

The abundance, richness and functional role of soil meso- and macrofauna in temperate grassland—A case study

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Received 16 June 2005; received in revised form 8 September 2005; accepted 2 November 2005

Abstract

This paper reviews the abundance and species richness, and factors that cause these parameters to vary, of mesofauna and macrofauna in an upland grassland soil studied intensively under the NERC Soil Biodiversity Programme. The concept that competitive exclusion does not act within soil communities is reviewed in light of these findings, which are placed in the context of the wider literature relating to earthworm, enchytraeid, collembolan and mite diversity, and factors that influence these, with particular reference to land management. The second half of the paper reviews laboratory and field ¹³C-tracer studies, carried out under the programme, that assess linkages between specific biota and ecosystem processes. The concept of functional redundancy in soil food webs is discussed in the context of these studies. We conclude that competitive interactions occur most widely amongst soil macrofauna, and that competitive exclusion amongst mesofauna is potentially limited by both fine-scale spatial heterogeneity and predation. The most profound impacts of soil fauna on soil properties at Sourhope appeared to be due to the presence of macrofauna in soil communities. There was also evidence for functional redundancy at the species level amongst soil biota, but this was dependent upon which ecosystem process was measured. We conclude that it is likely that functional redundancy at the species level occurs most widely in species rich faunal groups with generalist feeding behaviour.

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Keywords: Soil biodiversity; Fauna; Grassland; Competition; Functional redundancy

1. Introduction

The vast array of microbes and animals that live in soil constitute the decomposer food web, whose primary role in ecosystems is the cycling of organic matter derived from the above- and belowground, plant-

based food web (Bardgett, 2005). While processes of nutrient cycling are governed directly by microbes, such as bacteria and fungi, they are also affected by soil animals that live alongside them. Soil fauna affect decomposition processes both directly, through fragmentation and comminution of litter material, and indirectly by altering microbial function through grazing of the soil microbial biomass and through excretion of nutrient rich wastes (Petersen and Luxton, 1982; Cole and Bardgett, 2002). Further, the movement of animals through soil influences the dispersal of

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microbial propagules attached to the animal body surfaces or transiting through their guts (Visser, 1985). While all soil biota are involved in decomposition and nutrient mineralisation processes in soil, the mechanism by which they facilitate decomposition can be broadly correlated with their body size. It is generally believed that it is the larger, more mobile soil animals such as anecic earthworms that have the strongest direct effects on decomposition, by mixing litter into the soil profile, a form of ecosystem engineering (Jones et al., 1994). In contrast, the activity of smaller animals is more likely to arise as indirect impacts on soil microbial community structure and function through their selective grazing of the microbial biomass (Newell, 1984a,b; Klironomos and Kendrick, 1996).

There is currently much interest in understanding the factors that regulate the structure of soil faunal communities and the consequences of this for ecosystem function. We examine what was learnt about this from the NERC Soil Biodiversity Programme (SBP). A central objective of the Programme was to better understand the effects of a wide range of anthropogenic disturbances on soil biotic communities, such as agricultural intensification, and the deposition of nitrogenous pollutants, and the effects of the resultant depauperisation of the soil biota on ecosystem processes. The experiment was based at a single site, Sourhope, in southeast Scotland, which is described by Usher et al. (2006). We describe (1) the various components of the soil faunal community at Sourhope and how they were affected by nutrient and insecticide treatments applied to the site; and (2) the consequences of changes in soil faunal community composition for ecosystem processes.

2. Soil faunal communities of the temperate grassland

2.1. Mesofaunal communities and their response to manipulations

The adult or the largest larval stage of soil biota having a body width of between 0.1 and 2 mm are termed mesofauna (Swift et al., 1979), and comprise groups such as the Enchytraeidae (pot worms) and the microarthropods, the latter group including both Collembola (springtails) and Acari (mites). Cole et al. (2005) found that the soil microarthropod community at Sourhope was relatively species poor in comparison to records from other grassland sites; only 12 species of Collembola and 32 species of mite were identified from samples collected in August 2000.

In comparison, Salt et al. (1948) found 26 species of Collembola in pasture in the UK; Weis-Fogh (1948) recorded 58 prostigmatid and 59 oribatid species in a Danish ‘poor’ pasture; and Siepel and Vandebund (1988) reported up to 108 species of microarthropods in a 500 cm² area of soil of an unmanaged Dutch grassland. It was suggested that the low microarthropod diversity recorded at Sourhope might be a consequence of the shallow sampling of soils (top 5 cm only) and/or the omission of many Prostigmata and juvenile mites from these diversity estimates, due to difficulties with their taxonomy (Cole et al., 2005). In September 2000, eight species of enchytraeid were found in control plots at the site (Black et al., 2003), a richness similar to that of other unfertilised temperate grasslands (Standen, 1982).

At the site, microarthropod abundance was high, reaching almost 100,000 m⁻² in control plots receiving no nutrient additions (Cole et al., 2005). This density is approximately equivalent to that reported by Bardgett et al. (1993) for other semi-natural grasslands in the UK. The density of enchytraeids varied considerably between annual samplings being, in control plots, 160,000 m⁻² in August 2001 and 32,000 m⁻² in April 2002 (Thompson, 2003). In response to the nutrient manipulations at Sourhope, microarthropod abundance increased: after 15 months the addition of N increased mite and collembolan numbers by 19 and 23%, respectively (Fig. 1). In addition to mite abundance, the biomass of the Mesostigmata (predominantly predatory mites), was greater in plots receiving N (Cole et al., 2005). By contrast, although liming increased collembolan abundance (by 21%) it had no effect on the abundance of mites (Fig. 1). Despite the positive responses of the microarthropod densities to N, there was no change in overall microarthropod diversity (expressed either as the Shannon’s diversity or evenness

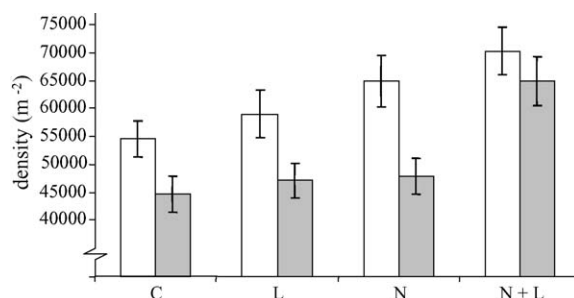


Fig. 1. Response of mite (open bars) and Collembola (shaded bars) population densities to nutrient manipulations (C = -lime, -N; L = +lime, -N; N = -lime, +N; N + L = +lime, +N). Error bars represent standard errors. Reproduced from Cole et al. (2005).

indices), although the diversity of Collembola alone was enhanced by N addition (Cole et al., 2005). Nevertheless, this response of collembolan diversity was not associated with a change in the dominance profiles of individual species: *Folsomia quadrioculata* and *Protaphorura armata* dominated collembolan communities in all plots (Cole et al., 2005), but not biocide plots (P. Murray, pers. commun.).

In contrast to microarthropods, the abundance of enchytraeids was reduced by lime addition, being only 38% of the density in control plots after 18 months of imposing treatments (A. Thompson, pers. commun.). Liming also altered the structure and richness of the enchytraeid community. In limed plots, the dominant enchytraeid species at the site (*Cognettia sphagnetorum*) was replaced by enchytraeids of the genus *Fridericia*, and limed plots had higher species richness than the control plots (13 as opposed to 8 species in the control plots, Black et al., 2003). This was taken to suggest that there was immigration of species into a more favourable environment and/or that, prior to liming, there were some species with abundances below detectable limits. Although the increase in enchytraeid species richness was associated with a modest reduction in their overall biomass (Table 1), biomass of enchytraeids of the genus *Fridericia* increased six-fold in the limed plots from 2.38 to 13.84 g m⁻². There was a simultaneous decline from 17.35 to 1.04 g m⁻² in the biomass of *C. sphagnetorum* (Black et al., 2003).

Unsurprisingly, the effect of the biocide (chlorpyrifos) treatment on microarthropods was dramatic, with most taxa being totally removed. These defaunated patches were initially re-colonised by *Ceratophysella denticulata* (Collembola: Poduridae) (M. Fountain, pers. commun.). A very similar result was obtained by Baweja (1939) who defaunated, then re-sowed, grass plots and recorded an explosion in *C. armata*. This

genus and the closely related *Hypogastrura* are known to occur in large numbers on recently disturbed areas (Hertzberg, 1997; Dunger, 2001; Shaw, 2003).

2.2. Macrofaunal communities and their response to manipulations

Soil biota having a body width >2 mm are termed macrofauna (Swift et al., 1979). The macrofaunal biomass at Sourhope was dominated by clitellate Oligochaetae (earthworms, Table 1) and larvae of the Tipulidae, *Agriotes* and Diptera (P. Murray, pers. commun.). In 1999, the total abundance and diversity of earthworm species was larger than was expected for acidic upland grassland with a mean abundance of 172 earthworms m⁻² (±1S.D. of 89) and up to 10 species being recorded (Bishop, 2003). Surprisingly, the most abundant species at the site was the acid intolerant, endogeic earthworm *Allolobophora chlorotica*, with a density of 65 m⁻². Acid intolerant species are generally found in soils with a pH > 4.5 (Satchell, 1955), but the pH at Sourhope was between 3.8 and 4.6. Species richness was, however, greatest amongst the epigeic species, which included *Dendrobaena octaedra*, *Dendrodrilus rubidus*, *Lumbricus festivus* and *Lumbricus rubellus* (Bishop, 2003). The anecic earthworm *Lumbricus terrestris* was also observed in Bishop's survey, albeit in low numbers; this was most likely due to a period of dry weather preceding sampling that forced this species below the sampling depth.

The most common insect root herbivore at the site was *Tipula paludosa*, with its soil-dwelling larvae reaching densities of 120 m⁻² in the control plots. This abundance exceeds the field damage threshold abundance of 85 m⁻² (Dawson et al., 2003). In the first year, other root herbivores found included chafers, *Agrotis* spp. (cutworms), *Agriotes* spp. (wireworms) and *Sitona*

Table 1
Biomass (mg m⁻²) of soil biota in untreated (control) and limed treatments

	Control	Lime	Sample date	Source
Collembola	2038	1539	August 2000	Cole et al. (2005)
Oribatida	496	508	August 2000	Cole et al. (2005)
Mesostigmata	196	208	August 2000	Cole et al. (2005)
Prostigmata	23	16	August 2000	Cole et al. (2005)
Enchytraeidae				
<i>Fridericia</i> spp.	2380	13840	September 2000	Black et al. (2003)
<i>Cognettia</i> spp.	17350	1040	September 2000	Black et al. (2003)
<i>Achaeta</i> spp.	250	870	September 2000	Black et al. (2003)
<i>Henlea</i> spp.	0	360	September 2000	Black et al. (2003)
Earthworms	43050	59066	October 2001	Bishop (2003)

spp. (clover weevils) but only at low densities, meaning that although tipulids were abundant overall root herbivory appeared to be low at the site. Following an insecticide application in June 1999, *T. paludosa* was eliminated from treated plots by October 1999.

Bishop (2003) repeated the earthworm survey after 3 years of lime addition at Sourhope, by which time soil pH was significantly greater in limed (mean pH 6.7) than unlimed plots (mean pH 4.5). The limed plots supported a significantly greater number of earthworms due to increased abundance of the species *D. rubidus*. *A. chlorotica* and *L. rubellus* also increased in abundance due to lime additions, albeit non-significantly, whereas the abundance of *D. octaedra* declined markedly. Three species that were not observed in the initial survey, *Aporrectodea rosea*, *Lumbricus castaneus* and *Octolasion cyaneum*, were also recorded at this time. It is likely that being endogeic, *O. cyaneum* had probably migrated to deep soil layers due to dry weather in the first survey and was therefore not recorded, whereas observations of *A. rosea* and *L. castaneus* were accounted for by an improvement in the author's taxonomic skills. Increased earthworm community biomass in response to liming was estimated from a parallel field study (Table 1).

2.3. Overview of responses of soil fauna to manipulations

Species richness of all groups, with the exception of microarthropods, was moderate for temperate grassland. That microarthropod and earthworm abundance increased concurrently with nutrient additions and an increase in plant productivity (Cole et al., 2005) supports the notion that soil biotic communities are predominately regulated by bottom-up forces (Moore and de Ruiter, 2000; Bardgett, 2002). The biomass of predatory mites was greatest in sites receiving N, suggesting that more energy was transferred to higher trophic levels in nutrient amended plots. This resulted in a shift in the trophic structure of the microarthropod community with increased soil fertility. Although microarthropod abundance strongly increased in response to increased soil fertility, Cole et al. (2005) found no change in the relative abundance of individual species; the same dominant species occurred in all plots, irrespective of the nutrient manipulations.

In contrast to the microarthropod responses, Thompson (2003) and Bishop (2003) reported significant shifts in species dominance within enchytraeid and earthworm communities in limed plots. Prior to lime addition, *C. sphagnetorum* was the dominant

enchytraeid species at Sourhope (Thompson, 2003). This species is considered a keystone organism of acid coniferous forest (Laakso and Setälä, 1999) and moorland (Cole et al., 2002) soils in terms of its biomass and role in soil processes. The abundance of *C. sphagnetorum* rapidly declined following lime addition to the soil, a response that has also been observed in fertilised hay meadows (Standen, 1982, 1984) and coniferous forest (Bäath et al., 1980). Concurrent with this, the contribution of enchytraeids to total oligochaete biomass declined from 32 to 18% following lime addition (Table 1). Enchytraeids comprised one-tenth of the biomass of oligochaetes in plots with pH > 5 (Standen, 1984), suggesting that at Sourhope further decreases in their biomass might follow. Standen (1984) proposed that the decline in enchytraeids in fertile soils could arise due to competitive exclusion by earthworms whose biomass also increases with improved soil fertility, particularly when pH is enhanced. Improved soil conditions through lime addition enabled the productivity of earthworms at Sourhope to increase (Bishop, 2003). The distribution of endogeic and anecic earthworms is known to be strongly limited by low pH in soils of Scottish grasslands (Boag et al., 1997) and northern boreal forests (Räty and Huhta, 2003). It is not known whether an antagonistic influence of earthworms on enchytraeid abundances occurs because of competition for resources, or from bioturbation by earthworms that cause small-scale disturbances that reduce enchytraeid densities. Standen (1984) proposed that roots of high yielding plants in fertile plots might physically inhibit the activities of enchytraeids, but concluded that improved plant litter quality derived from plants growing on fertile soil benefits earthworms, resulting in competitive exclusion of enchytraeids. Huhta and Viberg (1999) also concluded that competition for resources with earthworms was responsible for the decline in *C. sphagnetorum* in their study.

While competitive exclusion may account for the decline in enchytraeids at Sourhope, the existence of competition amongst soil biota is a contentious issue. It has been proposed that the majority of soil decomposer communities are not strongly regulated by competition, and that competitive exclusion does not occur when resource supply is increased (Bardgett, 2002, 2005; Wardle, 2002; Bardgett et al., 2005). That microarthropod abundance, but not diversity, was affected by the nutrient manipulations at Sourhope provides support for these ideas. Indeed, competitive exclusion amongst soil microarthropods at Sourhope may have been avoided through increased predation within this group (Cole et al., 2005). Further, the finding that enchytraeid

diversity increased in response to the nutrient manipulations, despite a reduction in biomass (Black et al., 2003; Thompson, 2003), suggests that competitive exclusion by earthworms is probably not the decisive factor in the decline of enchytraeids in limed plots. Rather, we propose that the keystone species, *C. sphagnetorum* – that is responsible for the widespread observations of reductions in enchytraeid biomass in limed soil – arises because this acid tolerant species might also be alkaline intolerant. In other words, it is primarily edaphic factors (increased pH) rather than biotic factors that caused this species to decline. Increased earthworm abundance may play a role in this decline by exacerbating the pH shift. This may occur because earthworms can increase the pH of their surroundings through increased incorporation of organic matter from the soil surface and excretion of cutaneous mucous (Haimi and Huhta, 1990; Schrader, 1994). This mechanism may account for the decline in enchytraeids reported in unfertilised soils in the microcosm studies of Rätty and Huhta (2003) and Huhta and Viberg (1999).

The one instance at Sourhope where competitive exclusion may be the mechanism underlying species shifts is within the earthworm community. That is, it is difficult to explain the reduction in abundance of the earthworm *D. octaedra* in limed plots without acknowledging the possibility of competition from other earthworm species. If true, then the fact that competitive interactions were observed between macrofaunal, but not mesofaunal, species adds weight to the hypothesis that the complex physical structure of soils permits extensive resource partitioning and niche differentiation that might limit competitive exclusion. For the larger-bodied and highly motile earthworms, the spatial heterogeneity in soil may be at too fine a scale to influence their interspecific interactions, such that the complementarity that is postulated to exist amongst microarthropod species (Siepel, 1996), and possibly enchytraeids, may not occur for earthworm species. Granted, the ecological classification system devised for earthworms is based on their spatial distribution in soil that correlates with differences in their feeding behaviour (Bouché, 1977), but Bishop (2003) reports that in limed soil at Sourhope, in the absence of the epigeic *L. rubellus*, the endogeic earthworm *A. chlorotica* fed on surface litter. This behaviour discords with its ecological classification, but might be more common than is currently assumed. Indeed, Neilson et al. (2000) were unable to discriminate amongst ecological groupings of earthworms using stable isotope ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{14}\text{N}/^{15}\text{N}$ at natural

abundance, suggesting that earthworm food sources may not be so clearly defined.

Bishop (2003) proposed that *D. rubidus* out-competed *D. octaedra* in limed soil due to changes in edaphic factors arising from management of the field site, irrespective of the nutrient manipulations. The regular homogenous mowing at the site was noted to alter plant community composition, with a decline of up to 40% in some vascular plant species across all nutrient manipulation treatments. This was coupled with an increase in the abundance of mosses that could have led to a gradual decline in soil nutrients, particularly calcium, which might account for the shifts in earthworm community structure (Bishop, 2003). That the abundance of the legume *Trifolium repens* was increased by lime addition at Sourhope (G. Burt-Smith, pers. commun.) might also explain the increased species richness of enchytraeidae in these sites, since the presence of legumes has been shown to increase species richness of other groups of soil biota in grasslands (Salamon et al., 2004). Therefore, it seems highly likely that it was not only direct effects of the nutrient manipulations that altered the diversity and abundance of soil biotic communities (as was the case for enchytraeids), but also site management in general. Moreover, the indirect effect of nutrient additions on plant diversity and productivity that alter the manner in which aboveground and belowground components interact to determine community composition may also have been at play (Bardgett and Wardle, 2003; Wardle et al., 2004).

3. Functions of soil fauna

It is well established that soil animals and their interactions with microorganisms play a primary role in the mineralisation of nutrients, and hence nutrient acquisition and the growth of plants (Coleman et al., 1983; Cole and Bardgett, 2002; Bardgett, 2005). Thus, changes in components of Earth's biodiversity not only cause concern for ethical and aesthetic reasons, but also because these changes are known to have the potential to alter ecosystem processes (Hooper et al., 2005). Processes such as plant growth are critical to the sustainability of natural systems and ensure the general functioning of the soil. Recent studies suggest that soil processes are augmented by the presence of a soil biotic community containing several taxonomic or trophic groups, compared to the presence of a single group or species alone (Mikola and Setälä, 1998; Bardgett and Chan, 1999). However, other studies have demonstrated that the presence of a single keystone species is

sufficient to evoke increased mineralisation and plant nutrient uptake (Laakso and Setälä, 1999; Cragg and Bardgett, 2001). The enchytraeid *C. sphagnetorum* has been identified as one such keystone organism (Laakso and Setälä, 1999); therefore the decline of this species in response to liming at Sourhope (Black et al., 2003) may have considerable consequences for both nutrient cycling and plant growth (Setälä and Huhta, 1991). In addition, *C. sphagnetorum* is instrumental in the release of dissolved organic carbon (DOC) from these upland organic soils (Briones et al., 1998; Cole et al., 2000), and thus its loss from the soil community might have serious implications for the C balance of such soils, which represent important stores of terrestrial carbon in the UK (Howard et al., 1995). Therefore, changes in the abundance of particular soil biota at Sourhope resulting from the site manipulations are likely to have consequences for the functioning of this grassland, especially given that density of soil animals can be a stronger driver of nutrient mineralisation rates than species richness (Cole et al., 2004a).

To investigate potential effects on ecosystem processes of changes in soil communities at Sourhope, a number of laboratory and field investigations were performed. Relationships between soil animal diversity and ecosystem functioning have been investigated by categorising animals by species (Scheu et al., 1999), trophic group (Ingham et al., 1985), body size (Setälä et al., 1996), habitat preference (Verhoef and Brussaard, 1990) or the successional community they belong to (De Deyn et al., 2003), and then relating this categorisation to function. Most studies conducted in the SBP focused on manipulating species within experimental microcosms or mesocosms, or on following a ^{13}C -label into a subset of species found within the managed plots at the Sourhope site. We now discuss how the functionality of different taxonomic and size class of groups of soil biota at Sourhope has been revealed by these approaches, and place these observations in the context of biodiversity. In particular, we discuss the extent to which functional redundancy is thought to occur in the soil food web.

3.1. Microcosm studies

3.1.1. Microarthropods

In a simple microcosm experiment, Cole et al. (2004b) used eight individual species of microarthropods taken from Sourhope, as well as multi-species (2, 4 and 8 species) combinations of these species, to test for individual species and richness effects of microarthropods on a range of soil microbial properties and plant

growth. In addition, a dual-labelled organic N source (glycine- $2\text{-}^{13}\text{C}$ - ^{15}N) was applied to microcosms to test for effects of soil microarthropod richness on the partitioning of N between the dominant grass species at Sourhope, *Agrostis capillaris*, and the soil microbial biomass. Certain species of Collembola influenced the soil microbial community: *F. quadrioculata* reduced microbial biomass, whereas *Mesaphorura macrochaeta* enhanced arbuscular mycorrhizal (AM) colonisation of *A. capillaris* roots (Fig. 2).

However, none of the species affected the growth of *A. capillaris*. Effects of increasing species richness of microarthropods on microbial biomass and AM colonisation were detected but these effects could be interpreted in relation to the presence or absence of individual species. Despite the influence of *F. quadrioculata* and

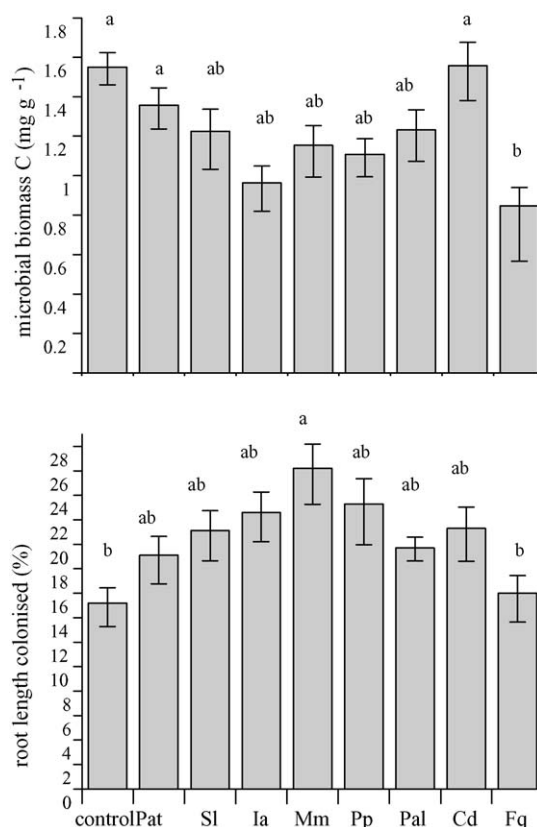


Fig. 2. (a) Microbial biomass C and (b) percentage root length colonised by AM fungi (means \pm 1 S.E., $n = 10$) in the absence (control) and presence of individual microarthropod species at the final sampling event. Treatment codes correspond to microarthropod species—Collembola are: *P. armata* (Pat), *Isotoma anglicana* (Ia), *Mesaphorura macrochaeta* (Mm), *Pseudosinella alba* (Pal), *Ceratophysella denticulata* (Cd) and *F. quadrioculata* (Fq), and mites are *Scheloribates laevigatus* (SI) and *Platynothrus peltifer* (Pp). Bars followed by the same letter do not differ at $P = 0.05$. Reproduced from Cole et al. (2004b).

M. macrochaeta on the microbial biomass, these effects were insufficient to affect microbial sequestration of the added ^{15}N , which averaged 28% of the total added. Consequently root and shoot uptake of ^{15}N was also largely unaffected by microarthropods, although the collembolan species *C. denticulata* reduced root ^{15}N capture when present in monoculture. The fact that individual collembolan species affected microbial biomass and AM colonisation, but did not affect the short-term immobilisation of N by the microbial biomass, might account for the lack of detectable effects of microarthropods on plant nutrition and growth in this study. This is in contrast to previously reported studies on the positive influence of collembolans on soil N availability and plant nutrition (e.g., Bardgett and Chan, 1999). Overall, the results of Cole et al.'s (2004b) study were taken to suggest that while single species and variations in diversity of microarthropods influenced microbial abundance, they did not cause detectable effects on microbial or plant function in terms of organic N uptake.

3.1.2. Tipulids

Treonis et al. (2005) examined the influence of *T. paludosa* larvae, at densities approaching those found in aggregated patches in the field, on the growth of some Sourhope grassland species. They found that tipulids reduced the biomass of *T. repens* and *Lolium perenne*, and increased organic carbon flow in the rhizosphere solution of these plant species. Grayston et al. (2001) and Dawson et al. (2004) employed a similar microcosm approach to Treonis et al. (2005) further to examine the impacts of root herbivory by tipulids on rhizosphere communities, and found that when plant species were grown in combination, e.g. *A. capillaris* and *T. repens*, tipulids preferentially grazed *T. repens* so that the biomass of *A. capillaris* was unaffected. This preferential feeding by root herbivores is thought to have direct consequences for plant community structure by altering competitive interactions between sward species.

Application of rhizosphere solution obtained from these microcosms to soil resulted in shifts in the microbial community structure, with increases in fungal biomass being recorded when solutions were derived from the rhizospheres of *L. perenne* and *A. capillaris*, and a decrease in gram negative bacteria for solutions obtained from *T. repens* (Treonis et al., 2005). The indirect effect of tipulid larvae on soil microbial communities through their influence on rhizosphere exudate chemistry was attributed to changes in the quantity and quality of root exudates. This was

indicated by differences in community level physiological profiles of microbial communities, with a greater utilization of sugars, amino and carboxylic acids in the presence of larvae (Grayston et al., 2001; Dawson et al., 2004; Treonis et al., 2005). These impacts of below-ground herbivory on rhizosphere chemistry could have consequences for soil nutrient availability and therefore plant performance, and might also have knock-on effects for the nutrition of soil mesofaunal communities, by altering the quality and quantity of their microbial food source.

3.1.3. Size classes

Another study, an integrated effort between multiple groups funded both within and outside the SBP, investigated the impact of soil organism body size on a suite of ecological processes (Bradford et al., 2002a,b). Body size provides a good functional classification because it correlates with metabolic rate, generation time, population density and food size (Peters, 1983). The physical structure of the soil habitat also constrains access to resources for certain body sizes and hence modulates interactions between organisms (Anderson, 1978; Brussaard, 1998). The rationale for the Bradford et al. (2002a) study was that while pot experiments have demonstrated the marked potential effects of loss of specific soil fauna and faunal groups on a range of ecosystem processes, the validity of extrapolating these studies to the field is questionable. They argued that what was required was an approach that used a soil faunal community with a species richness more akin to that of the field, which included a multi-species plant community and a reconstructed soil profile, and that measured the response of a suite of interacting variables. They used a microcosm approach, maintained within the Ecotron controlled environment facility (Lawton, 1996) to achieve these requirements, testing the role of one component of soil community composition, namely assemblages that differ in animal body sizes, on carbon flux, and microbial and plant community composition and abundance. Soil, plants, fauna, and microorganisms for microcosm construction were collected from the grassland at Sourhope.

Fauna were grouped into the following diameter classes: microfauna (<100 μm), mesofauna (100 μm to 2 mm) and macrofauna (>2 mm). Three treatment communities were established using these groupings to produce a gradient of increasing functional complexity: microfauna only; microfauna and mesofauna; and microfauna, mesofauna and macrofauna. Bradford et al. (2002a) expected that, due to widely reported

positive impacts of meso- and macrofauna on soil fertility and plant growth (e.g. Verhoef and Brussaard, 1990; Setälä et al., 1996; Bardgett and Chan, 1999), net primary productivity (NPP) and net ecosystem productivity (NEP) would both increase as larger-bodied fauna were included in the treatment communities. However, despite shifts in plant assemblage composition (increasing predominance of N rich groups and species in communities without macrofauna) neither aboveground NPP nor NEP responded to treatment. Bradford et al. (2002a) postulated that both variables were buffered by positive and negative effects of fauna that cancelled one another out and so resulted in no net ecosystem effects. For example, decomposition rate, which is generally positively correlated within a system with nutrient availability (Swift et al., 1979), was enhanced in the macrofauna treatment, but at the same time both mycorrhizal colonisation and root biomass were less abundant in the same treatment community. Bradford et al. (2002a) suggested that the lower root biomass and mycorrhizal infection might explain why plants in these communities were unable to capitalize on the higher nutrient availability. The existence of such simultaneous, but opposite, changes in variables develops Anderson's (1995) theory that soil process rates (e.g., N flux) at one scale may be maintained by sink and source processes (e.g., N immobilisation and N mineralisation) operating at finer scales.

The lack of response of net primary production to the manipulation of a soil assemblage lends support to the concept of functional redundancy within soil food webs. That net ecosystem productivity, estimated by Bradford et al. (2002a) as the net result of community photosynthesis and respiration, was also unresponsive only strengthens this idea. However, unpublished work by Bradford and others, using the same experimental communities, found that other measures of ecosystem carbon balance were responsive to the size class treatments but that a finer tool was required to detect these responses. They used ^{13}C -enrichment techniques to follow the assimilation, retention and pathways of recent, photosynthetically fixed carbon, and found that across the duration of their pulse-chase study (52 days), less of the photosynthetically fixed ^{13}C label was retained in the microcosm treatment containing microbiota and mesofauna, as opposed to a simpler or a more complex soil assemblage. Further, the rate of change with time in the rate of mineralisation (measured as the efflux of soil CO_2) of the ^{13}C label was greatest in the most functionally simple treatment. Together, these results suggest that the dynamics of recent photosynthetically fixed carbon is sensitive to

variations in the complexity of soil biotic assemblages (at least on the basis of size class), suggesting that functional attributes of soil assemblages may not conform to the commonly assumed models of redundancy (Andrén et al., 1999).

The classic way in which soil assemblage composition is manipulated by size class is through the use of litterbags with different mesh sizes. This approach has demonstrated marked positive effects of both meso- and macrofauna on rates of litter mass loss (Curry, 1969; Anderson, 1973; Vossbrinck et al., 1979; Wise and Schaefer, 1994; Setälä et al., 1996). As with the use of naphthalene to exclude larger-bodied fauna, the approach is associated with a number of limitations (Vossbrinck et al., 1979; Blair et al., 1989; Bradford et al., 2002b). One limitation is that the fauna in the soil surrounding the litterbag remain unmanipulated and thus may indirectly affect the decomposition of the litter patch. These indirect effects may involve soil fauna-mediated modifications of the abiotic environment and/or the decomposer assemblage in the bulk soil surrounding the decomposing material. For example, earthworm engineering may alter the soil moisture regime (Jones et al., 1994) and mesofauna regulation of fungal activity in the bulk soil may affect the initial rate of litter colonisation by fungi.

Using the experimental microcosms in the Ecotron, Bradford et al. (2002b) tested whether the composition of fauna in the soil environment surrounding litter

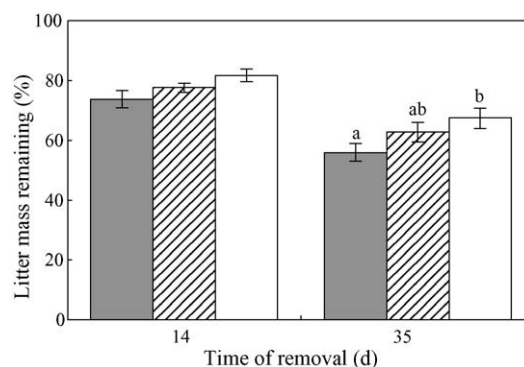


Fig. 3. Indirect effects of faunal communities on mass loss from litterbags with a mesh that restricts direct access to the litter to microbiota and mesofauna only. Mass remaining (mean \pm S.E.; percentage of original) after 14 and 35 days exposure to soil communities containing microbiota and mesofauna only (shaded bars), in addition to mesofauna (striped bars), and in addition to mesofauna and macrofauna (white bars) is shown. Means significantly different within one time point are marked by different letters ($P < 0.05$). There was significantly less mass loss when mesofauna and macrofauna were present in the soil communities. Reproduced from Bradford et al. (2002b).

patches has the potential to modify the decomposition activity of biota colonising the litter itself, as postulated by Beare et al. (1995) and Lavelle (1997). Bradford et al. (2002b) placed litterbags of different mesh sizes (to exclude mesofauna and macrofauna, or macrofauna only) into each of the three Ecotron soil assemblage treatments. In this way they could separate out mesh effects from effects due to excluding fauna from the environment surrounding the litterbags. They found that although meso- and macrofauna increased litter decomposition rate when these fauna could access the litter (i.e. larger mesh sizes), their effect mediated through the environment surrounding the litterbags on microfauna and microbially mediated decomposition (i.e. in the narrowest mesh bags) was to inhibit decomposition (Fig. 3). They concluded that while effects of meso- and macrofauna, such as litter comminution and direct litter consumption, increase litter decomposition overall, these larger-bodied fauna have the potential to inhibit decomposition by microfauna, bacteria and fungi through engineering impacts on the environment surrounding litter patches.

3.2. Field studies

3.2.1. Enchytraeids

Black et al. (2003) supplied a ^{13}C label to the aboveground vegetation of the control and limed plots, using the technique described in Ostle et al. (2000). The technique is used to label rhizosphere C sources, primarily root exudates, that can then be tracked through the soil food web (Staddon, 2004). The influence of lime was shown significantly to reduce the amount of ^{13}C assimilation (across 20 days) into tissue of individual enchytraeids of the genus *Cognettia* (Black et al., 2003) but not of the genus *Friderica*. Both genera continued to assimilate ^{13}C throughout the study period, most likely through consumption of roots or root-feeding microbes. That enchytraeids of the genus *Cognettia* were slower to assimilate rhizosphere C inputs in limed soils might reflect changes in the soil microbial community, or decreases in the activities of enchytraeid digestive enzymes, as a result of lime addition (Šustr et al., 1997). Based on these observations, Black et al. (2003) concluded that enchytraeids occupy a number of functional niches within the soil animal community and that environmental change, such as liming, may impact on the pattern of C assimilation of enchytraeids. This study also demonstrates that some soil biota assimilate rhizosphere C sources, most likely through their feeding on microbes that are associated with roots and that utilise root exudates.

3.2.2. Earthworms

In contrast to enchytraeids, earthworms increased their productivity in limed soils and were also observed to be more active. In a field-based mesocosm study, Bishop (2003) found that, in limed soil, earthworm activity increased the rate of comminution and incorporation of litter into the H horizon, significantly reducing the depth of the LF horizon. This reduction in the litter layer might be attributed to *A. chlorotica* whose abundance was increased by lime addition in mesocosms (Bishop, 2003; Spring, 2003). However, it is difficult to determine whether these effects on the LF horizon were primarily the result of increases in overall earthworm abundance or through species shifts in the community, or a result of the lime addition itself. Bishop (2003) concluded that the direct influences of earthworms on decomposition of organic matter in soil are less important than their effects on the incorporation and comminution of litter that regulates microbial decomposition.

3.3. Overview of functionality of soil fauna

Overall, the most profound impacts on soil properties at Sourhope appear to be due to the presence of macrofauna in soil communities (Bradford et al., 2002a,b). Potentially, this is because this size class of fauna contains the functionally important earthworm group. However, not all the effects observed can be assigned to earthworm activity. In the Ecotron facility, macrofauna were observed to reduce the foliar biomass of forbs and legumes and reduce root biomass, supporting the findings of Grayston et al. (2001) and Dawson et al. (2004) that herbivores, such as *T. paludosa* larvae, preferentially feed on legumes such as *T. repens*. Although root herbivory by macro-invertebrates was assumed to be low at the site (Dawson et al., 2003), selective herbivory by invertebrates might have reduced the presence of forbs (Brown and Gange, 1989) in the sward at Sourhope, possibly restricting treatment-induced shifts in plant community structure in the more fertile plots. This could account for the limited response of some biotic groups, such as the microarthropods, to the site manipulations since increases in richness of soil biota are generally correlated with the presence of plants that produce higher quality litter, such as forbs and herbs, rather than plant species richness per se (Hansen and Coleman, 1998; Hansen, 2000; Salamon et al., 2004). The presence of macrofauna was also shown to increase rates of nutrient mineralisation in soil and decomposition rate of *A. capillaris* litter (Bradford et al., 2002a,b),

confirming the positive role of groups such as earthworms on soil processes (Lavelle, 1998).

That the diversity effects reported by Cole et al. (2005) could be interpreted in relation to the presence or absence of individual species, supports the notion that traits of particular species in a community are more important for determining functionality than species richness (Mikola and Setälä, 1998; Laakso and Setälä, 1999; Cragg and Bardgett, 2001; Bardgett, 2005). Nevertheless, that only two of the eight species investigated had demonstrably different influences on some of the measured processes and not that of plant N capture or growth, lends weight to the concept of functional redundancy (Andrén et al., 1995, 1999). That a relatively species poor class of soil biota, the macrofauna, appeared to have the strongest impacts on soil processes in the studies of Bradford et al. (2002a,b), further implies marked functional redundancy in the soil food web at the species level (Laakso and Setälä, 1999). The studies of Bradford et al. (2002a) and Cole et al. (2004b) also suggest that soil fauna are redundant with respect to NPP. However, recent work by Bradford and others has demonstrated that some measures of ecosystem carbon dynamics are responsive to faunal assemblage composition. Bradford and others showed that communities containing different size classes of soil fauna all behaved differently when the dynamics of a photosynthetically fixed ^{13}C were investigated, highlighting functional attributes of soil assemblages that contradict the idea of redundancy (Andrén et al., 1995, 1999). Given that only a handful of studies within the programme addressed the concept of functional redundancy amongst soil fauna, a strong conclusion for or against it operating at Sourhope is not possible. However, it is likely that functional redundancy at the species level occurs most widely in species rich faunal groups (Bardgett, 2002) because of the generalist feeding behaviour that appears to predominate amongst soil biota under field conditions (Luxton, 1972; Ponsard and Ardit, 2000; Scheu and Falca, 2000; Scheu, 2002). That is, generalist soil biota will share similar trophic positions, enabling them to replace one another without influencing general soil functions (Andrén et al., 1995; Groffman and Bohlen, 1999).

It has been proposed that a large proportion of redundant species within an ecosystem infers stability, since subordinate species may be able to dominate under conditions where current dominants cannot thrive (Grime, 1998; Petchey et al., 1999; Walker et al., 1999). In this way, species that are functionally redundant prior to a perturbation act as 'spare wheels', maintaining function following environmental change (Andrén

et al., 1995; Loreau, 2000). For example, in limed soil at Sourhope, Bishop (2003) observed that *A. chlorotica* adopted a normally unobserved feeding behaviour in the absence of *L. rubellus*, a behaviour that might compensate for the loss of its competitor and thus confer ecosystem stability. Notably, Liiri et al. (2002) found no influence of increasing species richness of microarthropods on ecosystem stability, measured as the effect of drought on birch growth and nutrition. Potentially, the concept of stability through replacement of one (or many) species lost from a system, by others that were previously functionally redundant, applies only to macrofauna groups such as earthworms and not the numerically more abundant and species rich mesofauna. Alternatively, as Hooper et al. (2005) suggested, this buffering capacity of formerly redundant species might not become apparent until ecosystems have been exposed to multiple types of stresses (Griffiths et al., 2000; de Ruiter et al., 2002).

Black et al. (2003) found that the ability of the enchytraeid *C. sphagnetorum* to assimilate rhizosphere-derived C inputs was impaired in limed soil. However, this loss of role of *C. sphagnetorum* in limed soil might reflect either direct physiological effects of lime on enchytraeids or indirect effects of lime on rhizosphere inputs through altered plant and microbial community structure. These co-correlated plant, edaphic and biotic responses to experimental manipulations in the field system highlight the difficulty in determining the mechanism for shifts in functionality of individual species of soil biota in complex systems, and therefore the level of functional redundancy within soil food webs in changing environments. In a review of studies that have examined biodiversity–stability relationships, de Ruiter et al. (2002) also concluded that the environmental stress or disturbance might influence process stability more directly than a diversity effect. Given the observation that changed soil conditions can affect the functionality of individual soil biota, as well as determine their presence or absence in a community, we suggest that a combined knowledge of the effects of environmental change on biodiversity, and how this change affects soil faunal performance, is required so as to understand how soil biodiversity effects might feedback to alter the impact of environmental drivers on ecosystem function.

4. Conclusions

Nutrient additions and site management had direct and indirect effects on the abundance and structure of soil faunal communities. For example, lime addition

affected earthworm and enchytraeid community structure. In contrast, indirect effects of nutrient additions and management on soil microarthropod diversity were more subtle and difficult to ascribe, since these acted through treatments altering plant community structure and productivity, which in turn affected the soil community. One general observation was that the nutrient additions increased plant productivity, providing increased resources for soil fauna that resulted in increased biomass for some groups, demonstrating that soil biotic communities are predominately regulated by bottom-up forces. That competitive interactions were observed between macrofaunal, but not mesofaunal, species supports the notion that the complex physical structure of soils permits extensive resource partitioning and niche differentiation that might limit competitive exclusion and maintain soil biodiversity.

The most profound impacts of soil fauna on soil properties at Sourhope appeared to be due to the activities of macrofauna. Some authors also found evidence for functional redundancy at the species and size class level amongst soil biota, but this was dependent upon the ecosystem process being measured. All biota manipulations appeared to demonstrate redundancy with respect to NPP. Whilst the programme has delivered some insights into those factors that structure soil biotic communities and control soil biodiversity, much remains to be discovered regarding the functionality of soil meso- and macrofauna, especially under environmental change. We therefore identify an urgent need to examine these issues further in soil food webs.

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