

Biodiversity and Ecosystem Functioning in Soil

We review the current knowledge on biodiversity in soils, its role in ecosystem processes, its importance for human purposes, and its resilience against stress and disturbance. The number of existing species is vastly higher than the number described, even in the macroscopically visible taxa, and biogeographical syntheses are largely lacking. A major effort in taxonomy and the training of a new generation of systematists is imperative. This effort has to be focussed on the groups of soil organisms that, to the best of our knowledge, play key roles in ecosystem functioning. To identify such groups, spheres of influence (SOI) of soil biota—such as the root biota, the shredders of organic matter and the soil bioturbators—are recognized that presumably control ecosystem processes, for example, through interactions with plants. Within those SOI, functional groups of soil organisms are recognized. Research questions of the highest urgency are the assignment of species to functional groups and determining the redundancy of species within functional groups. These priorities follow from the need to address the extent of any loss of functioning in soils, associated with intensive agriculture, forest disturbance, pollution of the environment, and global environmental change. The soil biota considered at present to be most at risk are species-poor functional groups among macrofaunal shredders of organic matter, bioturbators of soil, specialized bacteria like nitrifiers and nitrogen fixers, and fungiforming mycorrhizas. An experimental approach in addressing these research priorities is needed, using long-term and large-scale field experiments and modern methods of geostatistics and geographic information systems.

INTRODUCTION

Much of the terrestrial biosphere resides in the soil, largely unnoticed by professional biologists and lay people. This is ironic because the soil provides the physical substratum for virtually all human activities, e.g., agriculture, buildings, transport; it provides resources for industrial use and waste management; and it is central in elemental cycles, without which agriculture would not be possible. Soil organisms are not just **inhabitants** of the soil, they are **part** of the soil (1), heavily influencing soil properties such as hydrology, aeration and gaseous composition, all of which are essential for primary production and the decomposition of organic residues and waste materials.

Whereas soils have been widely studied and classified in terms of physical and chemical characteristics, knowledge of soil biota lags far behind. This is partly due to a lack of recognition of the role of the biota in determining the physical and chemical properties and production potential of soils, and partly due to the bewildering diversity of soil organisms and the resulting taxonomic difficulties faced in identifying the soil's inhabitants. In high input agricultural systems, the importance of soil organisms has often been disregarded, as physical manipulation of the soil, disease and pest suppression, and nutrient supply have been increasingly provided by human inputs rather than by natural processes. However, the current shift towards sustainable land use, in particular sustainable agriculture and forestry, and the growing rec-

ognition of the pivotal role of the world's biota as the life-support system for planet Earth, has revived interest in soil biodiversity as an asset to conserve, to understand and to manage wisely in terms of its contribution to ecosystem services.

The objective of this paper is to review the knowledge on the diversity of soil biota and its role in ecosystem functioning, and to identify key areas for future research.

Although the diversity of soil organisms is worth conserving and studying in its own right, their functional roles offer a useful framework for making this effort more meaningful. We will first define functional roles in a utilitarian way as ecosystem services. We will then have a closer look at what we mean by biodiversity in soil, emphasizing spheres of influence (2; 'biological systems of regulation' in 3) of the biota in soil and various ways of assembling species in size-classes and functional groups. Subsequently, we relate soil biodiversity to ecosystem processes. Finally, we will address the issue of the knowledge gap and what we need to ascertain in order to relate soil biodiversity to ecosystem functioning and ecosystem services.

ECOSYSTEM SERVICES OF THE SOIL BIOTA

The soil biota provides a number of ecosystem services that are used by society for its own purposes.

Decomposition of organic matter. When defined simply as mineralization of carbon, 90% decomposition is carried out by microorganisms such as bacteria and fungi (4). It is greatly facilitated by soil animals such as mites, millipedes, earthworms and termites that shred the residues and disperse microbial propagules. Together they are called decomposers. The soil decomposer community is used for waste management and the purification of polluted soil.

Nutrient cycling is closely associated with organic matter decomposition. Here again, the microorganisms do the job, but the rate at which the processes operate is determined by small grazers such as protozoa and nematodes, while larger animals enhance the process in 'hot spots' such as the gut and excrements. Nutrient cycling by soil biota is essential for all forms of agriculture and forestry. Efficient nutrient cycling on land is also essential for water quality. Specific groups of soil bacteria are involved in autotrophic elemental transformations, i.e. they do not depend on organic matter as a food source.

Bioturbation. Plant roots, ants, termites, earthworms and other soil macrofauna create channels, pores, aggregates and mounds that profoundly influence the transport of gases and water in soil. In so doing they create or modify microhabitats for other, smaller, soil organisms. They are essential for maintaining the structure of soil in agriculture and forestry. Introduction of bioturbators is sometimes used to enhance the decomposition of organic pollutants in soil.

Suppression of soilborne diseases and pests. In natural ecosystems outbreaks of soilborne diseases and pests are relatively rare, whereas they are common in agriculture. It is widely assumed that low plant species diversity renders agroecosystems vulnerable to harmful soil organisms, but the causes of antagonism against pests and diseases in more species-rich systems can be manifold. The potential use of such antagonism in agriculture and forestry is enormous, but the subject is poorly studied.

Soil organisms—and, hence, soils as a whole—are affected

Table 1. Soil organisms discussed in this paper.

| Biota | Soil-dwelling species described | Global synthesis of biogeography | References |
|--------------------------|---------------------------------|----------------------------------|--|
| Microorganisms | | | |
| Bacteria and archaea | 3 200 ¹ | no | Stackebrandt (52) |
| Fungi | 18–35 000 | no | Hawksworth (11) |
| Amfungi | 200 | no | T.W. Kuyper (pers. comm.) |
| Ectomycorrhizal fungi | 10 000 | no | T.W. Kuyper (pers. comm.) |
| Microfauna | | | |
| Protozoa | 1 500 | no | |
| Ciliates | 400 | | Foissner (53) |
| Nematodes | 5000 | no | Andrassy (54) |
| Mesofauna | | | |
| Mites | c. 30 000 | no | |
| Collembola | 6500 | yes | Niedbala (55); Behan-Pelletier (56) |
| Enchytraeids | > 600 | no | Christiansen and Bellinger (57); Rusek (unpubl.) Didden (32) |
| Macrofauna | | | |
| Root herbivorous insects | c. 40 000 | no | |
| Termites | 2000 | yes | Brown and Gange (22) Pearce and Waite (58); Eggleton and Khambanpali (in prep.) |
| Ants | 8800 | yes | Hölldobler and Wilson (59) |
| Earthworms | 3627 | yes | Reynolds (60) |

¹ Total number; soil dwelling fraction is unknown.

by human-induced disturbances like agricultural practices, deforestation, pollution and global environmental change, with many negative consequences including: (i) loss of agricultural and forest production potential; (ii) loss of cleaning potential for waste materials; (iii) disruption or alteration of global elemental cycles; (iv) feedbacks on greenhouse gas fluxes; and (v) land degradation, including erosion and desertification (see Fig. 1; Table 1, in ref. 5).

BIODIVERSITY IN SOIL

Table 1 summarizes our current knowledge about species richness and distribution of major taxa of soil organisms. The species concept is problematic for bacteria and archaea. Currently, species are defined as “independent genomes” that are established by culturing and modern molecular methods. For even the relatively well-studied groups of soil invertebrates, we do not know the actual number of species, as the number described is still increasing rapidly. In many groups, such as viruses, yeasts, algae, oomycetes, chytridiomycetes, dictyostelids, myxomycetes, cyanobacteria, tardigrades, millipedes, pseudoscorpions, spiders, proturans, diplurans, pauropods, symphylans, rotifers, isopods, gastropods, turbellarians, aphids and centipedes, there is little knowledge or an imbalance in our knowledge of tropical and temperate species. All of these deserve much more effort in establishing their diversity and functional roles in the soil domain.

ECOSYSTEM PROCESSES INVOLVING SOIL BIOTA

Size relationships play an important role in biological interactions in soil, because the habitat is composed of differently-sized pores, interconnected by necks of various sizes. In spite of the fact that bioturbators create pores themselves, the soil biota can be meaningfully subdivided in size classes: microflora (e.g., archaea, bacteria and fungi) and microfauna (e.g., protozoa and nematodes), measuring < 200 µm in diameter; mesofauna (e.g., mites, collembola and enchytraeids), measuring 100 µm–2 mm in diameter; and macrofauna (e.g., earthworms, isopods and diplopods), measuring > 2 mm in diameter (6). These size classes are, for example, used to express the role of the soil biota in the most important biological process in soil, the decomposition of organic matter (Fig. 1).

In further assigning functional roles to soil organisms, we rec-

ognize a number of soil habitats, acting as spheres of influence of the biota in soil. One such SOI in soil is the rhizosphere or root zone with root biota, comprised of organisms that are beneficial to the plant, such as mycorrhiza-forming fungi, rhizobia and plant-growth promoting rhizobacteria; or detrimental, such as soilborne pests and diseases. Organisms feeding on leaves (foliar feeders) are included in Figure 2 to acknowledge that there are quantitatively important feedbacks, mediated by the plant, between above- and belowground herbivores. Another SOI is that of the decomposers, consisting of the soil meso- and macrofauna that shred organic matter (also called litter transformers, comminuters or shredders), and the microorganisms that are responsible for most of the biochemical transformation of organic matter, leading to nutrient mineralization and the complementary process of humification (Fig. 2, Ref. 5) (7). The third SOI of importance involves organisms that directly or indirectly modulate the availability of resources (like physical space and food) to other species, by causing physical state changes in soil; bioturbators or ecosystem engineers (8). Earthworms, ants and termites fall in this category, although at smaller spatial scales all organisms that transform the physical conditions of their habitats can be called (micro-)engineers. Figure 2 indicates that there are direct feedbacks between the root biota and plants, whereas the interactions between the decomposers and the plant are indirect (through the soil solution, following nutrient mineralization; indicated by ‘soil chemistry’ in Fig. 2) as are those between the bioturbators and the plant (through physical alteration of the soil; indicated by ‘soil physics’ in Fig. 2). In turn, predators and parasites may affect all other species and, therefore, are not indicated separately in Figure 2.

Although we can consider the diversity of the soil biota in a few size classes and spheres of influence, to fully appreciate the diversity of soil organisms and to understand the effects of human-induced stress and disturbance, we acknowledge that within these broad groups vast differences occur in life history, physiology, food preferences, feeding mode and microhabitat. These are the criteria for further recognition of ‘functional groups’. Although functional groups may consist of organisms from different taxa, this is rarely the case when the criteria are rigorously applied. For example, bacterivorous nematodes and protozoa differ according to at least two of these criteria and, therefore, are usually placed in different functional groups. For the same reason bacterial- and fungal-feeding nematodes are considered sepa-

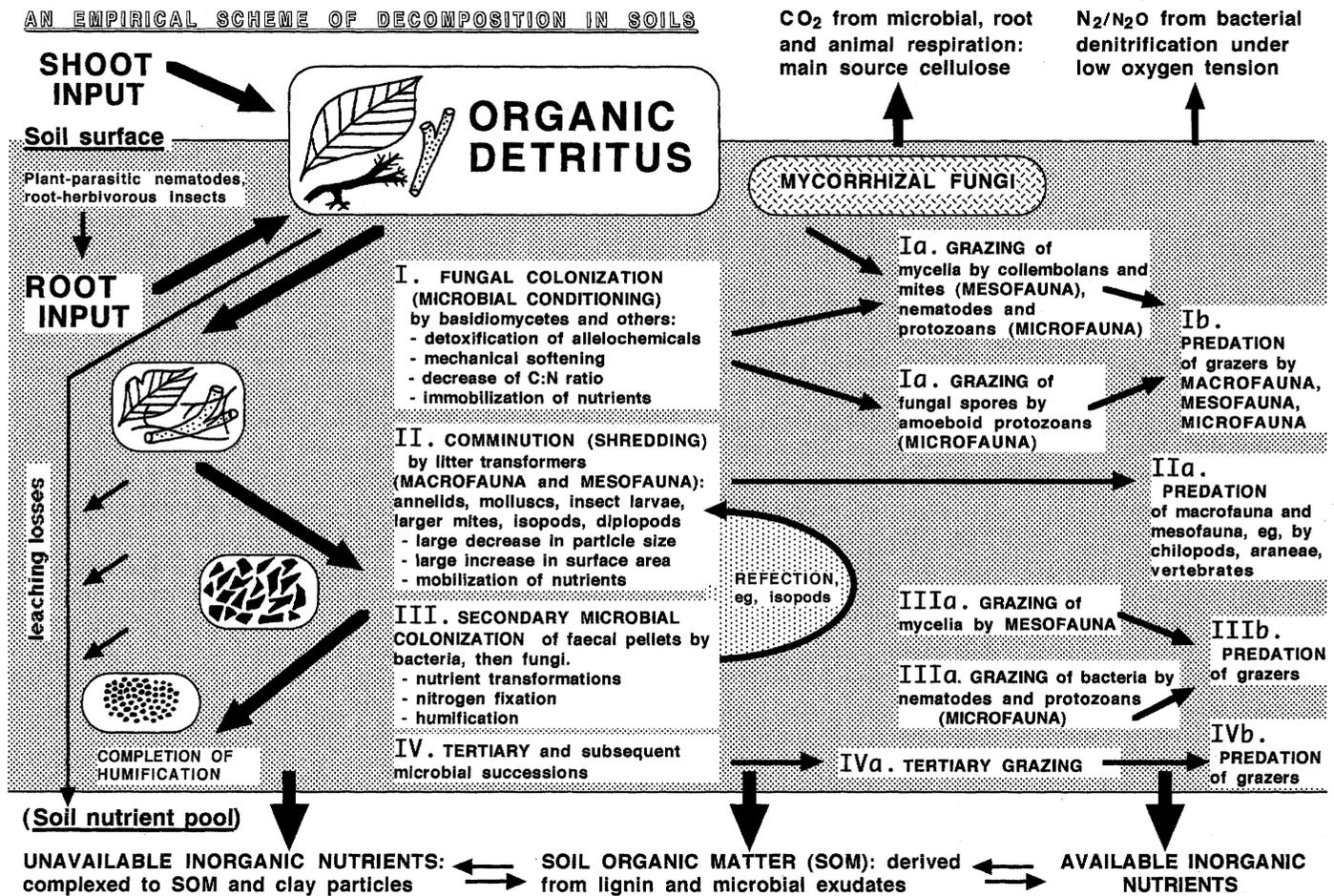


Figure 1. An empirical scheme of decomposition in soils (compiled by D.E. Bignell).

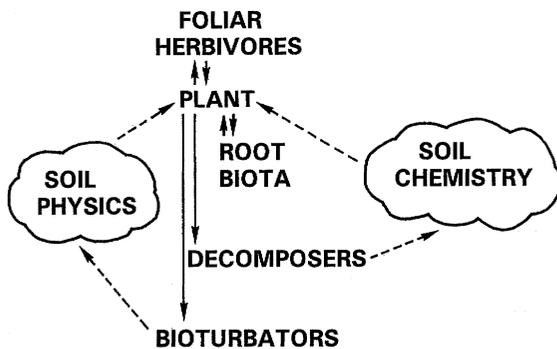


Figure 2. Conceptual diagram of an interaction web, showing the main spheres of influence of the biota in soil, interacting with plants directly (continuous arrows) or indirectly (hatched arrows) (60).

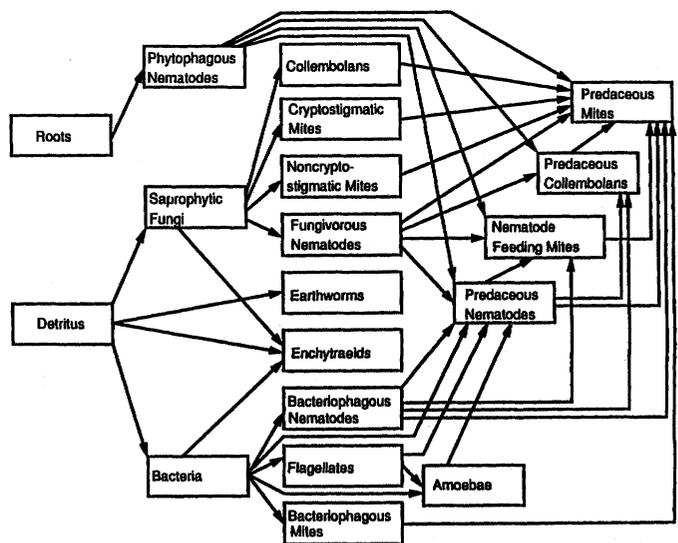


Figure 3. Food web in soil with functional groups (43).

Bacteria and Archaea

rately in functional terms. In cases where functional groups are comprised of higher taxa, such as bacteria, this reflects primarily our lack of knowledge of meaningful subdivision. Figure 3 is an example of a food web in soil ('micropredator foodweb' in 3), comprised of functional groups.

Table 2 summarizes the functional roles of the major taxonomic groups of soil organisms. As indicated above, these groups can be assembled in functional groups, according to the ecosystem process one is interested in. Below we complement Tables 1 and 2 with information on the biodiversity and roles of these groups in ecosystem processes.

Soil microbiologists originally focused on studies of pure cultures of bacteria that participate in different biogeochemical processes. For the last 25 years, the focus has shifted to measuring processes without much interest in the organisms responsible, but soon it was realized that the diversity of these organisms was much greater than previously recognized, and that perhaps only 1% of the bacteria could be cultivated. Molecular tools now provide more reliable detection of the unknown uncultured types and provide better differentiation of genera, species and ecotypes. With the new methods, it has become apparent that soil bacteria show a tremendously high diversity even at a scale of a few

Table 2. Functions of the major groups of soil organisms.

| Group | Functions |
|-------------------------|--|
| Free-living bacteria | Elemental immobilization; elemental mineralization; mutualistic intestinal associations; resource for grazing animals; genesis of biofilms; plant growth promoters; helpers in mycorrhizal associations; pathogens of plants; parasites and pathogens of soil animals; synthesis of humic materials; soil aggregation; decomposers of agrochemicals and xenobiotics |
| Rhizobial bacteria | N ₂ -fixing plants given competitive advantage; resource for root-feeding nematodes and other animals |
| Non-mycorrhizal fungi | Elemental immobilization; elemental mineralization; mutualistic and commensal associations; resource for arthropods and protozoan and nematode grazers, and for some other fungi; redistribution of nutrients; conditioning of detritus; parasites of arthropods and nematodes; synthesis of humic materials; soil aggregation; decomposers of agrochemicals and xenobiotics |
| Mycorrhizal fungi | Mycorrhizal plants given competitive advantage by the following mechanisms: mediation of transport of essential elements and water from soil to plant roots; mediation of plant-to-plant movement of essential elements and carbohydrates; sequestration of essential elements present in forms not available to plant; regulation of water and ion movements through plants; regulation of photosynthetic rate of plants; regulation of C allocation below ground; decreased seedling mortality; protection from root diseases and root herbivores. |
| Protozoa | Genesis of root mycosphere for bacteria; high-quality resource for mesofaunal and microfaunal grazers |
| Nematodes | Grazers of bacteria and fungi; enhance C and N availability to higher trophic levels; disperse bacteria and fungi; root herbivores / plant parasites; parasites / predators of microfauna, mesofauna and insects; prey for meso- and macrofauna |
| Mites | Grazers of bacteria and fungi; consumption of plant litter and animal carcasses; predators on nematodes and insects; root herbivores; dispersal of microorganisms; dispersal and vectoring of helminth parasites; host for protozoan parasites; parasites and parasitoids of insects and other arthropods; prey for macrofauna; micro-ecosystem engineers |
| Insects—General | Grazing of rhizosphere microorganisms; dispersal of microorganisms; predators of other soil organisms; decomposers of plant and animal matter |
| Insects—Root herbivores | Modification of plant performance below ground by root herbivory (modification of plant performance above ground by root herbivory and modification of herbivore populations above ground through changes in plant physiology resulting from herbivory below ground) |
| Insects—Collembola | Grazing of microflora and microfauna especially in rhizosphere; consumption of plant litter and animal carcasses; micropredators of nematodes, tardigrades, rotifers; dispersal of microorganisms; dispersal of helminths and cestode parasites; host for parasites; prey for macrofauna ; microecosystem engineers |
| Insects—Ants | Bioturbators; enhancement of microbial growth; keystone species for inquilinous fauna and plants associated with anthills |
| Insects—Termites | Bioturbators; enhancement of microbial growth; keystone species for inquilinous microorganisms and fauna and plants associated with mounds |
| Enchytraeids | Fragmentation of plant litter; enhancement of microbial growth; bioturbators; dispersal of microorganisms |
| Earthworms | Bioturbators; enhancement of microbial growth; dispersal of microorganisms and algae; host of protozoan and other parasites |

grams. Based on estimates of reannealing of soil DNA, Torsvik et al. (9) suggested 4000 independent bacterial genomes in 1 g of forest soil. Accounting common genes, the bacterial species definition, and extrapolation to rare species, this would amount to perhaps 20 000–40 000 bacterial species in 1 g of soil (10). The gap in knowledge is very apparent if this number is compared to described bacterial species; 4100, most of which are not soil inhabitants. The situation is even more primitive for soil archaea in which only a few methanogens and methylotrophs are known, but DNA analysis suggests many more types are present.

Certain functional groups of bacteria are important in cycles of specific elements. Although there is considerable redundancy among bacteria for these processes, e.g., N₂ fixation, there is growing recognition that there is considerable diversity at the kinetic, physiological, or niche level that is of importance to the process. It is this diversity that may be very important to ecosystem functioning. The main functional groups, listed according to the pertinent element, are:

Carbon: autotrophs; heterotrophs; methanotrophs, methylotrophs; methanogens.

Hydrogen: H₂ oxidizers; H₂ producers; butyrate oxidizers; propionate oxidizers.

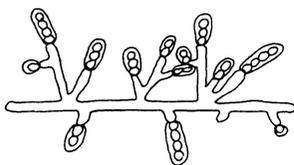
Nitrogen: N₂ fixers; denitrifiers; nitrifiers; DNRA (dissimilatory nitrate to ammonia reducers); mineralizers; immobilizers.

Sulfur: sulfur oxidizers; SO₄²⁻ reducers.

Iron: Fe²⁺ oxidizers; Fe³⁺ reducers.

Fungi

Fungi are involved in a large number of mutualistic and other organismal interactions in soil. The division between mutualistic and other fungi is not clear, since fungi are part of many complex ammensal, commensal and competitive relationships with other soil organisms. Saprotrophic food chains involving fungi and other organisms may be also mutualistic, but these relationships are poorly understood.



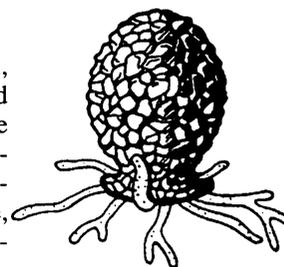
It is estimated that only 5% of living fungi have been described (11). The wide range of estimates (18 000–35 000 species of soil fungi) is caused by the fact that it is unknown how many of the approximately 72 000 described fungi are restricted to above-ground plant parts. Fungi forming macroscopical fruiting bodies can often be identified in the field in temperate and boreal forests and many partial inventories exist. The mycorrhizal fungi, i.e. fungi forming mutualistic associations with plant roots, present unique problems. The arbuscular mycorrhizal (AM) fungi are probably amongst the commonest fungi on earth. Many species seem to have a very wide distribution, but species concepts need to be reassessed by modern methods and adequate knowledge is available only for agricultural and similar soils and ecosystems. The ectomycorrhizal fungi show a much higher degree of specificity compared to the AM fungi (12). Many of them can be classified as macrofungi, and will thus be included in the inventories made by classical fungal taxonomists, but are difficult to identify in the soil when not forming aerial fruit bodies.

DNA techniques for identification of fungi, including mycorrhizal fungi that do not form fruiting structures are currently being developed, but with so many species involved this will take some time. Direct studies on DNA extracted from soil are not yet applicable.

Protozoa

Protozoa are microscopically small, unicellular organisms. It is assumed that only 10% of soil protozoans are known (13). Vickerman (14) suggested that the total number of species is close to 40 000. Protozoa are, with nematodes, the principal microbial grazers in terrestrial systems (15).

By classifying protozoa based on feeding preferences (bacterial or fungal), habitat preferences (acidophilic or neutrophilic) or ecological weightings, it may be possible to relate changes in diversity and/or biomass to ecosystem functioning (16).



Nematodes

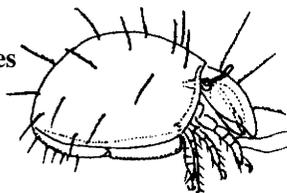
Soil nematodes are microscopic (about 1–1.5 mm) roundworms that live in waterfilms around soil particles. They are among the most numerous and diverse soil organisms, occurring in all soils on the globe. Most species are unknown and estimates indicate there are more than 100 000 soil nematode species to be described.

Nematodes are a major component of all soil food webs and thus comparisons of abundance, biomass and community structure can be made across ecosystems. Functional groups are based on morphology and known feeding habits of a few species, and in most soils include plant parasites and plant grazers, bacterivores, fungivores, predators, and omnivores. Plant parasites and plant grazers are the best known of soil nematodes, due to the damage they cause to agricultural crops, i.e. decreasing plant production, disrupting plant nutrient and water transfer, and decreasing fruit and tuber quality and size.

Soil disturbance, whether pollution, erosion, pesticides, or water quality, affects nematode species composition. For this reason they are used as indicators of soil disturbance (17–19).



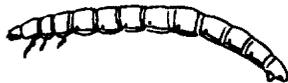
Mites



Mites are small spider-like invertebrates. The 45 000 described species of mites worldwide are thought to represent only 5% of the total number of

mite species (20). Mites are more diverse than any other single group of arthropods in soil, including insects, and this is reflected in the diversity of feeding habits in the group. Mites from the suborders Oribatida and Gamasida have been relatively well studied in agricultural soils (21). The response of oribatid mites to human perturbations has been categorized according to their life-history strategy (21).

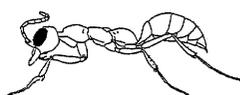
Insects



Many of the 29 insect orders have soil-dwelling representatives, which have the potential to realize a largely global distribution. However, at the level of family/genus/species, some are highly habitat specific, often being associated with particular plant species (22) and/or specific soil types. The soil insects associated with natural plant assemblages (with the possible exception of grasslands) have been grossly understudied. Other groups merely use the soil as a substrate for inactive stages of the life cycle, such as eggs or pupae, the soil providing buffering from abiotic and biotic factors.

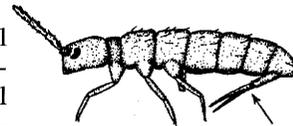
Only six insect orders are dominated by herbivorous species, but these insects exploit all belowground plant structures, and some also feed on and/or disperse propagules. Root herbivory may induce or increase the production of lignin and tannins, which can have important effects on ecosystem processes such as decomposition, by altering litter quality.

Termites are major decomposers in most tropical terrestrial ecosystems, responsible for the mineralization of up to 30% of net primary production (mostly as CO₂) in some systems and the breakdown of up to 60% of litterfall (23). Subterranean termites enhance macroporosity and infiltration with beneficial effects on soil water storage and primary productivity (24). Soil feeders have been little studied, but their role in soil processes is beginning to be documented (25).



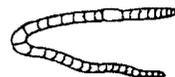
Ant species diversity declines with increasing latitude, altitude,

and aridity. Ant-plant communities are much more speciose in Amazonian than in temperate or other tropical areas of the world, and both patterns seem to be associated with habitat heterogeneity (26, 27). Soil ants (including mound builders) are representatives of predators, herbivores (granivores) and bioturbators, bringing about important changes in the physical and chemical properties of soils, as well as dispersing plant propagules. Networks of galleries and chambers increase the porosity of the soil, increasing drainage and soil aeration (28) and reducing bulk density (29).



Collembola or springtails are small wingless insects. They are well differentiated into ecomorphological groups occupying different soil horizons (30). Most are highly specialized feeders on soil microbiota (fungi, bacteria, actinomycetes, algae). Some mix small mineral particles with dead organic matter in their guts and contribute by their faecal pellets to soil microstructures (31).

Enchytraeids



Enchytraeids look like earthworms, but are much smaller. They live in moist places in soil. The highest species richness is found in grasslands (20–30 species) and deciduous forests (10–20 species) (32). In cold and acid soils such as in moors and coniferous forests they replace earthworms and constitute the dominant group of the soil fauna. Much less is known about their abundance in warmer and drier regions, although the available data suggest that they may be less important there. They are useful organisms for bio-indication purposes, as it is likely that specific soil types are inhabited by specific enchytraeid communities (33). Although previously regarded as purely saprophytrophagous, it is likely that they feed predominantly on microorganisms and exert their influence partly through grazing of microorganisms, and partly through fragmentation of organic material.

Earthworms



Earthworm species richness does not follow the classical latitudinal gradient and is rather similar (8–11 species) in temperate forests, Mediterranean forests, temperate pastures and tropical savannas (34). Similarly, Fragoso and Lavelle (35) concluded that the average number of species in tropical rainforests (6.5 spp) was not significantly different from that in temperate deciduous forests (5.7 spp.). Species diversity is determined by soil type and soil organic matter, nutrient content, and disturbance, more than by plant diversity. Bouché (36) classified earthworms as epigeic, endogeic and anecic, depending on whether they inhabit litter, soil or both. Each group has particular morphological and behavioral adaptations, which in turn produce different pedological effects (37).

SPECIES DIVERSITY, FUNCTIONAL DIVERSITY AND FUNCTIONAL COMPOSITION

Recently, the functional group concept has also become common in vegetation ecology. Tilman et al. (38) distinguish between the number of species (species diversity), the number of functional groups (functional diversity: C₃ grasses, C₄ grasses, forbs, woody plants and legumes), and the nature of the functional groups (functional composition). Hooper and Vitousek (39) make similar distinctions (although named differently). Although soil variables were measured in these studies, such as soil inorganic nitrogen, it is not clear whether soil biodiversity contributed to the observed effects, because it was not addressed. Microbial biomass C, soil respiration, denitrification potential,

potential N mineralization and nitrification were the response variables examined in different soils, sown to different grass species in a study by Groffman et al. (40). There were no significant differences between any of the grasses for any of the response variables. The hidden assumption in these studies seems to be that aboveground biodiversity or species composition determines soil properties and processes. This may be true on a short scale, but not in the long term. This can be illustrated by a study by Wardle et al. (41) on, among other parameters, plant litter decomposition and nitrogen mineralization on islands in an archipelago in the northern Swedish boreal forest zone. Large islands were in earlier successional stages than were small islands due to more frequent fires, associated with a higher incidence of lightnings in the large islands. The resulting higher plant species diversity on small islands was associated with lower ecosystem process rates and properties; e.g., basal soil respiration, substrate-induced respiration, microbial biomass, litter decomposition rate and nitrogen loss from buried litter. However, the higher rates on larger islands may have been due to the higher litter quality of the dominant plant species rather than to plant species diversity *per se*.

Similar experimental studies have not, or only partially, been done on soil biodiversity. Andrén et al. (42), using complete species redundancy as the null hypothesis, concluded that there is no need to address soil biodiversity in explaining the rate of decomposition of barley straw. In a food-web study on the role of different functional groups of soil organisms on net nitrogen mineralization, however, De Ruiter et al. (43, 44) found that model perturbations affecting specific functional groups often had quantitatively important effects on the simulated nitrogen mineralization. In another study, De Ruiter et al. (45) concluded that functional composition, i.e., the presence of groups exerting bottom-up effects on higher trophic levels and groups exerting top-down effects on lower trophic levels, was important for ecosystem stability by imposing stabilizing patterns of interaction strength. One of the few studies explicitly addressing soil biodiversity and litter decomposition was carried out by Naeem et al. (46). In this study, however, functional diversity was not explicitly taken into account in the species used, e.g., all treatments contained collembola (2, 4 or 7 species) and earthworms (1 species). No consistent relationship was found between species diversity and decomposition of litter. Perhaps the best experimental evidence on soil biodiversity and ecosystem processes is given by Faber and Verhoef (47). They carefully defaunated litter from a *Pinus nigra* stand and did or did not reintroduce (part of) the fauna in field mesocosms. When only one species of collembola was reintroduced, more nitrate was mineralized in soil in the presence of one species, but not in the presence of one of two other species. The 3 species together did not have an effect over and the above the case in which one species had an effect on soil nitrate, while re-introduction of the complete fauna showed a significant effect, which was, however, smaller than in the case with the 3 collembola. It appeared that the functional group to which the collembola belonged (from surface- to soil-dwelling) was decisive in the effect on soil nitrate.

Although the studies of De Ruiter et al. (45) and Faber and Verhoef (47) suggest that functional diversity and functional composition are important in determining the relationship between soil biodiversity and ecosystem processes, it is as yet an unresolved question what relationship exists between species diversity, functional diversity and functional composition with the occurrence and intensity of ecological processes. More precisely, what is the minimum number of functional groups, and species within functional groups, to ensure soil resilience against natural and anthropogenic stress and disturbance or is the presence of certain species decisive anyway (keystone species)? Most of the evidence is circumstantial. In the absence of hard data, stress and disturbance affecting functional groups that are comprised

of relatively few species are the most likely to cause loss of functioning. With reference to the section on *Ecosystem services of the soil biota*, this holds to the best of our knowledge for: shredders of organic matter (in particular the macrofaunal groups), with effects on decomposition; nitrifying and denitrifying bacteria and bacteria involved in CH₄, hydrogen, iron and sulfur transformations, with effects on element cycling and greenhouse gases; mycorrhizal fungi, with effects on plant health and competitive relationships; and bioturbators among the macrofauna, with effects on the production, purification and restoration potential of soil.

Meanwhile, it seems that a comprehensive study still waits to be done. We propose that, in determining the relationship between soil biodiversity and ecosystem processes, for each sphere of influence the number of functional groups (functional diversity), the number of species per functional group (species diversity), and the nature of the functional groups present (functional composition) should be experimentally manipulated and the effects on soil processes, such as decomposition and nutrient mineralization measured. Most meaningfully, treatments with different levels of plant diversity should be part of such a study in order to establish any feedbacks at the process level between aboveground and belowground biodiversity.

MAJOR GAPS OF KNOWLEDGE ON BIODIVERSITY AND ECOSYSTEM FUNCTIONING IN SOIL

For such an experimental approach to become feasible, major impediments will have to be overcome, some of which are as follows.

A recurrent theme is the lack of adequate techniques. Although there is an urgent need for standard protocols of sampling for each of the major taxa of soil organisms, perhaps more important is the development of strategies of data acquisition and analysis that account for the spatially heterogeneous and temporally variable occurrence of the soil biota. Geostatistics and geographic information systems appear to have a lot to contribute to the quantification of diversity and functioning among and within different soil types and land-use histories.

There is also a great need for a stronger development of taxonomy, resulting in easily accessible methods for identification of the species of soil organisms. Computer-aided diagnostic keys are becoming available for an increasing array of taxonomic groups. Molecular methods show promise for assessment of the diversity of soil organisms in which morphological taxonomy is difficult or even impossible. **The challenge here is to link molecular data to species, rather than broad taxonomic groups, and to performance in the field rather than just potential physiological capabilities.** For recent reviews on methods for the examination of organismal diversity in soil see Górný and Grüm (48) and Hall (49).

Functional groups are an indispensable aid in studying the role of the soil biota in maintaining ecosystem services. Similarity in life-history traits is an important criterion, in addition to a species' trophic role, since it is increasingly realized that the life-history traits of species, acquired over evolutionary time as a result of the interplay between genome and environment (both abiotic and biotic), determine their reactions to human-induced stress and disturbance. Functional groups operate in spheres of influence. Each SOI shapes the functioning of the ecosystem in a unique way. In Figure 2 the plant occupies a central position as the driving force of the soil ecosystem. The SOI in soil control ecosystem processes by direct interaction with the plant, by mineralization of carbon and nutrients and by physical alteration of the habitat, respectively. Alternatively, the structures (channels, pores, soil aggregates, excrements, etc.) that are produced by the soil biota (roots, shredders, bioturbators) may be the primary focus in designating SOI, determining the diversity

of, and within, functional groups as well as ecosystem processes in their spheres of influence at specific scales of space and time (2, 3). **The identification of functional groups of the soil biota that occupy key positions in ecosystem processes is a very high priority.** A fundamental problem, however, is the limited knowledge available at the species level to assign species to such groups. The vast majority of organisms living in the soil, have never been described. **Major advances in the systematics of the soil biota, and the training of a new generation of systematists, are imperative, with the highest priority for those groups that to the best of our knowledge are likely to fulfill key roles.**

Finally, most experimental work on soil organisms has been carried out in micro- and mesocosms. However, the interactions between soil fauna and microorganisms and plants, in terms of food selectivity and effects on communities and processes, remain difficult to assess and extrapolate to the ecosystem level, because the scale of micro- and mesocosms is too small and the biological interactions are too artificial. Furthermore, such small-scale studies ignore critical transition zones between domains, that exhibit high diversity and biogeochemical activity as described in Figure 1 and Table 1 in Freckman et al. (5). Hence, long-term and large-scale field experiments are needed to address questions of impacts on soil biodiversity of climate and land-use change.

CONCLUDING REMARKS

Except for a few studies, most research related to the diversity and functional role of different groups of soil organisms has been done for small assemblages of species. More comprehensive data

on the abundance and biomass of different members of the soil biota and their effects on functioning is required to determine the effects of disturbance and stress on ecosystem processes and stability.

In an article on ecological sustainability, Fresco and Kroonenberg (50) argue that biodiversity is the most vulnerable, least resilient natural resource *ex aequo* with topsoil/soil nutrients. They conclude that priority should be given to conservation of these resources in any decisions on future land use. The need for sound scientific knowledge on the relationship between soil biodiversity and ecosystem functioning cannot be expressed more urgently. It is obvious that soils cannot perform ecosystem services such as decomposition, nutrient cycling and disease suppression without an array of soil organisms being present. As both the biodiversity of soils and the functional roles of soil organisms become clearer, any relationship between the two will become apparent. Indeed, the two will be most meaningfully studied in research programs that are specifically designed to elucidate this relationship considering the possible effects of "normal" anthropogenic land-use practices as well as the effects of the major changes in climate, environment and land use that are sources of concern for mankind. Recent reviews of the state of the art (51) set the scene for such a major research effort.

References

- Hole, F.D. 1981. Effects of animals on soil. *Geoderma* 25, 75–112.
- Beare, M.H., Coleman, D.C., Crossley, D.A. Jr., Hendrix, P.F. and Odum, E.P. 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant Soil* 170, 5–22.
- Lavelle, P. 1996. Diversity of soil fauna and ecosystem function. *Biol. Int.* 33, 3–16.
- Swift, M.J. and Anderson, J.M. 1993. Biodiversity and ecosystem function in agricultural systems. In: *Biodiversity and Ecosystem Function*. Schulze, E.-D. and Mooney, H.H. Springer-Verlag, Berlin, 523 pp.
- Freckman, D.W. et al. 1997. Linking biodiversity and ecosystem functioning of soils and sediments. *Ambio* 26, 556–562.
- Swift, M.J., Heal, O.W., and Anderson, J.M. 1979. *Decomposition in Terrestrial Ecosystems, Studies in Ecology*. Vol. 5. Blackwell, Oxford.
- Brussaard, L. and Juma, N.G. 1996. Organisms and humus in soils. In: *Humic Substances in Terrestrial Ecosystems*. Piccolo, A. (ed.), pp. 329–359.
- Jones, C.G., Lawton, J.H. and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Torsvik, V., Goksøyr, J. and Daee, F.L. 1990. High diversity in DNA of soil bacteria. *Appl. Environ. Microbiol.* 56, 782–787.
- Tiedje, J.M. 1995. Approaches to the comprehensive evaluation of prokaryote diversity of a habitat. In: *Microbial Diversity and Ecosystem Functioning*. Allsopp, D., Hawksworth, D.L. and Colwell, R.R. (eds). CAB International, Wallingford, UK, pp. 73–87.
- Hawksworth, D.L. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycol. Res.* 95, 641–655.
- Smith, S.E. and Read, D.J. 1997. *Mycorrhizal Symbiosis*. 2nd edn Academic Press, San Diego, 605 pp.
- Foissner, W. 1994. Soil protozoa as bioindicators in ecosystems under human influence. In: *Soil Protozoa*. Darbyshire, J.F. (ed.). CAB International, Wallingford, UK, pp. 147–194.
- Vickerman, K. 1992. The diversity and ecological significance of Protozoa. *Biodiv. Conserv.* 1, 334–341.
- Gupta, V.V.S.R. 1994. The impact of soil and crop management practices on the dynamics of soil microfauna and mesofauna. In: *Soil Biota: Management in Sustainable Farming Systems*. Pankhurst, C.E., Doube, B.D., Gupta, V.V.S.R. and Grace, P.R. (eds). CSIRO, East Melbourne, Australia, pp. 107–124.
- Bamforth, S.S. 1997. Protozoa: recyclers and indicators of agroecosystem quality. In: *Fauna in Soil Ecosystems—Recycling Processes, Nutrient Fluxes and Agricultural Production*. Benckiser, G. (ed.). Marcel Dekker Inc., New York, USA, pp. 63–85.
- Bongers, T. 1990. The maturity index: an ecological measure of environmental disturbance. *Oecologia* 83, 14–19.
- Blair, J.M., Bohlen, P.J. and Freckman, D.W. 1996. Soil invertebrates as indicators of soil quality. In: *Methods for Assessing Soil Quality*. Doran, J.W. and Jones, A.J. (eds). Soil Sci. Soc. Am., Madison, WI, USA, pp. 273–291.
- Niles, R. K. and Freckman, D.W. 1997. From the ground up: nematode ecology in bioassessment and ecosystem health. In: *Plant-nematode Interactions*. Barker, K.R., Pederson, G.A. and Windham, G.L. (eds). Agronomy Monograph. American Society of Agronomy, Crop Science Society of America and Soil Science Society of America, Madison, WI, USA. (In press).
- Walter, D. E., Krantz, G. and Lindquist, E.E. 1996. Acari. In: *Tree of Life*. <http://phylogeny.arizona.edu/tree/eukaryotes/animals/arthropoda/arachnida/acari/acari.html>
- Siepel, H. 1995. Applications of microarthropod life-history tactics in nature management and ecotoxicology. *Biol. Fertil. Soils* 19, 75–83.
- Brown, V.K. and Gange, A.C. 1990. Insect herbivory below ground. *Adv. Ecol. Res.* 20, 1–58.
- Brian, M.V. 1978. Production ecology of ants and termites. *Int. Biol. Prog.* 13. Cambridge University Press, Cambridge.
- Wood, T.G. 1996. The agricultural importance of termites in the tropics. *Agric. Zool. Rev.* 7, 117–155.
- Garnier-Sillam, E. and Harry, M. 1995. Distribution of humic compounds in mounds of some soil-feeding termite species in tropical forests: its influence on soil structure stability. *Insectes Sociaux* 42, 167–185.
- Davidson, D.W. and McKey, D. 1993. The evolutionary ecology of symbiotic ant-plant relationships. *J. Hymen. Res.* 2, 13–83.
- Folgarait, P.J. 1996. Latitudinal variation in myrmecophytic *Cecropia*. *Bull. Ecol. Soc. Am.* 77, 143.
- Cherrett, J.M. 1989. Leaf-cutting ants. Biogeog. Ecol. studies. In: *Ecosystems of the World, Tropical Rain Forest Ecosystem*. Lieth H. and Werger, M.J. (eds). Elsevier, New York, pp. 473–488.
- Baxter, P.F. and Hole, H. 1967. Ant (*Formica cinerea*) pedoturbation in a prairie soil. *Soil Sci. Soc. Am. Proc.* 31, 425–428.
- Gisin, H. 1943. Oekologie und Lebensgemeinschaften der Collembolen im Schweizerischen Exkursionsgebiet Basels. *Rev. Suisse Zool.* 50, 183–189.
- Rusek, J. 1985. Soil microstructures—contributions on specific soil organisms. *Quaest. Entomol.* 21, 497–514.
- Didden, W.A.M. 1993. Ecology of terrestrial Enchytraeidae. *Pedobiol.* 37, 2–29.
- Graefe, U. 1993. Die Gliederung von Zersetzergesellschaften für die standortökologische Ansprache. *Mitt. Deutsch. Bodenk. Ges.* 69, 95–98.
- Lavelle, P. 1983. The structure of earthworm communities. In: *Earthworm Ecology: from Darwin to Vermiculture*. Satchell, J.E. (ed.). Chapman and Hall, London, pp. 449–466.
- Fragoso, C. and Lavelle, P. 1992. Earthworm communities of tropical rain forests. *Soil Biol. Biochem.* 24, 1397–1408.
- Bouché, M.B. 1972. Lombriciens de France. Ecologie et systématique. *Ann. Soc. Ecol. Anim.* 72, 1–671.
- Lavelle, P. 1988. Earthworm activities and the soil system. *Biol. Fertil. Soils* 6, 237–251.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302.
- Hooper, D.U. and Vitousek, P.M., 1997. The effect of plant composition and diversity on ecosystem processes. *Science* 277, 1302–1305.
- Groffman, P.M., Eagan, P., Sullivan, W.M. and Lemunyon, J.L. 1996. Grass species and soil type effects on microbial biomass and activity. *Plant Soil* 183, 61–67.
- Wardle, D.A., Zackrisson, O., Hömberg, G. and Gallet, C. 1997. The influence of island area on ecosystem properties. *Science* 277, 1296–1299.
- Andrén, O., Bengtsson, J. and Clarholm, M. 1995. Biodiversity and species redundancy among litter decomposers. In: *The Significance and Regulation of Soil Biodiversity*. Collins, H.P., Robertson, G.P. and Klug, M.J. (eds). Kluwer, pp. 141–151.
- De Ruiter, P.C., Moore, J.C., Zwart, K.B., Bouwman, L.A., Hassink, J., Bloem, J., De Vos, J.A., Marinissen, J.C.Y., Didden, W.A.M., Lebbink, G. and Brussaard, L. 1993. Simulation of nitrogen mineralization in the belowground food webs of two winter wheat fields. *J. Appl. Ecol.* 30, 95–106.
- De Ruiter, P.C., Neutel, A.M. and Moore, J.C. 1994. Modelling food webs and nutrient cycling in agro-ecosystems. *Trends Ecol. Evol.* 9, 378–383.
- De Ruiter, P.C., Neutel, A.M. and Moore, J.C. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269, 1256–1260.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368, 734–737.

47. Faber J.H. and Verhoef, H.A. 1991. Functional differences between closely-related soil arthropods with respect to decomposition processes in the presence or absence of pine tree roots. *Soil Biol. Biochem.* 23, 15–23.
48. Górný, M. and Grüm, L. (eds). 1993. *Methods in Soil Zoology*. Elsevier, Amsterdam, etc., 459 pp.
49. Hall, G.S. (ed.). 1996. *Methods for the Examination of Organismal Diversity in Soils and Sediments*. CAB International, Wallingford, 307 pp.
50. Fresco, L.O. and Kroonenberg, S. 1992. Time and spatial scales in ecological sustainability. *Land Use Policy*, July 1992, 155–174.
51. Swift, M.J. (ed.). 1997. Soil biodiversity, agricultural intensification, and agroecosystem function in the tropics. *Appl. Soil Ecol.* 6, 1–108.
52. Stackebrandt, E. 1996. From strains to domains. In: *Microbial Diversity in Space and Time*. Colwell, R.R., Simidu, U. and Ohwada, K. (eds). Plenum Press, New York, 20 pp.
53. Foissner, W. 1997. Global soil ciliate (protozoa, Ciliophora) diversity: A probability-based approach using large sample collectives from Africa, Australia, and Antarctica. *Abstracts 10th Int. Cong. Protozool.* Univ. Sydney, Australia, 86.
54. Andrassy, I. 1992. A short census of free-living nematodes. *Fundam. Appl. Nematology* 15, 187–188.
55. Niedbala, W. 1992. *Phthiracaroida (Acari, Oribatida) Systematic Studies*. Elsevier, Amsterdam, 612 pp.
56. Behan-Pelletier, V.M. 1993. Eremaeidae (Acari: Oribatida) of North America. *Mem. Ent. Soc. Can.* 168, 1–193.
57. Christiansen, K. and Bellinger, P. 1995. The biogeography of collembola. *Bull. Entomol. Pologne* 64, 279–294.
58. Pearce, M.J. and Waite, B. 1994. A list of termite genera with comments on taxonomic changes and regional distribution. *Sociobiol.* 23, 247–262.
59. Hölldobler, B. and Wilson, E.O. 1990. *The Ants*. Springer, Berlin etc., 732 pp.
60. Reynolds, J. 1994. Earthworms of the world. *Global Biodiv.* 4, 11–16.
61. Acknowledgements. The authors would like to thank the members of the soil domain editorial committee: Josef Rusek, Jim Tiedje, Vadakattu Gupta and David Bignell.

Corresponding author: Lijbert Brussaard is professor of soil biology at Wageningen Agricultural University. His research interests include rhizosphere ecology; the role of soil fauna in decomposition processes and nutrient cycling; and the relationships between belowground/ aboveground biodiversity, and ecosystem functioning in natural and agroecosystems. His address: Wageningen Agricultural University Dept. of Environmental Sciences, Soil Biology Group, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands.

Val M. Behan-Pelletier is a scientist with the Research Branch of Agriculture and Agri-Food Canada in Ottawa. Her research interest is the systematics, biogeography and ecology of oribatid mites (Acari). Her address: Biological Resources Program, ECORC, Agriculture and Agri-Food Canada, K.W. Neatby Bldg., Ottawa, Ontario, Canada K1A 0C6.

David E. Bignell is associate professor in the Tropical Biology and Conservation Unit, Universiti Malaysia Sabah. His interests span all aspects of termite biology, but especially their nutritional ecology and role in soil ecosystem processes. His current address: Tropical Biology and Conservation Unit, Universiti Malaysia Sabah, Kampus Jalan Tuaran, Kilometer 19 Jalan Tuaran, 88999 Kota Kinabalu, Sabah, Malaysia. His permanent address: School of Biological Sciences, Queen Mary & Westfield College, University of London, London E1 4NS, UK.

Valerie K. Brown is Director of the International Institute of Entomology. Her research interests are in experimental community ecology, with particular interests in the interactions between plants and soil-dwelling insects under environmental change. Her address: International Institute of Entomology, CAB International, 56 Queen's Gate, London SW7 5JR, UK.

Wim Didden is assistant professor of soil biology at the Agricultural University, Wageningen. His research interests include carbon and nutrient flows in terrestrial ecosystems, and the interactions of soil structure and soil biota, with emphasis on the ecology of oligochaeta. His address: Agricultural University, Dept. of Environmental Sciences, Soil Biology Group, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands.

Patricia Folgarait is a researcher from CONICET, Buenos Aires, Argentina. Her research interests include ant biodiversity and ecology in natural and agro-forestry systems, biological control of ants, and soil biodiversity and functioning with special emphasis on mechanisms maintaining soil fertility. Her address: IFEVA, Facultad de Agronomía, Universidad de Buenos Aires, Avenida San Martín 4453, 1417 Buenos Aires, Argentina.

Carlos Fragoso is in the Institute of Ecology in Xalapa, Mexico. His research interests include the ecology of tropical earthworm communities, the taxonomy and biogeography of earthworms and the influence of soil macrofauna on soil fertility. His address: Laboratorio de Suelos, Instituto de Ecología, 2.5 km Antigua Carretera a Coatepec, AP 63, 91000 Xalapa, Ver, Mexico.

Diana Wall Freckman is director of the Natural Resource Ecology Laboratory at Colorado State University. Her main research interests are the impact of environmental change on soil biodiversity and ecosystem processes, particularly the role of soil nematodes in biogeochemical processes. Her address: Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499, USA.

Vadakattu V.S.R. Gupta is a research fellow at the Cooperative Research Centre for Soil and Land Management in Adelaide, Australia. His research interests include microbial interactions and their impact on the turnover of carbon and nutrients, and the survival of introduced bacteria, special emphasis on protozoan-microfloral interactions. His address: CRC for Soil and Land Management, PMB No. 2, Glen Osmond, South Australia, SA 5064, Australia.

Tsutomu Hattori's main research interests include the phylogenetics and morphology of soil oligotrophic bacteria, the diversity of protozoa in soil microaggregates and the stochastic aspects of bacterial proliferation and protozoan excystment in soil. His address: Attic Lab, Komegafukuro 1-6-2-401, Aoba-Ku, Sendai 980, Japan.

David L. Hawksworth is the Director of the CAB International Mycological Institute in the UK. His address is: International Mycological Institute, Bakeham Lane, Egham, Surrey TW20 9TY, UK.

Carole Klopatek is currently working at the National Belowground Sustainability Program, USDA Forest Service, PO Box 96090, Washington DC 20090-6090. Her address: Department of Microbiology, USDA Forest Service, Arizona State University, Tempe, AZ 85287, USA.

Patrick Lavelle is professor of ecology at Université de Paris VI and Director of Laboratoire d'Ecologie des Sols Tropicaux at ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération). His research interests include general soil ecology with a special emphasis set on earthworm ecology and their management as part of sustainable practices in tropical environments. His address: LEST/ORSTOM, 32 rue H. Varagnat, 93143 BONDY cedex, France.

David W. Malloch is in the Department of Botany at the University of Toronto. His research is centered on fungal life histories, particularly those intersecting life histories of other organisms. Other research includes taxonomy of higher fungi and biology of *Penicillium* species occurring in indoor environments. His address: Department of Botany, University of Toronto, Toronto, Ontario, Canada, M5S 3B2.

Josef Rusek is Director of the Institute of Soil Biology, Academy of Sciences of the Czech Republic at Ceske Budejovice. His research interests include the ecology and taxonomy of soil fauna, especially Collembola and Protura, and its role in soil. His address: Institute of Soil Biology, Na sadkach 7, 370 05 Ceske Budejovice, Czech Republic.

Bengt Söderström is in the Department of Microbial Ecology at Lund University. His research interests include mycorrhizal formation, plant-fungus interactions, environmental effects on mycorrhizal function and soil processes and structure/function relations in mycorrhizal systems. His address: Dept. of Microbial Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden.

James M. Tiedje is at the Centre for Microbial Ecology at Michigan State University. His address: Centre for Microbial Ecology, Michigan State University, 540 Plant and Soil Science Building, East Lansing, MI 48824-1325, USA.

Ross A. Virginia is Professor of Environmental Studies at Dartmouth College. His research interests are focused on understanding the impacts of humans on biogeochemical cycles, with an emphasis on soil biota and carbon and nitrogen cycling in arid ecosystems of temperate and polar regions. His address: Environmental Studies Program, Dartmouth College, Hanover, NH 03755, USA.