PART I

Introduction

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

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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

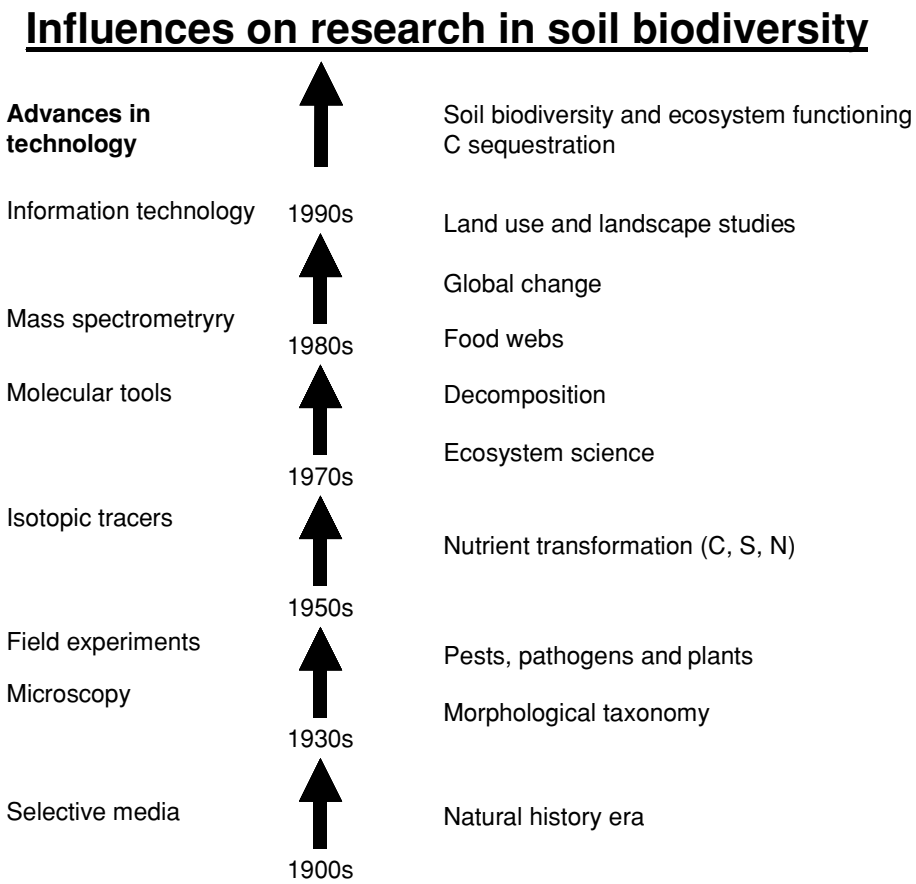

Figure 1.1. A brief history of recent accomplishments in soil biodiversity research.

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 CO_2 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