

CHAPTER ONE

Developing new perspectives from advances in soil biodiversity research

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SUMMARY

1. We use a historical context to examine the accomplishments of soil biodiversity and ecosystem research. These accomplishments provide a framework for future research, for enhancing and driving ecological theory, and for incorporating knowledge into sustainable management of soils and ecosystems.
2. A soil ecologist's view of the world differs from that of a terrestrial ecologist who focuses research primarily on above-ground organisms. We offer 'ten tenets of soil ecology' that illustrate the perspectives of a soil ecologist.
3. Challenges for the future are many and never has research in soil ecology been more exciting or more relevant. We highlight our view of 'challenges in soil ecology', in the hope of intensifying interactions among ecologists and other scientists, and stimulating the integration of soils research into the science of terrestrial ecology.
4. We conclude with the vision that healthy soils are the basis of global sustainability. As scientists, we cannot achieve our future goals of ecological sustainability without placing emphasis on the role of soil in terrestrial ecology.

Introduction

Despite the visionary appeals of an earlier generation of soil scientists, soil biologists and others (Jacks & Whyte 1939; Hyams 1952), above-ground ecologists have hitherto shown insufficient awareness of the significance and fragility of soils and the need to understand how life in soils relates to sustaining our global environment. However, many scientists, including microbial ecologists, atmospheric scientists, biogeochemists and agronomists, as well as economists and policy makers, are now starting to take heed of the multiple issues involving

soils and their biota, on both local and global scales. Phenomena that affect global sustainability via their impact on soil biota include wind and water erosion, pollution, the use of genetically engineered plants and microorganisms, invasive species, atmospheric deposition, land use change, and changes in soil structure. Such changes have rippling effects on the hydrologic cycle, loss of carbon and loss of fertile soils for cropping as well as societal needs. These issues pinpoint how little scientists knew about the relationship between soil biodiversity and ecosystem functioning, and whether scientists could, based on rigorous experiments, predict how future changes might impact human interactions with soil and their biota.

Papers throughout this volume summarise many of the recent results and how these might apply to future sustainability of soils, their biota and both ecosystem functions and processes. The advances and research priorities that they highlight need to be evaluated against short- and long-term needs for determining solutions to environmental problems. Recent data together with the immediacy of environmental changes that affect soil and soil biota create a mandate for

- assessing the present state of knowledge,
- developing and recording new challenges, and
- prioritising a new research agenda.

Past successes in research are the platform for new inquiry and preparation for future challenges. When combined with discussions and a synthesis and assessment of how the world works below-ground, they can serve to forge new ecological theories and directions. Future challenges for soil biodiversity and soil ecology research are a part of the broader global sustainability agenda that involves all academic disciplines and policy makers. Communication beyond the scientific community to the public, managers and government agencies about options for maintenance of soils and soil biodiversity must contribute to increasing public awareness of their dependence on soils. Such communication will highlight society's important role in decisions on sustaining soils for the functioning of the Earth's biosphere.

The definition of biodiversity we use here comes from the 1992 Convention on Biodiversity (CBD), the 'variability among living organisms, within species, between species, and of ecosystems'. Since the term was first coined (Takacs 1996), and as the global loss of biodiversity has escalated, there has been a dramatic increase in research on soil biodiversity. The literature survey by Morris *et al.* (2002) showed a ten-fold increase in publications from about 1985 to 2000 on such subjects as the rhizosphere, microbial habitats in soil and microbe-plant systems such as mycorrhiza. International conferences on mycorrhiza and soil ecology now routinely attract gatherings of around 500 scientists, which demonstrates the interest in this field. Inherent in research discussions is the additional consideration of the role of soil biodiversity in ecosystem functioning across temporal and spatial scales.

Soil ecology is the study of soil organisms and their interactions with their environment, and should therefore encompass the study of soil biodiversity in the broadest sense. We examine how a history of scientific accomplishments in soil biodiversity will contribute to new ecological perspectives and to global sustainability. Using past and present developments in soil biodiversity and soil ecological research as a foundation, we offer a list of 'ten tenets of soil ecology' and conclude with a discussion of our perspectives on six 'challenges in soil ecology'.

A brief history of advancements in soil biodiversity research

Many (Usher *et al.* 1979; Fitter 1985; Usher 1985; Wardle 2002) have proposed that a better understanding of soil ecology would present new ecological theories. As outlined by these authors and others (Coleman 1985; Coleman & Crossley 1996; Giller 1996), it is clear that above-ground ecological theories dominate present concepts in soil ecology. This is partially because we approach ecological questions based on differences in education and disciplinary training and from familiarity with the habitats and organisms we study. Rapid technical advances in molecular biology have enhanced research in all fields of soil biodiversity, and have transformed the study of microbial ecology both above and below-ground (Tiedje & Stein 1999; Tiedje *et al.* 2001). In some cases, soil biodiversity and microbial ecology are practised by scientists with little training in soils or ecology, using very different techniques and asking very different questions. Scientists trained in soil biodiversity gain a perspective that depends on an integrative, holistic and systems approach. For example, consider the question that permeates recent ecological research: does species diversity affect ecosystem functioning? Above-ground ecologists design experiments with many plants (species, traits, functional groups), across large spatial scales, and consider soil as a medium of physical and chemical properties needed for plant growth. They measure ecosystem process rates with rare consideration of soil biodiversity (Naeem *et al.* 1994, 2000; Tilman *et al.* 1997a, b). Soil ecologists, in contrast, must design field experiments with attention to both larger (m^2) scales for above-ground parameters and smaller (mm, cm) scales for soil organisms, and accordingly reduce the number of plant species to quantify effects on soil biodiversity (Bradford *et al.* 2002). This latter approach is integrated above and below-ground, but has a flip side: soil microbes and soil invertebrates are so abundant that researchers are limited to studying one or a few biotic groups at the species level. Identifying invertebrates to species level is labour intensive, often demanding molecular technologies. In short, above- and below-ground ecologists approach questions differently, and much less is known about below-ground biodiversity compared to that above-ground. Soil species have been minor players in past ecological studies due to the greater number of above-ground ecologists, the charismatic nature of many above-ground animals and plants, as well as human consumption and use of primarily plant shoots, leaves, flowers and other products.

Soil ecology, biodiversity and microbial process analyses have contributed and will continue to contribute to general ecological concepts and analysis of ecosystem functioning (Virginia & Wall 2000; Wardle 2002). Developments from numerous disciplines comprising soil ecology are crucial for studies of soils in managed ecosystems. The evolution of progress in soil biodiversity and ecosystem functioning has raised awareness in the terrestrial ecological community, as a whole, of the importance of inserting the interactions of soil organisms and ecosystem processes in what has traditionally been 'above-ground' ecology (Wardle 2002). The diversity and abundance of species (however defined) and operational taxonomic units (OTUs) in soil may be greater than the number above-ground (Virginia & Wall 2000; Wardle 2002). Thus, the inclusion of soil biodiversity in ecological research, as we include above-ground biodiversity, is critical if we are to manage soils as a renewable natural resource and in an environmentally sustainable manner.

The period 1900 to 1950 may be described as the era of 'soil biodiversity natural history' (Fig. 1.1). Soil ecologists compared extraction and culture techniques to enable quantification of major groups of organisms including soil invertebrates. However, in soil microbiology, ecology was regarded as a second-order problem, a view that is now being challenged. Fenchel (2003) credits Beijerinck with the ubiquitously quoted and (in retrospect) pernicious statement that any bacterial species can be found wherever its environmental needs are met ('the environment selects . . .'). The era was dominated largely by systematics and agriculture (soil science, plant pathogens). Quantification of soil pest and pathogen population dynamics, and establishing and modelling thresholds for plant damage, were integral to management of plant disease and increasing crop yields.

In natural, less-managed systems, experts continued to explore and measure the abundance and taxonomic diversity of groups of microbes and invertebrates. They documented geographic origin and dispersal mechanisms of pathogen species as a basis for plant quarantine regulations. During the early 1900s, general ecological theories were proposed and tested, based on larger above-ground and aquatic biota. For example, there were advances in plant and animal ecology in understanding the ecosystem (Tansley 1935; Clements 1936; see also Worster 1994), plant species community associations (Gleason 1926) and niche theory (Grinnell 1917; Elton 1927; Gause 1934). Soil ecology also was developing in Scandinavia (Bornebusch 1930) and elsewhere, and investigations in soil microbial ecology showed a succession of fungi occurring on various types of organic resources (Waksman 1932). Experiments on individual species, their food sources, microbial-faunal interactions and predator-prey relationships established the basis for soil food web research (Hunt *et al.* 1987; Killham 1994).

Field experiments with both radioactive and stable tracers in the 1950s to 1970s measured the processes involved in soil organic matter dynamics, nitrogen

Influences on research in soil biodiversity

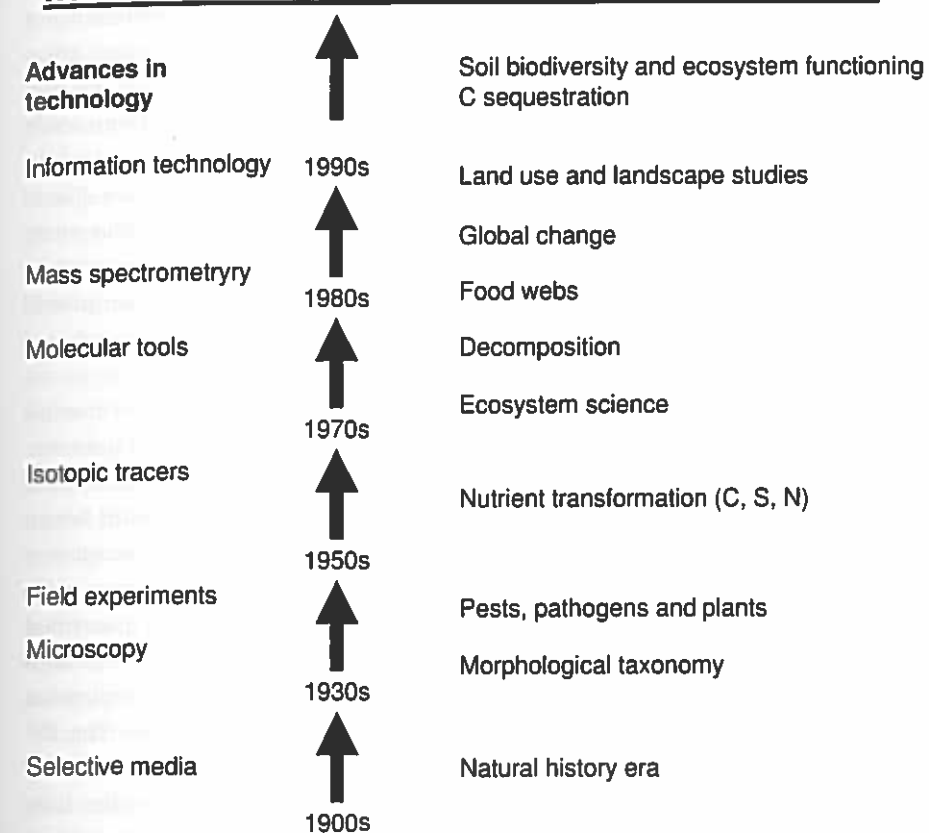


Figure 1.1. A brief history of recent accomplishments in soil biodiversity research.

mineralisation, nitrification, denitrification and nitrogen fixation, as well as the transformations and availability of sulphur and phosphorus. This period also saw the advent of chromatographic and other instrumental measurements, which were often associated with the use of metabolic inhibitors or the use of alternative substrates such as specific antibiotics, acetylene reduction and acetylene inhibition, to measure the same soil processes (Paul & Clark 1996). Selective media were often employed to determine the soil biota associated with these processes.

The late 1960s to mid 1970s saw the development of ecosystem science and further development of the concept of species diversity or 'biodiversity'. Investigations on species diversity accelerated after Hutchinson's (1959) article, asking 'why are there so many kinds of animals?' and, in the soil, Wallwork's (1976) *The Distribution and Diversity of Soil Fauna*. Some ecosystem highlights included Odum's (1969) ecosystem article, Swift *et al.*'s (1979) *Decomposition in Terrestrial Ecosystems*, and van Dyne's (1969) edited volume, *The Ecosystem Concept in Natural*

Resource Management. The International Biological Programme (IBP) marked the first occasion in which biologists throughout the world worked together for a common cause. The IBP microbial ecologists began to consider biomass, turnover and growth rates, and developed many new methods to establish the role of microbes in ecosystem processes. Extensive IBP publications (van Dyne 1969; Heal & French 1974; Stewart 1976; Breymeyer & van Dyne 1980) resulted in a wealth of scientific information still useful today for global analyses. These ecosystem-science studies stimulated scientists (ecologists, modellers and meteorologists) to consider the diversity of life through grouping of 'similar taxa', or functional groups, both above and below-ground. They also resulted in quantifying biotic processes in the common currencies of ecosystem science, energy flow and nutrient cycling.

Agricultural ecosystems were less emphasised by ecologists, but experimental manipulations flourished in the laboratory and field using biocides and soil management to reduce the activities of specific soil groups and measure the effect on decomposition rates or net primary productivity. These investigations began to establish the importance of functional groups of soil organisms on ecosystem functions and processes (Anderson 1975, 1978; Coleman 1976; Coleman *et al.* 1983). Petersen and Luxton's (1982) IBP synthesis paper compared and quantified the contribution of faunal groups in carbon budgets across biomes; although most soil fauna seemed relatively unimportant contributors to soil respiration compared to microbes, there were differences with taxa and biomes. The IBP was an extensive global network and a radical departure from traditional soil and above-ground ecology. In many ways, it set the stage for future studies linking soil organisms and ecosystem processes. The Swedish ecosystem project on arable land (Andrén *et al.* 1988), which synthesised the role of soil fauna and microorganisms in carbon and nitrogen cycling, is an example of a later initiative, as is Fox and MacDonald's (2003) project for soil biodiversity in Canadian agroecosystems.

There was increasing awareness that mycorrhizae and rhizobia played key roles in nutrient (phosphorus, nitrogen) transfer, a concept that had major implications for plant root competition and plant community development in managed ecosystems. The attention to the detritus food web and organic matter transformation became a major driver for soil ecology and ecosystem research during the 1970s. Today it is used as a foundation for understanding soil organic matter dynamics and nutrient availability in no-till agricultural systems (Groffman *et al.* 1986; Hendrix *et al.* 1986; Hunt *et al.* 1987; Frey *et al.* 1999). Research on soil biodiversity as a direct linkage to plants, e.g. the rhizosphere-soil food web, had less emphasis. These important research contributions from numerous ecosystems were major steps towards integrating soil research and extending awareness of soil food webs to ecology and ecosystem

science. Today's publications (Wardle 2002; Fox & MacDonald 2003) synthesising soil biodiversity in several ecosystems continue this successful approach.

Since the 1980s, research in soil ecology has exploded as a result of collective, individual and international scientific efforts, affirming the urgency of soil biodiversity research. Local concerns became global as we tackled issues such as the number of species on Earth (May 1988), the increased rate of species loss, changes in land use, environmental indicators, invasive species and atmospheric change. The Convention on Biological Diversity, Montreal Treaty, Kyoto Protocol and Desertification Treaty all had aspects that resulted in more attention to soil biodiversity and ecosystem processes. For example, global models were missing data on the allocation of carbon to plant roots and soils under elevated atmospheric CO₂ concentration. This fostered additional research on soil food webs.

A major question dominating ecology has been the role of biodiversity in ecosystem functioning. Results from a final Scientific Committee on Problems in the Environment (SCOPE) workshop (Schulze & Mooney 1994) recommended a synthesis of the relationship of biodiversity in soils and sediments to critical ecosystem processes. This led to another SCOPE committee which produced many synthetic papers that identified new areas of research (Wall Freckman *et al.* 1997; Groffman & Bohlen 1999; Adams & Wall 2000; Hooper *et al.* 2000; Bardgett *et al.* 2001; Wall *et al.* 2001b, c).

Experimentally, scientists asked how they could rigorously determine if species richness in soils directly affects the rate of an ecosystem process, given the large abundance and largely unknown diversity of soil microbes and invertebrates. To address this, a meeting was held in 1994 at the UK's Natural History Museum with disciplinary representatives from ecosystem science, ecology, systematics and soil science (Freckman 1994). The varying views resulted in a collective agreement on research priorities that became a basis for the UK's NERC Soil Biodiversity and Ecosystem Functioning (Soil Biodiversity) Programme (<http://mwnta.nmw.ac.uk/soilbio/index.html>), and, in the USA, a National Science Foundation US/UK collaborative soil biodiversity and ecosystem functioning grant (http://www.nrel.colostate.edu/projects/soil/us_uk/index.html). Major experimental networks were also leading and contributing to this focus in soils, including the Tropical Soil Biology and Fertility Program, the Macro Faunal Network, the Global Litter Invertebrate Decomposition Experiment, and the Long Term Ecological Research network (Symstad *et al.* 2003). Additionally, the European Union and European Science Foundation funded cross-EU experiments targeting, or including, soil biodiversity such as CLUE (Changing Land Use Experiment). These and other research projects in soil ecology are evolving to integrate soil biodiversity and ecosystem processes into research topics such as above-ground/below-ground coupling, multi-trophic interactions, biogeography,

soil carbon sequestration, land abandonment, invasive species and atmospheric change.

In general, most experiments on biodiversity and ecosystem functioning have been resolved for a group of soil organisms at the functional level or lower taxonomic resolution. It is widely accepted by ecologists that earthworms and termites are ecosystem 'engineers' (Lavelle & Spain 2001) and that microfauna such as mites, nematodes and protozoa affect rates of mineralisation (Coleman *et al.* 1983; Coleman 1985; Ingham *et al.* 1985). We know that groups of organisms, and in some cases species below-ground, can influence plant community composition and contribute to succession of plants (Read 1991; van der Heijden *et al.* 1998; de Deyn *et al.* 2003). We also have learned that disturbances, such as land fragmentation and agricultural intensification, decrease species diversity of earthworms with resulting changes in soil porosity and soil structure (Hooper *et al.* 2000; Bignell *et al.* in press; Giller *et al.* this volume). Evidence at the species level in microcosms and field experiments shows that there is considerable redundancy in soil species; this suggests little effect on rates of general decomposition processes with loss of soil species (Hunt & Wall 2002). As long as there is a functional group available to perform a particular role in a given ecosystem function, it may not matter whether there are many or few species within the functional group (see Setälä *et al.* this volume). However, there are situations where the abundance of a particular species can have a disproportionate impact on a process, such as with invasive species. The earthworm species *Aporrectodea tuberculata* and *Lumbricus terrestris* (which are two of only 45 introduced earthworm species in North America) homogenise upper soil horizons and increase erosion and runoff (Burtelow *et al.* 1998; Groffman & Bohlen 1999; Hendrix & Bohlen 2002). The nematode species *Bursaphelenchus xylophilus*, introduced from North America to Japan and Portugal (Mota *et al.* 1999), kills pine trees in plantations and forests within a couple of months (Mamiya 1983; Rutherford *et al.* 1990). These situations indicate that key species may sometimes strongly affect a range of soil-based ecosystem processes, including decomposition pathways, carbon and nitrogen cycling, hydrologic pathways and the maintenance of soil structure.

The multiple activities and experiments that have contributed to the present state of knowledge mark a new era of research in soil ecology. That is a recognition by ecologists and other disciplines that soil biodiversity at any taxonomic level is worthy of study for its own sake and as a major component of ecological and ecosystem research. There is a new fascination from terrestrial, atmospheric, aquatic and marine ecologists about these mostly unknown soil organisms and how they interact in ecosystems, where they are, whether general principles exist for below-ground microbes and fauna, and if these generalities might extend to microbes and invertebrate fauna elsewhere. Soils and their processes are a natural meeting place for fostering interdisciplinary studies, and it

is interdisciplinary studies that are going to be the key in solving environmental problems. Soil biodiversity, global changes and both nutrient transformations and movement, involve ecologists, agronomists, foresters, biogeochemists, biochemists, pedologists and geologists. Interdisciplinary studies tie together many terrestrial and aquatic processes, and are an excellent way of integrating otherwise difficult to integrate scientific disciplines. Thus, identifying general below-ground ecological principles from interdisciplinary research holds promise for broadening our understanding of ecosystems.

Ten tenets of soil ecology

Based on advances in soil biodiversity research over the past decades, we offer a short, unprioritised list that highlights the perspectives soil ecologists have when studying terrestrial ecosystems. These are the supporting groundwork for the 'challenges in soil ecology', which we discuss later.

1. *The terrestrial world is brown and black, not green.* Soils are brown to red and humus black. Despite our perception of the world as driven by photosynthesis, virtually all net primary production ends up as soil organic matter and, because of its relatively long residence time, soils contain twice as much carbon as vegetation (Schimel 1995). Consequently, more ecology occurs below than above-ground.
2. *The world seems primarily microscopic.* In soils, microbes and most groups of invertebrates (as adults or juveniles) are microscopic, or even at times at the electron microscope level, complicating studies of phylogeny, population and community ecology (Wilson 2002). However, some clones can be immense: fungal mycelia may be the largest organisms on Earth. Research is yet to determine whether ecological theory for larger organisms will apply to microbes (fungi and bacteria). However, microscopic is not a synonym for prokaryotic. Although life and all vitally associated processes could probably continue (as it did for two billion years) in the absence of vascular plants and vertebrate animals (Nabonne 2003), and despite Knoll's (2003) assertion that 'eukaryotic food webs form a crown - intricate and unnecessary - atop ecosystems maintained primarily by prokaryotic metabolism', modern ecosystems depend on a much broader range of organisms, still principally microscopic, but, in the case of several key groups (fungi, nematodes, arthropods), eukaryotic.
3. *We do not know their names or what they do.* Estimates indicate that less than 5% of species or less than 1% of operational taxonomic units (OTUs) in soils are described. One estimate based on DNA similarity was that there were 10^4 bacterial species per gram of soil (Torsvik *et al.* 1990). Hawksworth (2001) and Hawksworth and Rossman (1997) estimate 1.5×10^6 fungal species globally. Although molecular approaches enable the recognition of extreme

diversity in many soil-inhabiting taxa, we are only beginning to connect identity to function and consequently know little about what each species does. Today, using microarrays, we can determine hundreds of thousands of an organism's genes, but have only vague ideas of what most of the genes do. Similarly, we may discover millions of species in soils, but have little idea of what each does. Thus, field soil biodiversity experiments are rarely at the species level, even for invertebrates (Brussaard *et al.* 1997; Hooper *et al.* 2000). There are no soils where all species/OTUs of microbes or even all invertebrates have been described or quantified. Studies of natural history to determine food source and functional role are based on relatively few examples.

4. *Food webs do not follow traditional rules.* Omnivores are prevalent in soils (Moore *et al.* 1988; Moore & de Ruiter 1997). Many fungi are generalists and their extensive mycelial structure means that they may operate on a different spatial scale than their predators. Extreme environments may have no predators and few invertebrate species (Wall & Virginia 1999; Stevens & Hogg 2002). For example, in Antarctic Dry Valley soils, Stevens and Hogg (2002) noted only one mite species, *Stereotydeus mollis* (family Penthalodidae – not the predaceous mite family Tydeidae) and one Collembolan, *Gomphiocephalus hodgsoni*. Wall Freckman and Virginia (1998) found only one species of a nematode, *Eudorylaimus antarcticus*, capable of being a predator (Freckman & Virginia 1989). However, there is no evidence that these three species, which rarely co-occur, are predators (Fitzsimmons 1971; Block 1985; Davidson & Broady 1996; Sinclair & Sjursen 2001; Sjursen & Sinclair 2002). Soil food webs, unlike above-ground food webs, include a strong element of recycling within the decomposer component. For example, no-till agriculture favours a fungal-dominated food web on the soil surface (Beare *et al.* 1992; Frey *et al.* 1999), which leads to increased aggregation of soil particles, increased decomposition rates but overall greater soil carbon storage.
5. *Indirect effects can dominate, and are hard to quantify.* An individual species may have an identifiable effect on function in the field and laboratory, but the species richness in soils results in multiple species interactions that are indirect and difficult to measure. Facilitative interactions between species may be important to a process, but experiments are few. Thus, our knowledge of whether two, three or a succession of species are important in an ecosystem function is largely unknown. Based on a number of experiments to determine direct relationships between a single soil species and an ecosystem process, most species appear to be interchangeable (Setälä *et al.* this volume).
6. *Scale is a dividing issue between above- and below-ground ecology.* Spatial and temporal scales of most organisms above and below-ground are not in synchrony. The small spatial heterogeneity in soil allows for multiple complex

habitats and diversity. For example, the rhizosphere scale (mm to cm) can have extremely large diversity compared to the same scale above-ground. Consider the major differences in biodiversity and a process (nitrogen transformation) occurring vertically, from 0 to 30 cm soil depth and compare them to the same differences above-ground. The magnitude of change in a process is similar to that from a forest floor to a tree canopy. In soil, the species composition of the rhizosphere can differ from that of bulk soil organic matter a few centimetres away (Blackwood & Paul 2003). Organisms vary in their ability to cross scales (e.g. roots may spread for tens of metres; mycorrhizal fungi operate at the millimetre to metre scale between plants, whereas nematode species may move only a few centimetres, and some bacteria will be limited to spaces within aggregate microhabitats). Soil biota (fungi, invertebrates, vertebrates and roots) connects these otherwise isolated habitats through movement, mycelial structure and process reactions. Soils are also less temporally dynamic than above-ground systems, being buffered somewhat in nutrient dynamics from sudden change and human impact. Symptoms of damage to soils and their biota may take longer to observe than damage above-ground, and may be irreversible even before being identified (Amundson *et al.* 2003).

7. *Soil legacy imprints soil biodiversity (and can override plant effects).* Soils take hundreds to thousands of years to form, and their structure and biodiversity in an ecosystem today reflects past geologic, climatic and vegetative history. Soil horizons change slowly over time until disturbed. Soil organic matter, even at only 50 cm depth in the field, can be 1400 years older than that at the surface (Paul *et al.* 2001). Yet, when brought into the laboratory it decomposes at the same rate as that from the surface (Collins *et al.* 2000). The age and amount of carbon held in soils is greater than above-ground, and as it becomes available, provides an energy base for biodiversity, above and below-ground. This evolution of physical and chemical patterning over eons, as well as consequences of biological evolution, produces many characteristic and complex biotic habitats within and across ecosystems, and may have a greater impact on patterning of soil biodiversity than plants in some ecosystems (Virginia & Wall 1999; Kaufmann 2001; Williamson & Harrison 2002).
8. *Soils and their biota are not isolated in terrestrial ecosystems: they have multiple landscape connections.* Soils and biota are often separately examined, yet there are many important soil interactions including the mediation of plant productivity by soil-dwelling animals (Warnock *et al.* 1982; Masters *et al.* 1993). Soils are linked physically and biologically to sediments of freshwater, estuaries and marine systems (Wall Freckman *et al.* 1997; Wall *et al.* 2001c), and the atmosphere. They also are an intermediary habitat for above-ground animals. For example, the mountain plover (*Charadrius montanus*) nests in

bare soil of the US shortgrass prairie, but due to decreasing habitat, began nesting in agricultural soils where spring ploughing contributed to loss of nests and its decline (Knopf & Rupert 1999; US Fish and Wildlife Service 1999). A species of amphibian, *Oscacilia ochrocephala* (a Caecilian), moves to 10 m depth in tropical soils (Wake 1983, 1993), and various soil invertebrates, as juveniles and adults, serve as food for above-ground vertebrates. Soils and biota are subjected to fluctuations and inputs from erosion and flooding, which change the biotic interactions. The lateral connections of biodiversity from soils to sediments in aquatic systems are studied less than in clearly defined ecosystems (e.g. soils vs. aquatic systems) but are often interdependent (Polis *et al.* 1997). Detrital food webs and process controls are similar in soils and sediments, as are major taxonomic groups, but species differ.

9. *Small creatures have biogeography too.* Our knowledge of latitudinal and landscape patterns of soil biodiversity is sketchy (Bardgett *et al.* this volume). Most process studies are conducted on relatively flat land in northern temperate ecosystems with very little information from the large part of our Earth that is hilly or tropical. We know little about how diversity and processes differ at depth (Jackson *et al.* 2002) because the majority of reports on soil species diversity and processes are from within the top 30 cm of the soil profile (Schenk & Jackson 2002) where, globally, 50% of root biomass occurs. However, many roots occur below 1 m (Schenk & Jackson 2002) and diversity and biological processes occur wherever conditions and energy can support life, which, in aquifers and buried deposits, is often well below the rooting layer.
10. *Decomposition is one of the two major life-generating processes.* Decomposition pairs with photosynthesis to maintain the function of ecosystems and the balance of the atmosphere. It differs from photosynthesis in the enormous diversity of organisms involved. As a tenet of soil ecology, we believe it is important to emphasise that one process does not dominate: these two processes must be considered of parallel importance for research in soil ecology and the consideration of our sustainable future. A small fraction of photosynthetic products and biotic degradation products is protected from decomposition in soil, and this forms the core of soil organic matter.

Challenges in soil ecology

Recent advances in technologies that can be applied to studying soil biota have been exceptionally rapid, and they will accelerate. We are virtually unlimited in the types of questions we can ask and the hypotheses we can test. Our confidence in extending findings from many taxonomic groups at higher resolution

will be tested at multiple scales. However, we have to take advantage of many developments occurring now. For example, model organisms (e.g. the nematode *Caenorhabditis elegans*) might extend our knowledge, in soil, of bacterial-feeding nematode physiological ecology (survival rates, life stages, periodicity, mechanisms) and life history (life cycle length, death), as well as the effects of agronomic management and sustainable agriculture. Availability of annotated gene sequences for soil organisms or their close relatives will enable investigations of links between diversity and function. Use of stable isotopes to track carbon and nitrogen transformations is revolutionising our ideas of nutrient sources through species and food webs (Johnson *et al.* 2002; Manefield *et al.* 2002; Radajewski *et al.* 2002). Multiple technologies, and concurrent use of technologies (e.g. NMR and chemical fractionation techniques), will open new frontiers for soil biodiversity. Global research networks such as the Below-ground Biodiversity (BGBD) Network (Tropical Soil Biology and Fertility (TSBF) Institute of the International Center for Tropical Agriculture (CIAT); see Giller *et al.* this volume) magnify our understanding of sustainable soil management.

While the issue of scale, both temporal and spatial, will continue to be an overriding challenge, in the following list of six questions we have not highlighted it, nor have we highlighted technologies such as global positioning system (GPS) and remote sensing. These challenges are not unique to soil ecology, and overlap with many issues, questions and priorities listed elsewhere (Cracraft 2002). We see the following as challenges that will radically change our view of life in soils and how soils are intertwined with the Earth system.

What are the organisms?

Species as we once knew them, even for invertebrates, no longer really exist. We are now dealing with a new 'tree of life'. 'What is a species?' is considered by Cracraft (2002) as one of the seven great questions for systematic biology, and is integral to many experiments we do. The species concept has been continually evolving and many of the recently tested ecological hypotheses and resulting conclusions are based on concepts of a species, derived from studies of organisms in which reproduction is normally sexual and individuals are easily defined (Cohan 2002). We must have an idea of our organism or OTU if we are to accept the soil as a living habitat and if we are to propose hypotheses at broader scales. How will we test what is considered 'a defined species' above-ground (e.g. plants and large vertebrates and invertebrates) when for 'soil species' (e.g. invertebrates, protozoa and microbes) we have OTUs or even different resolution of DNA sequence data? This uncertainty about the nature of ecological and evolutionary units in soil ecosystems has profound operational consequences. Simply quantifying biodiversity in soil (how many species and how abundant are they?) is challenging.

Building on that quantification, we need to be able to link diversity – now typically measured by some attribute of DNA sequence variation – with function. Yet most of the organisms appear to be unculturable, so that without new and imaginative experimental protocols, technologies such as stable isotope probing (Radajewski *et al.* 2002) and accelerator mass spectrometry (Staddon *et al.* 2003b), we will not be able to say which organisms perform which processes. A further problem in addressing soil biodiversity and ecosystem functioning at the species level is the difficulty of experimentally teasing apart the massive number of species interactions that occur in soil.

Where are they?

There is a missing field of study in soil ecology: biogeography (Bardgett *et al.* this volume). We do not know what geographical patterns of soil biodiversity exist. Can we predict where most soil organisms will be found? Are there endemic species and hot spots of diversity that are related to ecosystem functions at different scales (Usher this volume)? Are these based on soil physical and chemical coupling, climate, geology or plant characteristics? Can such knowledge be used to predict soil fertility and ecosystem productivity in a changing, anthropogenically stressed environment? The words of Whitaker *et al.* (2003), on bacteria in an isolated hot spring, challenge the original model of Beijerinck (see Fenchel 2003) in which unrestricted dispersal constrains species richness. C. B. Blackwood (personal communication), using DNA analysis and multi-variate spatial statistics, showed significant differences in types of bacteria at the scale of 1 mg to 1 g of soil. Another break occurred at 10^3 to 10^5 g of soil where spatial organisation was hypothesised to be controlled by plant type and density.

What do the organisms do?

It has become unfashionable (and unfindable) simply to study an organism to discover how it operates in the wild (although funding sometimes is available to do the same for a gene). Consequently, we extrapolate understanding of functional groups in an ecosystem process based on life histories and physiologies of a few hopefully representative species and sites. Using stable isotopes to track sources of carbon and nitrogen in species of enchytraeids previously placed within the same feeding group indicates problems with lumping together species of similar morphology (Cole *et al.* 2002). Somehow, we need to compile more information on more taxa to determine generalities (for example, what are the food sources and who eats what?) if we are to build predictive models of many soil taxa and processes. How does periodicity in feeding affect transfer of nutrients? What aspects of physiological ecology make organisms in the same location either vulnerable or successful? Under what conditions does a facultative organism become a pathogen? How do multiple species interact? How

do multiple element interactions change through the soil food web? And, how do multiple species affect root architecture, rooting depth, plant community succession and feedbacks to organic matter dynamics? How do rhizosphere and root symbionts and parasites affect nutrient and carbon flux when interacting with species of detrital food webs? Can we extend knowledge of interactions (facultative, competitive) horizontally across soils and sediments, and vertically to above-surface processes?

What are commonalities in survival and dispersal mechanisms at the species level that occur under different environmental stresses? How do multiple species and microbes respond to simple changes in soil moisture? We know different organisms enter a survival state under water stress at different moisture potentials. We also know that in soils a large proportion of soil organisms are in the resting state (Paul & Clark 1996). When do the organisms become active? The resting nature of much of the microbiota represented by isolated DNA makes it difficult to interpret activity and process studies based on DNA analysis of gene frequency and abundance. This problem of a comprehensive lack of natural history of our organisms is acute for the generally uncharismatic soil biota. For birds, mammals, plants and many insects, there is a great wealth of enthusiastic amateurs, often extremely knowledgeable, whose commitment to the gathering of information can be put to productive use. Who will do the same for collembola, nematodes, ascomycetes or archaea?

Do soil species matter in ecosystem processes?

One of the most frequently recurring questions in soil ecology is whether there is a link between biodiversity and the way in which an ecosystem operates. A first problem is how to pose this question in an interesting and yet experimentally tractable form. The UK Soil Biodiversity Programme focused on carbon fluxes within soil as a measure of ecosystem function. With stable isotopes, these can now be quantified in the field (e.g. Johnson *et al.* 2002; Staddon *et al.* 2003a), but we still have only the crudest techniques for manipulating biodiversity. As part of the programme, Bradford *et al.* (2002) recreated a field system in a controlled environment and varied maximum body size of the soil fauna – the most remarkable result was how robust the system was to such a major perturbation.

In most soils, there is a surprising balance between carbon inputs and losses. This is one reason why soils take so long to form. We have little idea as to why this should be, nor the extent to which soil organic matter and soil biodiversity are related. The accumulation of organic carbon in soil is closely linked to nitrogen dynamics. In soils of high carbon : nitrogen ratio, partially decomposed organic matter tends to accumulate because the decomposers are limited by substrate quality, pH and oxygen. This accumulation, however, locks up potentially huge amounts of nitrogen, exacerbating the problem. Similar relationships must exist with phosphorous and probably other elements.

How will soil species respond to a changing world?

How predictable are species changes? Can we use evolutionary and geologic history to predict the impact of future changes on soil communities, and on their survival or dispersal? Soils are the geologic legacy that produced heterogeneity in soil biodiversity. Soil parent material and climate contributed to individual habitats (and species that evolved in those habitats). Recent estimates indicate 4.5% of US soil series are in danger of serious loss or extinction (Amundson *et al.* 2003). We need to examine how soils and geologic history of plant-animal-microbe associations have or have not imprinted today's soil communities. Additionally, we know little about the environmental ranges of soil biota so we cannot easily predict how it will respond to change. Above-ground ecologists and soil systematists have long recognised the power of preserved specimens to provide clarification of geographic patterns and local diversity patterns. Many are now aggressively intensifying analyses of museum collection data with GIS, climate data and overlying major groups of plants and animals in a region. These museum collections provide a phylogenetic context that allows systematists to place past ecological and natural history collections in a historical and global framework and broaden the database to predict how species distributions will react in the future. These and ongoing global experiments when synthesised provide modellers with the ability to answer questions such as what happens to ecosystem functions when soil warms, or how effectively can soil microbes disperse (Finlay 2002).

Should we care?

While the first five questions have relevance to global environmental problems, there must also be a targeted research effort, and an effort to extend and communicate our findings, and to make them relevant to society as a whole. Management of soil biota and its functions is critical for carbon sequestration, for agriculture, for forestry and for watersheds. In the past 50 years we have advanced considerably in indirect management of decomposers and soil engineers (termites, earthworms), and in direct management of symbionts and pathogens/pests (the latter while reducing pesticide use, such as methyl bromide; Swift & Anderson 1994; Giller *et al.* this volume). The molecular revolution may offer the opportunity to influence the soil community through genetic manipulation of the plant, by altering the biochemical signals sent out to the soil. Society, at least in some countries outside Europe, is starting to accept the introduction of genetically engineered plants (or genetically modified organisms, GMOs), but not GM microorganisms. Yet one of the most widely used GMO plants, incorporating resistance to insects with Bt, which is derived from soil bacteria. Its effects on soil invertebrates and the soil food web are only beginning to be known (Stotzky & Bollag 1992; Hopkins & Gregorich 2003). There is

great need for compiling and synthesising the overlapping data from soils, climate and soil biodiversity to use in a predictable manner for problems such as desertification and abandoned land (and other land use changes).

How comfortable are we at extending the evidence we have now gathered towards pressing global problems? Can we extend our knowledge to explain, for example, how we manage soil ecologically to decrease plant, animal and human disease in the light of global change? Our knowledge of soil organisms as vectors or pathogens under varying environmental or soil conditions is, at present, scattered (Jamieson 1988; Hendrix & Bohlen 2002).

Ecosystem services are now an accepted part of our socio-economic system. These include a broad variety of functions from soil and water decontamination, prevention of the spread of plant and animal diseases, and responses to stresses such as global and climatic change to visual landscape diversity (Wall *et al.* 2001a). The soil biota is an integral part in all the above. For example, can associated mycorrhiza move rapidly enough to allow whole forests to adapt to changing temperatures? Will society be more willing to pay for desirable habitats and landscapes?

Conclusions

The question arises, how can we possibly tackle all these challenges? It can be done. The British Ecological Society (BES) conference in 2003 on Soil Biodiversity and Ecosystem Functioning was one of the largest conferences held by the BES. Repercussions of this meeting are multiple and very promising. Delegates of all disciplines were energised with recent experimental progress, and with their cutting edge technologies, and are ready to work towards meeting these challenges and to test and develop below-ground theory.

There are several ways to proceed. These include terrestrial ecology institutes that integrate all aspects of soil ecology from organism to global models and cross disciplines (e.g. the Tropical Soil Biology and Fertility Institute of the International Center for Tropical Agriculture, http://www.ciat.cgiar.org/tsbf_institute/index.tsbf.htm). Others include integrated international experimental networks focused on long-term or short-term projects, such as the Integrated Tundra Experimental Network, ITEX (Marion *et al.* 1997; Welker *et al.* 1997); Global Litter Decomposition Experiment, GLIDE, <http://www.nrel.colostate.edu/projects/glide/index.html>; the EU project, Conservation of Soil Biodiversity under Global Change, CONSIDER, <http://www.nioo.knaw.nl/CTE/MTI/Index.htm>; and International Long Term Ecological Research, ILTER, <http://www.ilternet.edu>.

Biodiversity research needs by definition to be extended in time. Will long-term, well-organised global research sites and networks, such as agricultural and forest experimental stations (e.g. Fluxnet and Precipnet), highlight soil

biodiversity and help to synthesise the vastly different disciplines needed to manage soils? Projects need to emphasise informatics and utilise statistical analysis to synthesise information hidden in taxonomic collections and relate it to soil characteristics. There are many ongoing efforts to link scientists and managers; an example is the FAO Portal on Soil Biodiversity (<http://www.fao.org/landandwater/agll/soilbiod/activity.stm>), which also has links to soil biodiversity projects. It is perhaps time to link knowledge on soil biodiversity, from these various disciplines and networks in natural and managed ecosystems, into a global soil assessment that could provide information useful for the future management and sustainability of soils. A synthesis of the ecosystem goods and services provided by the functioning of soils and soil biodiversity, and an evaluation of their vulnerability under future scenarios for global change (land use, atmospheric, climatic and biotic), are both critically needed, but must involve all disciplines involved in soil research as well as economists and social scientists.

There is now a great international interest in the subject of soil sustainability. The International Technical Workshop on Biological Management of Soil Ecosystems for Sustainable Agriculture (Embrapa 2002) states 'Sustainable agriculture including forestry involves the successful management of agricultural resources to satisfy human needs while maintaining or enhancing environmental quality and conserving natural resources for future generations'. The effective management of crop species, soil fertility, soil physical factors and water availability as well as pests and diseases are all involved in soil sustainability. Soil biodiversity and biological processes are both impacted by the above and in turn have major roles to play in understanding and management of the processes involved. The general indicators of soil sustainability involve soil structure maintained by the interaction of physical and biotic forces, soil organic matter levels and soil biotic populations as well as a healthy, economically successful crop. We hope that the tenets of soil biodiversity and the challenges in this field can be used to enhance our understanding further, and even future improvement, of the sustainability of soils. The present melding of the various fields of soil science with ecosystem ecology and soil biodiversity research, the great advances in molecular biology and the close relationship of soil biodiversity research to present programmes in global change carbon scenarios, as well as in organic agriculture, make us believe there is great hope for the future.

This chapter echoes May's (1997) statement that implicitly emphasises the need for research in soil biodiversity, 'A full understanding of the causes and consequences of biological diversity, in all its richness, probably cannot be had until the contribution made by decomposers to the structure and functioning of ecosystems is fully understood'. The urgency to provide information and concepts that can be a general theory for soil biodiversity, and contribute to sustainability of ecosystems at local, regional and global levels, is a goal for all of us.

Acknowledgements

The authors thank Byron Adams, Emma Broos, Johnson Nkem, Mike Swift, two anonymous referees and the editors for their critical and helpful comments. D. Wall acknowledges Holley Zadeh, Lily Huddleson and US National Science Foundation Grants, DEB 98 06437 and OPP #9810219.

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