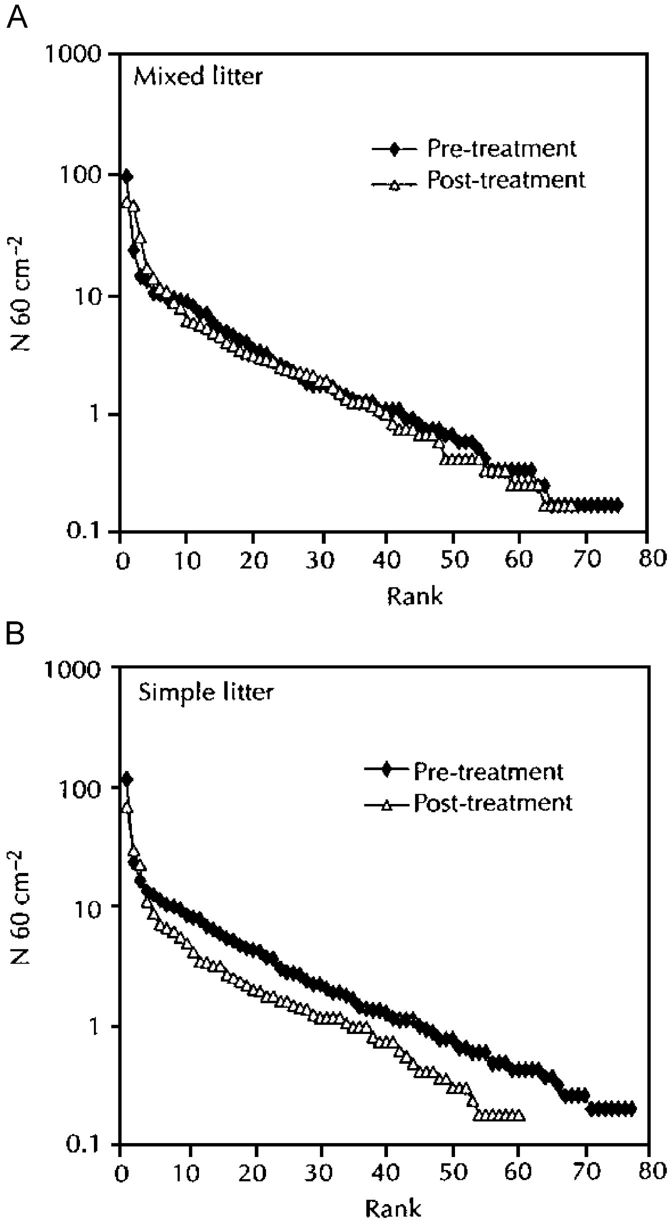

Fig. 8. Average rank vs. abundance curves for the oribatid assemblages pretreatment and 3 years post-treatment in simple and mixed litter plots at Coweeta LTER site, western North Carolina. Species were ranked according to their mean abundance in each of the five litter types. Data shown are the abundance 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, 2000a).

attributed to the lower physical and chemical diversity of available microhabitats from polyspecific to oligospecific litters, including leaf petioles, which specialized feeders such as phthiracarid mites would occupy preferentially (Hansen, 1999). In addition, the synchronized decomposition of uniform substrates in the monospecific litters could have led to a "boom-bust" cycle in microbial resources that was unfavorable to oribatid mites and their conservative life histories (Hansen, 2000b). This spatial aspect of biocomplexity mechanism is in accord with the niche-differentiation mechanisms in O horizon layers (O_i, O_e and O_a = L, F, and H in the European terminology) suggested earlier by Anderson (1975, 1978).

A testable hypothesis is that relatively high oribatid species richness in the oligospecific leaf litter of a forest floor is strongly influenced by the species richness of the decomposer fungal community. Hence feeding specificity, as noted by several authors (Schuster, 1956; Luxton, 1972) could be a primary causal factor of niche partitioning, hence giving rise to the very speciose nature of oribatid mites. 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. When eight species of litter decomposing fungi were offered to 10 oribatid species, a wide range of responses, some narrow, and others wide in species consumed, led Schneider and Maraun (2005) to suggest that although trophic niche differentiation in oribatids was limited it may contribute to the high diversity of these mites in the field. Molecular probes to examine the species richness of decomposer fungi and bacteria are being steadily improved and should help provide an answer to this apparent conundrum (Coleman and Whitman, 2005).

An evaluation of the distribution of species within a guild, such as shown by data in Hansen (2000a) in relation to the unified neutral theory of biodiversity and biogeography (Hubbell, 2001) is worthy of consideration. The species rank order curves in Fig. 8, with monospecific or polyspecific leaf litters, show descending S curves similar to ones presented in Chapter 1 of Hubbell (2001). This is impressive, given the much more heterogeneous environment that oribatid mites inhabit, compared with trees in a tropical rain forest. In calculations made using Hansen's (2000a) data, S. Hubbell (pers. commun., 2004) verified the conclusions made above. A more general consideration of the species rank orders in a wide range of soil-inhabiting taxa awaits further investigation.

Impacts of oribatid mites farther up the food chain, in ways not often considered by soil ecologists, have been demonstrated recently. In tropical America and probably in the tropics more generally, oribatids as a group contain as many as 80 alkaloids and represent a major dietary source of alkaloids in poison frogs (Saporito et al., 2007). A conservative assumption is that they accumulate alkaloids from their food sources. To what extent do fungi or other organisms contribute alkaloids to the oribatids' diet?

4.4. *Collembolans: a model system for gene transfer?*

Another group of microarthropods, the collembola, have been a mainstay of studies of microbial–faunal interactions for several decades. Recent research has focused on the possible role of collembolan guts serving as "hot spots" not only for nutrient transfer, but also for possible gene transfer between microorganisms. In an analogy to the fact that transfer rates of bacterial genes in rhizospheres are much higher than in bulk soil, Tebbe et al. (2006) considered that collembola could be a "hot spot" for bacterial gene transfer. The total volume of the gut of *Folsomia candida* is small (20 nl), but large enough to harbor thousands of bacteria simultaneously. With an average gut transit time of only 1 h, the processes occur relatively rapidly. In studies using strains of *E. coli* ingested by *F. candida*, with *Folsomia* guts as the experimental "reactor," Tebbe et al. (2006) found that transfer of narrow-host range plasmids could not be detected. However, conjugative plasmids and mobilizable plasmids, with the mobilizing genes in the donor cells, were transferred to indigenous gut bacteria. Plasmid mobilization by indigenous gut bacteria was not detected, but Tebbe et al. (2006) assume that conditions may be favorable for that at various times in the life-span of the collembolan.

Although not yet studied in a similar fashion, one might well expect to find similar processes and patterns in mite guts as well. Indeed, the consequences of gut activities in numerous invertebrates (e.g., comminution, enzymatic activities, often with accompanying pH changes, etc.), including earthworms, gastropods and termites (Brauman et al., 2000), are often overlooked or underappreciated by many soil biologists.

4.5. *Trophic interactions in soil biodiversity*

In the full range of ecological factors affecting soil organisms, there are undoubtedly some "top-down" forces of predation that would have an influence, and some "sideways" forces of interspecific competition as well. An interesting example from soil systems is given by Wardle (2002), who noted that in microcosms Hedlund and Augustsson (1995) found that hyphal length of the fungus *Mortierella isabellina* was greatest when subjected to intermediate intensities (in contrast to low and high levels) of grazing by the enchytraeid *Cognettia sphagnetorum*. This finding is clear proof of an overcompensatory response to grazing. Similar findings were cited by Wardle (2002) for collembola grazing on the fungus *Botrytis cinerea*. Indeed, below-ground communities could differ from their above-ground counterparts in that soil biodiversity is not so strongly regulated by competition, and competitive exclusion does not occur when resource availability in soil is increased (Wardle, 2002, Bardgett et al., 2005).

Concerns about the roles of oribatid mites as vectors for soil microfungi led Renker et al. (2005), using cultural and molecular (DNA extraction and PCR analyses) techniques, to investigate the extent of fungal dispersal in soils. Surprisingly, Renker et al. (2005) found that several saprotrophic and a few parasitic genera, including *Beauveria* were associated with four of the most common oribatid species in a temperate deciduous forest, but no mycorrhizal fungi were detected. Ingestion of certain arbuscular mycorrhizal (AM) spores by collembola in culture was demonstrated by Moore et al. (1985). Collembola seem to feed preferentially on saprotrophic fungi under field conditions however, perhaps allowing AM fungi to gain space on the root surface (Gange and Brown, 2002). An additional aspect of microarthropod feeding effects is the suppression of pathogenic fungi, e.g., *Rhizoctonia solani* on cotton plants by collembola (*Proisotoma minuta*) under field conditions in Alabama, USA (Lartey et al., 1994).

As in many other aspects of ecology, temporal considerations are of paramount importance in soil food web dynamics. In a $^{13}CO_2$ pulse-chase experiment, followed by sampling of soil mesofauna over the next 20 days, Ostle et al. (2007) measured a significant increase in tracer ^{13}C uptake by both collembolans and mites. This pattern was increased markedly by defoliation of subplots within 1 week of the pulse. Thus, short-term rhizodeposition patterns affect soil food web dynamics; a pattern that was observed also by Garrett et al. (2001).

A recent synthesis of ecosystem effects of biodiversity comments that: "soil processes in particular appear to be primarily influenced by the functional characteristics of dominant species rather than by the number of species present" (Hooper et al., 2005). These processes include decomposition, soil OM dynamics, nutrient uptake by soil organisms and nutrient retention. All of these are more strongly influenced by differences in functional traits (leaf chemistry, etc.) of the dominant plant species than by the diversity of plant species. Hooper et al. (2005) admit that "less is known about how the diversity of soil organisms affects rates of decomposition and nutrient cycling." This is a key point, deserving of much more study. Recent studies of synthesized soil food webs suggest that food web composition, rather than the diversity of the organisms within trophic levels, drives decomposition properties, and omnivory plays a key regulating role as well (Mikola and Setälä, 1998; Moore et al., 2004) and plant productivity (Laakso and Setälä, 1999).

4.6. *Effects of bottom-up vs. top-down forces in soil systems*

A comprehensive study of bottom-up and top-down forces in a temperate deciduous forest studied the response of three major biotic components to the addition of resources (Salamon et al., 2006). They hypothesized that bottom-up effects would be strongest on lower trophic levels, leading to increases in bacteria and fungi. These effects would propagate to higher trophic levels, but with decreasing intensity due to high connectivity, omnivory and generalist feeding. The components were: microorganisms, animal decomposers and predators (Staphylinid beetles, Araneida, Lithobiid centipedes, Pseudoscorpionida, Prostigmata, Uropodina, Gamasina, certain Nematode taxa). Organic additions were added fortnightly to $1\,m^2$ experimental enclosures set up in a randomized complete block design, and the experiment was run for 17 months. The organic additions, in ascending C-to-N ratio were: wheat bran (18), pet food (22), CNP (31) and beech wood (1080).

Microbial biomass increased only moderately after resource addition, and some animal groups increased (lumbricids, nematodes, collembolans, gamasid mites, staphylinids), densities of several other groups decreased (oribatids, prostigmatids and lithobiids), and several others remained unaffected (enchytraeids, millipedes, uropodine mites, pseudoscorpions and spiders). Salamon et al. (2006) concluded that: (a) bottom-up forces are of limited importance in soils of temperate deciduous forests; (b) large primary decomposers such as earthworms do not depend on microorganisms for food but consume organic matter directly; (c) the link between microorganisms and microbivores such as collembolans, is weak because collembolan density increased even though microbial biomass was unaffected; (d) prostigmatid mites and centipedes respond to habitat modification by ecosystem engineers such as earthworms and (e) the soil food web is rather resistant, responding little to changes in resource supply. Interestingly, species often commonly assigned to a single trophic group, e.g., collembolans, responded differentially to changes in the base of the food web. Thus increased fungal biomass led to an increase in densities of *Folsomia quadrioculata* and *Isotomiella minor*, whereas increased bacterial biomass was accompanied by increased density of *Ceratophysella denticulata* and *Isotoma notabilis*. One might question some of the experimental conditions and assumptions, namely: microorganisms were estimated from respiration and not fumigation, ergosterol may not decompose as was assumed, but the study represents an impressive attempt at a holistic study and merits further studies by other ecologists to ascertain the generalities of some of Salamon et al. (2006) conclusions.

A more theoretical approach to the study of the coexistence of soil organisms addresses the coexistence of strong competitors in soils. Soil community feedback in plant–soil systems can be strongly negative, and generated by a variety of complementary soil microbial mechanisms, including host-specific changes in the composition of rhizosphere bacteria, nematodes, pathogenic and mycorrhizal fungi (Bever, 2003). To date, there are no empirical demonstrations that negative feedback can permit coexistence of plant species that might otherwise competitively exclude each other. Bever (2003) observed that it may prove useful to develop mechanistic models of competition that include soil microbial dynamics and soil feedback, as discussed by van der Heijden (2002).

5. Additional major themes in soil ecology

The above commentary on the mechanisms for coexistence of soil organisms reflects one of several major themes running through soil ecology. Others include new advances in knowledge of root production and turnover and their impacts on soil ecosystems; soil biota, rhizodeposition, and soil aggregation phenomena; the biology of invasive species in soils; soil biodiversity, legacies and linkages to soil processes and soil biodiversity and ecosystem functional responses. I consider these themes in turn, and finally suggest some interesting topics that would benefit from research in the future.

5.1. Root-related processes

Beginning with inputs, the ways in which root production and turnover are being measured is remarkable, compared with the crude methods such as ^{14}C pulse labeling, which were in use a generation ago. By using a combination of $\delta^{13}C$ and ^{14}C tracing with mass spectrometry and accelerator mass spectrometry, Gaudinski et al. (2000) have been able to decipher root production and persistence at different layers in the soil profile, providing much useful information for researchers at the plot and watershed scales, as well as regional scales of resolution. In recent studies of AM, Driver et al. (2005) discovered that the glycoprotein Glomalin seems to be more associated with AM hyphae rather than being expressed as an exudation or secretion. Glomalin-related soil protein (GRSP) is problematic yet, and seems to be confounded with some humic materials. It may not be correlated directly with substances produced by AM hyphae (Rosier et al., 2006; Schindler et al., 2007; Whiffen et al., 2007).

Jastrow et al. (1998) developed a system-level comparison of physical binding effects of roots, fungal hyphae and their secretions that are key agents in soil aggregation in the Tallgrass prairie restoration at the Fermilab, Argonne, Illinois, USA. Using path analysis, they determined direct and indirect effects of fine roots, microorganisms and organic matter, with roots and mycorrhiza playing dominant roles (Fig. 9). The ways in which aggregates are formed, disassembled and reassembled have been reviewed by Six et al. (1999) (Fig. 10).

The roles of AM species in diversity and ecosystem functioning have been the subject of considerable research in recent years. Considering the fact that most AMF species can colonize many plants, this in turn means that most plants host several different AMF species concurrently (Allen, 1996). Thus, not only do mycorrhizal plants acquire more nutrients, they are able to share them via an underground network of hyphal connections linking individuals within and between species (Hart and Klironomos, 2002; Simard et al., 2002).

Ectomycorrhizal fungi (EMF) are similarly influential in affecting nutrient uptake, affecting uptake via flow through the Hartig net (the interface between the plant and the fungus) or traveling through the apoplast of the fungal mantle (Simard et al., 2002). Soil community dynamics in the New Jersey pine barrens ecosystem, dominated by pitch pine (*Pinus rigida*), showed a significant EMF by microarthropod interaction, with collembola (principally *Folsomia* spp.) showing positive or negative correlations (hence inferred feeding) with various EMF morphotypes in leaf litters in experimental incubations. There were no responses to EMF strains exhibited by the mite species in this ecosystem (Jonsson et al., 2006).

The rhizosphere is a well-known "hot spot" for microbial and faunal activity (Beare et al., 1995). The interaction between plant roots, root exudates and microorganisms is multi-faceted and the role of soil micro and meso-fauna in enhancing nutrient turnover and plant growth (Elliott et al., 1979; Ingham et al., 1985) is becoming more widely appreciated. Cardon and Gage (2006) summarize numerous studies of stable isotope probing and microbial bioreporters of gene products, indicating activities within the rhizosphere. With little direct proof, Bonkowski et al. (2000) suggested that the additional effects of release of phytohormones by protists grazing on bacteria may have an influence beyond that of direct nutrient release. This assertion remains

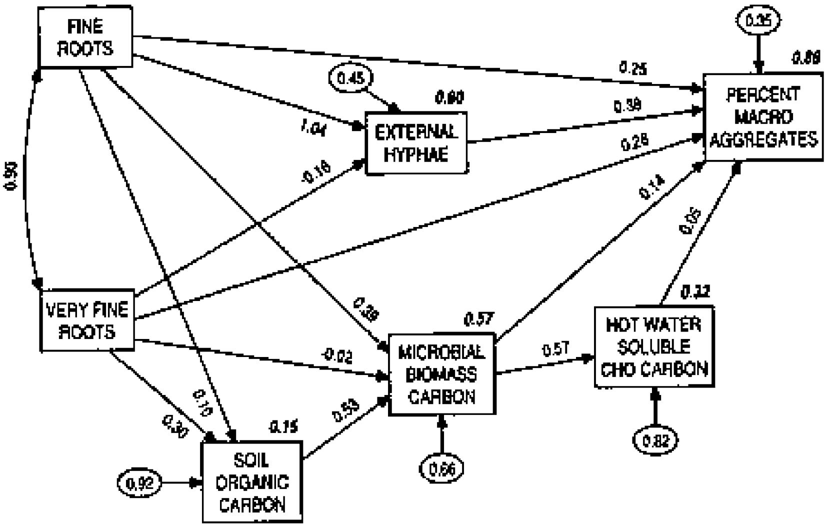

Fig. 9. Path model of hypothesized causal relationships among the lengths of roots and mycorrhizal fungal hyphae, three soil C pools and the percentage of water-stable aggregates in a chronosequence of prairie restorations. Numbers are path coefficients and proportion of total variance explained (r^2; shown in bold italics) for each endogenous variable. The numbers within ellipses represent the proportion of unexplained variance and, thus, indicate the relative contribution of all unmeasured or unknown factors to each dependent variable (from Jastrow et al., 1998).

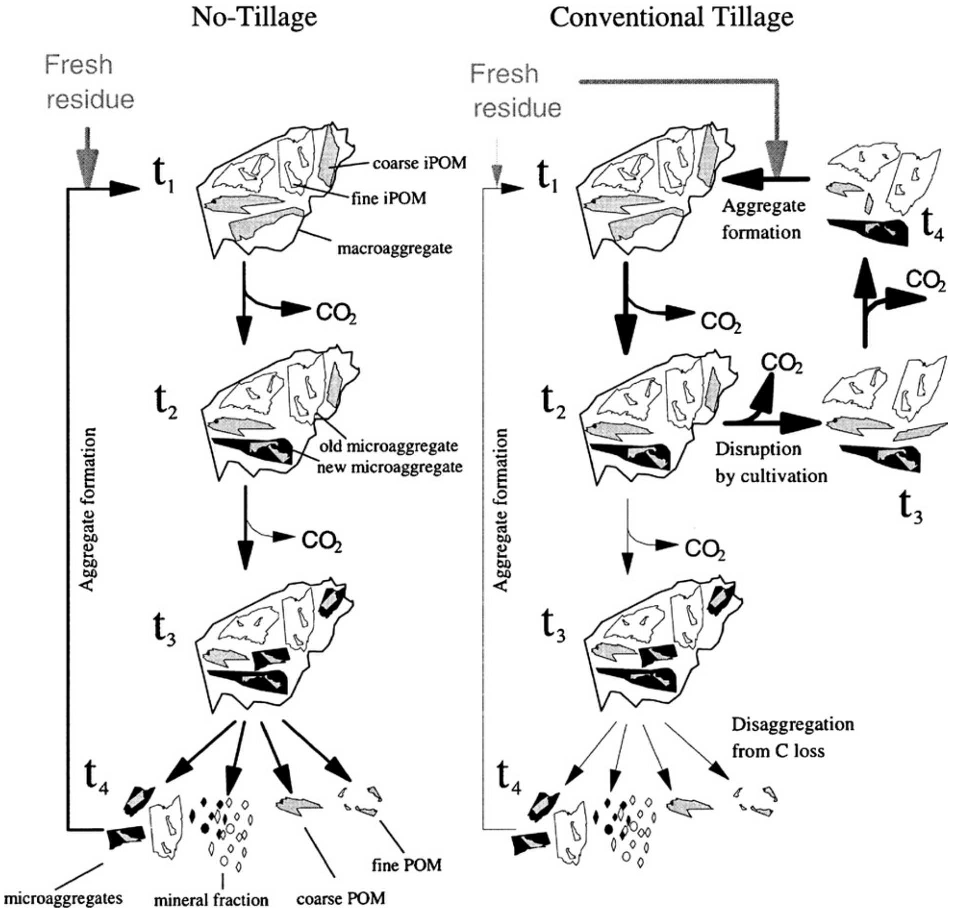

Fig. 10. Diagram of NT and CT macro- and micro-aggregate stability. Note less stable regime in CT (Six et al., 1999).

controversial across the decades, having been raised initially by Russian workers in Uzbekistan (Nikolyuk and Geltzer, 1972). Additional research in the area of chemical ecology in the soil is certainly warranted.

5.2. Mycorrhizosphere

The field of mycorrhizosphere (the volume immediately surrounding fungal mutualists (mycorrhizae) associated with roots) research has leapt forward with elegant microscopic methods in conjunction with molecular tools to pinpoint co-associated organisms. Artursson and Jansson (2003) used the thymidine analog bromodeoxyuridine (BrdU) to identify active bacteria associated with 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. *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. 11). This study is a model of how to use molecular and traditional approaches to isolate, identify and visualize a specific bacterium that is active in soil and associates with another organism.

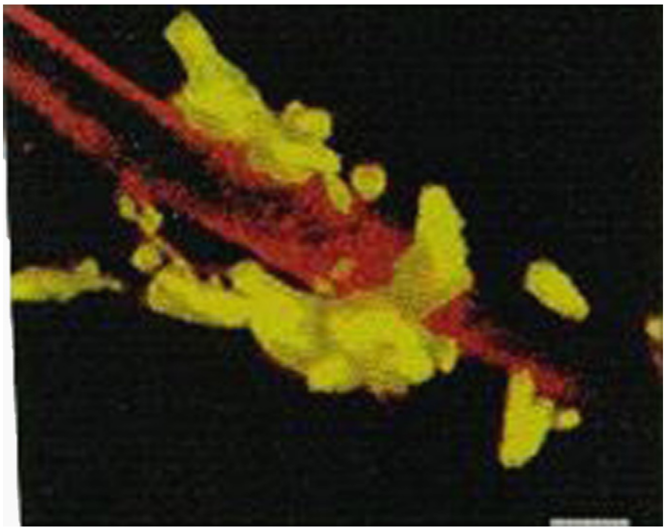

Fig. 11. Immunofluorescent-labeled *Bacillus cereus* associated with an arbuscular mycorrhiza in an undisturbed fallow field near Uppsala, Sweden (Artursson and Jansson, 2003).

5.3. Soil biodiversity and legacies

Soils are rife with historical signs and legacies, as has been made evident by studies (e.g., Pawluk, 1987) using soil

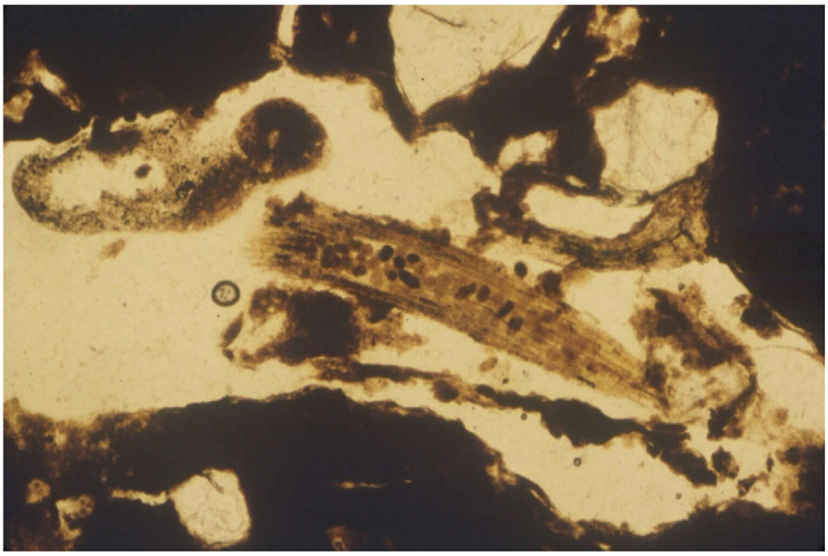

Fig. 12. Soil thin section (5-cm depth), showing microarthropod feces associated with sorghum litter breakdown in a Georgia piedmont agroecosystem, Griffin, GA (L.T. West pers. commun.).

thin sections showing mite fecal pellets (wrapped in chitin-rich peritrophic membranes) in the soil profile that persist for years (Fig. 12). The pellets act as a slow-release nitrogen fertilizer within the humification layer in soils. Radiotracer and stable isotope studies have also demonstrated organic matter legacies in soil profiles (Gaudinski et al., 2000).

5.4. *Effects of invasive species on soil processes*

The impacts of invasive plants on ecosystems have been investigated in a wide range of sites. System-level changes ranged from increase in available nitrate and elevated pH due to changes in root growth and activity patterns (Ehrenfeld et al., 2001), to changes in litter quality and lower species richness and numbers of soil invertebrates, and altered percentage ground cover with the invasion of *Bromus tectorum* in three study sites in the Canyonlands of southeastern Utah (Belnap and Phillips, 2001). The invasion of exotic plant species has markedly altered the distribution and abundance of pathogenic and/or mutualistic fungi, which in turn affects the establishment, growth and biotic interactions between exotic and native plants (Wolfe and Klironomos, 2005).

Earthworm invasion has a marked potential to alter (usually reduce) soil C storage on local and regional scales (Alban and Berry, 1994; Bohlen et al., 2004a). Previous site history has a significant impact on organic matter dynamics. For example, in a comparison of storage of soil C and changes in C:N ratios in two sugar maple (*Acer saccharum*)-dominated forests in New York State, USA, Bohlen et al. (2004b) found that exotic earthworm species eliminated the thick forest floor, decreased soil C storage in the upper 12 cm by 28%, and reduced soil C:N ratios from 19.2 to 15.3. At a previously cultivated forest site with little forest floor, earthworms did not change the storage of soil C or N or soil C:N ratios. Additional analyses of stable isotopic signatures revealed that earthworms significantly increased the loss of forest floor C but not N from the site with the thick forest floor. An increase in total microbial biomass after earthworm invasion may act as a strong immobilization sink for available N in C-rich soils (Groffman et al., 2004). These results suggest that the effect of earthworm invasion on the distribution, retention, and solution chemistry of soil C and N in northern temperate forests may depend on the initial quantity and quality of soil organic matter at invaded sites.

Few studies have been carried out in the field across several years to ascertain the impacts of invasive exotic earthworms on soil microbial community responses. One noteworthy example in western Alberta, Canada, followed the response of soil fungi to the invasion of *Dendrobaena octaedra* into pine forest soils. In the long term, fungal community diversity and richness decreased and dominance among fungi increased, apparently due to the disruption of fungal hyphae, lowered resource availability, and reduced spatial heterogeneity as the organic layers in the forest floor became homogenized (McLean and Parkinson, 2000). Competition among fungi was reduced soon after the invasion, perhaps due to the addition of nutrients or as a result of disturbances due to burrowing and deposition of casts into the organic layers (McLean and Parkinson, 1998). For a summary of the impacts of non-native earthworms on temperate forests, see the review by Bohlen et al. (2004c). The policy implications for monitoring the movement and impacts of invasive earthworms were reviewed by Hendrix and Bohlen (2002). For additional examples of impacts of invasive animals and potential for their biological control in agroecosystems see Robertson and Swinton (2005).

5.5. Levels of disturbance; effects on soil biodiversity

The impact of invasive species on plants and soil organisms is a subset of a more general phenomenon: the effects of various levels of disturbance on soil biodiversity. Several studies summarized by Bardgett et al. (2005) have shown little support for optimization of local soil animal diversity at intermediate levels of disturbance. In fact, Wardle (1995) found that a wide range of disturbances of soil by tillage could strongly elevate or reduce macrofaunal group diversity, but the diversity of microfauna was little affected. Apparently the magnitude of these effects depends on soil type, climate and tillage operation. The overall consensus seems to be that in conversion from natural vegetation to agriculture, the diversity of a wide range of microbial communities and faunal groups, ranging from nematodes to earthworms and termites, is significantly reduced in the disturbed agro-ecosystems (Bardgett et al., 2005). Rigorous experimental testing of the disturbance–diversity relationship is still needed to ascertain its importance as a regulator of below-ground diversity (Bardgett et al., 2005). We must keep in mind the spatio-temporal aspects of soil communities. Thus enhanced habitat complexity and diversity of available food resources will support localized "hot spots" of more diverse mite communities, as noted in Section 4.2 above (Hansen, 2000a, b; Bardgett et al., 2005). This is addressed further in Section 6.4 below.

A more general aspect of disturbance studies is that related to land-use and global change phenomena. Noting some significant differences in bacterial- and fungal-based soil food webs, with organisms in the latter pathway considered more sensitive to disturbance, Hedlund et al. (2004) concluded that disturbance-induced changes in plant community composition will change the soil food web composition. Organisms involved in direct interactions with plants (i.e., AM fungi) were also predicted to be vulnerable to disturbance. A very useful general model for the nature of aboveground and belowground interactions between principal functional groups (as noted in Fig. 2) in soil is provided by Schröter et al. (2004).

5.6. Soil biodiversity and ecosystem functional responses

Numerous factors influence the magnitude and stability of ecosystem properties, including climate, geography, and soil or sediment type. These abiotic controls interact with functional traits of organisms to control ecosystem properties (Fig. 13, Hooper et al., 2005). These in turn have feedbacks on biodiversity. Assuming that there is an increase in ecosystem function with increasing diversity, they could arise from two principal mechanisms: (1) only one or a few species might have a large effect on any given ecosystem property. Increasing species richness increases the likelihood that these species would be present, and assumes that competitive success and high productivity are positively associated at the species level (Fig. 14A, Hooper et al., 2005; Tilman, 2001); (2) species or functional richness could increase ecosystem properties through positive interactions among species. Two primary mechanisms for this are complementarity and facilitation, leading to the phenomenon of overyielding. All these effects are expected to show a similar saturating response as diversity increases (Fig. 14B, Hooper et al., 2005).

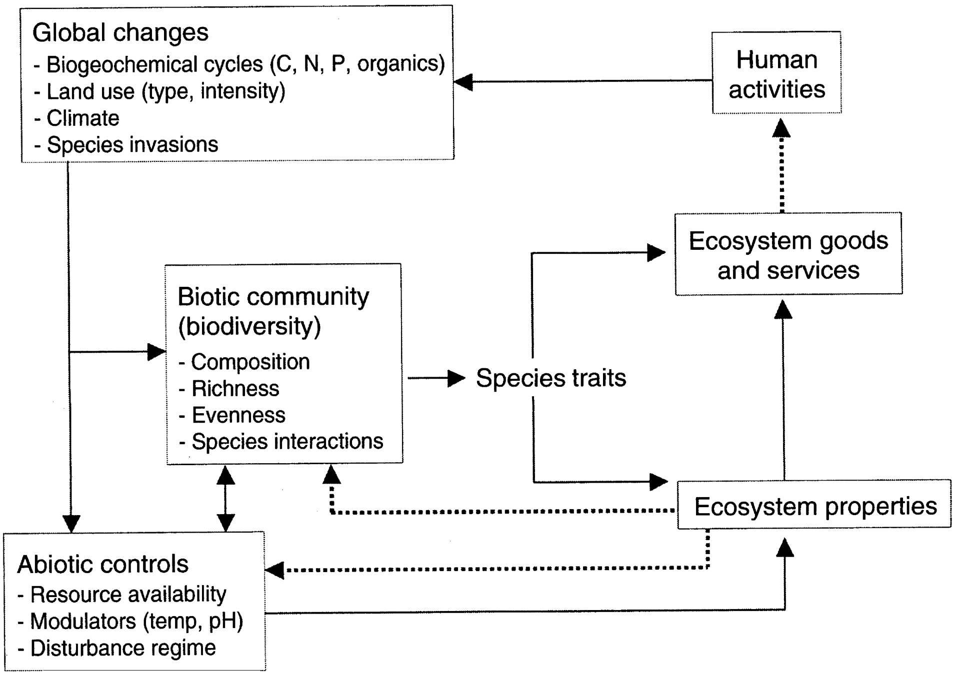

Fig. 13. Feedbacks between human activities, global changes, and biotic and abiotic controls on ecosystem properties (modified from Chapin et al., 2000; Hooper et al., 2005).

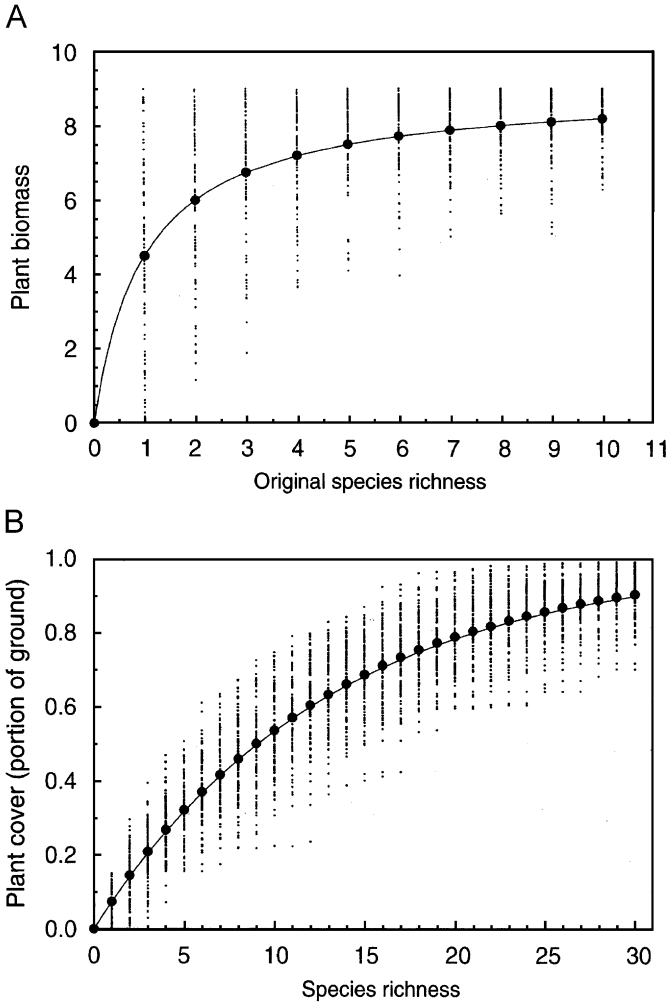

Fig. 14. Theoretical examples of how changing species diversity could affect ecosystem properties. Lines show average response, and points show individual treatments. (A) Selection effect for a dominant species: average ecosystem properties increase with increasing species richness, but maximal response is also achievable with particular combinations even at low diversity. (B) Complementarity and/or positive interactions among species, illustrated for plant cover as an index of aboveground primary productivity in a system with all new aboveground growth each year (figures from Tilman, 1997; Hooper et al., 2005).

Experimental evidence from field and microcosm studies generally supports the concept that increasing species richness increases stability of ecosystem properties, if one can sort through other confounding variables. Thus, coefficient of variation of aboveground biomass decreased with increasing species richness (Fig. 15A, Hooper et al., 2005). In a microcosm study, the standard deviation of CO_2 efflux from a microbial microcosm decreased with increasing species richness (Fig. 15B, Hooper et al., 2005).

6. Soil and terrestrial ecology in the 21st century

6.1. Linking organisms and activities

It is essential to bear in mind the advice and counsel of one of our pioneers: "The indications are the soil, despite its complexity, can be studied biologically and rationally. If we can detect the centers of activity, the sites of particular stages of decomposition processes, and link these to specific organisms, we should be able to isolate those centers of activity and processes which are important in particular soils and the organisms which are associated with them" (Macfadyen, 1969).

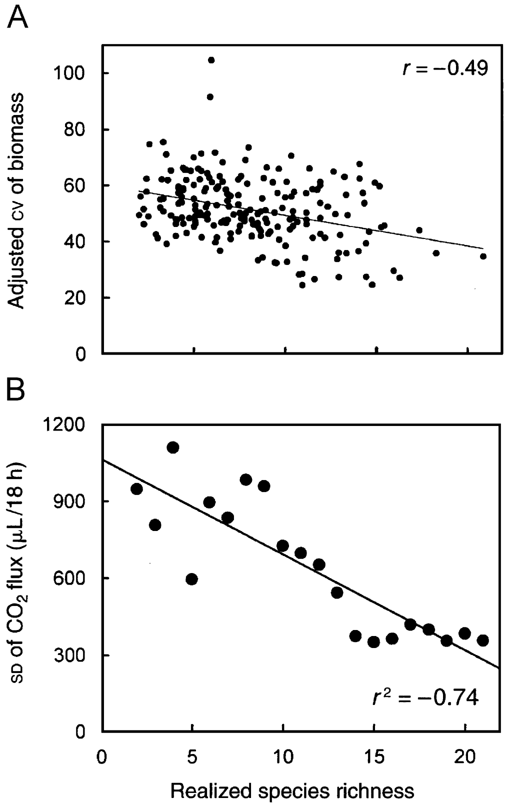

Fig. 15. Increasing stability with increasing species richness in ecological experiments. In both cases, the overall patterns are as predicted from theory, but the underlying mechanisms may coincide only in part. (A) Temporal variability (coefficient of variation, CV) in aboveground plant biomass. The gradient in species richness results from different levels of nutrient addition. (B) Standard deviation (SD) of net ecosystem CO_2 flux in a microbial microcosm. The decrease in variability with increasing diversity may result from both decreased temporal variability and increased compositional similarity among replicates (Hooper et al., 2005).

6.2. Miniaturization and sensor arrays

To make significant strides in the future, we need to be aware of and utilize the benefits of miniaturization. This includes "smart dust," miniature nanosensors that enable the investigator to track the location and physiological activities of individual soil organisms. Imagine the ability to track literally tens of thousands of members of the soil biota with Global Positioning Systems (GPS) and other sensors, simultaneously and in real time! This research has expanded to additional nanoproducts, such as fullerenes (nC60). Tong et al. (2007) found that fullerenes had little impact on the soil microbial community and microbial processes.

In addition, in situ measurements of pools and processing of particular compounds in soil are possible using miniaturized sensors the size of a small thermocouple (Johnston et al., 2004) (Fig. 16). The possibilities truly defy comprehension of those of us who grew up with simple Tullgren funnels and rotary calculators and later on, IBM main frame computers and punch card machines.

6.3. Integrative long-term experiments

We need long-term experiments in above- and below-ground ecology, perhaps utilizing some of the International Long-term Ecological Research (LTER) network of sites. This enables us to answer questions across space and time. An example follows: what is the fate of plant detritus, or "litter," in soil systems? A network of long-term, large-scale field experiments has been established across the North American continent to examine its fate. The Detritus Input Removals and Transfers (DIRT) experiments were established by Nadelhoffer et al. (2004), drawing on the initial inspiration and results of Francis Hole and colleagues at the University of Wisconsin. Treatments consist of chronically altered above- and below-ground inputs in the following fashion: 1, double litter; 2, no roots (using trenched and root barrier containing plots; 3, no litter; 4, no inputs, and 5, O/A-less plots (Fig. 17; Johnston et al., 2004). For more information on the DIRT network of sites, see the description in Johnston et al. (2004). This approach builds upon other, perhaps better-known long-term studies at Abisko (Sweden) and Rothamsted (UK). What makes the DIRT studies intriguing is the fact that they have been replicated across many different ecosystems and biomes, thus permitting soil ecologists to explore the generalities of some of the principles of decomposition across a very wide range of biotic, climatic and pedological conditions.

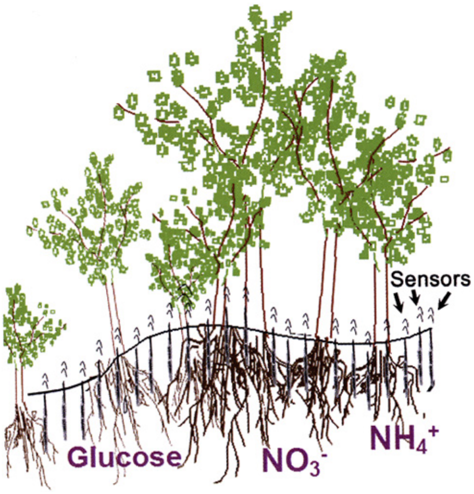

Fig. 16. Networks of autonomous soil sensors envisioned for continuous quantification of pools of compounds in situ in the field (e.g., in the rhizosphere, Johnston et al., 2004).

6.4. Biocomplexity and "tangled nature" in soils

The complexities inherent in soils are leading to a new appreciation of the conceptual framework that comprises the physico-chemical–biological combination that makes soils so fascinating. This milieu is an ideal location to test some of the ideas contained in the "Tangled Nature" model of evolutionary ecology (Christensen et al., 2002). They consider species as emergent structures, and extinction, origination and diversity are viewed as a consequence of co-evolutionary interaction between individuals. They consider both asexual and sexually reproducing populations. In either case, the system evolves through periods of hectic reorganization separated by periods of coherent stable coexistence. The "Tangled Nature" model concerns the evolution of thousands of interacting agents in a high-dimensional genotype space, which is precisely what soils are. This system lends itself to some of the ideas of

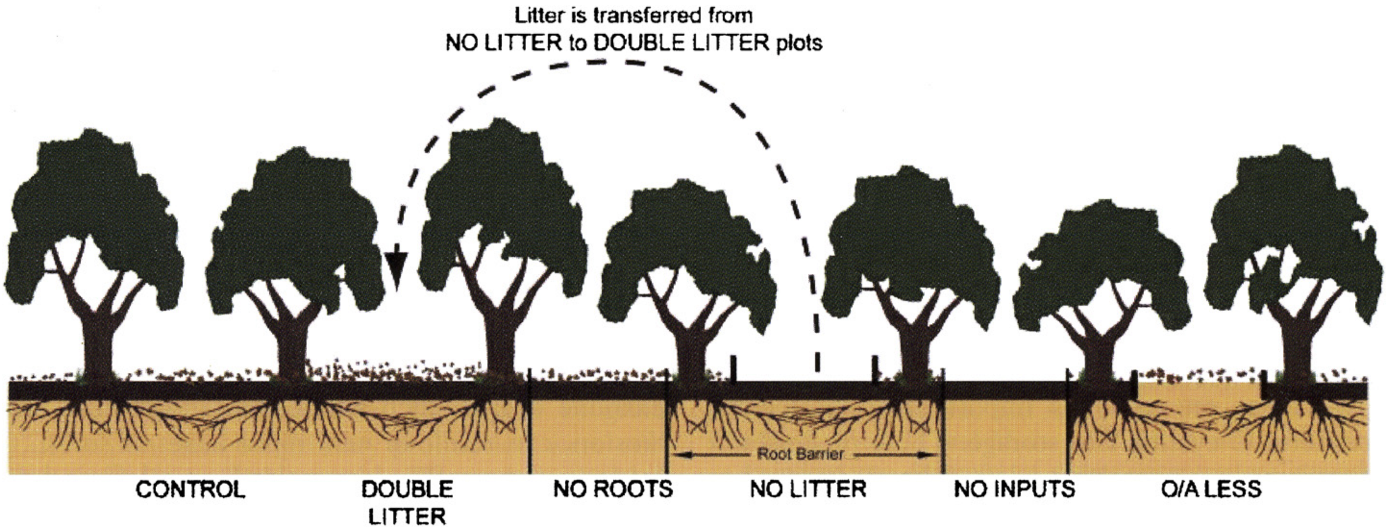

Fig. 17. Design of the Detritus Input Removal and Transfers (DIRT) experiment; see text (Nadelhoffer et al., 2004 from Johnston et al., 2004).

Complex Adaptive Systems in Gaia (Crawford et al., 2005), in which the macroscopic properties of ecosystems emerge as a consequence of interactions between the many individual parts and where the emergent properties can feed back to affect the subsequent nature of the interactions. As noted in Section 4.5, the prevalence of omnivory in soil food webs plays a major stabilizing role in ecosystem function (Moore et al., 2004; Setälä et al., 2005).

System-level considerations must be borne in mind when addressing such topics as the high microbial richness in soils. Dejonghe et al. (2001) propose that microbes follow "Pareto's Law", in which 20% of the species govern 80% of the energy flux of the ecosystem. This is eminently testable, and increases the interest in determining what species or groups of species play quantitatively key roles in the ecosystem of concern.

7. Summary

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. In addition to the highly heterogeneous environment, a high degree of omnivory prevails in resource-use among decomposer organisms, tending to reduce competition, and hence plays a major role in explaining the high degree of functional complementarity in decomposer communities. This is another way of considering soils as organizing centers in terrestrial ecosystems, as noted at the beginning of this review.

There are pitfalls to be encountered in soil ecological studies, as in any research projects. The chances of drawing the incorrect or wrong conclusions from studies that do not use two or more methods of measuring key variables or processes of interest seem to become greater with time. By the same token, chances of finding out new and exciting results are also enhanced by suitably well-designed experiments, utilizing fully the range of tools available (Coleman, 1985).

Thus, the time seems ripe for major advances in the exciting and fast-changing multidimensional milieu that characterizes soil. The ped is opaque, but the illumination of the research of a new generation of researchers in soil ecology is shining ever brighter!

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