16 Soil Biodiversity and Food Webs

Franciscus X. Susilo, Anje Margriet Neutel, Meine van Noordwijk,
Kurniatun Hairiah, Georg Brown and Mike J. Swift

Key questions

1. How does below-ground biodiversity vary with land-use practices?
2. What is the function of soil biodiversity in ecosystems?
3. Can the food-web concept be used to approach soil biodiversity problems?
4. Under what conditions is managing specific soil biota rather than overall diversity relevant?

16.1 Introduction

Although it is not apparent to the naked eye, soil is one of the most complex habitats on earth, containing one of the most diverse assemblages of living organisms (Lavelle and Spain, 2002). Over 1000 species of invertebrates were identified in 1 m^2 of soil in temperate forests in Germany (Schaefer and Schauermann, 1990). The diversity of the microbial component of soil may be even greater than that of the invertebrate component. However, this is only just beginning to be realized, as a result of phylogenetic and ecological studies using molecular methods (Torsvik *et al.*, 1996). A single gram of soil is estimated to contain several thousand species of bacteria (Giller *et al.*, 1997a). Of the 1.5 million species of fungi estimated to exist worldwide, remarkably little is known about soil fungi, apart from common fungal pathogens and mycorrhizal species. Some 100,000 species of protozoa, 500,000 species of nematodes and 7000 species of earthworms are estimated to exist (Reynolds, 1994), not to mention the other invertebrate groups of the mesofauna (e.g. springtails, mites and potworms) and macrofauna (e.g. ants, termites, beetles and spiders) (Brussaard *et al.*, 1997). Few data are available from tropical regions, where it is suspected that the highest levels of diversity may be found. Consequently, although the biological diversity of the community of organisms below the ground is probably higher in most cases than that above ground, it has generally been ignored in surveys of ecosystem biodiversity. The lower visibility of below-ground organisms and an absence of 'charismatic' species (those that attract atten-

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tion) have previously led to less attention being focused on below-ground biodiversity. Yet, below-ground biodiversity is of direct relevance to the health of crops, trees and other desirable plants, and soil organisms play key roles in the maintenance of soil structure and in closing nutrient cycles by releasing nutrients from dead organic material. But as such studies proceed, driven by the new concerns about biodiversity loss and global change, it becomes more and more apparent that below-ground biodiversity is significantly in excess of earlier predictions (e.g. Eggleton *et al.*, 1995; Giller, 1996).

Soil organisms contribute a wide range of essential services to the sustainable function of all ecosystems. They act as the primary driving agents of nutrient cycling, regulating the dynamics of soil organic matter and soil carbon sequestration (see Chapter 11, this volume). They play key roles in the absorption and emission of greenhouse gases (see Chapter 12, this volume) and modify soil physical structure and water regimes. They can enhance the amount and efficiency of nutrient acquisition by the vegetation through mycorrhiza (see Chapter 14, this volume) and N_2-fixing bacteria (see Chapter 13, this volume) and they influence plant health through the interaction of pathogens and pests with their natural predators and parasites (see Chapter 15, this volume). Although the study of soil biology has a long history – including the famous studies by Darwin (1837, 1881) on the role of earthworms in soil formation – the links between the diversity of the soil biota and its functional value are still poorly established (Giller *et al.*, 1997a). The obvious methodological difficulties associated with obtaining species inventories (e.g. taxonomy and sampling) and making assessments of the functional significance of below-ground diversity (in terms of both direct and indirect effects) have hampered such investigations, as have the shortage of conceptual models that might help us answer the 'so what?' question.

Whilst above-ground the conversion of a tropical rainforest, through slash-and-burn land clearing, into food-crop, pasture or tree-crop production systems has an obvious and dramatic effect on all forms of life, the below-ground changes are smaller and take more time (except for the litter layer and top few centimetres of soil directly affected by the burn) to detect. However, due to more limited dispersal means for many soil organisms, changes below-ground may also be more difficult to reverse.

From a purely agronomic perspective, many functions modulated by soil biota can be substituted for by the use of agrochemicals (fertilizer, pesticides) and fossil-fuel energy (soil tillage). However, learning to work through or with, rather than against, the soil biota, is often seen as one of the pillars of a more ecological and sustainable approach to 'healthy agriculture'. As summarized in Fig. 16.1, we can analyse the relationship between land-use practices and below-ground biodiversity in a number of steps or questions:

1. How do land-use change and specific management practices within broad land-use categories impact on soil biota?
2. What are the key functional roles of soil biota in agroecosystems? And which groups play these roles?
3. How do the various soil biota function in below-ground food webs in different ecosystems?
4. How can farmers, as managers of agroecosystems, work through (or with), rather than against soil biota?
5. How does the presence of specific soil biota, and the diversity of the below-ground ecosystem as such, contribute to the overall cost–benefit balance at the farm, landscape and global levels?

In this chapter we will review the first four questions, as the basic data and approaches necessary for answering question 5 are still lacking, except perhaps for some N_2-fixing bacteria in annual cropping systems (e.g. Hungria and Campo, 2000). Box 16.1 and Fig. B16.1 give a quick overview of the broad groups of organisms included in this discussion. A conventional indicator of ecosystem diversity is species richness, or the number of species per unit area. This implicitly assumes that all species are of potentially equal value – but how can

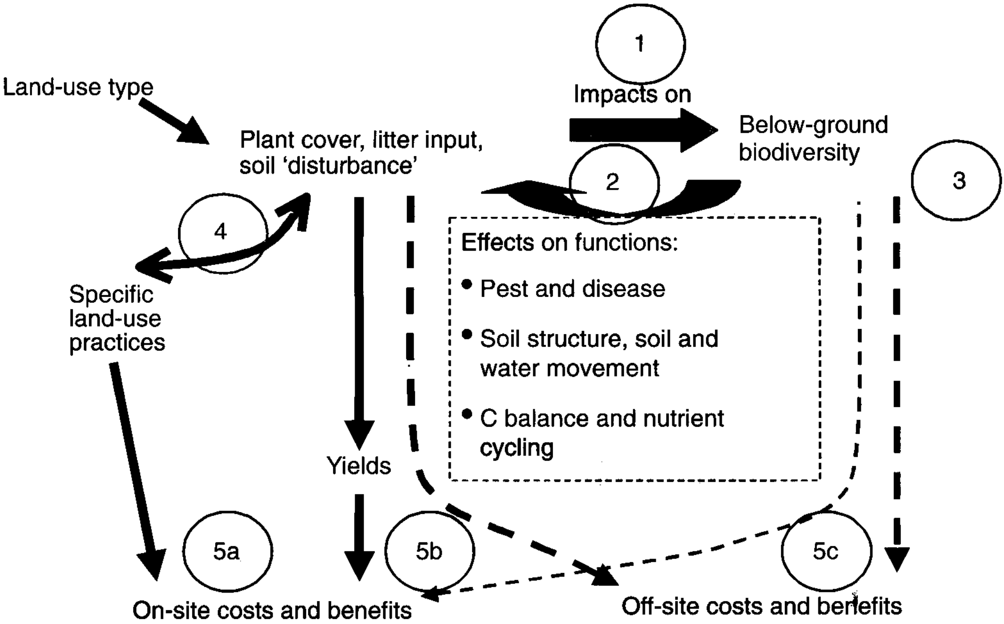

Fig. 16.1. Schematic representation of the impacts of land-use practices on below-ground biodiversity (BGBD) and the consequences this may have for internal regulation of BGBD by representatives within below-ground communities and for key functions in the agroecosystem. The numbers refer to questions raised in the text.

we know whether one additional earthworm species is equivalent to 0.5, 1.0, 10 or 100 additional species of mites or fungi? Therefore, in ecological thought this notion is inadequate. As a result, many biologists lost interest in the concept of species richness, after community ecologists showed that one predator species could not be treated as functionally equivalent to one plant species.

Hence, as the overall diversity of organisms is too large and too complex to be fully understood and interpreted, ecologists often use the concept of 'functional groups'. This does not mean that there also are non-functional (or 'redundant') groups, but merely introduces a term for groups of soil organisms that contribute to ecosystem functioning in a similar way (Brussaard *et al.*, 1997). Functional groups can therefore include soil organisms that are not taxonomically related, e.g. termites and earthworms are often included in the functional group of 'ecosystem engineers'.

Numerous problems are associated with the measurement of biodiversity indicators (Paoletti, 1999). Problems in the sampling and extraction of organisms from soil are common to many groups (Swift and Bignell, 2001). Sample size must be determined by a knowledge of both the ecology of the organism in question and of the spatial heterogeneity extant within the habitat under study, and thus cannot be generalized across groups. Larger soil animals (such as termites) can forage over distances of more than 50 m from their nests (Wood, 1988), and can disperse over much larger distances when they fly, whereas smaller animals are relatively sedentary (Giller *et al.*, 1997a). Basidiomycete fungi can forage for several metres (Dowson *et al.*, 1988), and a single individual has been shown to cover an area of more than 15 ha (Smith *et al.*, 1992). By contrast, the habitat range for bacterial colonies is better estimated in microscopic terms of (micro) aggregates.

Box 16.1. A quick refresher on 'who is who in the below-ground zoo'.

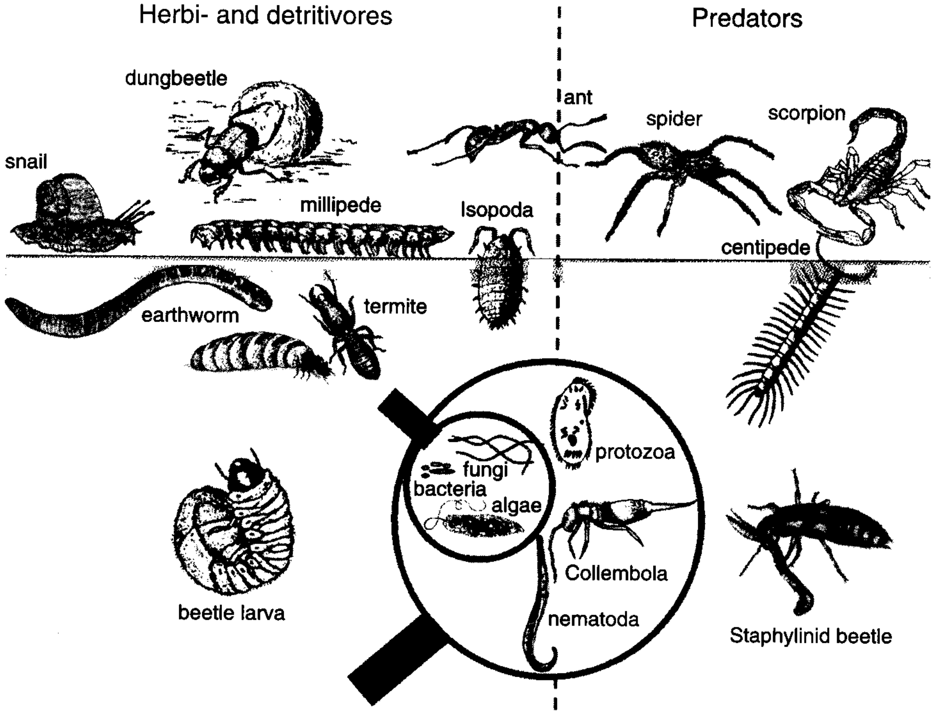

Fig. B16.1. Litter layer and soil with some of its inhabitants (see Table B16.1 for details, drawing by Wiyono).

Three groups of 'below-ground' soil biota can be distinguished (Swift and Bignell, 2001).

1. Epigeic species are biota that live and feed on the soil surface. These invertebrates effect litter comminution (reduction in litter size) and mineralization (nutrient release), but do not actively redistribute plant materials. They mainly consist of predatory and/or saprophagic arthropods (e.g. ants, beetles, cockroaches, centipedes, millipedes, woodlice and orthopterans (grasshopper-type insects)), as well as gastropods (snails) and small, entirely pigmented (dark-coloured) earthworms. These 'surface-active' macrofauna can be sampled using baits and/or pitfall traps (water-filled containers sunk into the ground into which the animals tumble and are caught).
2. Anecic species are biota that take litter from the soil surface and transport it to the deeper soil layers. Through their feeding activities, a considerable amount of topsoil, minerals and organic materials become distributed through the soil profile; this is also accompanied by the formation of channels that alter soil structure, increasing soil porosity. Fauna included in this group are earthworms, non-soil-feeding termites, some beetle larvae and ants (e.g. leaf-cutting *Atta* species).
3. Endogeic species are biota that live in the soil and feed on organic matter and dead roots, also ingesting large quantities of mineral materials. Fauna included in this group are non-pigmented earthworms and soil-feeding termites.

Box 16.1. *Continued.*

Table B16.1. Examples of groups of soil biota, their habitats and food preferences.

		Where do they live?			
Group	Size: approximate body length	Litter layer?	Soil?	Rhizosphere (around plant roots)?	What do they eat?
Bacteria	< 1–5 μm, i.e. visible only under microscope (× 1000)	X	X	X	• Organic substrates ('organotrophs') • Inorganic substrates like CO_2 from the air, NH_4^+, NO_2^-, Fe^{2+}, S^- and $S_2O_3^{2-}$ ('lithotrophs')
Actinomycetes (filamentous bacteria)	< 1–5 μm, i.e. visible only under microscope (× 1000)	X	X	X	Organic substrates; they play an important role in the early stages of decomposition, by mineralizing C and N.
Fungi	Some microscopic, but some above-ground parts can reach up to 40 cm!	X	X	x	Carbon and other nutrients from organic matter in the litter and soil. Fungi are the major decomposers of cellulose, hemicellulose, lignin and pectin in plant cell walls.
Protozoa (single-celled organisms)	0.002–0.2 mm	X	X	X	Bacteria, yeasts and algae and sometimes other small protozoa as well. They feed by engulfing the other organisms.
Nematodes (roundworms)	250–5500 μm	X	X	X	Bacteria, fungi (including yeasts) protozoa and other small nematodes. Some nematodes parasitize invertebrates, vertebrates (including humans), and particularly plants, affecting roots and all above-ground parts.
Springtails (Collembola)	1–10 mm	X	X		Grazing on fungi and other microbes in decaying vegetation. Some feed on live plants or their roots and may be predatory. One family (Onychiuridae) may feed in the rhizosphere and ingest mycorrhizas. Springtails are also effective in biological control of various plant pathogenic fungi.
Mites (Acarina)	0.1–6 mm	X	X		Fungi, decomposing vegetable matter, or both, nematodes, collembola (predatory).
Wood lice (Isopoda)	5–20 mm	X	Under rocks and in decaying wood		Fungi and dead organic matter: occasionally roots and foliage of seedlings.
Millipedes (Diplopoda)	2–250 mm	X	X		Organic debris, but they avoid leaf litter with high polyphenol content and favour litter with a high calcium (Ca) content.

Continued

Box 16.1. *Continued.*

Table B16.1. *Continued.*

Group	Size: approximate body length	Where do they live? Litter layer?	Soil?	Rhizosphere (around plant roots)?	What do they eat?
Centipedes (Chilopoda)	25–280 mm	X	X		Predators of various fauna (collembola, mites, worms).
Scorpions (Scorpionidae)	Average 6 cm, minimum 12 mm, maximum 18 cm	X	Under rocks or logs		Carnivores. Predators of other arthropods, lizards, mice and birds; they are also cannibalistic.
Spiders (Arachnida)	0.5–90 mm	X	X		Carnivores. Above-ground predators.
Ants (Formicidae)	1–25 mm	X	X		Predatory (carnivores), fungi, plant leaves, wood.
Termites (Isoptera)	0.5–20 mm	X	X		Wood, plants, humus, fungi.
Beetles (Coleoptera)	0.5–200 mm	X	X		Larvae and adults have very diverse feeding habits: roots, plant litter, animal dung and carcasses, predators (millipedes, various arthropods, and worms).
Earthworms (Oligochaeta)	2–200 cm	X	X		Organic litter, soil, microorganisms.

16.2 Effects of Land-use (Change) on Soil Biota

Below-ground biota include fungi, bacteria, protists and representatives of the majority of terrestrial invertebrate phyla. No survey can realistically hope to cover all groups, and the degree to which any group can be used as an 'indicator' for all other non-studied groups remains hotly debated (Eggleton *et al.*, 2002; Touyama *et al.*, 2002). Contrary to widely held views, there is remarkably little detailed evidence that agricultural intensification results in a loss of biodiversity in the soil (Giller *et al.*, 1997a). 'Intensification' is here used in a broad sense, and includes an increase in the time that land is cropped, the use of fertilizer, pesticides, mechanization and/or control of soil water content by irrigation and drainage. Even less is known about the thresholds in biodiversity change that are likely to affect soil functions with little reversibility (Swift *et al.*, 1996). Indeed, a number of hypotheses and questions that need to be answered have been identified by Giller *et al.* (1997a).

Studies on soil macrofauna, particularly earthworms (Fragoso *et al.*, 1997), have shown that significant changes in soil biodiversity do indeed occur with land-use change (Lavelle and Pashanasi, 1989) and that these can have functional consequences (Pashanasi *et al.*, 1996). Chauvel *et al.* (1999) showed that conversion of Amazonian rainforest into pasture led to a major reduction in macrofaunal and earthworm diversity, to the extent that only a single species of earthworm survived, resulting in soil compaction due to its surface-casting activity. That changes in land-use have impacts on termites and nematodes has been shown for the Cameroon rainforest (Eggleton *et al.*, 1996, 2002; Hodda *et al.*, 1997). As a result, significant shifts in system carbon fluxes were anticipated. Swift *et al.* (1998) have summarized a number of other studies across a range of environments. Provided external inputs replace biological functions, many of the soils used for temperate-zone agriculture can, however, be mistreated to a remarkable extent and still continue to support crop yields that are close to the theoretical maximum.

A comprehensive approach to the investigation of the relationship between land-use change and soil biodiversity in Indonesia, Cameroon, Brazil and Peru has been initiated by the Alternatives to Slash-and-Burn (ASB) Program. Methods have been standardized (Swift and Bignell, 2001) and overviews of the initial results are now available (Hairiah *et al.*, 2001; Bignell *et al.*, 2002). The main hypotheses underlying this work relate below-ground biodiversity to above-ground biodiversity and the overall C balance of land-use systems, so the work was carried out as part of an integrated survey. Results of the ASB surveys in Indonesia (Fig. 16.2) showed that dramatic land-use change (from rainforest to *Imperata cylindrica* grassland or cassava fields) had a relatively small effect on the number of broad functional groups (orders) represented in a single sample point for the soil fauna. However, it had a greater effect on the surface fauna and especially on the total number of orders encountered per land-use class in the survey. Where we expected to find a drastic difference between the forest and agroforest land-use category (which maintain a year-round litter layer) and the more open land-use classes (which lack such a layer), the survey found that most groups (including spiders, centipedes, millipedes) were still present (at least at the 'order' level). When we 'zoom in' on specific groups, we see little effect on the number of soil nematode genera, or on the diversity of arbuscular mycorrhizal fungi (as judged from the numbers of

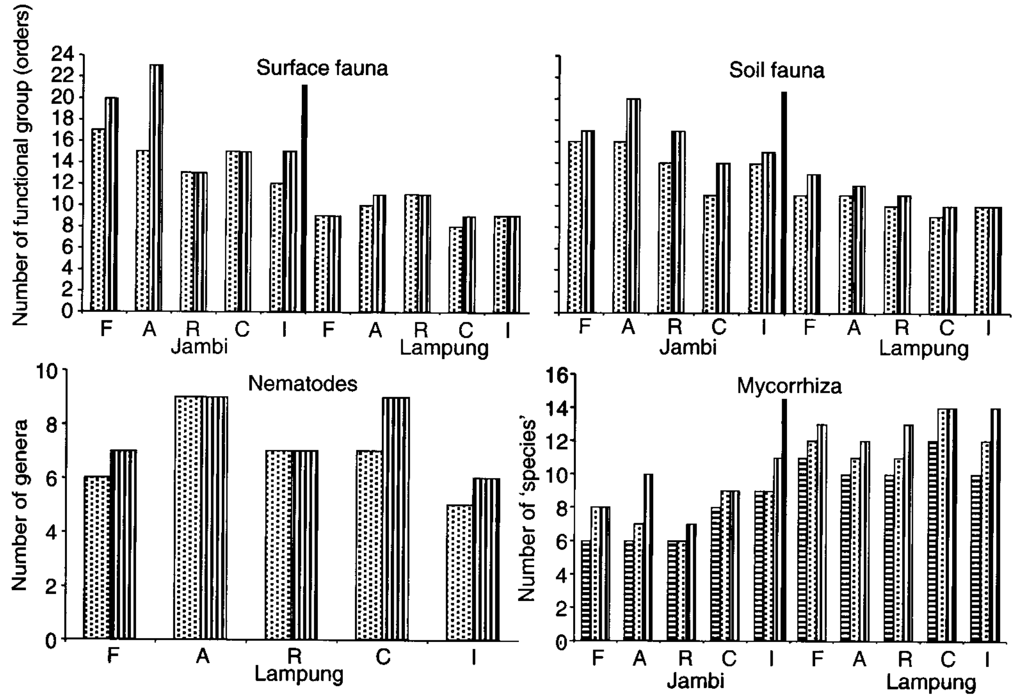

Fig. 16.2. Results of below-ground biodiversity surveys by ASB (Alternatives to Slash-and-Burn) of representative land-use systems in Jambi and Lampung in Indonesia. The data were grouped into five classes: F, forest (in Jambi: approximately natural or logged-over, in Lampung: logged-over, degraded); A, agroforest (rubber agroforest or mixed fruit trees); R, regrowing trees, young plantations and agroforests; C, cassava, potentially in rotation with *Imperata* grassland; I, *Imperata* grassland, potentially in rotation with cassava. Data collection included soil fauna of the litter layer and the upper layers of the soil. As a first approximation presence/absence was evaluated of a number of 'functional groups', roughly representing Orders as taxonomic units (e.g. millipedes, centipedes, cockroaches, beetles, spiders ...). Data are here represented as the maximum number of groups observed for a given location or land cover. Modified from Hairiah *et al.* (2001).

spore 'morphospecies'). Although such overall diversity indicators change little (and may remain below the threshold of statistical significance as there is considerable variation between replicates), considerable shifts can be observed if we compare the presence/absence of species or genera (Hairiah *et al.*, 2001). Specific nematodes, such as the plant-parasitic *Meloidogyne* spp., were prominent in cassava fields in the ASB surveys, and occurred in smaller numbers in other land-use classes.

Two other cases are worthy of note: the first in the Colombian savannahs (Decäens *et al.*, 2001) and the second in Brazilian Amazonia (Barros, 1999). In these studies, soil macrofauna diversity was assessed at the 'morphospecies' level, in order to evaluate the impact of transformation of the native vegetation to various agricultural uses. In Colombia, between 31 and 57 morphospecies were found in the native savannah, whereas between 42 and 55 were found in various types of pasture. Although the total was similar, only 54% of all morphospecies found occurred in both the natural and the disturbed ecosystems. North of Manaus (Brazil), 151 morphospecies were found in the rainforest, whereas only 48 were found in pasture. Only 15% of the morphospecies were found to occur in both the natural and the disturbed ecosystems.

Although survey data can establish to what degree the presence/absence or relative abundance of various groups has apparently changed, we have very little understanding of how these changes result from changes in reproduction and mortality at the population level. A comparison of the pathways for the impact that land use change has on above-ground and below-ground organisms (Fig. 16.3, Table 16.1) indicates that directly induced mortality (pesticides) and lack of food sources may be the dominant causes of a loss of soil fauna and flora. 'Loss of habitat' (which is a dominant cause of loss of fauna and flora above-ground), may only cause the loss of below-ground organisms that are susceptible to the reduction of soil macropore space that occurs as a result of soil compaction or the loss of all topsoil under serious erosion.

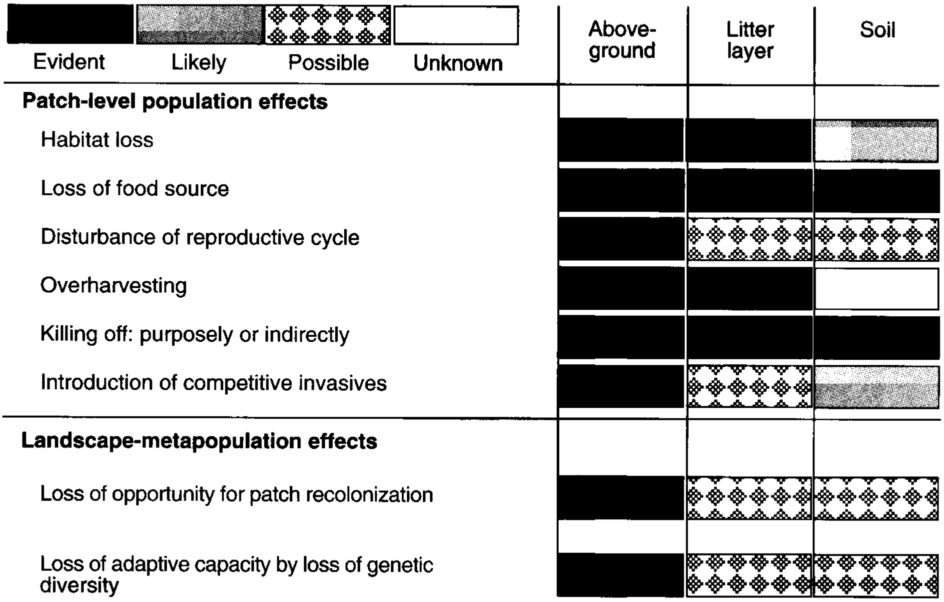

Fig. 16.3. Schematic comparison of the various pathways by which land-use change is likely to indirectly affect the above- and below-ground biodiversity, through specific effects on the patch and landscape level populations of soil biota (Table 16.1 gives further details for each of the cells).

Table 16.1. Pathways for impacts of land use on biodiversity (see also Fig. 16.3).

	Agricultural intensification aspects		
	Above-ground		'Below-ground'
	Vegetation and fauna	Litter layer microflora and fauna	Soil microflora and fauna
Effects on 'patch-level' populations			
Habitat loss	Strong effects on vegetation structure and species composition	Removal of litter layer by slash-and-burn practices, tillage, or overland waterflows; lack of litterfall to reestablish litter layers	Soil compaction reduces macropores and habitat availability
Loss of food source	Effects on flora and fauna via change in species composition of vegetation	Decrease in quantity and/ or diversity or resource qualities, e.g. C/N ratio, content of lignin, polyphenolics and other secondary metabolites; shifts between 'fungal' and 'bacterial' pathways	Clear, for specific rhizosphere symbionts and 'soilborne pests'
Disturbance of reproductive cycle	Loss of pollinators and seed dispersers; loss of nesting and breeding sites	No evidence	No evidence?
Overharvesting	Common in 'bush meat' and birds	Discussion (but little evidence) on fungal fruiting bodies (mushrooms)	Large worms for fish bait in Brazil
Killing off: purposely or indirectly	Insecticides, rodenticides	Surface-applied insecticides and fungicides	Use of fungicides, nematicides, soil fumigation
Introduction of invasive species	Competition with 'weeds', exotic fauna, grazing animals	Leaf-burying worms and dung beetles	E.g. flatworm effects on earthworms
Landscape-level effects			
Loss of opportunity for patch recolonization	Coarsening of land-use mosaic pattern can substantially change dispersal opportunities	Coarsening of land-use mosaic pattern	Dispersal distances either small ('creepy crawlies') or large (airborne spores or adults)
Loss of adaptive capacity by loss of genetic diversity	Potentially serious, evidence mainly for 'domesticated' plants and animals	Potentially serious, little hard evidence	Potentially serious, little hard evidence

16.3 Functions of Soil Biota in Ecosystems

16.3.1 General ecological roles

The terms 'epigeic', 'anecic', and 'endogeic' (see Box 16.1) indicate the overall habitat of soil organisms. The 'anecics', by definition, play a role in functionally connecting the litter layer and mineral soil. Further indications of 'functional roles' are needed, however. A different way of classifying organisms into functional groups distinguishes rhizosphere biota ('rhizospherics'), decomposers and litter transformers, ecosystem engineers, grazers, micropredators and mid-top predators.

Rhizosphere biota are organisms that live close to, or in symbiotic relationship with, plant roots, and can thus directly influence plant performance in a positive or negative way. From a plant or an agronomic perspective, a conventional subdivision distinguishes: (i) organisms that increase nutrient amounts (such as the symbiotic N_2-fixing bacteria discussed in Chapter 13, this volume); (ii) organisms that increase nutrient availability for the plant (such as the mycorrhizal fungi discussed in Chapter 14, this volume); and (iii) organisms that interfere with root functions, such as plant-pathogenic fungi, plant-parasitic nematodes (Chapter 15, this volume) and rhizovorous ('root herbivorous') insects. From the perspective of all rhizosphere biota, growing roots release an appreciable amount of organic C and N into the rhizosphere (Chapter 5, this volume). The three major sources of this organic C and N are:

- free exudates (substances exuded from roots, i.e. low-molecular-weight organic compounds);
- mucilage (high-molecular-weight gelatinous ('slimy') materials, which are produced by root tips);
- sloughed-off cells and tissues and their decomposition products ('lysates').

The true symbionts and invasive parasites have access to the resources of the living root cells as well.

Ecosystem engineers have a major influence on the structure of a soil, creating a network of pores and contributing to aggregation (the way elementary soil particles, clay, silt and/or sand, stick together). Earthworms, termites and some ants can create macropores by pushing their bodies into the soil (thus causing compaction of a zone of soil around the channel that can persist for some time), or by eating their way through the soil and removing soil particles. Earthworms and other animals that feed on soil, produce excrement that contains resistant organomineral structures that may persist for long periods of time (from months to years) and which profoundly affect nutrient cycling and the environment for smaller organisms (Lavelle *et al.*, 1997; Brown *et al.*, 2000). Sometimes these are built into elaborate structures (e.g. termite nests). Earthworms and termites can do this because they have a 'gut flora' of bacteria. These organisms condition the soil as a habitat for other organisms by 'bioturbation' and aggregate formation. Bioturbation is the moving of soil particles, from one horizon to another, by soil biota, in such a way as to affect and determine physical structure and the distribution of organic material in the soil profile. Examples of ecosystem engineers are earthworms and the larvae of some species of scarab beetle of the anecic group (species that live in the soil and feed on surface litter) and earthworms, ants and termites of the endogeic group (species that live and feed in the subsoil).

Grazers and micropredators are small invertebrates, mainly protozoa and nematodes, which feed on microorganisms and fungi. They live free in the soil and do not develop mutualistic relationships with microflora. Predation of microorganisms, particularly by nematodes and protozoa, plays an important role in regulating the biomass of microorganisms and is likely to assist in the maintenance of diversity, by preventing the dominance of particular groups. This is arguably more important for bacteria, which tend to be strongly regulated by predation, than for fungi, which are less susceptible to grazing as they are more complex both chemically and structurally (Wardle and Lavelle, 1997). Current models of below-ground food-webs (see below) are reasonably successful in predicting the time pattern of N mineralization for a given structure of the foodweb and abundance of functional groups (de Ruiter *et al.*, 1995). Application of such models to tropical ecosystems is, however, still very fragmentary.

Mid-top predators are the ants, centipedes, beetles (e.g. carabids), spiders and other arachnids (scorpions, pseudoscorpions, harvestmen (opilionids) and predatory mites) that prey on decomposers and micropredators. As they are more common in the litter layer than in the soil as such, they may cross the below-ground versus above-ground divide. Where they also climb into plants and prey on herbivores they may play an important ecological role relative to their biomass.

Finally, the most important functional group is probably that of the *decomposers and litter transformers*, as all nutrient cycling would come to a halt in the absence of decomposition. The major contributors to decomposition are fungi and bacteria that have the enzymatic capacity to breakdown complex organic molecules and release the nitrogen, phosphorus and sulphur compounds they contain. Soil fauna can improve the access of bacteria and fungi to these molecules by their 'comminutive' action, breaking the material into smaller particles with a larger surface area. Important 'detritivorous' fauna include:

- some species of earthworms (epigeics living in the litter layer on top of the mineral soil);
- wood-eating ('xylophagous') termites;
- pot worms (Enchytraeidae, in the class of Oligochaeta).

16.3.2 Relationships between above-ground and below-ground biota

Above-ground diversity consists of plants and nearly all animal groups; but plants play the dominant role by providing both the 'infrastructure' of the vegetation, and the basis of the foodweb – by capturing energy from sunlight and sequestering CO_2 into energy-rich carbohydrates, proteins and other organic substrates. Most plants, however, live only partly above-ground – their below-ground organs (roots) are essential for their survival and functioning. We may expect a strong linkage between above-ground and below-ground diversity, primarily because plants and plant diversity determine the functioning of the below-ground ecosystem via factors (van Noordwijk and Swift, 1999) such as:

- plant litter quality, quantity and timing;
- the soil water balance and microclimate in the surface layer;
- root activity, which changes the rhizosphere.

Plant diversity can lead to a wider array and/or a more continuous supply of substrates for the below-ground system. In return, the below-ground community provides a number of 'environmental services' to the plants. However, the functions involved in mineralization and decomposition are broad-based, and there is little evidence to suggest either that specific groups are needed, or that more diverse systems function better from a plant's perspective. Specific relationships with plants do occur in the symbionts, diseases and their antagonists, and it is here that below-ground diversity may facilitate above-ground diversity.

Functional relations between above-ground and below-ground biodiversity, mediated by roots, are likely to involve time lags and may be poorly reversible. Soil organisms tend to have less effective means of dispersal than most above-ground organisms and may thus become a rate-limiting step for ecosystem adjustment in as far as they are critical to the functioning of above-ground vegetation. This is most likely to be the case for specialized obligate symbionts such as mycorrhizal fungi and specific rhizosphere organisms. The impact of soil biota on vegetation change may have been underestimated. The rate of establishment of plant-parasitic nematodes (and not changes in nutrient availability as previously assumed) was shown to be a major determinant of primary succession in sand dunes in The Netherlands (van der Putten *et al.*, 1993).

As herbivores and their below-ground counterparts (rhizovores; van Noordwijk *et al.*, 1998c) exert a considerable selection pressure, it is understandable that plants devote a considerable part of their energy and nutrient resources to the making of 'secondary metabolites', which play a primary role in making them less attractive as food (Brown and Gange, 1991). Several antinutritional factors, such as silica needles and polyphenols, continue to inhibit animal activity after the death of the plant organ, restricting comminution and decomposition. Such relations have been poorly quantified so far, but recent observations (Min Ha Fagerstrom, 2001, Hanoi, personal communication) of limited earthworm activity under fallows of *Tephrosia candida* (a species with a high rotenone content) may provide an explanation for the surface accumulation of its litter. Crop domestication has often led to a reduction in such substances, in order to increase the crop's harvestable yield and consumption value. Interestingly, where the labour efforts required to guard crops without chemical defences from herbivores exceed the labour required for removing the toxins in food processing (as is true in the case of the 'bitter cassava' preferred by African farmers for out-fields) plant chemical defence properties may be retained during domestication. However, due to a general loss of antinutritional factors in today's crops, decomposition may be accelerated in agroecosystems, as compared with natural ecosystems. In addition, the quantity and diversity of organic inputs are lower in agroecosystems. Thus, there may be less need to maintain an assembly of specialists in order to secure decomposition processes.

16.4 Food-web Theory and Below-ground Biodiversity

Important aspects of the structure, functioning and stability of the below-ground part of agroecosystems can be captured in the study of the dynamics of the soil food web. A food web is a network of feeding interactions between species or, more generally, groups of organisms. It is a web of interacting food chains. The food-chain concept is basic to ecology and represents an ecosystem in a simple way, as a chain of species where one species is preyed upon by the next. A generic form can be written as: plant, plant-eater, eater of plant-eater, and eater of eater of plant-eater. Well-known examples are the terrestrial (above-ground) plant–herbivore–carnivore chain and the aquatic algae–zooplankton–fish chain. The chains also depict how energy (fixed by plants as primary producers) is transferred over trophic levels to the top consumers. The transfer of energy through the food chain is necessarily accompanied by loss when organisms convert their food into new biomass. This is why we speak of 'trophic pyramids', a concept referring to the decrease in energy consumption that occurs with an increase in trophic levels, often accompanied by a decrease in biomass (Odum, 1971).

Like most natural communities, soil communities are not simple chains of species. They are diverse, complex systems, in which species often feed from more than one trophic level. Ecologists use food-web models to try to capture the interconnected dynamics of populations in such complex communities. By studying soil food webs, ecologists have gained insight into such system processes as overall energy flow and nutrient cycling, as well as into the relationships between the shapes of trophic pyramids and the stability of communities and their environments.

16.4.1 Food-web models

When organisms decompose organic matter they transform a proportion of the energy and nutrients into new biomass, and release the rest in mineral or gaseous form. Hunt *et al.* (1987) described the soil food web as a community of 'functional groups', with detritus (i.e. plant litter or other forms of dead organic matter), and live plant roots as the base. A simple representation of a below-ground food web for tropical agroecosystems is shown in Fig. 16.4.

The functional groups in food-web diagrams are not taxonomic categories, but groups of species having a similar choice of prey and similar population dynamics. The detail with which groups are distinguished depends on practical limitations imposed by field measurements and on the level of interest of the researcher. When constructing a food web, the practical decision to distinguish just two groups of microbes, fungi and bacteria (as in Fig. 16.4, for example), leads logically to the distinction of two microbivorous groups, fungivores and bacteriovores. Using this functional-groups approach, de Ruiter *et al.* (1994) evaluated overall annual nitrogen mineralization and respiration rates in a series of agricultural and natural soils. Using observations on population sizes (biomass per unit land area), and data on species' physiologies (in particular the species' natural turnover rates and food-conversion efficiencies), they calculated annual equilibrium feeding rates in

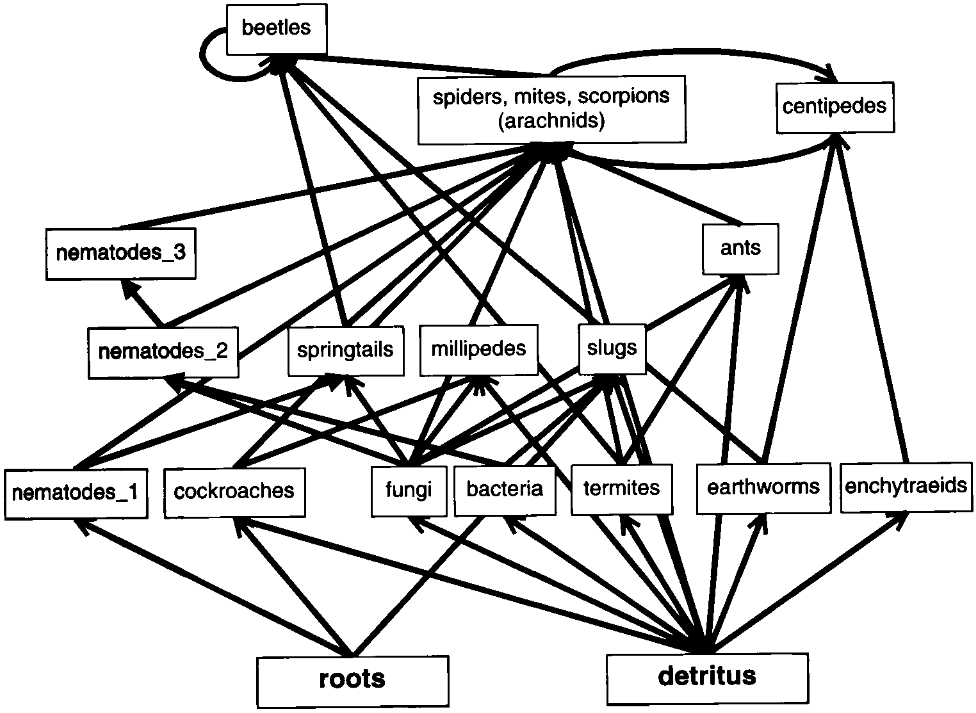

Fig. 16.4. Generic food web of the below-ground community in a tropical soil.

the food webs, which determine mineralization and respiration rates. Equilibrium is a state where for each species the population size is constant (i.e. growth rates are equal to loss rates). De Ruiter and colleagues also showed how these functional processes are linked to system stability, based on the stability of all populations in the community. Stability calculations require estimates of the 'interaction strengths' (May, 1973), the effects of species on each other's dynamics near equilibrium, that can be derived from the equilibrium feeding rates (de Ruiter *et al.*, 1995).

16.4.2 Stability

When talking about system stability, we may think of many aspects of a system and different types of disturbance. Stability is concerned with the ability to deal with disturbances. It may be associated with concepts such as *'constancy'*, which simply states that a system stays the same over time. However, this does not tell us anything of the way the system handles disturbances.

First we should ask what is a 'disturbance'? Let us say that a disturbance starts with a change in the environment of the system, and can 'propagate' within the system through the response of (local) subcommunities or those populations that make up the biological community. We may distinguish three different levels of system stability: the first is 'resistance' (resisting change), which states that the system and its components withstand change altogether. The second is 'resilience' (coping with change), which states that the components may change, but the system and its components are drawn back, at a certain speed, either to their original state, or to the same domain of attraction. The third is 'adapting' to change: the system and its components end up in another state or domain; but, at a higher level of abstraction, the system stays essentially the same, i.e. it functions in a similar way. Think of the first form (resistance) as a pile of bricks or a brick building, the second (resilience) as a wooden house or a flexible rope bridge, and the third (adapting) as a tree, e.g. it adapts its growth direction, loses some leaves or even branches, but remains the same tree. Our current mathematical concept of the stability of food-web models comes closest to the second level (resilience). But, instead of picturing that level as a more or less static object, it would be better to think of it as a group of people all pulling on the same rope but in different directions. When the rope does not move, all forces are in equilibrium. When an outside disturbance leads to one of the people pulling harder, or letting go, the change in force may affect the other people, leading to all kinds of other changes. When, finally, everyone holding the rope exerts equal force once more, and the centre of the rope is in the same area, we would call this stable behaviour. Instability would be the probability of not returning to this area. The degree of stability could be measured by, for example, determining the maximum disturbance from which a recovery would be possible.

The debate on the relationship between biodiversity and ecosystem stability has a long history. A classical idea in ecology holds that complex and diverse communities or ecosystems are more 'stable', in an unspecified sense, than simple ones (Elton, 1927; MacArthur, 1955; Odum, 1971). This is often illustrated by the example of a well-developed tropical rainforest and a monoculture in an arable field. The rainforest, a highly diverse system with (supposedly) small fluctuations in population abundances and steady nutrient cycles, is regarded as a stable system. The relatively simple agricultural system does not have that many feedback mechanisms and is very susceptible to, for example, pest outbreaks or adverse weather conditions. However, it has been difficult to get operational definitions of stability in order to apply a direct experimental approach to these issues. With the introduction of the use of mathematical models in ecology, it became possible to define and distinguish more explicitly the various aspects of stability. The study of the mathematical stability of a community (i.e. of the ability of the community, when perturbed from a state of equilibrium, to return to equilibrium) has led to the idea that complexity in communities gives instability (May, 1972). The larger the number of species or the higher the density of interactions ('connectance') in a system, the less likely the system is to return to a state of equilibrium following a small perturbation from said equilibrium. This difference between experience from the field and the results of mathematical models, in ideas on the relationship between complexity and stability, is one of the central controversies in ecology. But, the two perspectives can be reconciled (May, 1973), if we reverse the presumed cause–effect chain: diversity itself does not lead to a stable system, but a stable environment is required for diversity to develop. Relative to temperate and subarctic systems, tropical ecosystems have developed under relatively constant conditions. Moreover, when developing, they have also created their own environment (their own microclimate), which in turn acts as a buffer against outside disturbance.

16.4.3 Food-web theory on diversity, stability and energetic organization

Recently, the discussion on whether biodiversity leads to stability or instability (or vice versa) has been given new impetus, through studies that point to both the stabilizing effects of (weak) interactions (McCann *et al.*, 1998) and the importance of community organization, indicating that more diversity as such does not make a community more (or less) stable. Rather, it is the organization of diversity (the pattern of strong and weak interactions) that determines stability (McCann *et al.*, 1998; Neutel *et al.*, 2002). Observations on soil food webs give some insight into what constitutes this stabilizing organization. In general, ecosystems are biomass pyramids, i.e. by far the most biomass is at the base of the food chains, and the higher up the chains we look, the less biomass we find (Odum, 1971). Neutel *et al.* (2002) found that this phenomenon is an important stabilizing property of food webs. In two series of soil food webs occurring along gradients of primary vegetation succession, below-ground complexity and food-chain length increase with developmental (successional) age. It was not this complexity that determined the stability of the system, however. Rather, it was the shape of the biomass pyramid of the food webs that turned out to be a good indicator of food-web stability. The stronger the biomass decrease over trophic levels in the bacterial 'chain', the more stable the food web (Neutel, 2001; Fig. 16.5).

16.4.4 Perspectives on soil ecology in tropical agroecosystems

For soil ecologists in the tropics, this food-web approach may offer the possibility to compare different soil communities in the field, and analyse their diversity and stability at a system level. There are, however, a number of methodological and conceptual issues to take into account.

The first issue pertains to the complexity of many tropical systems, and the difficulty of collecting complete and detailed data sets. Because of this, simple indicators of community structure are required. Instead of trying to accomplish the almost impossible task of identifying and quantify-

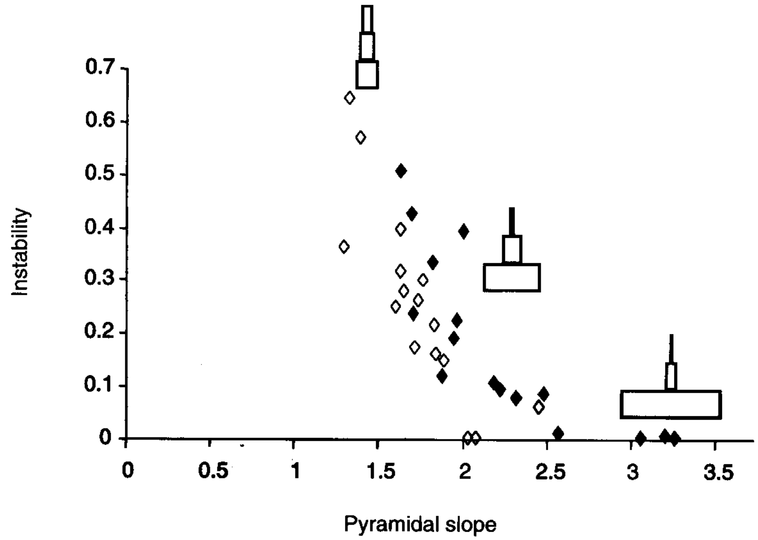

Fig. 16.5. Relationship between the slope of the biomass pyramid and an index of instability of the foodweb, in two series of below-ground food webs in Dutch dune soils. Filled diamonds represent food webs from coastal dunes on the island of Schiermonnikoog, unfilled diamonds represent food webs from sand dunes on Hulshorsterzand (part of a nature reserve on the Veluwe), both in The Netherlands. Each symbol represents a food-web replication in one of the series. The pyramidal slope is the decrease over trophic levels of the species' biomass (densities) in the bacterial 'chain'. This decrease was expressed as a power of 10, i.e. pyramidal slopes of 1 and 2 mean a tenfold and a 100-fold decrease in biomass over trophic levels, respectively. In the bacterial chain, trophic level 1 consisted of bacteria, trophic level 2 consisted of bacterivorous nematodes, flagellates and amoebae, and bacterivorous mites, trophic level 2.5 consisted of predatory nematodes, and trophic level 3 consisted of nematophagous mites and predatory collembola. Instability is defined here as the level of intraspecific interaction the populations need for the food web to be (mathematically) stable. Intraspecific interaction, or self-limitation, counteracts destabilizing effects of interaction between the populations. A system that needs a high level of intraspecific interaction is relatively unstable. Based on A.M. Neutel, J. van de Koppel, F. Berendse, P.C. de Ruiter, unpublished.

ing all the feeding relations in a soil food web (Fig. 16.4), we may start by first characterizing systems according to the shape of their associated trophic pyramids. Probably the simplest indicator is the ratio (in orders of magnitude or powers of 10) between the top and the base of the pyramid. In a study of the impacts of above-ground land-use intensification on below-ground biodiversity (Fig. 16.2), we explored this approach. The comparison of five land-use types, in two locations, showed some differences in the top-to-base ratios, i.e. top trophic level biomass and (base) annual organic matter input (Table 16.2) in below-ground pyramids (Fig. 16.6a,b). The first thing to note, however, is the remarkable similarity of the amount of top predator biomass per unit organic input: approximately 5×10^{-6} kg top predator biomass per kilogram of annual organic input per year (Fig. 16.6c). The values for Jambi province are higher than those for Lampung, which might suggest that these pyramids would be less stable (and associated with a more stable climate and an environment with less disturbance). Compared with Fig. 16.5, however, we may conclude that extremes such as the pure sands that form the start of the successional series in those data are missing, and all points may be in the range 1.5–2.0 of that figure (assuming three trophic levels and a biomass turnover of 1 year for the top predators as a first guess).

As expected, the (base) organic matter inputs to the soil food web showed a decreasing trend over the land-use gradients (Fig. 16.6a,b). This trend reflects degradation of above-ground vegetation

Table 16.2. Assumptions underlying the estimate of annual organic matter input to the soil in five different land-cover types (Fig. 16.2), sampled in Indonesia as part of the Alternatives to Slash-and-Burn Program.

	Forest	Agroforestry	Regrowth	Crops	*Imperata* grassland
Standing biomass stocks (Mg/ha)					
Woody above-ground	350	120	20	0	0
Leaf and twig	10	10	8	4	6
Coarse roots	50	17	3	1	3
Fine roots	3	3	3	2	3
Coarse roots from previous vegetation	5	10	10	10	10
Estimated turnover rates (per year)					
Woody above-ground	0.02	0.02	0.02	0.02	0.02
Leaf and twig	1.0	1.0	1.0	1.0	1.0
Coarse roots	0.02	0.02	0.02	0.02	0.02
Fine roots	1.0	1.0	1.0	1.0	1.0
Above-ground inputs lost by fire	0.0	0.0	0.0	0.0	0.5
Organic matter input to the soil (Mg/ha/year)					
Above-ground coarse litterfall	7.0	2.4	0.4	0.0	0.0
Leaf and twig litterfall	10.0	10.0	8.0	4.0	3.0
Coarse root turnover	1.1	0.5	0.3	0.2	0.3
Fine root turnover	2.5	2.5	2.5	1.5	2.5
Exudation	1.3	1.3	1.3	0.8	1.3
Annual change in Corg/Cref[a] – Jambi	0	0	−0.05	−0.01	0
Annual change in Corg/Cref – Lampung	0	0	0	−0.01	0
Net change in Corg – Jambi	0.0	0.0	−3.0	−0.6	0.0
Net change in Corg – Jambi	0.0	0.0	0.0	-0.6	0.0
Total (Mg/ha/year) – Jambi	21.9	16.7	15.4	7.1	7.0
Total (Mg/ha/year) – Lampung	21.9	16.7	12.4	7.1	7.0

[a] Corg/Cref, soil organic carbon content relative to that for forest soils of the same texture and pH.

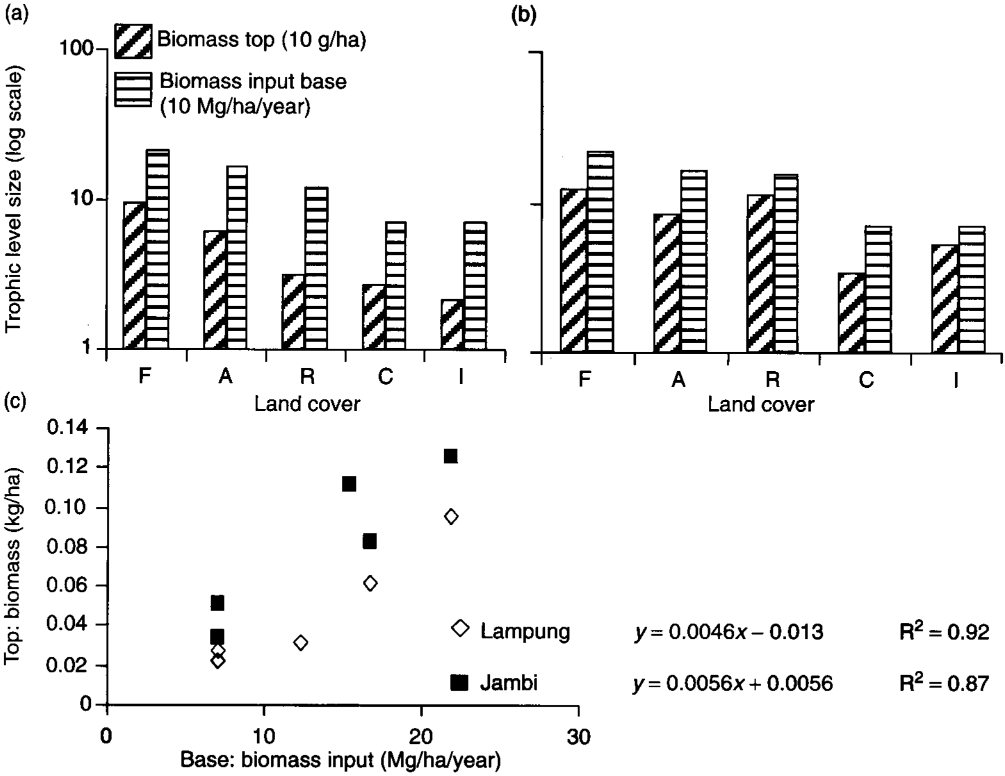

Fig. 16.6. Comparison of the base of the below-ground foodweb (estimates of the annual above- and below-ground organic inputs) and the top predators (biomass of arachnids, ants plus centipedes); land cover codes (F, forest; A, agroforest; R, plantation; C, cassava; I, *Imperata* grassland), data from the ASB-Indonesia consortium. (a) Data for Lampung; (b) data for Jambi; (c) correlation graph.

and suggests that below-ground community structure and functioning followed changes in above-ground vegetation. The correspondence between the above-ground and below-ground community is not self-evident; when single trophic groups were compared with organic matter input the relations were much less clear (data not shown).

The second issue to be considered is that of spatial structure. How do spatial compartments affect stability? Where does 'below-ground' end and 'above-ground' start? This is a general issue of course, but is all the more eye-catching in tropical systems. Should we distinguish a litter and a soil food-web compartment? Above-ground vegetation, particularly as regards the presence or absence of trees, could have important consequences for below-ground spatial structure and, consequently, for the dynamics of the litter–soil system (Fig. 16.7). Theory to deal with this aspect is lacking. Investigation of spatial heterogeneity could make an important contribution to our understanding of plant–soil interactions, as well as to food-web theory in general.

The third and final issue pertains to the fact that, although the energy flow constraints placed on food-web structure do not directly allow us to make predictions about below-ground biodiversity, there may be opportunities to link them with the theory developed by Hubbell (2001). In this 'neutral' theory of biodiversity and biogeography, Hubbell proposed that species richness within functional groups can be understood

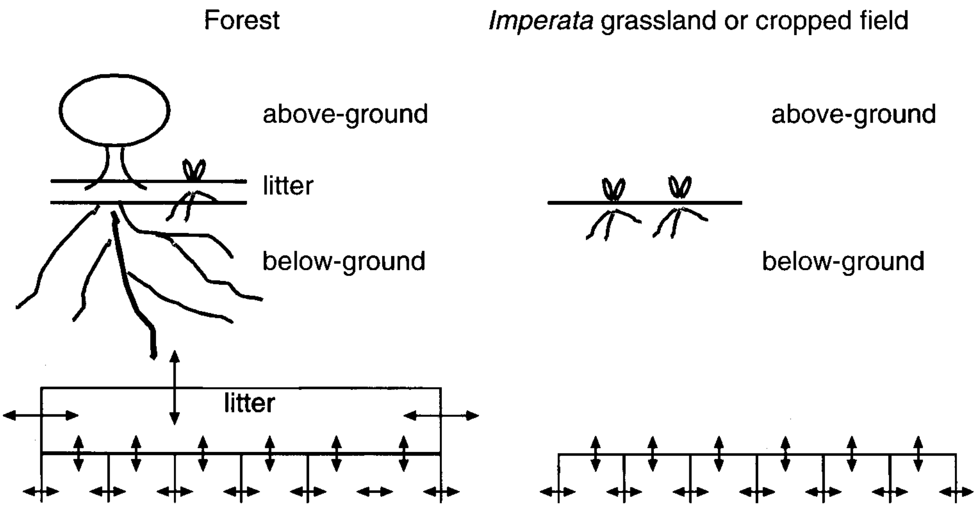

Fig. 16.7. Schematic representation of the spatial structure of the below-ground community in forests (or other vegetation with a permanent litter layer) and grasslands of cropped fields without such a layer. The litter layer allows organisms to move over much larger distances than most organisms living in the soil. These organisms transport organic material vertically to and from the soil, and/or horizontally over the surface rather than via the soil. The lateral flows in the litter layer could have important consequences for the dynamics of the soil community and allow for a stronger presence of 'top of the pyramid' organisms.

by assuming that interspecific interactions are approximately equal to intraspecific ones. Increases and decreases in the abundance of individual species can then be seen as 'random walks', with the probability of local disappearance depending on total energy flow to the group and the probability of recolonization from neighbouring sites within the same 'metapopulation' depending on the accessibility and the dispersal means of the species. Combining this theory with food-web theory may prove to be productive.

16.5 Farmers and Below-ground Biodiversity: Many Questions Remain

Is below-ground biodiversity a concept that has relevance for farmers? Or should they focus on specific soil biota, especially those that are harmful to their crops (pests, plant pathogens, weeds and their symbionts) or that favour their crops (including symbionts, natural enemies and competitors of the pestiferous biota)? What are the options for 'managing' populations of organisms in the context of the existing food webs and pathways for energy flow? Is 'feeding the soil food web' through organic matter inputs a generally safe way of securing 'healthy soil life'? Is there a need for more specific management? In general, questions such as these cannot yet be answered, despite all the research efforts made thus far; however, we can see that, for specific situations, the balance between 'beneficial' and 'harmful' is a delicate one (Swift and Anderson, 1993; Susilo *et al.*, 1999; Bekunda, 2000).

It is no surprise that changes in land management may change below-ground diversity. But does it matter if one species disappears? Can other species replace its function? Is the function consistently predictable for a wide array of agroecosystems? We all believe that under low-input agricultural systems, earthworms play very important (beneficial) roles in terms of maintaining soil fertility and crop productivity (Box 16.2). But an example exists of earthworms becoming destructive pests in irrigated rice fields in the Philippines (Box 16.3).

Box 16.2. Case study: decline in species richness of earthworms as a result of land management (Hairiah *et al.*, 2001).

Changes in land management may change soil organic matter (SOM) status and subsequently affect the abundance and diversity of 'soil engineers'. Most soil biota respond to litter quality (e.g. termites respond more to low-quality material, ants respond to high-quality, and earthworms appear not respond to litter quality). Brown *et al.* (1998) showed that when forest was converted into agricultural land in Kenya, Tanzania, Zambia and Zimbabwe, faunal diversity and density were reduced from an average of > 16 orders and 9 g/m^2 to < 7 orders and 5 g/m^2. However in some pastures and crop fields, biomass was higher than that found in forests, reaching > 20 g/m^2. This is primarily a result of the stimulation of earthworm, Coleoptera (beetle) or termite populations.

Organic matter management practices (such as hedgerow intercropping systems) can have a great impact on decomposition, nutrient mineralization and microbial activity. Work on secondary forest in North Lampung (Indonesia) showed that this area had a higher microbial biomass (10^6 mg/kg), a higher total number of microbes (224×10^4 colony-forming units (cfu)) and higher microbial activity (7 mg/kg/day of CO_2) than 8-year-old plots in hedgerow intercropping systems, which benefited from inputs from the pruning of *Peltophorum*, *Gliricidia*, *Calliandra*, *Leucaena* or *Flemingia* hedgerows (Priyanto, 1996). In the same plots, Wibowo (1999) found that the seven species of earthworm found under secondary forest was reduced to six species in hedgerow intercropping systems (*Peltophorum*, *Gliricidia* and mixed *Peltophorum* + *Gliricidia*) and five species in the control plot used (without hedgerows) (Table B16.2).

Table B16.2. Species richness of earthworm under secondary forest and agricultural land in North Lampung in dry (D) and rainy (R) seasons (Wibowo, 1999).

			Hedgerow intercropping								
	Forest		Pelto		Gliri		Pelto+Gliri		Control		Ecological group
Species	D	R	D	R	D	R	D	R	D	R	
Megascolex filiciseta	V	V	V	V	V	V	V	V	V	V	Anecic
Glyphidrilus papillatus	V	V	V	V	V	V	V	V	V	V	Endogeic
Drawida burchardi	V	V	V	V	V	V	V	V	V	V	Anecic
Dichogaster affinis	V	V	V	V	V	V	V	V	V	V	Endogeic
Dichogaster crawi	V	V	V	V	V	V	V	V	-	-	Endogeic
Pontoscolex corethrurus	V	V	V	V	V	V	V	V	V	V	Endogeic
Metapheretima carolinensis	V	V	-	-	-	-	-	-	-	-	Epigeic
Total number of species	7	7	6	6	6	6	6	6	5	5	

Pelto, *Peltophorum dasyrrachis*; Gliri, *Gliricidia sepium*; V, present.

In a simplified causal diagram of the intermediary role that soil biota play in the relationship between 'crop management' and 'yield', a number of intervention points can be identified. Box 16.4 gives an example of how ants, as epigeic soil biota, can play a role in the control of 'above-ground' pests (intervention point 7 in Fig. 16.8). This indicates that the split between below-ground and above-ground biota is artificial: the litter layer fauna in particular can play an intermediary role.

Similar to the view expressed in Chapter 14, this volume, with regard to the management of mycorrhizal fungi, the dominant paradigm in applied soil ecology is based on maintaining the energy resource base for biota through the regular supply of organic inputs to the soil (which could be summed up by the saying 'no litter, no money'). However, where the relationship between the litter layer and the soil has been disturbed, strategic deep placement of organic inputs in soil trenches, along with the stimulation of worm activity, can have spectacular effects on crop production (Box 16.5).

Box 16.3. Case study: earthworms in the Ifugao rice terraces (IRTs), the Philippines.

'Soil engineers' that make macropores in the soil (such as earthworms) are not always welcome. This is particularly true in bunded rice fields. Farmers who own such fields work to destroy soil structure, and so reduce its porosity, by puddling, and build dykes to contain the water in the field. 'Soil engineers' counteract all this hard work.

Surveys were conducted across three municipalities containing IRTs (Banaue, Hungduan and Mayoyao). A total of 150 farmers were randomly selected to be respondents (Joshi *et al.*, 1999). The survey was intended to help researchers learn about farmers' knowledge, attitudes and practices concerning both the extent and nature of the problem caused by earthworms in such irrigated rice fields. Of 150 farmer-respondents interviewed, 125 farmers ranked earthworms as the most important pest of terraced rice fields. The farmers described the problem as follows:

The earthworms seem to cause damage to the rice fields by making tunnels along the terrace walls, causing leaks, resulting in undesired water drainage from the fields.

The species of earthworm in the area can be divided into two groups:

1. Terrace-dwelling species
- *Polypheretima elongata* (the dominant species)
- Large worm species belonging to either of the genera *Pheretima* or *Metaphire*
- *Pontoscolex corethrurus* (Müller)
- *Pithemera bicinta* (Perrier)
- *Amynthas diffringens* (Baird)

2. Non-terrace-dwelling species
- *Polypheretima* sp. – a hitherto undescribed species.
- *Pheretima* sp. – a hitherto undescribed species
- *Pleinogaster* sp.

Of all the terrace-dwelling species, only *Pontoscolex corethrurus* was found to be present in the neighbouring forest area. The others may be native, new to the area or exotic species. Such invasions occur most often in locations affected by human activity, and rarely in natural vegetation with a resident earthworm fauna. In general, native earthworms are vulnerable to habitat disturbance and invasion by exotic species (Fragoso *et al.*, 1997).

Besides mechanical control (e.g. tillage), farmers used indigenous methods of control, e.g. the use of ground wild sunflower (*Tithonia diversifolia*) or ground seeds of the neem tree (*Azadirachta indica*) mixed with water and poured evenly over the plot, in order to kill the worms.

Box 16.4. Case study: the changing roles of ants in agroecosystems in Lampung Province (Indonesia).

From a farmers' perspective, the fire ant *Solenopsis* sp. can be both beneficial and destructive. The ants function as a very effective predator of the eggs of the noxious armyworms (*Spodoptera litura*), which affect soybean (Waraspati, 1997; Table B16.3), and may in fact be the key factor limiting outbreaks of armyworms in Lampung soybean fields (Sudarsono *et al.*, 1995).

However, the same ants are seen as pests themselves in pineapple plantations (Rusmiati, 2001). The ants have a symbiotic relationship with the mealy bug (*Dysmicoccus brevipes*), which lives on and sucks the sap of the pineapple leaves, and indirectly functions as the vector of pineapple wilt virus (PWV). The mealy bug picks up the virus from diseased plants and transmits it into new, healthy plants upon feeding. The direct and indirect effects of the mealy bug are economically significant. However, the bug is quite difficult to control, because it is resistant to various insecticides. The plantation companies have considered the possibility that managing the ants (e.g. intervention point 9 on Fig. 16.8) would be a more promising way of controlling the PWV than directly controlling its vector (mealy bug).

Box 16.4. *Continued.*

Ants can also be pestiferous when associated with the banana aphid (*Pentalonia nigronervosa*). In this case the ants play a role in the transmission of the bunchy-top virus (BTV) disease in banana plants. In Indonesia the disease is one of the three most important diseases of banana, though in Sumatra it has only been found in Lampung. The aphid pierces the diseased plant and sucks the virus-containing sap for 1–2 h: it then transmits the viruses to a healthy banana plant at a later feeding. The aphid remains capable of transmitting the virus for about 13 days. The ants are surface dwellers (epigeic) involved in a symbiotic relationship with the aphids, which live at, and feed on, the base of the plant. The ants protect the aphid from predators (seraphic flies, coccinellids, chrysopids) and in return the aphids produce honeydew, a sweet tasting, nutritious substance harvested by the ants. More ants mean more aphids, and more aphids result in more damage to the plantation.

Table B16.3. Populations of the pestiferous armyworm (*Spodoptera litura*) and the predatory fire ant (*Solenopsis* sp.), and soybean yield in Seputih Mataram-Central Lampung, 1997 (Waraspati, 1997).

Variables	Time (weeks)	Without exclusion of ants	With exclusion of ants
Spodoptera litura (armyworm) population (individuals/hill)	3	46.3 a	177.5 b
	4	19.8 a	120.8 b
	5	1.3 a	17.3 b
Solenopsis sp. (ant) population (individuals/pitfall trap)*	3	9.8 a	16.8 a
	4	9.3 a	7.5 a
	5	18.8 a	6.8 a
Grain yields (g of soybean seeds/plant)	17.2 a	11.0 b	

*Pit diameter = 13.5 cm; average values in the same row followed by the same letters are not significantly different at $P < 0.05$.

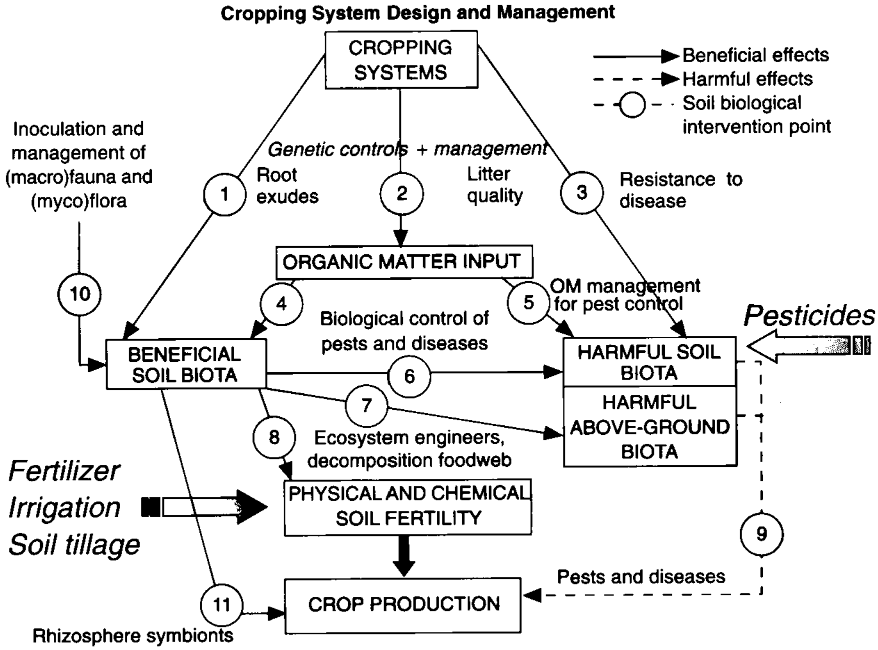

Fig. 16.8. The potential entry points for biological management of beneficial and pest soil organisms, cropping systems, organic matter (OM) inputs and soil fertility, affecting crop production. Adapted from Bekunda (2000) and Swift (1999).

Box 16.5. Restoring soil fertility and enhancing productivity in tea plantations through the use of earthworms and organic fertilizers: a case study from Tamil Nadu, India (Senapati *et al.*, 2002).

Between the 1950s and the 1980s, tea production in India increased from 1000 to 1800 kg/ha/year, whilst leguminous shade trees disappeared from the tea plantations. This was the result of fertilizer and pesticide use and a shift towards new cultivars that grow better in full sunlight. Currently, national yields have stagnated as decades of intensive cultivation have left soil fertility greatly depleted. On some tea plantations, not even the use of external inputs and plant growth hormones has overcome 100 or more years of intensive exploitation.

Soil degradation on tea plantations is seen in the following: (i) the loss of soil biota (losses can be as high as 70%); (ii) a decrease in organic matter content; (iii) acidification (pH levels can be as low as 3.8); (iv) a decrease in cation exchange capacity; (v) aluminium toxicity; (vi) reduced water retention; (vii) soil compaction; (viii) soil erosion; (ix) nutrient leaching; and (x) the accumulation of toxins (polyphenols) from tea leaves.

In an effort to restore soil fertility and improve tea production using organic matter and earthworms, researchers worked in close collaboration with plantation managers to develop alternative management practices based on locally available organic resources. Tea prunings, high-quality organic matter, and vermicultured earthworms were applied in trenches between tea rows, in order to evaluate the effects had on tea yields. Improvements in the structural and biological properties of soils were expected to produce higher tea yields – and tea yields at one of the estates did indeed increase by a factor of 2.4 in the first year, whilst profits rose by a factor of 3. Trenching is an old practice, and has been mostly abandoned on plantations because it involves high human labour costs. However, researchers in this study thought that trenches would minimize soil loss and improve moisture and aeration conditions, so enhancing nutrient-cycling processes. Lower responses at the other plantations were due to site-specific conditions, including delays in soil recovery that were proportional to the degree of soil degradation.

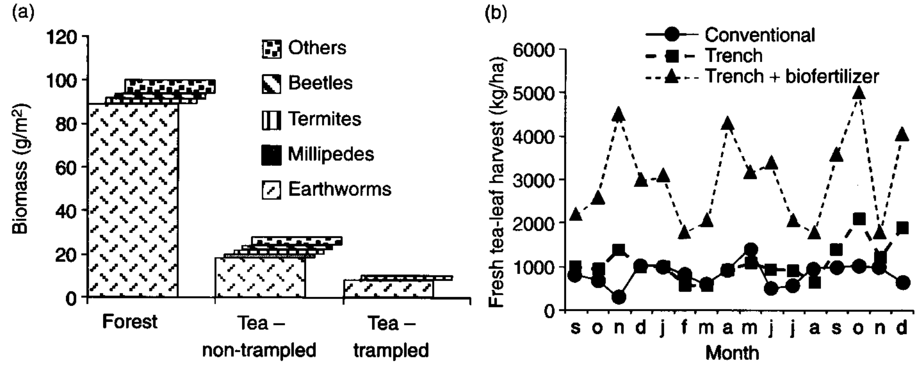

Fig. B16.2. (a) Biomass of main groups of soil biota in forests and tea gardens in Tamil Nadu, India. (Redrawn from Senapati *et al.*, 1994.) (b) Effects on harvested tea-leaf yields (fresh weight, kg/ha) of two soil amelioration treatments that involved deep trenches with or without a (patented) biofertilizer formulation, which included cultured earthworms. Conventional = no amelioration treatment (Senapati *et al.*, 1999; Lavelle *et al.*, 1998).

Conclusions

1. Initial changes in below-ground biodiversity, caused by changes in land-use practices, are less pronounced than those above ground. However, as the dispersal abilities of many soil organisms are more limited than those of organisms above ground, these changes may be less reversible.
2. Soil organisms play important roles in agroecosystems by maintaining and restoring soil structure, modifying pest and disease pressures and securing decomposition and nutrient cycles; specific information on the relevance of diversity within 'functional groups' is still scarce.
3. The 'food-web' and 'energy pyramid' concepts offer a basic understanding of the abundance of various trophic layers, related to the total amount of organic inputs, and may help to quantify system stability and resilience.
4. The scope for managing specific soil biota is limited to the (re-)introduction of species and to the use of specific chemicals. Overall the provision of regular, substantial and diverse organic inputs may be the simplest way to maintain below-ground biodiversity in agroecosystems.

Future research needs

1. How biodiversity at the 'functional group' level varies with land-use practices should be systematically evaluated, as should the biodiversity of specific target groups at the levels of taxonomic and/or genetic diversity. Such an evaluation should span as wide a range of land uses as possible, including natural, degraded and intensively used lands.
2. In order to better understand the function of soil biodiversity in agroecosystems, new models should be developed. These should include soil, litter-layer and above-ground dynamics, a water balance, nutrient and carbon cycles, and pest and disease relationships.
3. In order to refine our understanding and improve our models of the food web, the essential biology and life history of the various groups involved should be further investigated. Such investigations should include dispersal, feeding preferences, longevity, seasonality, and energy-use efficiency.
4. Research undertaken to address a specific challenge to an agroecosystem (e.g. research linked to the control of pests and diseases) may have to balance the prospects of managing specific soil biota with the opportunity of maintaining the 'below-ground zoo' by feeding it.