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ESSAY REVIEW

Biodiversity and ecosystem function in soil

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Summary

1. Soils are one of the last great frontiers for biodiversity research and are home to an extraordinary range of microbial and animal groups. Biological activities in soils drive many of the key ecosystem processes that govern the global system, especially in the cycling of elements such as carbon, nitrogen and phosphorus.

2. We cannot currently make firm statements about the scale of biodiversity in soils, or about the roles played by soil organisms in the transformations of organic materials that underlie those cycles. The recent UK Soil Biodiversity Programme (SBP) has brought a unique concentration of researchers to bear on a single soil in Scotland, and has generated a large amount of data concerning biodiversity, carbon flux and resilience in the soil ecosystem.

3. One of the key discoveries of the SBP was the extreme diversity of small organisms: researchers in the programme identified over 100 species of bacteria, 350 protozoa, 140 nematodes and 24 distinct types of arbuscular mycorrhizal fungi. Statistical analysis of these results suggests a much greater 'hidden diversity'. In contrast, there was no unusual richness in other organisms, such as higher fungi, mites, collembola and annelids.

4. Stable-isotope (^{13}C) technology was used to measure carbon fluxes and map the path of carbon through the food web. A novel finding was the rapidity with which carbon moves through the soil biota, revealing an extraordinarily dynamic soil ecosystem.

5. The combination of taxonomic diversity and rapid carbon flux makes the soil ecosystem highly resistant to perturbation through either changing soil structure or removing selected groups of organisms.

Key-words: bacteria, ^{13}C, carbon flux, fungi, models, resilience, soil fauna, Sourhope

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Introduction

Establishing the linkage between ecosystem function and ecosystem biodiversity is a substantial scientific challenge. Nowhere is this challenge greater than in soils. Fundamental processes within the carbon and nitrogen cycles occur in soils. The precise role of many soil organisms in these cycles is unknown, although the great diversity and abundance of microbial, plant and animal life in soil seems likely to influence ecosystem function in various ways. There have been several reports of remarkable microbial diversity (Torsvik, Goksoyr & Daae 1990; Tiedje *et al*. 1999; Torsvik, Ovreas & Thingstad 2002). Although no-one has ever counted all the microbial species in a natural soil, estimates suggest anything up to 10^4 bacterial species per g soil, of which at least half (and perhaps as many as 95%) are as yet unculturable (Sait, Hugenholtz & Janssen 2002; Joseph *et al*. 2003). An understanding of the linkages between soil biodiversity and the processes of C and N cycling is essential given the potential impact of both natural events and human activity on soil communities, but experiments are rarely performed in a context where their significance to ecosystem-level processes can be reliably inferred.

This review reports key ecological findings from a major research programme, Soil Biodiversity and Ecosystem Function (aka the Soil Biodiversity Programme or SBP), funded by the UK Natural Environment Research Council. The SBP had the specific aim of combining both traditional and molecular approaches to the

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Box 1. Novel technologies to probe soil biodiversity and function

The biggest hurdle encountered by researchers in soil biodiversity is that most of the organisms are not identifiable by conventional morphological taxonomy. Prokaryotes and many fungi (especially the symbiotic fungi that form arbuscular mycorrhizas with plant roots) are largely unculturable, and so could be identified morphologically only from structures that can be recovered from field samples. Typically these are inadequate for any useful taxonomy. Even where organisms are large enough to be extracted intact from soil, as is true of most animals, morphology may be a poor guide to genetic differentiation. Molecular techniques are therefore essential.

Estimating the diversity of microbial taxa in a sample can be achieved by extracting the DNA, cutting it with one or more restriction enzymes and separating out the fragments on an electrophoresis gel. A range of such techniques was used in the SBP, such as denaturing gradient gel electrophoresis (Kowalchuk, Gerards & Woldendorp 1997) and terminal restriction fragment-length polymorphism (Liu *et al*. 1997).

Identifying the taxa relies ultimately on sequencing DNA after amplifying it using PCR. Selecting an appropriate gene for sequencing is critical: it must be sufficiently conserved to be consistent within a species, but offer enough variation to be a useful discriminator among species. Often ribosomal genes are used. However, most sequences that are discovered within environmental samples come from unknown organisms, so 'identification' often means no more than giving a sequence a unique identifier and making some statement about its phylogenetic relationships.

Identifying the organisms is only half the story: we also need to know which ones are acquiring and metabolizing soil resources. The stable-isotope technology we used relies on distinguishing the heavy ^{13}C atoms from background ^{12}C using mass spectrometry. Bulk samples or individual organisms or parts of them can be analysed to reveal the pathway of C movement. At Sourhope this approach was facilitated by the development of a mobile laboratory, designed by Professor Phil Ineson (University of York), that can control the supply of an air stream containing pure $^{13}CO_2$ at ambient concentration along 18 gas lines simultaneously, enabling different patches of vegetation to fix the ^{13}C pulse: 99·9 at % ^{13}C-labelled CO_2 was provided to vegetation at ambient concentrations (355 μmol mol^{-1}; Ostle *et al*. 2000).

The novel ^{13}C techniques developed in the SBP involved measuring the ^{13}C content of specific molecules. Stable-isotope probing builds on the classic Meselson & Stahl (1958) experiment, and relies on separating the DNA (or RNA) from a sample along a density gradient and then amplifying the separated bands to identify the organisms that have become labelled (Radajewski *et al*. 2000). It is a powerful technique for measuring the activity of unculturable microbes. By starting with RNA, and including a reverse transcription step, an even more precise focus on metabolic activity can be achieved, as RNA is much more labile than DNA (Ostle *et al*. 2003). If the organisms are larger and can be separated from soil visually, then there is no need for stable-isotope probing, and compound-specific infrared mass spectrometry can be used to measure the ^{13}C content of specific compounds (so avoiding the danger that, for example, gut contents rather than the animal's tissues are measured). This approach has been pioneered by Professor Richard Evershed of the Organic Geochemistry Unit, University of Bristol.

analysis of diversity (Box 1) with novel experimental investigations of the C cycling activities of different types of soil organism. The SBP ran from 1997 to 2004; its unique feature was that £5·85 million of research funds were all expended on a single site, a rather dull hectare of grassland at Sourhope (Box 2) in the Scottish Borders. Choosing a single site for 27 distinct but related research projects allowed an unprecedented insight into the workings of a soil ecosystem. Choosing a biologically unexceptional site which does not display especially great richness in plant diversity means that explanations for diversity in the soil cannot fall back on the argument that the below-ground community is driven by that above ground.

By undertaking all the experimental activity on one site, a single experimental design could be used and the results from many related projects integrated into one model. The scope for collaboration and cross-fertilization between separate projects was also improved using this strategy. The Sourhope site is part of the UK Environmental Change Network, and is also the most thoroughly studied site in the MicroNet programme funded by the Scottish Executive. The site studies were complemented by laboratory-scale investigations using the Ecotron facility at the Centre for Population Biology, Imperial College, London, in which a simplified grassland ecosystem was recreated with defined faunal communities differentiated on body size.

To achieve the SBP's objective, the ecosystem at Sourhope was perturbed by removing taxa using a biocide or by artificially manipulating their population numbers, and by subjecting plots to various treatments representative of anthropogenic inputs and designed to affect biodiversity. Thirty plots, each 12×20 m, were laid out and five treatments applied: a factorial of limestone and N addition, with an extra control and a biocide treatment. These treatments were intended to alter both diversity and function and allow investigators to look for correlated changes. Then the research teams were let loose: between them they studied a remarkable range of taxa, processes and treatments (Box 2).

The SBP did not aim to compile an all-taxa biodiversity inventory (e.g. www.dlia.org/atbi/index.html) – that would have been a massive task, and probably unachievable at a time when systematic concepts for many soil organisms remain so fluid.

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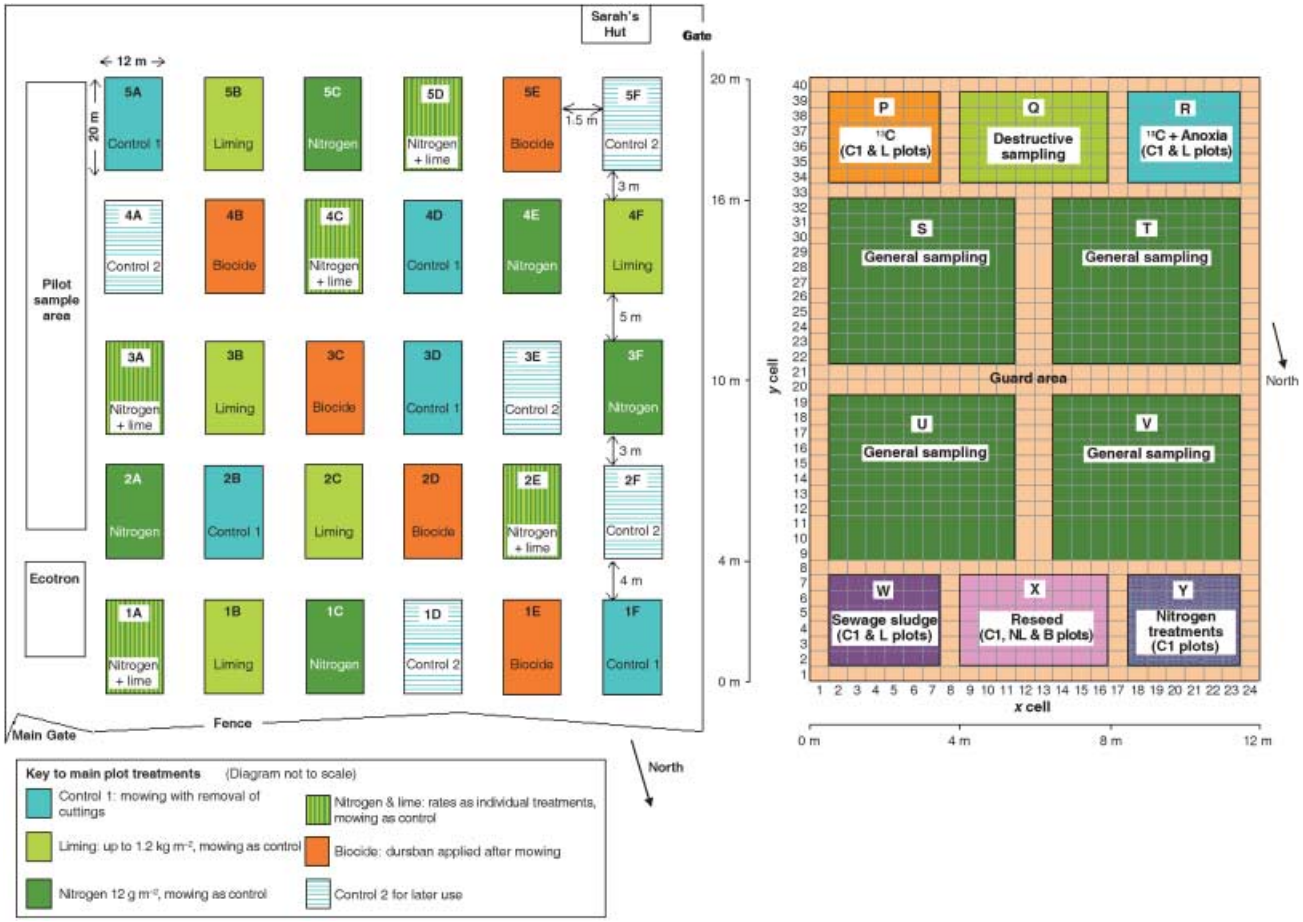
Box 2. The Sourhope experiment

The field site at Sourhope (grid reference NT855197), an experimental farm managed by the Macaulay Land Use Research Institute, Aberdeen, UK, was ≈1 ha of semi-improved grassland 320 m above sea level (see www.soilbio.nerc.ac.uk). The main plant species were common grasses of upland Britain such as *Agrostis capillaris*, *Festuca rubra* and *Poa pratensis*; dicots were relatively scarce. At the start of the experiment the site was fenced and sheep grazing was replaced by regular mowing. Although this change of management indubitably affected the vegetation and hence the soil communities, it was an essential logistical step: many of the experiments would have been impossible had sheep roamed freely across the site.

The experimental design comprised 30 plots, each 12 × 20 m, and each subdivided into 10 subplots, four of which (5 × 5 m) were used as nested plots within each main plot; the other six (3 × 3 m) were for special treatments (see figure). The main plots received one of five treatments:

1,2 two controls
3 limestone added at 600 g m^{-2} annually in spring
4 nitrogen added at 12 g m^{-2} twice a year
5 both limestone and N
6 biocide (Dursban), added at 0·15 ml m^{-2} five times a year.

Each subplot was divided into 0·25 m^2 grid squares, and all sampling activity was recorded to that resolution so that a complete record of all the programme activities is available in space and time. The experiment is being maintained for at least another 3 years, and other experimenters are welcome to make use of what is now one of the best known plots of soil in the world.



Box 2 Fig. 1. Design of the Sourhope field experiment. There were five treatments (the controls were duplicated) and five blocks. The major treatments were a factorial of N and lime additions, intended to shift productivity and hence diversity of the system. Each plot was subdivided into a series of subplots; the four main subplots were intended for the main sampling activities, and the smaller subplots for specialized activities that needed to be segregated from the main sampling programme. Each sampling act was precisely located on a 50 × 50 cm scale grid, and full details were recorded. All data are deposited in the Soil Biodiversity data archive (www.soilbio.nerc.ac.uk).

Diversity of small things is very great

Bacterial diversity had already been determined by the research group of Professor Jim Prosser (University of Aberdeen), at a site a few hundred metres away from that used in the SBP. They identified around 100 species, but statistical estimation of diversity from these data suggests that there may be between 500 and 5000 species of bacteria at Sourhope (McCaig, Glover & Prosser 2001; Curtis, Sloan & Scannell 2002), perhaps unsurprisingly if other estimates that soils harbour 10^3–10^4 bacterial species g^{-1} are correct (Torsvik *et al*. 2002). Importantly, the SBP has shown that this richness is mirrored at Sourhope in other taxa. The team led by Dr Bland Finlay (Centre for Ecology and Hydrology) recorded 365 species of protozoa, representing one-third of the global total of non-marine species (Finlay & Fenchel 2001). That proportion is high, but similar values for protozoa have been recorded previously at other sites (Finlay *et al*. 2001). However, those identifications were morphological, raising the question of whether each morphospecies comprises several genetically distinct groups. The latter explanation may well apply to nematodes: the group led by Dr Mark Blaxter's group (University of Edinburgh) examined 3500 individual nematodes and found that they represented ≈140 species defined using molecular, not morphological, criteria (Floyd *et al*. 2002). Where it was possible to compare the two approaches there was a good match, except that morphology, as expected, often failed to reveal the presence of genetically distinct taxa. Using a collector's curve approach, the estimate is that the Sourhope hectare is home to over 400 species of nematode. Those data compare with the richest site previously studied in the UK – Porton Down, a biologically diverse chalk grassland, with 125 nematode species; and to the richest site previously studied in the world – Mbalmayo forest, Cameroon, with 431 morphospecies (Bloemers *et al*. 1997).

A similar result, on a different scale, was found for the symbiotic fungi in the phylum Glomeromycota that form arbuscular mycorrhizas (AM). Only 150–200 morphospecies of these fungi have been described worldwide (Morton, Bentivenga & Bever 1995), yet the group led by Professor Peter Young (University of York) found 17 distinct molecular types in a few roots of a single plant species (white clover, *Trifolium repens*), and 24 when the grass *Agrostis capillaris* was also sampled (Vandenkoornhuyse *et al*. 2002). There were quite distinct communities of AM fungi in roots of these two species and of a second grass species, *Poa pratensis* (Vandenkoornhuyse *et al*. 2003). Even allowing for our uncertainty as to the relationship between sequence diversity and species diversity in this phylum (Pawlowska & Taylor 2004), it is pertinent to ask whether 10% of all AM fungal species can occur on a few roots of a single plant species at Sourhope; alternatively, is the diversity of these key symbionts much greater than we have allowed? In contrast to the Glomeromycota, the diversity of saprotrophic fungi (mainly Ascomycota and Basidiomycota) at Sourhope appeared low, with only 57 taxa (counted as genera) isolated from litter soil and basidiomes (C. H. Robinson and E. J. Pryce Miller, unpublished data). However, cryptic species may have been missed.

In contrast to the high diversity of these small organisms, there was no unusual richness in the larger soil species. Just 44 species of mites and collembola and 19 annelids (five earthworms and 14 enchytraeids) were discovered. Their low diversity does not make them ecologically unimportant: Professor Donald Davidson's group (University of Stirling) showed that 90% of the soil organic matter at Sourhope has been processed by annelids, and the upper horizons of the soil at Sourhope are largely composed of annelid excrement (Davidson *et al*. 2002). The disproportionately high diversity of small – but not the larger – organisms (Table 1) is unexplained and represents a new ecological challenge: it is likely that it reflects great unidentified global diversity in these small-organism taxa. This pattern could be related to the extreme heterogeneity of soils on all spatial scales, and the limited migration ability of most of these species, resulting in systems that are always far from equilibrium. This explanation is supported by data of Zhou *et al*. (2002), who found that saturated soils had fewer and more evenly distributed bacterial taxa than did well drained soils: in the latter, migration and dispersal through the soil's water-filled pores would be less effective.

A related question is whether the high diversity reflects the global distribution of microbial and other small-organism taxa, as postulated for protozoa (Finlay *et al*. 2001); in other words, do microbes have biogeography or are microbial species ubiquitous, with local communities selected by environmental preferences from a universal species pool? The latter view has been the dominant one in microbial ecology since

Table 1. Species diversity of some groups of organisms measured at the Sourhope site compared with UK and global diversity (where known)

Taxon	Global diversity	UK species total	Sourhope diversity	
			Measured	Estimated
Bacteria: Eubacteria	6000		~100	500–5000
Protozoa: non-marine taxa excluding Mycetozoa	1050		365	
Fungi: Glomeromycota	150		24*	
Fungi: other phyla		14773†	57‡	
Nematodes: soil spp.	3000	200	129–143	400–500
Insecta: Collembola	20000	300	12	
Arachnida: Acari	45000		32	
Annelida: Enchytraeidae	143	111§	14	
Annelida: Lumbricinae	1200	25	5	

Data sources for Sourhope as in text; others from Groombridge (1992) except where specified.
*, As phylotypes from two plant species only (Vandenkoornhuyse *et al*. 2002).
†, P.M. Kirk, personal communication.
‡, Counted as genera (C. Robinson and J. Pryce Miller, personal communication).
§, European total.

Beijerinck (Horner-Devine, Carney & Bohannon 2004; Wall, Paul & Fitter, 2005), but is increasingly challenged. Data on *Pseudomonas* from locations on four continents (Cho & Tiedje 2000), and from the archaean genus *Sulfolobus* from geographically distributed hot springs (Whittaker, Grogan & Taylor 2003), suggest that there are significant biogeographical patterns to be discovered, described and explained for microbes, as does the demonstration of taxon–area relationships for bacterial communities (Horner-Devine *et al*. 2004b). Parallel studies at other sites will be needed to reveal how general these results are.

Carbon flux is rapid

The SBP used stable-isotope technology (Staddon 2004) to measure the rates and routes of carbon movement through the soil food web. By allowing vegetation to photosynthesize in an atmosphere of $^{13}CO_2$ for a day, the appearance of that label could be traced in successive recipients within the food web: first to AM fungi, rhizosphere bacteria and root-feeding animals, then to predators of these, and ultimately to higher-level predators. A novel feature was the use of a mobile laboratory to ensure very high enrichment with the stable isotope ^{13}C, allowing the label to be applied at ambient CO_2 concentration: if excessive CO_2 concentrations had been used, for example by releasing CO_2 from carbonate within a sealed chamber, that would have altered C allocation between shoot and root (Suter *et al*. 2002) and biased the results.

The most striking finding from these experiments was the speed with which C moves into the soil biota. Laser ablation spectroscopy revealed that only 10% of the roots received ^{13}C after the pulse (Bruneau *et al*. 2002). This presumably reflected either high rates of root turnover, the presence of many dead or moribund roots, or possibly non-uniform transport of ^{13}C from labelled shoots to roots. In any case, over 70% of the labelled C was released from the plants as either respired CO_2 or exudates within 48 h (Ostle *et al*. 2000). Furthermore, a strong signal was observed in AM fungi within an hour of the end of the short pulse (Fig. 1; Johnson *et al*. 2002), and liming the soil increased the rate of transfer of ^{13}C to soil organisms (Staddon *et al*. 2003a). About 5–8% of the ^{13}C fixed by plants during the pulse went to mycorrhizal fungi and ≈2% to the bacteria (Ostle *et al*. 2003). There have been numerous attempts to quantify these transfers in laboratory conditions: the SBP data are the first to be obtained in the field, and demonstrate the importance of this fast pathway for C transfer in the cycle.

One major uncertainty is how long C stays in particular soil pools. Accelerator mass spectrometry (AMS) and natural ^{14}C tracing was applied in a novel manner to obtain the first measurements of C residence time in AM fungal hyphae (Staddon *et al*. 2003b). A pulse of CO_2 from a fossil source was used, which therefore contained no ^{14}C, and this created a recognizable signal

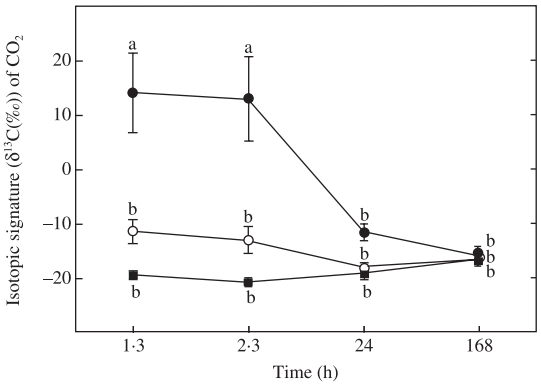


Fig. 1. Recovery of ^{13}C in CO_2 released by respiration from soil cores in the field at intervals after exposure of plants to $^{13}CO_2$. The isotopic signature ($\delta^{13}C(‰)$) of CO_2 is much greater in soil from cores into which mycorrhizal mycelium had been allowed to grow through a fine (20 μm) mesh (solid circles) than where the cores had been rotated (open circles), severing the mycelium and preventing the fungus entering the core. Solid triangles represent data from rotated cores in unlabelled plots (± SE). Points sharing a letter are not significantly different ($P > 0{\cdot}05$). From Johnson *et al*. (2002).

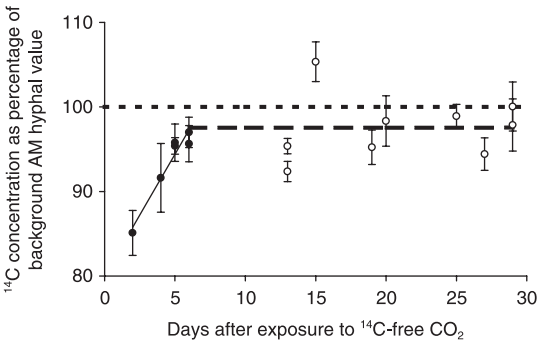


Fig. 2. The ^{14}C concentration of extraradical AM hyphae recovers to the natural background value within 5–6 days after plants are allowed to photosynthesize in an atmosphere of ^{14}C-free CO_2 at ambient concentration (350 μmol mol^{-1}), which reduces the background ^{14}C concentration in plant and fungal tissue. The intercept suggests that 15–20% of the AM mycelium was labelled, confirming the estimate of turnover rate (Staddon *et al*. 2003a).

in the fungal tissue. The rate at which the signal returned to background was then measured, as newly fixed C from atmospheric CO_2 was transferred to the fungi (Fig. 2). The extraordinary sensitivity of AMS means that these minute differences could be detected in samples of <100 μg hypha, and showed that the C turnover time was ≈5 days. This rapid turnover appears to be even faster than for bacteria: measurements of ^{13}C in bacterial RNA at Sourhope show a turnover time of about 11 days (Ostle *et al*. 2003).

These data reveal an exceptionally dynamic ecosystem in soil, and have large implications for the construction of global C cycle models. What remains to emerge from the data is identification of the pathway followed by the bulk of C in the food web. We know that some ^{13}C remains in root systems much longer than the

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rapidly moving component that goes to AM fungi and rhizosphere bacteria. Ultimately, earthworms and enchytraeids process around 90% of the root-derived C. Initially, this slower pool is picked up by saprotrophic fungi and root grazers, and from them goes to predators such as fungivorous collembola. Although earthworms typically accounted for >80% of faunal biomass, most (0·1%) of the ^{13}C label in the fauna was found in mites and collembola, even though they comprised only 3% of the biomass (P. Ineson, unpublished data). However, this figure is small compared with the ^{13}C in the microbial biomass, which peaked at 8% of the label fixed by plants. Nevertheless, it appears that whereas earthworms have a large indirect influence on soil biodiversity and C flux, mesofauna have a more important direct effect on C dynamics. ^{13}C labelling reveals the biological role of individual species. By measuring the $\delta^{13}C$ of cholesterol isolated from individual enchytraeid worms, these organisms, previously assumed to feed wholly on detritus, were shown to be feeding directly on material in the rhizosphere, and some species to a much greater extent than others (H. Black, unpublished data). These techniques therefore reveal new aspects of the fundamental biology of soil organisms.

The next step in understanding the role played by different soil organisms in the C cycle will be achieved using stable-isotope probing (Box 1). In theory, the paths of C to all the genetically distinguishable taxa in soil can be resolved. Several groups within the SBP are applying stable-isotope probing and are developing it to use mRNA rather than DNA (Manefield *et al*. 2002), as RNA is more labile and so likely to reveal the taxa that are actively metabolizing C *in situ*.

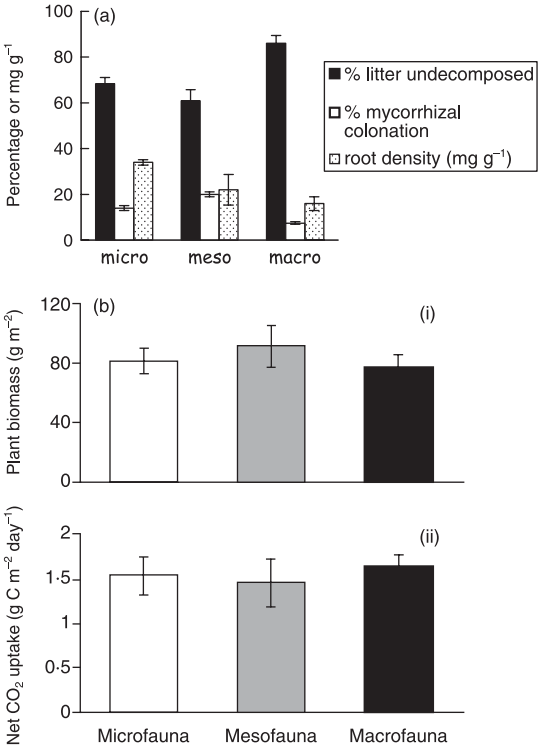


Fig. 3. (a) Effect of faunal treatment on three system variables in the reconstructed Sourhope ecosystems in the Ecotron at Imperial College, UK. Litter decomposition was measured in litter bags. The three treatments are microbes only (micro, <100 μm diameter); microbes plus mesofauna (meso; <2 mm); and these plus macrofauna (macro). Note that units vary for different variables on the *y* axis. (b) Aboveground net primary productivity (i) and net ecosystem productivity (ii) of communities exposed to the same increasing gradient of soil faunal complexity.

Does the diversity matter?

What is the impact of altering the structure and diversity of such a complex and dynamic ecosystem? This key question was tackled in three ways in the SBP, by:

1. exploring correlated changes in diversity and ecosystem processes in the treatments in the field;
2. reconstructing the ecosystem in a progressive manner in a controlled environment; and
3. modelling the system.

The treatments had the expected substantial impacts. Liming increased soil pH; raised plant productivity; and substantially altered the composition of many groups of soil biota, from bacteria through saprotrophic fungi to enchytraeid worms. However, liming had no detectable effect on the rate of soil respiration, suggesting that the system was resistant to perturbation (Gray *et al*. 2003). Similar results were obtained by imposing specific stresses on the system, including drought, heat and the application of sewage sludge (Griffiths *et al*. 2003).

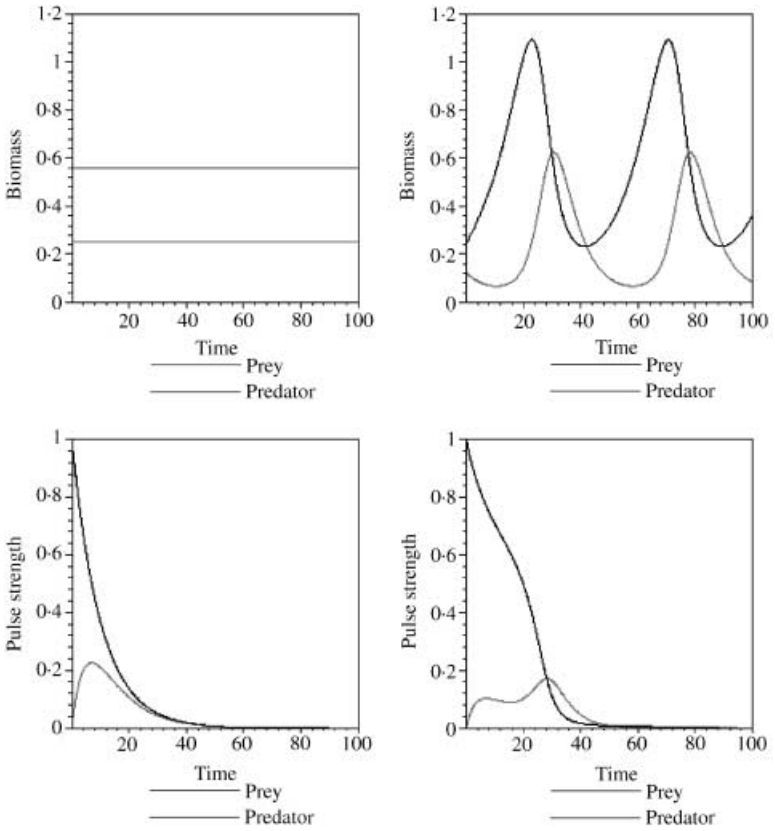
The most explicit test of the system's resilience came from a major reconstruction experiment. Soil was taken from the site and used to rebuild the community in the controlled environment of the Ecotron (Bradford *et al*. 2002). The distinct soil horizons were restored and then the biota added back, either as just the microbes (<100 μm diameter); or as the microbes plus the mesofauna (100 μm^{-2} mm); or both those with the macrofauna (>2 mm) as well. These very different communities exhibited large differences in parameters such as root growth, AM colonization and decomposition rate (Fig. 3a). The biggest differences were between the macrofauna treatment and the others, suggesting that predators such as beetle larvae feeding on the mesofauna are major controlling agents, even if the predators are neither especially abundant nor diverse in the system. For example, the extraradical mycelium of AM fungi was least well developed in the mesofauna treatment, probably because the fungivores could operate without predator restraint: this result mirrors the finding that AM fungal diversity was greater in the field plots that had received insecticide (Vandenkoornhuyse *et al*. 2003). Remarkably, however, despite these radical differences in the composition of the soil community, the reconstructed systems showed no differences in overall productivity or ecosystem C exchange rate, even after 9 months (Fig. 3b), suggesting that these systems are

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Box 3. Static models, dynamic ecosystems

The Hunt *et al*. (1987) model assumes constant biomass: inputs exactly balance outputs at all times in each compartment. This assumption is restrictive, and this figure illustrates a potential pitfall in its application. Identical models (from the static point of view) with identical parameters can produce radically different signals in pulse dynamics, driven simply by the timing of pulsing relative to the population dynamics.

When pulse data show a consistent pattern in timing and magnitude of peaks, we can infer that *either* the population dynamics are slow relative to the overall C flux, *or* the pulse was administered at a sufficiently large spatial scale to average out any local heterogeneities.



Box 3 Fig. 1. Simulated pulses in a Lotka–Volterra predator–prey system. Panels on the left show population dynamics (top) and pulse signal (bottom) for a situation where populations remain close to equilibrium. Panels on the right show the same model with identical parameters, but with initial conditions chosen to induce oscillatory dynamics. Note that, although the models are identical, the timing of the observed pulse peak in predators changes from <10 to >30 days.

extremely resilient, and perhaps that significant changes cannot be expected in short-term experiments.

Soil ecosystems are so complex that all experimental approaches to them pose major problems, of either realism (as in reconstruction experiments), or precision (as in the perturbations in the field). An alternative is to express the key features of the system in a model. This was achieved by adapting the well known and widely applied Hunt model (Hunt *et al*. 1987; Berg *et al*. 2001; Hunt & Wall 2002) to the Sourhope food web. That model is flexible, in that it can handle any number of compartments, and C can flow between them. A version of the model has been implemented that allows the fate of a ^{13}C pulse to be followed in any food web; it can be downloaded from www-users.york.ac.uk/~jwp5. Running the model with communities based on data from the Ecotron experiment reveals ^{13}C dynamics in, for example, the bacteria and AM fungi: these outputs can be used to generate testable hypotheses for experimenters to examine (L. Austin, unpublished data).

However, the Hunt *et al*. model has one feature that is obviously unrealistic: it assumes constant biomass. C flows through the model system because the top predator consumes a quantity of prey in a time interval, and those prey must consume an equal quantity (plus what they lose by respiration) to permit that predation. This effect then cascades through the web. However, soil ecosystems do not exhibit constant biomass in all compartments. Through a series of workshops that brought together soil biologists, mathematicians and modellers, the SBP developed dynamic versions of this static model: incorporation of Lotka–Volterra dynamics

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reveals that the size, duration and timing of the peaks in ^{13}C seen in a particular trophic group in the soil depends on the dynamics of the population (Box 3). This has serious implications for experimenters: in the simplest case of constant populations, the dynamics of a ^{13}C pulse are characterized by a single monotonic peak in ^{13}C in the target group. In such a case, relatively few samples would be sufficient to reveal the position and magnitude of the peak. However, the more complex signals implied by the dynamic model could not easily be resolved experimentally without an intensive sampling campaign. This is an area requiring careful exploration in planning future field experiments.

Conclusions

The Soil Biodiversity Programme is unique in the scale of the effort that has been expended on understanding a single patch of soil. It represents new thinking by ecologists about the importance of model systems. Microbiologists use *Escherichia coli*; developmental biologists use *Drosophila melanogaster* or *Arabidopsis thaliana*; ecologists have tended to use their own species or system. Consequently, we have always found it hard to synthesize data from different studies. The focus on Sourhope has revealed that there is extensive unexplored diversity across a range of microbial and small eukaryotic taxa, but not especially of large organisms. This diversity exists in a system deliberately chosen for its apparent biological dullness: it would be less surprising to find it in a known diversity hotspot, and what awaits us in soils in such places remains to be seen (Husband *et al*. 2002). Ecosystem processes in the Sourhope soil are also exceptionally dynamic, as shown by measurements of C flux. Again, the single-site focus enables us to compare fluxes across functional groups: the early steps in the C cycle appear to be much more rapid than we anticipated, and root-associated microbes (AM fungi and bacteria) play a key role in them. Later steps are, as we expected, much slower, and the biological roles of some soil taxa in them are beginning to reveal big surprises. However, one consequence of taxonomic richness appears to be substantial resilience in the face of external forces: soils appear able to retain function even when their biological structure has been radically altered. For how long they can do that, and how far we can push them, remain to be seen.

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References

Berg, M., De Ruiter, P., Didden, W., Jansen, M., Schouten, T. & Verhoef, H. (2001) Community food web, decomposition and nitrogen mineralization in a stratified Scots pine forest soil. *Oikos* **94**, 130–142.

Bloemers, G.F., Hodda, M., Lambshead, P.J.D., Lawton, J.H. & Wanless, F.R. (1997) The effects of forest disturbance on diversity of tropical soil nematodes. *Oecologia* **111**, 575–582.

Bradford, M.A., Jones, T.H., Bardgett, R.D. *et al.* (2002) Impacts of soil faunal community composition on model grassland ecosystems. *Science* **298**, 615–618.

Bruneau, P.M.C., Ostle, N., Davidson, D.A., Grieve, I.C. & Fallick, A.E. (2002) Determination of rhizosphere C-13 pulse signals in soil thin sections by laser ablation isotope ratio mass spectrometry. *Rapid Communications in Mass Spectrometry* **16**, 2190–2194.

Cho, J.C. & Tiedje, J.M. (2000) Biogeography and degree of endemicity of fluorescent *Pseudomonas* strains in soil. *Applied and Environmental Microbiology* **66**, 5448–5456.

Curtis, T.P., Sloan, W.T. & Scannell, J.W. (2002) Estimating prokaryotic diversity and its limits. *Proceedings of the National Academy of Sciences, USA* **99**, 10494–10499.

Davidson, D.A., Bruneau, P.M.C., Grieve, I.C. & Young, I.M. (2002) Impacts of fauna on an upland grassland soil as determined by micromorphological analysis. *Applied Soil Ecology* **20**, 133–143.

Finlay, B.J. & Fenchel, T. (2001) Protozoan community structure in a fractal soil environment. *Protist* **152**, 203–218.

Finlay, B.J., Esteban, G.F., Clarke, K.J. & Olmo, J.L. (2001) Biodiversity of terrestrial protozoa appears homogeneous across local and global spatial scales. *Protist* **152**, 355–366.

Floyd, R., Abebe, E., Pepert, A. & Blaxter, M. (2002) Molecular barcodes for soil nematode identification. *Molecular Ecology* **11**, 839–850.

Gray, N.D., Hastings, R.C., Sheppard, S.K *et al.* (2003) Effects of soil improvement treatments on bacterial community structure and soil processes in an upland grassland soil. *FEMS Microbiology Ecology* **46**, 11–22.

Griffiths, R.I., Whiteley, A.S., O'Donnell, A.G. & Bailey, M.J. (2003) Physiological and community responses of established grassland bacterial populations to water stress. *Applied and Environmental Microbiology* **69**, 6961–6968.

Groombridge, B. (1992) *Global Biodiversity*. Chapman & Hall, London.

Horner-Devine, M.C., Carney, K.M. & Bohannan, B.J.M. (2004a) An ecological perspective on bacterial biodiversity. *Proceedings of the Royal Society of London, Series B* **271**, 113–122.

Horner-Devine, M.C., Lage, M., Hughes, J.B. & Bohannan, B.J.M. (2004b) A taxa–area relationship for bacteria. *Nature* **432**, 750–753.

Hunt, H.W. & Wall, D.H. (2002) Modelling the effects of the loss of soil biodiversity on ecosystem function. *Global Change Biology* **8**, 33–50.

Hunt, H.W., Coleman, D.C., Ingham, E.R. *et al.* (1987) The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* **3**, 57–68.

Husband, R., Herre, E.A., Turner, S.L., Gallery, R. & Young, J.P.W. (2002) Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. *Molecular Ecology* **11**, 2669–2678.

Johnson, D., Leake, J.R., Ostle, N., Ineson, P. & Read, D.J. (2002) *In situ* (CO_2)-C^{13} pulse-labelling of upland grassland demonstrates a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. *New Phytologist* **153**, 327–334.

Joseph, S.J., Hugenholtz, P., Sangwan, P., Osborne, C.A. & Janssen, P.H. (2003) Laboratory cultivation of widespread

and previously uncultured soil bacteria. *Applied and Environmental Microbiology* **69**, 7210–7215.

Kowalchuk, G.A., Gerards, S. & Woldendorp, J.W. (1997) Detection and characterization of fungal infections of *Ammophila arenaria* (marram grass) roots by denaturing gradient gel electrophoresis of specifically amplified 18S rDNA. *Applied and Environmental Microbiology* **63** (10), 3858–3865.

Liu, W.T., Marsh, T.L., Cheng, H. & Forney, L.J. (1997) Characterization of microbial diversity by determining terminal restriction fragment length polymorphisms of genes encoding 16S rRNA. *Applied and Environmental Microbiology* **63** (11), 4516–4522.

Manefield, M., Whiteley, A.S., Griffiths, R.I. & Bailey, M.J. (2002) RNA stable isotope probing, a novel means of linking microbial community function to phylogeny. *Applied and Environmental Microbiology* **68**, 5367–5373.

McCaig, A., Glover, L.A. & Prosser, J.I. (2001) Numerical analysis of grassland bacterial community structure under different land management regimens by using 16S ribosomal DNA sequence data and denaturing gradient gel electrophoresis banding patterns. *Applied and Environmental Microbiology* **67**, 4554–4559.

Meselson, M. & Stahl, F.W. (1958) The replication of DNA. *Cold Spring Harbor Symposium in Quantitative Biology* **23**, 9–12.

Morton, J.B., Bentivenga, S.P. & Bever, J.D. (1995) Discovery, measurement, and interpretation of diversity in arbuscular endomycorrhizal fungi (Glomales, Zygomycetes). *Canadian Journal of Botany* **73**, S25–S32.

Ostle, N., Ineson, P., Benham, D. & Sleep, D. (2000) Carbon assimilation and turnover in grassland vegetation using an *in situ* (CO_2)-C-13 pulse labelling system. *Rapid Communications in Mass Spectrometry* **14**, 1345–1350.

Ostle, N., Whiteley, A.S., Bailey, M.J., Sleep, D., Ineson, P. & Manefield, M. (2003) Active microbial RNA turnover in a grassland soil estimated using a (CO_2)-C^{13} spike. *Soil Biology and Biochemistry* **35**, 877–885.

Pawlowska, T.E. & Taylor, J.W. (2004) Organization of genetic variation in individuals of arbuscular mycorrhizal fungi. *Nature* **427**, 733–737.

Radajewski, S., Ineson, P., Parekh, N.R. & Murrell, J.C. (2000) Stable-isotope probing as a tool in microbial ecology. *Nature* **403**, 646–649.

Sait, M., Hugenholtz, P. & Janssen, P.H. (2002) Cultivation of genetically distinct soil bacteria from phylogenetic lineages previously only detected in culture-independent surveys. *Environmental Microbiology* **4**, 654–666.

Staddon, P.L. (2004) Carbon isotopes in functional soil ecology. *Trends in Ecology and Evolution* **19**, 148–154.

Staddon, P.L., Ostle, N., Dawson, L.A. & Fitter, A.H. (2003a) The speed of soil carbon throughput in an upland soil is increased by liming. *Journal of Experimental Botany* **54**, 1461–1469.

Staddon, P.L., Ramsey, C.B., Ostle, N., Ineson, P. & Fitter, A.H. (2003b) Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of ^{14}C. *Science* **300**, 1138–1140.

Suter, D., Frehner, M., Fischer, B.U., Nosberger, J. & Luscher, A. (2002) Elevated CO_2 increases carbon allocation to the roots of *Lolium perenne* under free-air CO_2 enrichment but not in a controlled environment. *New Phytologist* **154**, 65–75.

Tiedje, J.M., Asuming-Brempong, S., Nusslein, K., Marsh, T.L. & Flynn, S.J. (1999) Opening the black box of soil microbial diversity. *Applied Soil Ecology* **13**, 109–122.

Torsvik, V., Goksoyr, J. & Daae, F.L. (1990) High diversity of DNA in soil bacteria. *Applied and Environmental Microbiology* **56**, 783–787.

Torsvik, V., Ovreas, L. & Thingstad, T.F. (2002) Prokaryotic diversity – magnitude, dynamics, and controlling factors. *Science* **296**, 1064–1066.

Vandenkoornhuyse, P., Husband, R., Daniell, T.J. *et al.* (2002) Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. *Molecular Ecology* **11**, 1555–1564.

Vandenkoornhuyse, P., Ridgway, K.P., Watson, I.J., Fitter, A.H. & Young, J.P.W. (2003) Co-existing grass species have distinctive arbuscular mycorrhizal communities. *Molecular Ecology* **12**, 3085–3095.

Wall, D., Paul, E.A. & Fitter, A.H. (2005) Developing new perspectives from advances in soil biodiversity research. *Soil Biodiversity and Function, 44th Symposium of the British Ecological Society* (eds R. Bardgett & M.B. Usher), pp. 000–000. Blackwell Scientific Publications, Oxford (in press).

Whitaker, R.J., Grogan, D.W. & Taylor, J.W. (2003) Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science* **301**, 976–978.

Zhou, J.Z., Xia, B.C., Treves, D.S. *et al.* (2002) Spatial and resource factors influencing high microbial diversity in soil. *Applied and Environmental Microbiology* **68**, 326–334.

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