

Influence of disturbance and nitrogen addition on plant and soil animal diversity in grassland

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Abstract

Two key determinants of biological diversity that have been examined in aboveground and aquatic systems are productivity, or resource supply, and physical disturbance. In this study, we examined how these factors interact under field conditions to determine belowground diversity using microarthropods (mites and Collembola) as our test community. To do this, we established a field manipulation experiment consisting of crossed, continuous gradients of nitrogenous (N) fertilizer addition (up to 240 kg N ha⁻¹) and disturbance (imitated trampling by cattle) to produce a gradient of soil nutrient availability and disturbance. Due to the relatively short-term nature of our study (i.e. 2 years), we only detected minimal changes in plant diversity due to the experimental manipulations; in the longer term we would expect to detect changes in plant diversity that could potentially impact on soil fauna. However, disturbance reduced, and additions of N increased, aboveground biomass, reflecting the potential effects of these manipulations on resource availability for soil fauna. We found that disturbance strongly reduced the abundance, diversity, and species richness of oribatid mites and Collembola, but had little effect on predatory mites (Mesostigmata). In contrast, N addition, and therefore resource availability, had little effect on microarthropod community structure, but did increase mesostigmatan mite richness and collembolan abundance at high levels of disturbance. Oribatid community structure was mostly influenced by disturbance, whereas collembolan and mesostigmatan diversity were responsive to N addition, suggesting bottom-up control. That maximal species richness of microarthropod groups overall occurred in undisturbed plots, suggests that the microarthropod community was negatively affected by disturbance. We found no change in microarthropod species richness with high N additions, where plant productivity was greatest, indicating that soil biotic communities are unlikely to be strongly regulated by competition. We conclude that the diversity of soil animals is best explained as a combination of their many varied life history tactics, phenology and the heterogeneity of soils that enable so many species to co-exist.

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1. Introduction

Understanding the factors that explain the co-existence of species and thereby the maintenance of biodiversity is a major theme of community ecology. To date, most studies that have considered this issue have been conducted on either marine or aboveground communities (Huston, 1994; Lawton, 2000; Mittelbach et al., 2001). Until recently, far less attention has been given to understanding how soil biodiversity is maintained, despite soil being the habitat for

the majority of Earth's terrestrial species (Wardle, 2002). Now there is a growing interest in this belowground diversity, largely as a result of advances in techniques that enable us to more readily characterize belowground diversity (e.g. Blaxter and Floyd, 2003; Young and Crawford, 2004), but also because of an increasing recognition amongst ecologists that soil biota have important roles in ecosystem function, especially organic matter turnover and nutrient mineralization (Hooper et al., 2000; Wardle, 2002; Heemsbergen et al., 2004; Wardle et al., 2004; Bardgett, 2005) and the flow of material through ecosystems (Bardgett et al., 2005a). As a consequence, understanding the factors that regulate soil

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biological diversity now represents a major challenge in community and ecosystem ecology.

Two key determinants of diversity that have been examined in aboveground and aquatic systems are productivity, or resource supply, and physical disturbance. At local scales, peak diversity is often observed to occur at intermediate levels of productivity, creating the hump-backed model (e.g. Grime, 1973a, b; Al Mufti et al., 1977; Grace, 1999), with declining diversity at higher levels of productivity being due to competitive exclusion. However, periodic mortality events such as predation or physical disturbance can limit competitive exclusion also resulting in unimodal relationships between disturbance frequency or intensity and diversity, as hypothesized by the “intermediate disturbance hypothesis” of Connell (1978). Assuming the same rules apply belowground, this would result in aboveground and belowground diversity being positively related (Wardle et al., 2004).

The response of the soil microbial community to stress and disturbance gradients has been examined experimentally by Degens et al. (2001), who observed unimodal patterns of soil microbial diversity in response to stress (metal toxicity and pH) and disturbance (frequency of freeze–thaw) gradients, a pattern consistent with Grime’s model. This suggests that some components of the soil community, particularly microbes, might be structured by the same kinds of mechanisms that structure plant communities, and that competitive exclusion might be an important feature determining the abundance and components of some groups of soil biota, especially fungi (Wardle, 2001, 2002). However, in a review of studies that examined the responses of a wide range of decomposer soil organisms to stress and disturbance gradients, Wardle (2002) concluded that since most species were not excluded by competition when resource supply was elevated, soil biodiversity is not strongly regulated by competition. In a previous study, Cole et al. (2005) examined how alleviating soil nutrient stress (by using field-scale plots that had received factorial additions of fertilizer and lime) influenced microarthropod community structure and diversity in temperate grassland. From this study, Cole et al. (2005) also found little evidence of competitive exclusion of microarthropod species, concluding that increased predation in microarthropod communities of more fertile sites might limit competitive interactions. However, this study was conducted under conditions of limited soil disturbance and had single levels of resource addition, via fertilizer nitrogen (N) addition.

In this second, but independent, study we aimed to examine under field conditions how soil disturbance and nutrient availability interact to determine belowground diversity. To do this, we established a field manipulation experiment based on that of Burke and Grime (1996) that consists of crossed, continuous gradients of fertilizer addition and disturbance intensity to produce a gradient of soil nutrient stress (resource addition) and disturbance. In this study, we doubled the quantity of N fertilizer that

was applied by Cole et al. (2005) to further enhance resource availability, and therefore the possibility of invoking competitive interactions amongst microarthropods. Our highest level of disturbance was designed to mimic an infrequent, but intense period of cattle trampling (Burke and Grime, 1996). We used microarthropods (mites and Collembola) as our test community, since numerically they are the most abundant and diverse meso-faunal group in temperate grassland soils (Bardgett and Cook, 1998) and they are known to be functionally important in these situations, in terms of their role in decomposition processes (Cragg and Bardgett, 2001; Cole et al., 2006) and nutrient supply to plants (Bardgett and Chan, 1999; Cole et al., 2004). In accordance with ecological theory (Grime, 1973a, b), we test whether maximal species richness of the microarthropod community occurred at intermediate levels of nutrient stress and soil disturbance. Due to the relatively short-term nature of our study (2 years), we did not expect significant changes in plant community composition and diversity to occur. However, we did expect changes in plant biomass to respond significantly to the nutrient availability and disturbance treatments. Since soil animal abundance and diversity are known to be highly dependant upon the quality and quantity of plant-derived resources available (Hansen, 2000; Hansen and Coleman, 1998), we also report on short-term changes in plant community productivity and structure.

2. Materials and methods

2.1. Site description and experimental design

The study site was the N.E.R.C. Soil Biodiversity Programme site at Sourhope in the Cheviot Hills, South-east Scotland, UK (55°28′30″N/2°14′W). The site is a semi-improved upland grassland at an altitude of circa 350 m, with annual rainfall of 1117 mm and air temperatures in the range of 3.8–12.2 °C (Grayston et al., 2001). The plant community is dominated by *Agrostis capillaris*, *Festuca ovina*, *Poa pratensis* and *Anthoxanthum odoratum*. The grassland type corresponds to U4b in the UK National Vegetation Classification (NVC), described as an *Agrostis–Festuca–Galium* grassland (Rodwell, 1992). The soil is a humic brown soil from the Sourhope series (SH 74711) (Kenny, 1998). The main experimental design at the site consists of five replicate blocks, with each block containing six plots (12 m × 20 m) with a range of treatments allocated randomly to plots by site management (Usher et al., 2006). In December 1999, we set up an experiment within the main soil biodiversity experiment, by establishing experimental plots within a control plot (one per block) that was not treated by the Sourhope site management, resulting in five replicated and randomly positioned experimental areas, each of 3 m × 3 m size. Within each of these five experimental areas, we established a crossed, continuous gradient of fertilizer addition (0, 60, 120, 180 and 240 kg N ha⁻¹) and disturbance intensity (0%, 25%, 50%,

75% and 100% ground cover disturbed), using the design of Burke and Grime (1996) (Fig. 1). This involved setting up a continuous and crossed grid of 25 individual 0.5 m² sub-plots, each with a 0.5 m border that acted as a “buffer” zone where the vegetation received the same treatment as the sub-plot immediately adjacent to it; this reduced the possibility of the surrounding vegetation and soil contributing to any “edge” effects. Orientation of the nitrogen and disturbance treatments to these plots was randomly assigned according to the design of Burke and Grime (1996).

Annual applications of N as ammonium nitrate fertilizer were made to the individual sub-plots within the experimental gradient in February 2000 and April 2001. Following the initial setup and disturbance of the plots in December 1999, plots were disturbed on a second occasion in December 2000. The various levels of disturbance were achieved by breaking up the soil structure across the required area cover within each 0.5 m² sub-plot using an implement that consisted of a metal pipe (4 cm diameter) with a cross blade (4 cm × 4 cm) welded to one end. The implement was driven into the ground to approximately 10 cm depth and twisted to mimic the effects of cattle trampling.

2.2. Sampling

Assessments of plant diversity were made on the plots on 1–18 August 2000 and 20–23 August 2001 using point quadrat techniques. Relative species abundance for both plants and microarthropods were expressed as the Shannon Wiener diversity index (H), an evenness index (J) and as cumulative species richness (R), calculated as described in Begon et al. (1996). Diversity indices for microarthropods as a whole (mites + Collembola) were calculated, as well as indices for these groups individually. Further, as a coarse indicator of functional diversity belowground, indices were calculated for the diversity of predatory and non-predatory

mites separately. To assess the influence of our treatments on aboveground productivity, vegetation on all the plots was cut to a sward height of 6 cm on 17–18 August 2000 and 28–29 August 2001. Vegetation from each sub-plot was oven dried at 70 °C for 1 week prior to being weighed to obtain aboveground biomass.

Three soil cores (3 cm diameter to 5 cm depth) were taken from each plot (0.5 m²) with 0%, 50% and 100% disturbance and 0, 120 and 240 kg N ha⁻¹ only on 17 August 2000 and 10 July 2001. Microarthropods were extracted from the three cores combined by Tullgren funnel for 96 h. Microarthropods were stored in 70% industrial methylated spirits containing 5% glycerol. Total counts of mites and collembolans were made on samples collected both in 2000 and 2001, but microarthropod species abundance was only recorded on samples collected in 2001. Collembola were identified according to Hopkin (2000) and adult oribatid and mesotigmatid mite species were identified using a variety of taxonomic descriptions, but mostly based on the descriptions of Krantz (1978).

2.3. Data analysis

Annual variability in plant biomass, plant diversity measures and microarthropod abundance, and their response to the site manipulations, were examined by repeated measures ANOVA using SAS v 8 (SAS, 1989, 1990) with nitrogen and disturbance as main factors and year as repeat. The response of measures of microarthropod group diversity and abundance in 2001 to the experimental manipulations was examined by two-way ANOVA in SAS (SAS, 1990) with nitrogen and disturbance as main factors. When treatment effects were found to be significant ($P < 0.05$), a Tukey's HSD multiple comparisons test was used to compare treatment means. Square root transformations of some variables were necessary to meet homogeneity criteria for ANOVA and Mauchly's test of sphericity for repeated measures ANOVA (SAS, 1990).

3. Results

3.1. Plant community

Aboveground biomass was significantly reduced by disturbance (Table 1), but this effect was only seen in 2000 (Fig. 2a) when the highest level of disturbance reduced plant biomass by 74% relative to the control. Plant biomass only responded to the N treatments at the second year's sampling (Fig. 2b), with plant biomass being 64% greater in the plots receiving 240 kg N ha⁻¹ yr⁻¹ than in control plots. In contrast, disturbance had no effect on plant diversity (Fig. 2c), evenness or richness (Table 1). Plant species diversity, measured using the Shannon Wiener index, was seen to respond to the N fertilizer early in the study (2000), being maximal at intermediate levels of N addition (Fig. 2d). Overall, more plant species were

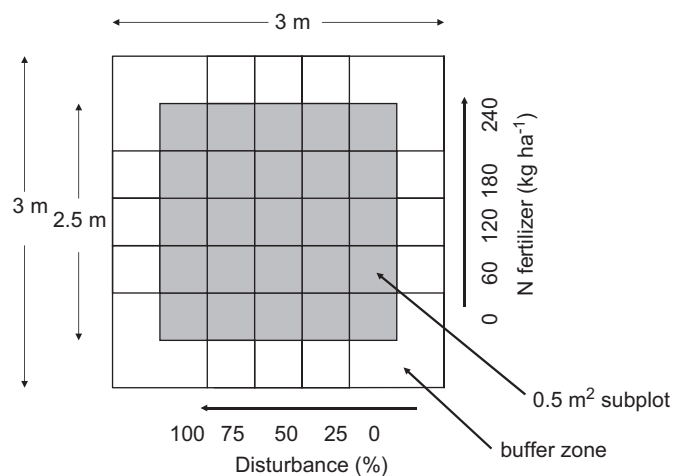


Fig. 1. The layout of the disturbance–N addition experimental plots (Burke and Grime, 1996).

Table 1
F-statistics from repeated measures analysis of variance among measures of plant community structure and biomass and mite and collembolan abundance

	d.f.	Shoot biomass ^a	Plant <i>H</i>	Plant <i>J</i> ^a	Plant <i>R</i> ^a	Total mites (Oribatida + Mesostigmata) ^a	Collembola abundance ^a
Between subjects effects:							
Disturbance	2	8.15**	0.67	0.27	1.03	7.47**	7.03**
Nitrogen	2	2.28	1.76	1.23	1.35	0.37	2.48
Disturbance × Nitrogen	4	0.11	0.29	0.23	0.12	1.03	2.11
Within subjects effects:							
Year	1	24.84***	12.74 **	0.29	28.85***	52.41***	17.79**
Year × disturbance	2	21.95***	0.14	0.76	1.62	0.65	0.19
Year × Nitrogen	2	4.80*	3.52*	1.01	3.16	0.11	0.75
Year × disturbance × nitrogen	4	1.16	0.51	0.33	1.67	2.48	3.32*

^aSquare root transformed.

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

***Significant at $P < 0.0001$.

recorded on the experimental plots in 2001, but while this was significant, the data show that this corresponded to only a couple of additional species being recorded.

3.2. Microarthropod abundance

Irrespective of the N manipulations, disturbance reduced the density of mites (oribatids + mesostigmatans) after 1 year (2000), but only significantly so for the highest disturbance treatment, where mite numbers were 57% lower than in the control plots (Fig. 2e; Table 1). By the second sampling date in 2001, this trend remained but was no longer significant (Fig. 2e). However, when individual groups of mites were considered, disturbance significantly reduced oribatid mite abundance, but not mesostigmatan abundance, in 2001 (Table 2; Fig. 3a). In contrast, there was no effect of N addition on the abundance of mites collected from the plots in either year.

Collembola densities were also reduced by disturbance (Fig. 3a); mean densities in the control plots were 28,256 m⁻², whereas in the most disturbed plots densities were only 21,651 m⁻², representing a reduction of 23%. However, the addition of N to plots had a marked influence on this response; at high levels of disturbance (100%) collembolan densities increased with increasing N addition (Table 3, Fig. 4c). Further, maximal collembolan density (43,906 m⁻²) was achieved at intermediate levels of both stress and disturbance in 2001 (Fig. 4b). Overall, greater densities of both mites and Collembola were collected from the experimental plots in the second year of sampling, with mean densities being 21,007 and 18,668 m⁻² in 2000, and 42,752 and 27,323 m⁻² in 2001, for mites and Collembola, respectively.

3.3. Microarthropod diversity

Disturbance reduced almost all our measures of diversity of the microarthropod groups, other than the Mesostigma

(Table 2). At the highest level of disturbance, there was a significant reduction in the diversity index for oribatids and Collembola (Fig. 3b). Species richness of oribatids and Collembola was also significantly reduced by the highest level of disturbance, although intermediate levels of disturbance (i.e. 50%) did not significantly reduce collembolan richness relative to the control (Fig. 3c). In contrast, N addition had very little effect on microarthropod community structure, although there was significant interactive effect of N and disturbance on mesostigmatan mite richness; mean species richness increased from 1.1 to 1.4 when 240 kg N ha⁻¹ yr⁻¹ was added to plots that were disturbed (100%), whereas in the control plots (0% disturbance), mesostigmatan richness decreased from 1.4 to 1 with N addition (240 kg N ha⁻¹ yr⁻¹).

4. Discussion

We set out to test how belowground animal communities responded to resource addition, in the form of N fertilizer, and disturbance, which are two major determinants of aboveground diversity. We found that all microarthropod groups showed marked responses to the nutrient-disturbance manipulations, but there was no evidence to suggest that microarthropod diversity at the local scale conforms to the hump-backed model of Grime (1973a, b), at least in the short term. In addition, in contrast to the intermediate disturbance hypothesis (Connell 1978) that states that maximal diversity occurs at intermediate levels of disturbance, we found that maximal diversity and species richness of all microarthropod groups occurred in undisturbed plots, suggesting that the microarthropod community was negatively related to disturbance. We did find, however, that the response of soil organisms to N addition could be predicted, to some extent, by their taxonomic identity, in that the response of species within broad taxonomic groups to N addition was similar. In particular, the structure and dynamics of the oribatid community were

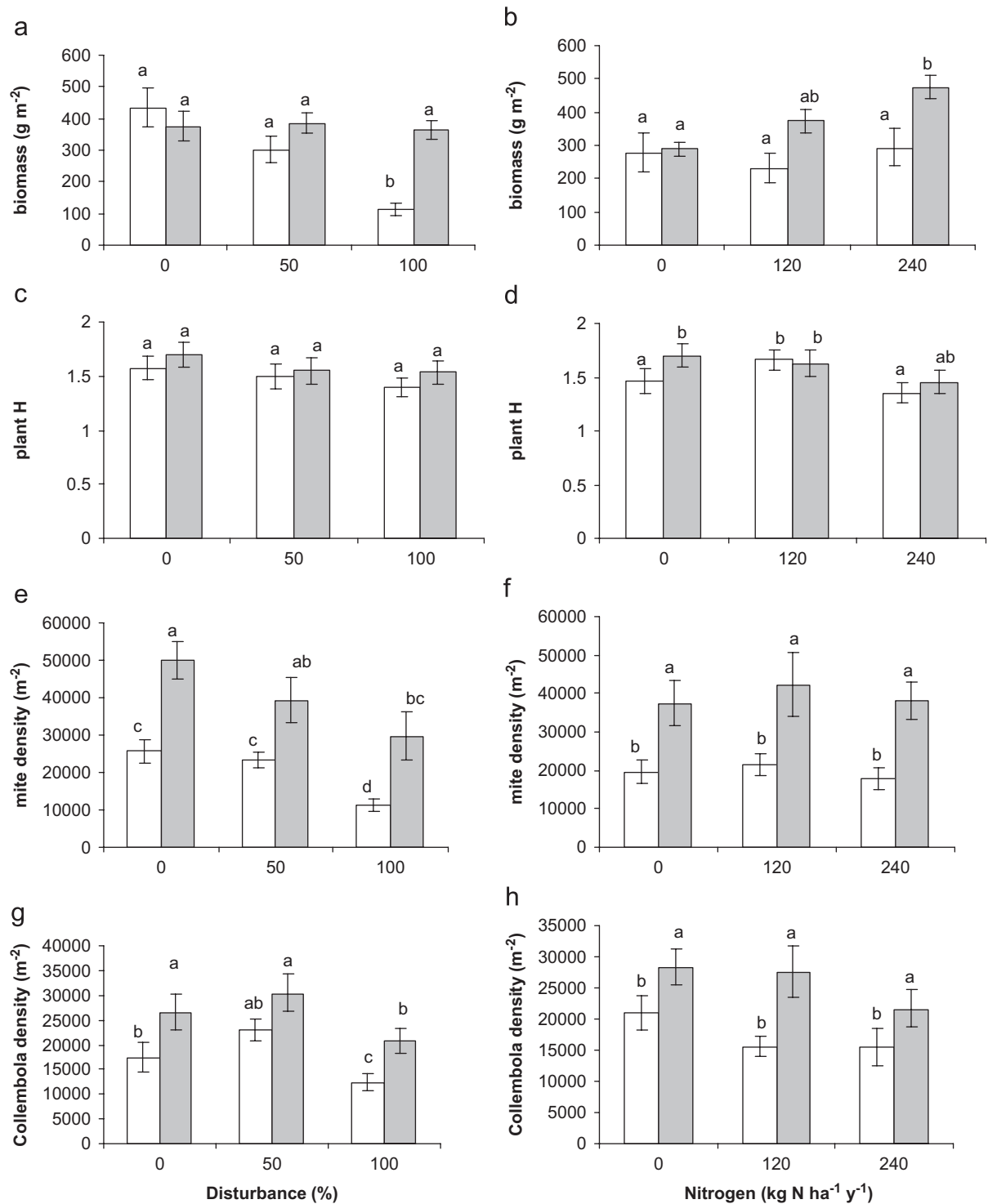


Fig. 2. Response of plant biomass, plant diversity (H), Collembola and total mite abundances to disturbance and nitrogen manipulations in 2000 (open bars) and 2001 (shaded bars). Error bars represent standard errors and bars bearing the same letter do not differ at $P < 0.05$.

most strongly influenced by top-down forces (disturbance), whereas Collembola and mesostigmatan diversity was most responsive to bottom-up controls (i.e. resource availability). In line with our hypothesis that aboveground diversity would not respond to the manipulations in the time frame of our experiment, we detected minimal changes in plant diversity. We discuss these findings in turn.

4.1. Response of plant community

Disturbance had no effect on plant diversity overall and only reduced aboveground plant biomass in the first year of study. Recovery of plant biomass by the second year of study might have been promoted by soil improvement through N additions, since plant biomass only responded

Table 2
F-statistics from analysis of variance for measures of microarthropod group abundance in 2001

	d.f.	Total mites (Oribatida + Mesostigmata)	Oribatida ^a	Mesostigmata	Collembola
Disturbance	2	2.07	11.98***	0.43	3.59*
Nitrogen	2	0.52	0.02	0.10	1.84
Disturbance × Nitrogen	4	1.55	0.77	1.80	3.59*

^aSquare root transformed.

*Significant at $P < 0.05$.

***Significant at $P < 0.0001$.

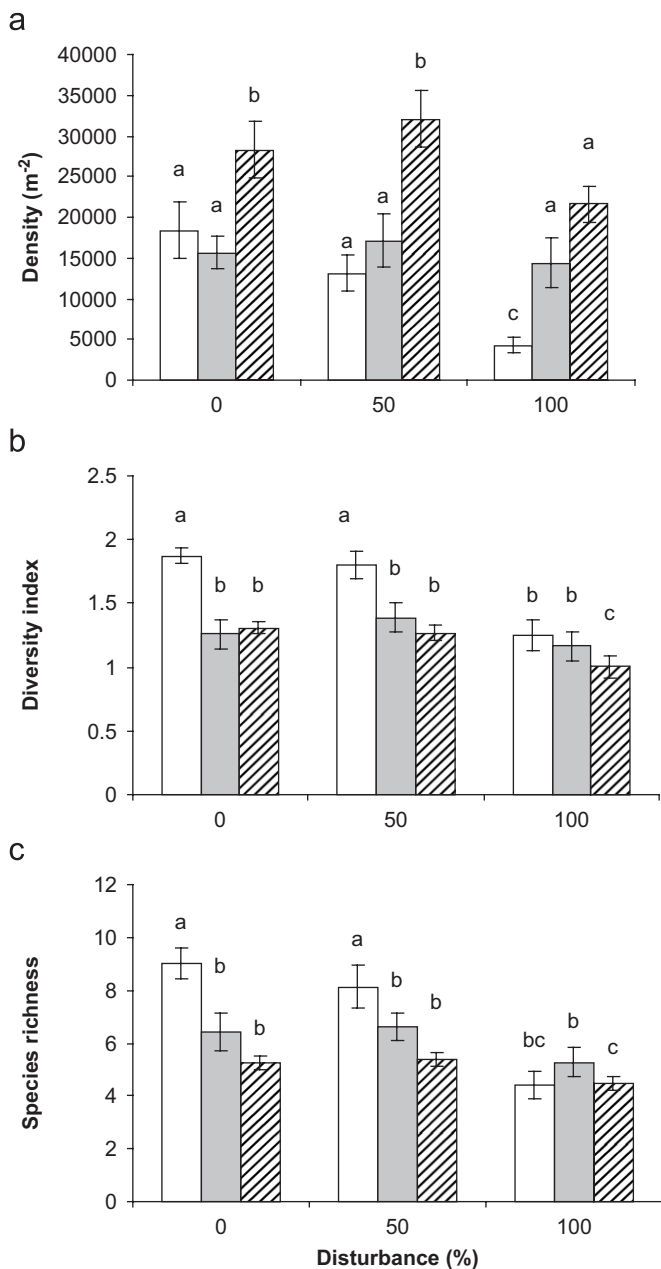


Fig. 3. Response of Oribatida (open bars), Mesostigmata (shaded bars) and Collembola (hatched bars): (a) abundance, (b) diversity, and (c) richness of species to disturbance treatments in 2001. Error bars represent standard errors and bars bearing the same letter do not differ at $P < 0.05$.

to N in 2001. Despite the lack of response of plant diversity to disturbance, intense levels of disturbance created areas of bare ground, in accordance with the study of [Burke and Grime \(1996\)](#). In the longer term, we would expect to detect changes in plant diversity resulting from our treatments, which could potentially impact on soil fauna via a variety of mechanisms.

4.2. Response of microarthropod community

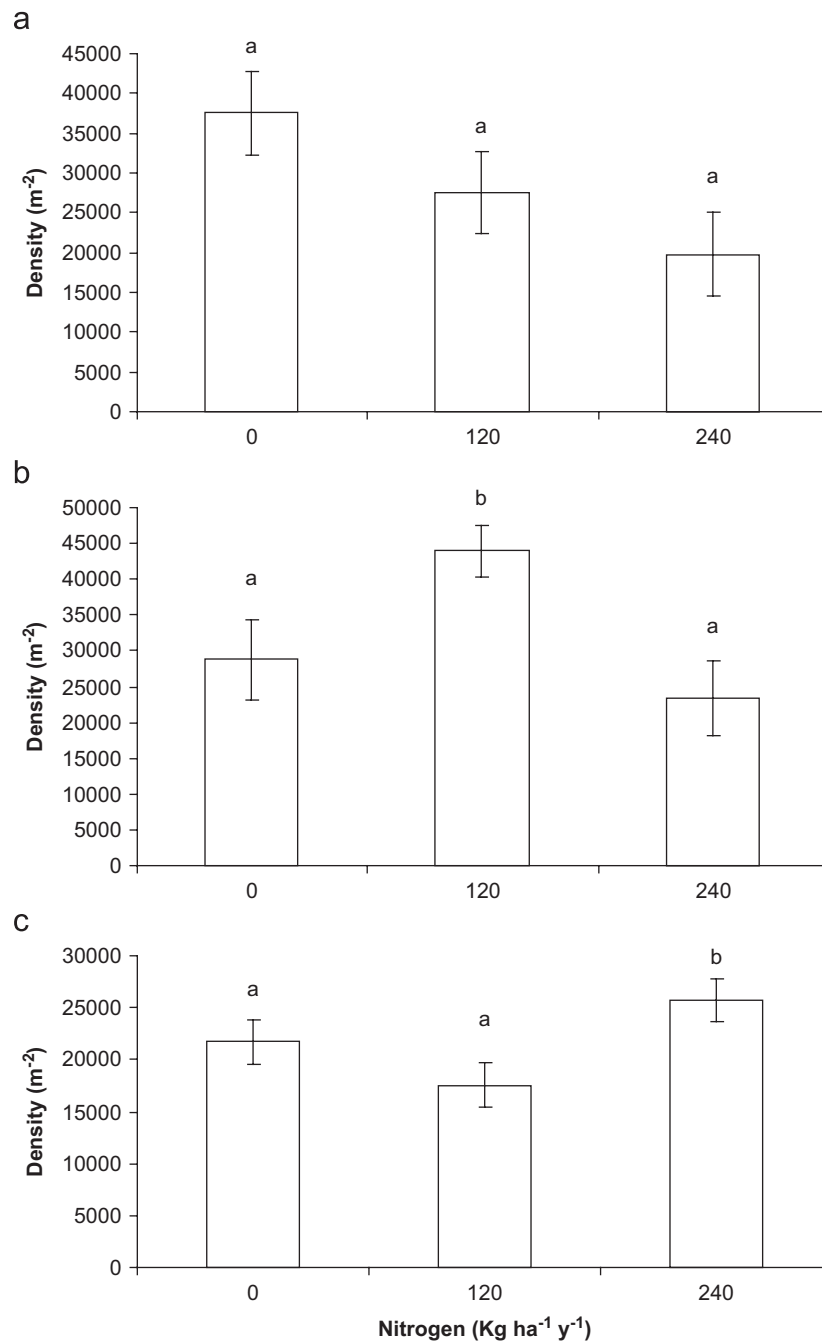
Physical disturbance to the soil using an implement to mimic a short, but intense, period of cattle trampling, strongly reduced the population densities of both mites and Collembola in the first year. This is in accordance with other studies which reveal that disturbance from cultivation and soil mixing has a negative impact on microarthropods ([Petersen and Luxton, 1982](#); [Crossley et al., 1992](#); [Berch et al., 2007](#)). However, by the second year, given time for recovery between the disturbance events, microarthropod population densities had increased compared to the previous year, and only the abundances of two microarthropod groups (oribatids and Collembola) were reduced by the most intense level of disturbance. This increase in population size in the second year's sampling suggest some adaptation of the community to disturbance by the second year. Climatic conditions in the second year of sampling are unlikely to account for these differences since rainfall and soil temperatures were generally lower in the months preceding sampling in 2001 than in 2000 (data from <http://soilbio.nerc.ac.uk/weather.asp>).

The microarthropod group that was most consistently affected by disturbance was the oribatids; disturbance reduced their abundance, diversity and richness. In contrast, increased resource availability, resulting from N addition, had no effect on either the abundance or diversity of oribatids. That oribatids were most sensitive to disturbance is not surprising; of the microarthropod groups tested they have traits that most closely correspond to "k-selected" species in that their reproduction is usually sexual and they have relatively long generation times. Many species have strategies that are pre-adapted to stress conditions, e.g. quiescent life stages, semelparity or seasonal iteroparity and moderate to high egg production ([Siepel, 1994](#)); however, their slow generation times and

Table 3

F-statistics from analysis of variance for measures of microarthropod community structure

	d.f.	Oribatida			Mesostigmata			Collembola		
		<i>H</i>	<i>J</i>	<i>R</i>	<i>H</i>	<i>J</i>	<i>R</i>	<i>H</i>	<i>J</i>	<i>R</i>
Disturbance	2	9.99**	0.76	13.12***	1.08	0.13	1.63	5.43**	3.38*	3.66*
Nitrogen	2	0.48	0.46	0.17	1.46	0.98	0.31	0.40	1.26	0.34
Disturbance × Nitrogen	4	0.26	0.92	0.55	2.04	1.00	2.76*	0.31	0.16	0.95

*Significant at $P < 0.05$.**Significant at $P < 0.01$.***Significant at $P < 0.0001$.Fig. 4. Density of collembolans with increasing nitrogen additions at (a) 0% disturbance, (b) 50% disturbance, and (c) 100% disturbance. Error bars represent standard errors and bars followed by the same letter do not differ at $P < 0.05$.

low dispersal capacity (Norton, 1980) reduces their tolerance to habitat disturbance (Prinzinger et al., 2002). Indeed, it has been shown that oribatid communities may not recover from a single disturbance event for considerable amounts of time (Zaitsev et al., 2002; Siepel, 1992).

Intense disturbance to the soil also reduced collembolan density and species richness, but this effect was not as great as was observed for the oribatids. Indeed, some species of Collembola, namely *P. armata*, *M. macrochaeta* and *C. denticulata*, appeared to be associated with plots that were moderately disturbed (data not shown). Maraun et al. (2003a) similarly reported that Collembola of the genus *Mesaphorura* and *Protaphorura* partially benefited from disturbance, leading to the suggestion that moderate amounts of disturbance, such as that arising from agricultural practices, might promote the diversity of some faunal groups (Wardle, 2001). Further, increased resource availability from the application of N fertilizer, increased collembolan population size at the highest level of disturbance, possibly reflecting improved soil conditions and increased soil microbial abundance despite reductions in aboveground plant biomass. Seastedt et al. (1988) also reported a dramatic increase in microarthropod density in response to a single application of N fertilizer, most likely through increased resource availability.

That N additions ameliorated the response to soil disturbance suggests that resource availability is a greater determinant of collembolan community dynamics than disturbance. This is consistent with the knowledge that some collembolans share traits with competitive species (Siepel, 1994), being able to increase their population size when resources are increased due to their relatively short generation and development times arising from both sexual and asexual reproduction in collembolans, with continuous, low to moderate iteroparity (egg production). That these organisms respond positively to resource addition has also been shown in field studies of grassland, where application of N fertilizer has increased population densities (Bardgett et al., 1993; Cole et al., 2005).

In contrast to the other microarthropod groups, the Mesostigmata were unaffected by physical disturbance to the soil, and two species, *U. minima* and mites of the genus *Rhodacarus*, were found to be associated with disturbed plots (data not shown). That Mesostigmata were mostly unaffected by disturbance can be explained by their life history traits that include high dispersal capability of some species (e.g. *U. minima*) and, in comparison to other microarthropod groups, relatively rapid generation times (Siepel, 1994). For those plots that were disturbed and also received N, an increase in mesostigmatan richness was also observed.

In summary, each taxonomic group responded differently to resource availability and disturbance, the response being dependant upon their predominant life history strategy. Oribatid community structure and dynamics appear to be strongly regulated by top-down control (i.e. disturbance), whereas Collembola and mesostigmatan

diversity are more strongly determined by bottom-up forces driven by increased resource availability.

4.3. Comparison of responses to known patterns

Grime (1973a, b) demonstrated that plant diversity was maximised by stress or disturbance factors that promoted intermediate levels of standing biomass. This pattern has been observed along natural gradients (Grime, 1973a) and in experimental manipulation studies where opportunity for invasion was made available to plant species not naturally present at the site by under sowing the plots with seed mixtures (Burke and Grime, 1996). In 2001, while we observed moderate levels of aboveground plant biomass at intermediate levels of N addition (Fig. 1b), there was no corresponding increase in diversity, providing no evidence that the plant community response to our imposed gradients of stress and disturbance resulted in plant diversity being maximal at intermediate levels of productivity, in accordance with Grime's theory (Grime, 1973a, b). In our study, however, little opportunity was available for either plant or microarthropod species to invade plots, other than those that were already present at the site. Further, 2 years is an insufficient time period to observe these changes in the plant community structure; in the study of Burke and Grime (1996) these patterns only became apparent after 9 years.

That microarthropods did not conform to nutrient and disturbance gradients consistent with Grime's model is in contrast to the findings of Degens et al. (2001), who concluded that competitive exclusion might be important for determining the abundance and community structure of soil microbial communities. In our study, we detected no decline in the abundance or diversity of microarthropods with increasing N addition, suggesting that there was no competitive exclusion of microarthropods at the highest N level. However, we do acknowledge that the time frame of our study might be too short to detect such changes, in that N only increased plant productivity in the second year of our study, so this feedback to the microarthropod community as increased resource availability through rhizosphere and litter inputs might only be detectable following a further time lag, that went beyond our sampling period. Also, while we saw that animal densities increased with N additions, these densities might not be sufficient to induce competitive interactions. Scheu and Schulz (1996) studied the development of an oribatid mite community across different stages of secondary succession, and observed that changes in oribatid species composition followed the successional stages in plants, with the greatest number of oribatid mite species being found in the climax (beech wood) ecosystem. Scheu and Schulz (1996) concluded that this contradicted inhibition models of succession, indicating that interspecific competition amongst oribatid mite species is of little importance. Nevertheless, Scheu and Schulz (1996) suggested that the large biomass of earthworms observed in the beech wood ecosystem

might partly explain the high diversity of oribatids found there, since earthworm activity causes frequent disturbance of intermediate intensity that would promote maximal diversity according to the intermediate disturbance hypothesis of Connell (1978).

This notion of a lack of competitive interactions between soil biota has puzzled ecologists for a long time (e.g. Anderson, 1975), especially since soil fauna are thought to be quite generalist in their feeding behaviour, preferring similar fungal taxa (Maraun et al., 2003b) and hence competing for similar resources. The wide ranging life history tactics employed by decomposer fauna (Siepel, 1994, 1996), coupled with the complex structure of soils that creates extensive opportunity for niche partitioning (Bardgett, 2002; Bardgett et al., 2005b), might best explain the wealth of diversity in soil. Indeed, trophic niche differentiation in oribatids has been detected using stable isotope ratios, despite their being thought of as generalist feeders (Schneider et al., 2004).

5. Conclusions

Our data show that while responses of soil animal diversity to nutrient addition and disturbance were detected, these responses were not unimodal, at least in the short term of this study. This is in contrast to aboveground communities where unimodal responses of diversity to disturbance and productivity are common. This difference, therefore, suggests that different mechanisms structure plant and soil communities, and in particular that competitive exclusion is unlikely to be as important a driver of soil faunal diversity as it is for aboveground diversity. We conclude that soil animal diversity is not strongly regulated by competition and, rather, it is best explained by the evolution of varied life history tactics and phenology (Siepel, 1994) and the heterogeneity of soil (Young and Crawford, 2004; Bardgett et al., 2005b), thereby enabling so many species to co-exist.

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