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Multitrophic effects of nutrient addition in upland grassland

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Abstract

Although the effects of nutrient enhancement on aquatic systems are well documented, the consequences of nutritional supplements on soil food webs are poorly understood, and results of past research examining bottom-up effects are often conflicting. In addition, many studies have failed to separate the effects of nutrient enrichment and the physical effects of adding organic matter. In this field study, we hypothesised that the addition of nitrogen to soil would result in a trophic cascade, through detritivores (Collembola) to predators (spiders), increasing invertebrate numbers and diversity.

Nitrogen and lime were added to plots in an upland grassland in a randomised block design. Populations of Collembola and spiders were sampled by means of pitfall traps and identified to species.

Seventeen species of Collembola were identified from the nitrogen plus lime (N + L) and control plots. Species assemblage, diversity, richness, evenness and total number were not affected by nutrient additions. However, there was an increase in the number of Isotomidae juveniles and *Parisotoma anglicana* trapped in the N + L plots.

Of the 44 spider species identified, over 80% were Linyphiidae. An effect on species assemblage from the addition of N + L to the plots was observed on two of the four sampling dates (July 2002 and June 2003). The linyphiid, *Oedothorax retusus*, was the only species significantly affected by the treatments and was more likely to be trapped in the control plots.

The increased number of juvenile Collembola, and change in community composition of spiders, were consequences of the bottom-up effect caused by nutrient inputs. However, despite efforts to eliminate the indirect effects of nutrient inputs, a reduction in soil moisture in the N + L plots cannot be eliminated as a cause of the invertebrate population changes observed. Even so, this experiment was not confounded by the physical effects of habitat structure reported in most previous studies. It provides evidence of moderate bottom-up influences of epigeic soil invertebrate food webs and distinguishes between

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nutrient addition and plant physical structure effects. It also emphasises the importance of understanding the effects of soil management practices on soil biodiversity, which is under increasing pressure from land development and food production.

Keywords: bottom-up, Collembola, community structure, lime, nitrogen, spiders

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Introduction

Populations of soil invertebrates are exposed to many anthropogenic activities including agricultural (cultivation, harvesting, crop residues, chemical inputs), pollution (acidification, nitrogen deposition, heavy metals etc.) and other land management practices, which render them vulnerable to physical and chemical stresses. Such activities often lead to changes in invertebrate species assemblages, trophic interactions and community structure (e.g. Wardle *et al*., 1995; Symondson *et al*., 1996; Chapin *et al*., 1997; Wardle *et al*., 1998; Rusek & Marshall, 2000; Smit *et al*., 2002; Frampton, 2002; Fountain & Hopkin, 2004; Hooper *et al*., 2005).

Recently, there has been much interest in the plant-mediated links between above- and below-ground organisms (Wardle *et al*., 2004a,b). Studies have shown that a variety of subterranean organisms, including mycorrhizas, rhizophagous insects, earthworms and Collembola, can affect the growth of above-ground phytophagous insects, usually through nutritional changes in the host plant (Masters *et al*., 1993; Gange & Nice, 1997; Gange, 2000; Gange & Brown, 2002) and that above-ground consumers are, in turn, able to affect soil food webs (Wardle *et al*., 2004a,b, 2005). These changes can often be linked to a change in the nitrogen content of the host plant, but whether nitrogen addition itself can alter above-/below-ground interactions is poorly understood. This is important since nitrogenous fertilisers are applied in large quantities to a variety of crops in the UK, including long-term pasture.

There is considerable interest in the relative importance of top-down and bottom-up forces controlling organisms at each trophic level (Hairston & Hairston, 1993; Polis & Strong, 1996; Jefferies, 1999), but there have been an inadequate number of studies in this area of ecology for consistent patterns to emerge (Chen & Wise, 1999), particularly in relation to the soil environment (Wardle, 1999). More recent work above ground suggests that both forces play a role, but it is poorly known if these forces act differently on herbivores in the same assemblage and what factors underlie this variation (Denno *et al*., 2003). Top-down control may depend on the niches that species occupy. For example, in experiments by Denno *et al*. (2003), only sap-feeders were adversely affected by predation from spiders. Likewise, the release from predation by spiders increased Tomoceridae Collembola, but not other endemic collembolan families in a study by Wise (2004). Where below-ground systems have been examined, the results have been conflicting (see review of studies in coniferous forest soils by Huhta *et al*. (1998)) and, in some cases, failed to detect any effect of carnivores on lower trophic levels and plant productivity (Laakso & Setälä, 1999; Strong *et al*., 1999) or effects of nutrient enhancement on higher trophic levels (Niklaus *et al*., 2003). Other studies have, however, shown that trophic links in the soil may be strong. Santos *et al*. (1981) found that experimental reduction of predaceous mites increased bacterivorous nematode numbers, reduced bacterial numbers and reduced rates of decomposition. Wardle *et al*. (1995, 1998) also considered that top-down effects can be important in soil food webs, with evidence that trophic cascades may exist. Salminen *et al*. (1997) assessed the performance of a predatory mesostigmatid mite on soil communities. The mite regulated the densities of some prey species, which, in turn, decreased microbial activity, indicating that decomposers and decomposition in soil were, to some extent, top-down controlled. Top-down effects are also seen around the root rhizosphere where protozoans regulate rhizobacteria, thereby releasing nutrients available for plant root uptake (Moore *et al*., 2003; Bonkowski, 2004).

Bottom-up influences can operate by regulating nitrogen availability to predators (Fagan & Denno, 2004). De Deyn *et al*. (2004) and Murray *et al*. (2006) showed that an increased root biomass and increased nitrogen addition to soil ecosystems increased root feeding nematodes, respectively. However, it has been demonstrated that the effect on invertebrate fauna, after the addition of carbon, nitrogen and phosphorus to soil, did not equal the effect observed on the soil microbial biomass (Scheu & Schaefer, 1998). This indicated that the manipulation of soil invertebrates by increasing soil microbial biomass was not straightforward, and it was suggested that the unparalleled response was partly attributable to competition between soil invertebrates and microorganisms.

A major confounding factor in the studies to date has been the lack of a clear separation between the physical effects of adding organic matter in the form of detritus (compost, manure etc.) and the enhancement of soil nutrients. Detritus may increase invertebrate abundance by providing, for example, additional food (directly as organic material and indirectly through fungal growth), refugia, websites for spiders, moisture and an altered microclimate. Nutrients will leach into the soil as detritus breaks down, but the direct and indirect effects of such nutrient subsidies cannot be measured separately where these materials are used. Detrital subsidies are well known to have positive effects on some invertebrates. For example, Chen & Wise (1999) found that augmentation of the resource base with detritus led to a ten-fold increase in the density of detritivores and fungivores, and the predatory Staphylinidae and Carabidae beetles that feed on them. Similar results were found by Halaj & Wise (2002), whilst Axelsen & Kristensen (2000) revealed that incorporation of green manure into the soil also increased numbers of Collembola. Rypstra & Marshall (2005), by contrast, found no effects of a detrital subsidy on herbivores and insect predators, but an

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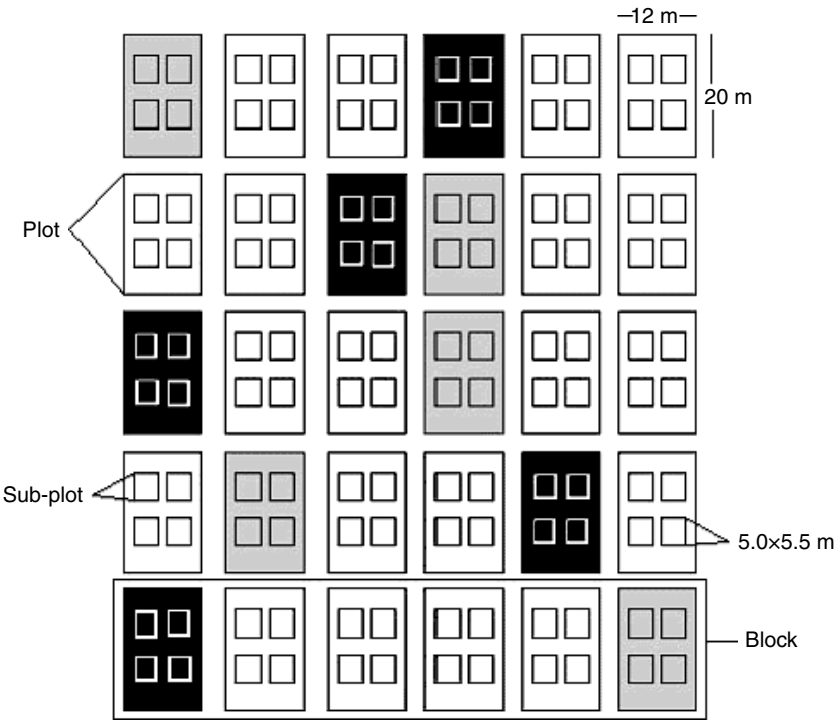


Fig. 1. The experimental site at Sourhope showing dimensions and positions of plots and subplots. Plots coloured black were treated with nitrogen plus lime (N + L) and plots coloured grey received no additions (■, N + L plot; ▩, Control plot; □, Control plot used).

increase in foliage-dwelling spider numbers and size was observed. These effects may not have been a result of increasing nutrient availability in the soil.

The effects of nutrients on invertebrate communities (that have been added directly rather than through detritus) have rarely been studied. Bird *et al*. (2000) showed that arthropod species richness increased in a Texas pine plantation after the application of nitrogen and phosphorus. It was suggested that this was probably in response to increased numbers of fungivores and detritivores in the food chain. Similarly, Gratton & Denno (2003) found an increase in linyphiid spider numbers where nitrogen and phosphate were added to plots in a salt marsh. Hemerik and Brussaard (2002) demonstrated that an impoverishment of grassland soil nutrients reduced the total number of individuals of macroinvertebrate species.

In the upland grassland ecosystem study presented here, we tested the hypothesis that adding nitrogen and lime would positively affect the numbers and diversity of epigeic (surface dwelling) Collembola and spiders. It was predicted that the addition of an enhanced resource would be reflected though the food web to the higher invertebrates, in this case spiders. Collembola were chosen to represent fungal feeders as they are important prey to spiders (Marcussen *et al*., 1999; Agusti *et al*., 2003; Harwood *et al*., 2003, 2004). Methods of soil community manipulation have been used successfully to determine changes in soil food webs and ecosystem properties in Ecotron experiments under controlled conditions (Naeem *et al*., 1994; Bradford *et al*., 2002). This study, by contrast, was designed to examine the effects of nutrient addition directly in the field.

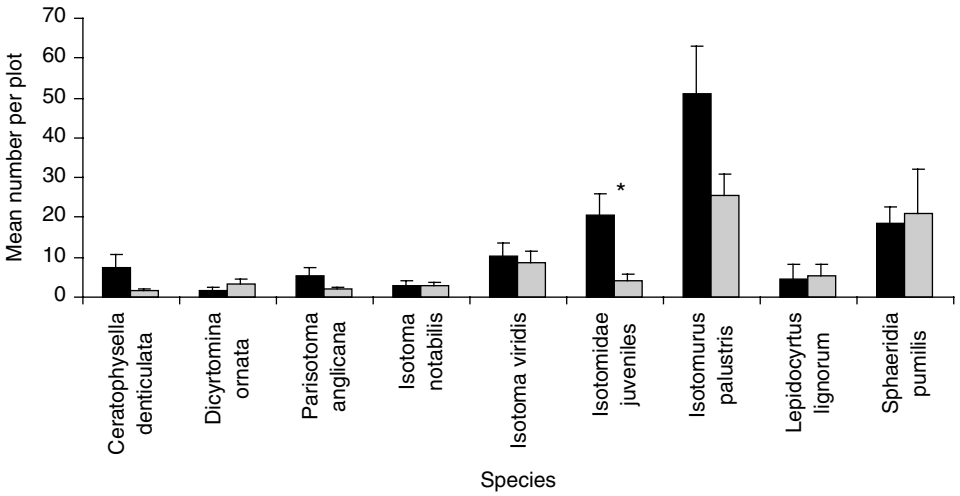
Materials and methods

Field site and treatments

The Sourhope Research Station field site (Lat: 55 : 28 : 11N; Lon: 2 : 13 : 51W) is located in the Bowmont Valley, south of Kelso in the Scottish Borders, UK. The site lies between 300–350 m in altitude and the annual rainfall is 950 mm (ten-year mean). Historically, the area was used for cereal and oat production, but more recently (the last 50 years) the area has been permanent grassland for sheep and cattle grazing (Davidson *et al*., 2002). Since 1998, when experimental work on this site began, grazing animals have been excluded. The soil is a brown podzol, of the Sourhope series (SH74711), and has been described in detail by Davidson *et al*. (2002). The site is dominated by Agrostis and Festuca grasses and has a UK National Vegetation Classification U4d (Rodwell, 1992).

In this study, we determined invertebrate species numbers in nitrogen plus lime treated plots (N + L) and untreated, control plots. The experiment was a randomised complete block design consisting of five replicate blocks (fig. 1). Each treatment was allocated at random to a plot, which measured 20×12 m. Within each main plot were four sub-plots (5×5.5 m). The treatments commenced in April 1999, as part of the long term Soil Biodiversity Programme funded by the Natural Environmental Research Council, UK. Nitrogen was added each year in early and late spring, with lime applied between the two N applications. Nitrogen was applied in the form of NH_4NO_3 granules at a rate of 240 kg ha^{-1}, and lime was applied in the form of $CaCO_3$ powder at a rate of 6000 kg ha^{-1}. Nitrogen and lime are often added together in this type of grassland system to

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Collembola species trapped, but not included in the histogram: Hypogastruridae; *Ceratophysella gibbosa*, Onychiuridae; *Protaphorura aurantiaca*, Entomobryidae; *Entomobrya nivalis*, Isotomidae; *Folsomia* sp., *Desria tigrina, Isotoma violacea,* Sminthuridae; *Dicyrtoma fusca, Dicyrtomina minuta, Sminthurides schoetti.*

Fig. 2. Mean number of Collembola of each species in the untreated (control) and nitrogen plus lime (N + L) plots from the July 2002 sampling ($n = 5$, ±SE). Data from species where there were less than two individuals per trap in both treatments have been omitted for clarity. Only Isotomidae juveniles showed a significant difference (*) (■, N + L; □, Control).

maintain soil pH at an optimum (about 6) for nitrogen uptake by plants, which results in an increased production of sward for grazing livestock. The site was mown every four weeks between May and September and the cut material removed (the sward was maintained at a height of approximately 6 cm).

Invertebrate sampling

Invertebrate sampling took place in July and October 2002, and April and June 2003, at times selected to reflect peak activity of the target invertebrate groups. Spiders and epigeic (surface dwelling) Collembola were sampled by means of pitfall traps (11 cm deep, 8 cm diameter), which were quarter filled with 25% ethylene glycol. Four traps were placed in each plot (one in each sub-plot; fig. 1) 6 m apart (total of 40 traps on each sampling occasion). The traps were removed after one week and the fauna preserved in 70% alcohol.

Identification of invertebrates

Spiders from all four sampling occasions were identified to species. Due to the time and difficulty of identifying large numbers of Collembola (Hopkin, 2000), only individuals from the July 2002 sampling were identified to species. Collembolan identification was carried out according to Fjellberg (1998) and Hopkin (2000). The key by Roberts (1993) was used for the diagnosis of spider species.

Statistical analyses

The effect of the treatments on the spider and Collembola assemblages was examined using the Canoco for Windows package (version 4.51). Following analyses using Detrended Correspondance Analysis, the community data were log transformed (Log_{10} (x + 1)) to stabilise variances and examined using Redundancy Analyses (RDA). This analysis is a canonical form of principal components analysis and was used to detect unimodal relationships between species and the treatments, allowing a distinction to be made between the communities where present.

For closer examination of the invertebrate assemblages, means for individual species were compared using one-way (Collembola data) and two-way (spider and total numbers data) ANOVAs (data were log transformed (Log_{10} (x + 1)) before analyses using Genstat 7th Edition, 7.1.0.198. Diversity indices (Shannon-Wiener, Richness and Evenness) were calculated using the 'Species Diversity and Richness II Package' (Pisces Conservation Ltd, England) and then compared using two sample *t*-tests (Minitab version 10.51Extra).

Results

Collembola

A total of 17 epigeic Collembola species were identified from the pitfall traps (fig. 2). There was no significant difference in the total number of Collembola in the control plots compared to the N + L (nutrient enhancement) plots (table 1). There was also no significant difference between the N + L and control plots in terms of Collembola species assemblage (table 2), with the exception of juvenile Isotomidae ($P = 0.01$), which were more likely to be trapped in the N + L than the control plots (table 1, fig. 2). Although not significant ($P = 0.05$), the number of *Parisotoma anglicana* was also higher in the N + L plots than the control plots. Thus, the N + L treatment had no effect on collembolan species composition but may have increased the recruitment of Isotomidae species. Consequently, species richness, evenness and diversity were not significantly different for

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Table 1. Two-way (spider and total number data, degrees of freedom = 28) and one-way (Collembola data, degrees of freedom = 4) ANOVAs showing significant differences in spider and Collembola numbers between the control (C) and nitrogen plus lime (N + L) plots in an upland grassland.

	Jul 2002		Oct 2002		Apr 2003		Jun 2003		Treatment			Time			Treatment × Time		
	C	N + L	C	N + L	C	N + L	C	N + L	F prob	SED	LSD	F prob	SED	LSD	F prob	SED	LSD
Total Collembola	74.0	144.0	73.0	57.0	61.0	94.0	96.0	278.0	NS	–	–	0.017	0.34	0.70	NS	–	–
Parisotoma anglicana	2.0	4.5	–	–	–	–	–	–	0.050	0.10	0.27	–	–	–	–	–	–
Juv Isotomidae	4.2	20.6	–	–	–	–	–	–	0.010	0.14	0.39	–	–	–	–	–	–
Total Spiders	60.2	72.6	10.4	12.0	21.6	16.6	84.0	65.4	NS	–	–	< 0.001	0.34	0.69	NS	–	–
Agyneta decora	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.40	< 0.001	0.07	0.12	< 0.001	0.11	0.22	< 0.001	0.15	0.30
Allomengea scopigera	0.0	0.0	2.4	4.2	0.0	0.0	0.0	0.00	NS	–	–	< 0.001	0.16	0.33	NS	–	–
Bathyphantes gracilis	0.0	0.0	0.0	0.0	0.2	2.4	1.6	7.20	< 0.001	0.11	0.22	< 0.001	0.15	0.31	< 0.001	0.21	0.44
Bolyphantes luteolus	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.00	NS	–	–	0.031	0.08	0.16	NS	–	–
Centromerita bicolor	0.0	0.0	0.8	1.6	3.4	3.8	0.0	0.20	NS	–	–	< 0.001	0.19	0.39	NS	–	–
Dicymbium tibiale	0.6	2.2	0.6	0.4	3.0	2.4	4.0	1.60	NS	–	–	0.019	0.26	0.54	NS	–	–
Erigone atra	0.6	3.4	0.0	0.2	1.8	2.0	0.6	7.40	< 0.001	0.19	0.38	0.002	0.27	0.54	0.026	0.38	0.77
Erigone dentipalpis	3.6	15.2	0.0	0.2	0.8	0.8	1.6	3.00	0.012	0.19	0.40	< 0.001	0.27	0.56	0.047	0.39	0.79
Lepthyphantes ericaeus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.4	NS	–	–	< 0.001	0.08	0.17	NS	–	–
Lepthyphantes tenuis	0.0	0.2	0.2	0.2	1.0	0.2	2.0	2.0	NS	–	–	< 0.001	0.19	0.39	NS	–	–
Monocephalus fuscipes	0.0	0.0	0.0	0.0	0.8	0.6	0.0	0.2	NS	–	–	0.008	0.13	0.26	NS	–	–
Oedothorax retusus	28.8	21.4	0.6	0.0	1.0	0.4	32.4	17.8	0.002	0.11	0.23	< 0.001	0.16	0.33	NS	–	–
Pachygnatha degeeri	2.6	0.8	0.2	0.4	1.4	0.8	0.6	1.8	NS	–	–	0.007	0.17	0.35	0.007	0.25	0.50
Pardosa palustris	2.0	0.8	0.0	0.2	0.8	0.4	8.2	5.2	NS	–	–	< 0.001	0.26	0.54	NS	–	–
Pardosa pullata	0.4	0.0	0.0	0.0	0.2	0.0	2.8	0.4	< 0.001	0.09	0.19	< 0.001	0.13	0.26	< 0.005	0.18	0.37
Savignya frontata	0.6	1.0	0.0	0.0	0.2	0.4	0.4	0.8	NS	–	–	0.026	0.17	0.34	NS	–	–
Tiso vagans	5.0	6.8	0.2	0.0	7.4	3.8	12.2	7.6	NS	–	–	< 0.001	0.24	0.48	NS	–	–
Trochosa ruricola	0.0	0.0	0.0	0.0	3.4	0.8	0.2	0.0	0.009	0.10	0.20	< 0.001	0.13	0.28	0.004	0.19	0.39
Walckenaeria vigilax	0.6	0.4	0.0	0.0	0.0	0.0	0.0	0.00	NS	–	–	< 0.001	0.08	0.17	NS	–	–
Juvenile Linyphiidae	12.0	18.4	3.2	2.8	1.4	1.2	7.0	4.2	NS	–	–	< 0.001	0.16	0.33	NS	–	–
Juvenile Tetragnathidae	0.0	0.0	0.6	0.2	0.0	0.0	0.0	0.0	NS	–	–	0.025	0.09	0.19	NS	–	–

Differences are shown for the effects of sampling date and treatment, and the interaction between these variables. Species data where there were no significant differences (NS) for any of the variables are omitted for clarity. Data was analysed using $\log_{10}(+1)$ transformed data. The means are actual means ($n = 5$). A full list of Collembola and spider species is available in figs 2 and 3.

Table 2. Redundancy analyses (RDAs) comparing communities of Collembola and spiders in the nitrogen plus lime (N + L) and untreated (control) plots in an upland grassland ($n = 5$).

Date	Invertebrate group	F-ratio	*P*-value
July 2002	Collembola	1.11	0.34
	Spiders	**3.20**	**0.02**
October 2002	Spiders	1.04	0.35
April 2003	Spiders	1.78	0.07
June 2003	Spiders	**5.82**	**0.00**
All dates	Spiders	**3.97**	**0.00**

N + L communities which differed significantly from the control are highlighted in bold.

the Collembola in the N + L compared to the control plots (table 3).

Spiders

Forty-four spider species belonging to four families were identified, including six Lycosidae and only one Thomididae and Tetragnathidae (fig. 3). More than 80% of the species were Linyphiidae (36 species). In July 2002 and June 2003, the effect of N + L applications on the community composition was significant (table 2), with the N + L plots having a different species assemblage compared to the control plots (fig 3). *Erigone atra*, *Erigone dentipalpis*, *Bathyphantes gracilis*, *Pardosa pullata* and *Trochosa ruricola* were more prevalent in the N + L plots, whilst *Oedothorax retusus* and *Agynatha decora* were significantly more abundant in the control plots (table 1). However, only *O. retusus* had no time treatment interaction and, therefore, only this species can be concluded to have been influenced by the addition of N + L to the plots. Despite this, the diversity indices failed to show any significant differences between the N + L and control communities (table 3).

There were no treatment differences in abundance or species composition in October 2002 or April 2003 between either total numbers or species of spiders. The number of individuals caught per plot was very low: 10.0 ± 3.1 and 21.6 ± 8.7, and 12.0 ± 2.7and 16.6 ± 5.3 in the control and N + L treatments, respectively, for each year (mean number ±SE). This was a particularly dry time of year and may have been the cause of low numbers of invertebrates. There were no differences in species assemblages at these times (table 2).

Discussion

In contrast to the hypothesis, the effect of enhancing the resource base three years prior to sampling the invertebrate community of upland grassland was no increase in invertebrate (Collembola and spiders) abundance accompanied by no change in species diversity of the invertebrate communities at the Sourhope site. However, the species composition did change. Litter-dwelling isotomid Collembola increased in number in the nutrient enhanced (N + L) plots. Total numbers of spiders did not increase significantly, but species composition did change (tables 1 and 2, fig. 3), due mainly to an increase in the number of *O. retusus* in the control plots. Conversely, trends in the Collembola were different from those of Cole *et al*. (2005, soil samples taken from different areas of the same plots in this study) at the same field site, who found that soil-dwelling (euedaphic) Collembola numbers increased in the N + L plots at the Sourhope site compared to the control (dominated by *Folsomia quadrioculata* and *Protophorura armata*) with no significant difference in species diversity between the treated and untreated plots (sampled in 1999 and 2000). In the control plots, the surface-dwelling (epigeic) species in our study had a higher species diversity (Shannon-Weiner Index 1.6) than did the euedaphic Collembola in the study by Cole *et al*. (2005) (Shannon-Weiner Index 1.24). However, in the N + L plots, species diversity was identical (Shannon-Weiner Index 1.53). In the study by Cole *et al*. (2005), soil-dwelling predatory mite biomass increased in response to N + L, unlike the density of spiders in our study. In agreement with our study, Salamon *et al*. (2006) found very weak bottom-up effects of nutrient addition with spider density remaining unchanged. Their study also found a moderate increase in Collembola density (due mainly to increased numbers of Isotomidae) in plots with various forms of nutrient resources added.

Only one species of spider and one group of Collembola in the epigeic arthropod communities responded to the bottom-up effects of three years of chemical inputs. Importantly, changes were induced that were unrelated to the confounding physical effects of the organic matter (manures, compost etc.) used in most previous studies.

Collembola

The N + L (nutrient enhanced) and control plots were fairly similar in species composition and total number. Juvenile Isotomidae and *P. anglicana* were more abundant (although the latter was not significant) in the resource-enhanced treatments. It is uncertain whether this is a direct effect, since increased resources may have caused indirect effects, for example, as a consequence of an altered microflora and/or -fauna. Plant biomass on the site was reported to be consistently higher in the N + L compared to the control plots over the course of the experiment (see report by Burt-Smith, 2003), and this increase in plant productivity was shown to generate dryer soils (Burt-Smith, 2003). Despite the removal of mown plant material from the site, Burt-Smith (2003) estimated that soils in the N + L plots contained more dead plant material than soils from the control plots. This organic material is likely to be a factor in promoting microbial colonisation (Lohm *et al*., 1977) and possible increased feeding opportunities and habitat for Collembola, thereby changing the species composition of spiders (bottom-up effect). Lindberg & Persson (2004) also reported no effect on collembolan numbers with nitrogen inputs into a boreal forest soil, but there was a shift in the species of Collembola present.

Spiders

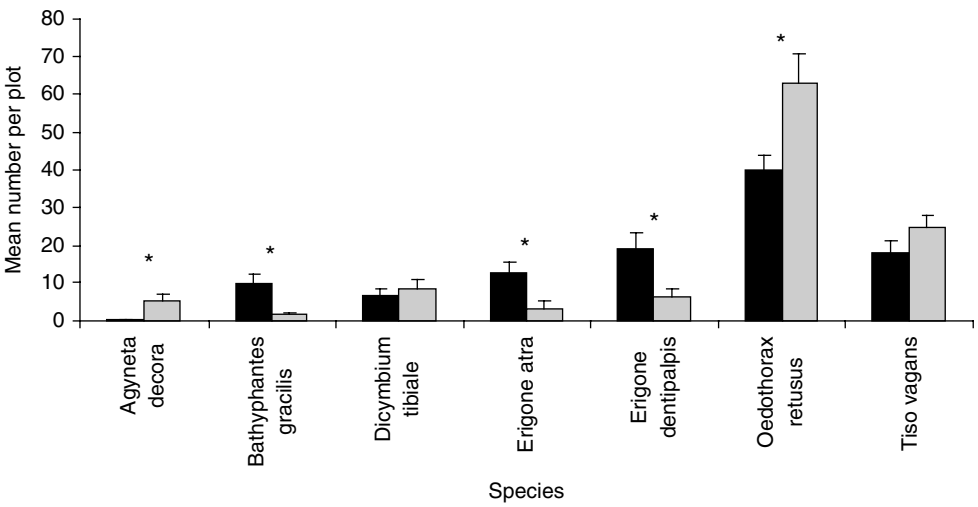
For many of the spider species in this study, there was an effect of sampling time (table 2) as species become more or less abundant at different times of the year. The spider community at Sourhope was similar to those found in other studies of British upland grassland spiders using pitfall trapping (Coulson & Butterfield, 1986; Rushton *et al*., 1987), with many species being aeronauts (e.g. *E. dentipalpis* and *B. gracilis*). The number of non-Linyphiidae species is known to decrease with altitude, whilst the number of Linyphiidae

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Table 3. Mean diversity indices (Shannon-Wiener, Species Richness and Evenness) for spider and Collembola assemblages on the nitrogen plus lime (N+L) and untreated (control) plots in an upland grassland.

Indices	Spiders (all dates)		Collembola (July 2002)	
	N+L	Control	N+L	Control
Shannon Wiener	2.30±0.02	2.10±0.11	1.53±0.10	1.60±0.12
Species Richness	19.60±0.93	20.60±1.70	8.80±0.37	8.00±0.71
Evenness	0.62±0.01	0.56±0.03	0.54±0.04	0.56±0.04

There were no significant differences in diversity between the two treatments (two-sample *t*-tests, $n=5$, means±SE).



Spider species trapped, but not included in the histogram: Lycosidae; *Pardosa palustris*, *Pardosa pullata*, *Trochosa terricola*, *Xerolycosa miniata*, *Trochosa ruricola*, *Alopecosa pulverulenta*, Tetragnathidae; *Pachygnatha degeeri*, Thomisidae; *Xysticus cristatus*, Linyphiidae; *Ceratinella brevipes*, *Walckenaeria vigilax*, *Walckenaeria atrotibialis*, *Walckenaeria acuminate*, *Dicymbium nigrum*, *Pocadicnemis juncea Hypomma bituberculatum*, *Oedothorax gibbosus*, *Silometopus elegans*, *Tapinocyba praecox*, *Monocephalus fuscipes*, *Lophomma punctatum*, *Gongylidiellum vivum*, *Savignya frontata*, *Micrargus herbigradus*, *Erigonella hiemalis*, *Centromerita bicolour*, *Centromerita concinna*, *Bathyphantes approximates*, *Bathyphantes parvulus*, *Bolyphantes luteolus*, *Lepthyphantes tenuis*, *Lepthyphantes zimmermanni*, *Lepthyphantes mengei*, *Lepthyphantes flavipes*, *Lepthyphantes tenebricola*, *Lepthyphantes ericaeus*, *Microlinyphia pusilla*, *Allomengea scopigera*.

Fig. 3. Mean number of spiders of each species per pitfall trap in the untreated (control) and nitrogen plus lime (N+L) plots from all sampling dates combined ($n=5$, ±SE). Only species where abundances were >6 per plot in both treatments or where there was a significant difference (*) are plotted (■, N+L; □, Control).

species shows no decline (Coulson & Butterfield, 1986). Many of the species trapped on the site are associated with wet habitats (e.g. *Allomengea scopigera* and *Hypomma bituberculatum*). Rushton *et al*. (1987) found that from the 49 species they trapped, five species preferred open highly-managed, temporary leys. This may be a consequence of the aeronautic ability of many Linyphiidae (Bell *et al*., 2005), making them capable of early colonisation.

The spider assemblages on the plots were dominated by *E. atra*, *E. dentipalpis* and *O. retusus* and *Tiso vagans* (table 1, fig. 3). All of these species are characteristic of grasslands, common and highly dispersive due to their aeronautic abilities (Harvey *et al*., 2002), and *E. atra* and *E. dentipalpis* are often found together in the same habitat (Thornhill, 1983). The increase in nutrient resources resulted not only in an increased plant biomass (reported in Burt-Smith, 2003) but also in increased numbers of juvenile Isotomid collembolans. Collembola are an important food source to Linyphiidae (Marcussen *et al*., 1999; Agusti *et al*., 2003; Harwood *et al*., 2003, 2004). However, the slight change in species assemblage did not considerably influence the community composition of the spiders. Interestingly, the above spider species have been reported to be common in arable fields where soils are well fertilised and kept neutral or calcareous (Agusti *et al*., 2003; Harwood *et al*., 2003, 2004).

Bird *et al*. (2000) found that the species richness of soil and litter arthropods increased and that there was no change in Shannon diversity in response to nutrient enhancement following the addition of nitrogen and phosphorus to a pine plantation. The communities at Sourhope showed no significant change in Shannon diversity or species richness (table 3) although there was a significant change in response

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to nutrient enrichment in the number of individuals per species for some taxa (table 1), indicating that there was a change in community composition. In grassland systems under restoration, macroinvertebrate diversity was found to be highest at intermediate stages of soil fertilisation (Berg & Hemerik, 2004). Indeed, Enchytraeid and Collembola numbers were found to increase only 2–3 years after a nitrogenous input ($90\,kg\,N\,ha^{-1}$) into a forest soil (Huhta *et al*., 1967; Huhta *et al*., 1969).

Chen & Wise (1999) also found a significant bottom-up effect of nutrient addition to leaf litter invertebrates with the addition of chopped mushrooms and potatoes (spiders and Collembola increased two- and three-fold, respectively). Likewise, experiments enhancing detritus in an agro-ecosystem resulted in an increase in Collembola populations by 2–4 times and ground beetles two- to three-fold (Halaj & Wise, 2002). However, these two studies were also likely to have changed the physical properties of the soil surface layer (contributing to shelter, fungi, moisture etc.) and the results confound the effects of enhanced nutrients alone. The altered communities in our experiment were not subject to structural change.

Model-based predictions, using experimentally assembled grassland food chains, have implied a predominance of bottom-up control in food chain structure (Schmitz, 1993). Nutrient supply directly enhanced primary productivity and plant and herbivore biomass (Schmitz, 1994). Experimentally changing spider abundance caused a classic 'trophic cascade' in which herbivore biomass increased and edible plant biomass decreased (Schmitz, 1994). However, the effect of top-down control in soil ecosystems appears to be weaker and less consistent (Kajak, 1995). Wise & Chen (1999), for example, found that densities of the wolf spider *Schizocosa* were not affected by predation from higher predators (e.g. birds) in exclusion experiments.

Gratton & Denno (2003) demonstrated an increase in Linyphiidae on fertilised plots ($44.5\,g\,m^{-2}$ ammonium nitrate, $13.8\,g\,m^{-2}$ acid phosphate). The response of particular herbivores and predators to the increased nutrient resources was believed to be, in part, habitat dependent (increase in plant biomass).

Moisture and vegetation height have an effect on spider species communities (Rushton *et al*., 1987; Marc *et al*., 1999; Moretti *et al*., 2002; Harwood *et al*., 2003). Above-ground arthropod species richness and abundance of four trophic groups (detritivores, herbivores, parasites and predators) were increased in plots where nitrogen fertiliser was added and plant production was higher (Siemann, 1998). This study also made a distinction between modern and historically nutrient enriched sites, stating that plant diversity and composition are influential in the control of herbivores by determining available resources and influencing herbivore and parasite/predator interactions (Siemann, 1998).

The influence of vegetation structure in our study was kept to a minimum with regular cutting of the plots during the growing season. However, the effect of nitrogen on plant productivity decreased moisture in the N + L plots, presumably through increased plant biomass and evaporation (Murray *et al*., 2006). So, although we maintained a relatively uniform plant structure by cutting, our efforts to remove the physical effects of nutrient enhancement on the microclimate were not entirely met. Thus, an indirect effect of nutrient enhancement, other than an altered micro-flora and -fauna, may have been involved.

Other considerations

Liming, a commonly employed practice in grassland management, raises soil pH. Ormerod & Rundle (1998) demonstrated that, five and six years after either acidifying or liming soils, the total numbers of spiders were reduced. At our study site, a decrease in spider numbers was not evident, even though the mean soil pH at the site increased in the N + L plots (control 4.54, N + L 6.87, reported by Burt-Smith (2003)).

Our study highlights the importance of multiple sampling occasions to assess treatment effects. It is one of a few demonstrating a moderate effect of nutrient inputs on invertebrate community structure (Salamon *et al*., 2006) and, to our knowledge, only one of three in which an upland grassland has been the focus (Cole *et al*., 2005; Murray *et al*., 2006). Indeed, it is suggested that a study examining experimental reductions of predator numbers in grassland communities would give an indication of the importance of top-down forces in this system. Further studies of other invertebrate groups, such as predatory Coleoptera and their prey, would be worthwhile in order to address consistency of effects.

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