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Impacts of Soil Faunal Community Composition on Model Grassland Ecosystems

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Human impacts, including global change, may alter the composition of soil faunal communities, but consequences for ecosystem functioning are poorly understood. We constructed model grassland systems in the Ecotron controlled environment facility and manipulated soil community composition through assemblages of different animal body sizes. Plant community composition, microbial and root biomass, decomposition rate, and mycorrhizal colonization were all markedly affected. However, two key ecosystem processes, aboveground net primary productivity and net ecosystem productivity, were surprisingly resistant to these changes. We hypothesize that positive and negative faunal-mediated effects in soil communities cancel each other out, causing no net ecosystem effects.

Soil fauna are essential to efficient nutrient cycling, organic matter turnover, and maintenance of soil physical structure, processes that are key determinants of primary production and ecosystem carbon storage (*1–3*). Consequently, there is considerable concern about impacts on ecosystem functioning that might result from shifts in the community composition of soil fauna mediated through global change (*4–6*). Predictions based on theoretical considerations of soil communities are ambivalent. Indeterminate and unexpected impacts are predicted from food web theory (*7*, *8*). Redundancy is also postulated to be common (*9*), with large changes in community composition having minimal effects. Anderson (*10*) argued that net effects may be positive, negative, or zero, depending on the balance between sink and source processes operating at finer scales. Keystone species theory (*11*) and distinct bacterial versus fungal energy channels (*12*, *13*) further cloud the predictions. Therefore, an empirical approach is essential for predicting the impacts of shifts in soil community composition on ecosystem functioning.

Pot experiments with soil, soil organisms, and sometimes an individual plant or plant species have demonstrated the marked potential effects of loss of specific soil fauna and faunal groups on a range of ecosystem processes (*14–16*). However, the validity of extrapolating these studies to the field is questionable given the low species numbers of soil fauna and plants (if present) typically used, the artificiality of the soil, and the limited number of variables measured. What is required is an approach that manipulates the composition of a soil faunal community with a species richness more akin to that in the field, which includes a multispecies plant community and a reconstructed soil profile and measures the response of a suite of interacting variables. To manipulate the soil community in the field, and maintain it over biologically meaningful temporal and spatial scales, is logistically difficult (*17*). Ecological microcosms make such investigations eminently more feasible. We used the Ecotron controlled environment facility (*18*) to test 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.

We constructed 15 terrestrial microcosms over a period of 7 months (*19*) as analogs of a temperate, acid, sheep-grazed grassland (a habitat that occurs widely across the upland regions of northern Britain). We maintained the microcosms in the Ecotron under constant environmental conditions (*19*) for a further 8.5 months. Soil, plants, fauna, and microorganisms for microcosm construction were collected from the grassland (*19*). Soil fauna were assigned to a functional group according to body width (*20*, *21*) of the adult or, if the adult was not soil dwelling, largest larval stage. Body size provides a good functional classification because it correlates with metabolic rate, generation time, population density, and food size (*22*).

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Table 1. Biomass and numbers of soil organisms in the microfauna, mesofauna, and macrofauna treatment communities at the end of the experiment. Data for groups common to all treatments (body width < 0.1 mm) were analyzed by analysis of variance, and significant differences ($P < 0.05$) within a row are marked by asterisks and daggers. Data are means ± 1 SE ($n = 5$). Microbial biomass carbon was determined by modified chloroform fumigation extraction (in K_2SO_4). Biomass and numbers of earthworms and *T. paludosa* larvae in macrofauna columns are those added at the beginning of the experiment. Mean weekly earthworm cast and *T. paludosa* adult counts are provided from the last 4 weeks of the experiment to demonstrate activity of these organisms. Not applicable, na; not determined, nd.

Organism group	Biomass per treatment (mg m^{-2})			Individuals per treatment (number m^{-2})		
	Microfauna	Mesofauna	Macrofauna	Microfauna	Mesofauna	Macrofauna
			<0.1 mm			
Microbial (carbon)	$454 \times 10^2 \pm 326.3 \times 10^1$*	$453 \times 10^2 \pm 179.0 \times 10^1$*	$358 \times 10^2 \pm 173.7 \times 10^1$†	na	na	na
Nematode worms	185 ± 31.7	208 ± 20.4	152 ± 14.4	$859 \times 10^3 \pm 161.7 \times 10^3$*	$132 \times 10^4 \pm 390.5 \times 10^3$*	$151 \times 10^4 \pm 371.5 \times 10^2$†
Protozoa	nd	nd	nd	$188 \times 10^7 \pm 651.5 \times 10^6$	$188 \times 10^7 \pm 316.4 \times 10^6$	$220 \times 10^7 \pm 298.4 \times 10^6$
			0.1 to 2 mm			
Enchytraeid worms	0	199 ± 84.8	297 ± 92.9	0	$825 \times 10^1 \pm 268.8. \times 10^1$	$112 \times 10^2 \pm 369.3 \times 10^1$
Entomobryoidea (Collembola)	0	182 ± 42.0	123 ± 27.4	0	$575 \times 10^2 \pm 199.6 \times 10^2$	$404 \times 10^2 \pm 739.5 \times 10^1$
Poduroidea (Collembola)	0	494 ± 349.8	48 ± 6.7	0	$140 \times 10^3 \pm 877.3 \times 10^2$	$315 \times 10^2 \pm 806.2 \times 10^1$
Oribatid mites	0	13 ± 5.8	13 ± 6.9	0	$667 \times 10^1 \pm 338.6 \times 10^1$	$733 \times 10^1 \pm 434.2 \times 10^1$
Gamasid mites	0	120 ± 28.7	108 ± 19.9	0	$962 \times 10^1 \pm 222.8 \times 10^1$	$815 \times 10^1 \pm 171.2 \times 10^1$
Prostigmatid mites	0	2 ± 0.7	1 ± 0.3	0	$250 \times 10^1 \pm 868.7$	$127 \times 10^1 \pm 290.3$
Featherwing beetles (adult; Ptiliidae)	0	20 ± 8.3	7 ± 4.5	0	458 ± 187.1	153 ± 101.8
			>2 mm			
Rove beetles (adult; Staphylinidae)	0	0	546 ± 337.2	0	0	764 ± 426.1
Chilopoda (centipedes)	0	0	81 ± 20.4	0	0	204 ± 50.9
Lumbricus rubellus (earthworm)	0	0	$115 \times 10^2 \pm 129.9$	0	0	75 ± 2.9
Allolobophora caliginosa (earthworm)	0	0	$843 \times 10^1 \pm 8.8$	0	0	171 ± 1.9
Earthworm casts	na	na	na	0	0	95 ± 14.7
Arion ater (mollusk)	0	0	253 ± 132.8	0	0	2 ± 1.0
Tipula paludosa (larvae; Diptera)	0	0	$161 \times 10^1 \pm 2.2$	0	0	29 ± 0.3
T. paludosa (adult)	nd	nd	nd	0	0	8 ± 1.4

The physical structure of the soil habitat also constrains access to resources for certain body sizes and hence modulates interactions between organisms (*21*). We grouped fauna into the following size classes [see (*23*)]: microfauna (<100 μm diameter), mesofauna (100 μm to 2 mm diameter), and macrofauna (>2 mm diameter). We established three treatment communities using these groupings to produce a gradient of increasing functional complexity: (i) microfauna only; (ii) microfauna and mesofauna; and (iii) microfauna, mesofauna, and macrofauna. We refer to these treatments as microfauna, mesofauna, and macrofauna communities, respectively. All treatments included bacteria and fungi. End of experiment numbers and biomass of soil organism groups are shown in Table 1 (initial inoculation densities are shown in table S1).

We predicted that plant community composition would change and aboveground net primary productivity (NPP) would increase, in mesofauna and macrofauna communities, because of widely reported positive effects of these fauna on soil fertility and plant growth (*14*, *16*, *24*). In addition, we postulated that net ecosystem productivity (NEP; a measure of total ecosystem carbon balance) would be greater in the more complex communities because of the combined effects of increased carbon input and soil organic matter stabilization (*25*). As predicted, plant functional group (grass, forb, or legume) and species composition were markedly affected by the treatments. Foliar biomass of both forbs and legumes decreased in macrofauna communities, whereas their biomass increased over time in the other two treatment communities (Fig. 1). This shift toward the more nitrogen-rich plant functional groups was reflected in shifts in grass species composition: *Holcus mollis* L., the most nitrogen-rich graminoid species, increased in biomass in microfauna and mesofauna communities (*19*, *26*). In contrast to our predictions, and despite the plant community compositional change, aboveground NPP and NEP were not affected by the treatments (Fig. 2) (*19*).

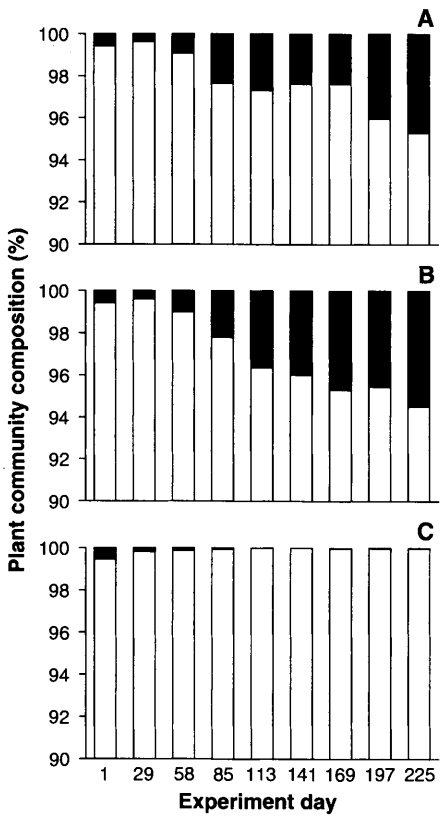

Fig. 1. Change in plant functional group aboveground composition of communities exposed to an increasing gradient of soil faunal complexity over time. Data (mean biomass proportion; $n = 5$) for microfauna (**A**), mesofauna (**B**), and macrofauna (**C**) treatment communities are given. Grass biomass proportion is represented by open bars, and forb and legume biomass proportion is indicated by solid bars. Forb and legume data are pooled, with proportion data shown for clarity; statistical analyses were performed on absolute biomass data. Forb and legume biomass was significantly lower in macrofauna communities (time × treatment interaction: forbs, $F_{14,56} = 1.9$, $P < 0.05$; legumes, $F_{14,56} = 10$, $P < 0.001$). From day 169 for forbs, and day 113 for legumes, individual time point analyses of variance were highly significant ($P < 0.001$) and macrofauna communities had consistently lower forb and legume biomass than microfauna and mesofauna communities ($P < 0.05$). Grass biomass was not significantly affected (time × treatment interaction; $F_{14,56} = 1.7$, $P > 0.05$).

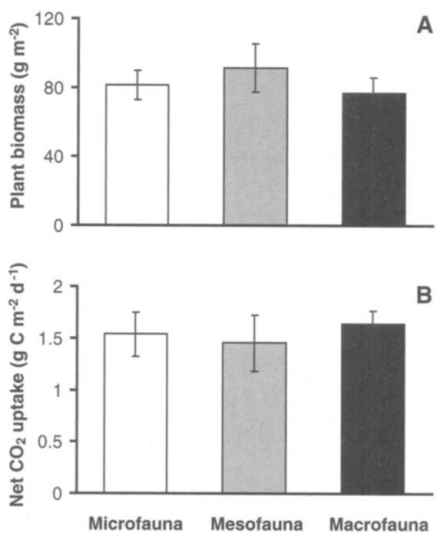

Fig. 2. Aboveground NPP (**A**) and NEP (**B**) of communities exposed to an increasing gradient of soil faunal complexity. Data (means ± SE; $n = 5$) for microfauna, mesofauna, and macrofauna treatment communities are given for the final sampling event; statistical analysis was done with repeated measures analysis of variance across all sampling events. There was no significant treatment effect on NPP (time × treatment interaction; $F_{14,56} = 0.16$, $P > 0.05$) or NEP (significant time × treatment interaction; $F_{8,32} = 2.4$, $P < 0.05$; but no consistent overall treatment effect; $F_{2,8} = 0.24$, $P > 0.05$).

That the magnitudes of two key ecosystem processes, NPP and NEP, were resistant to such a major shift in soil-faunal community composition was surprising. We investigated the responses of a range of variables within the soil habitat to explain the observed resistance. Although we observed no marked changes in soil physical properties (*19*) that could have contributed to changed soil fertility (*27*), decomposition rate (*19*) was significantly enhanced ($P < 0.05$) in the most complex faunal treatment (*28*); see also (*14*). As decomposition rate is generally positively correlated, within a system, to nutrient availability (*23*), we might have expected NPP to increase in response in macrofauna communities. However, both mycorrhizal colonization and root biomass (*19*, *29*) were less abundant in macrofauna communities, and these decreases may explain why plants in these communities were unable to capitalize on the potentially higher nutrient availability. The existence of such simultaneous but opposite changes in variables, which in this case appeared to buffer NPP, develops Anderson's (*10*) theory that soil process rates (for example, nitrogen flux) at one scale may be maintained by sink and source processes (for example, nitrogen immobilization and nitrogen mineralization) operating at finer scales.

As with NPP, NEP may have been buffered by positive and negative responses to fauna that occurred within the soil habitat. NEP is the sum of photosynthesis and respiration (*19*), and a change in the rate of either contributing process affects the net CO_2 flux of the system. Given the resistance of NPP to the treatment gradient, it is perhaps not surprising that photosynthesis (*19*) was similarly resistant ($P > 0.05$). However, marked decreases in both root and microbial biomass (Table 1), the two main contributors to grassland respiration, occurred in macrofauna communities. Thus, we would have expected community respiration (*19*) to decrease (and NEP to increase), but CO_2 efflux was not significantly different between treatments ($P > 0.05$). Respiration was probably buffered in the macrofauna communities by the combined stimulatory effect of both mesofauna and macrofauna on microbes (*16*, *30*), which served to maintain microbial activity (*19*) at a level equivalent to that in the microfauna and mesofauna communities (*31*).

Similarly, we predict that plant community composition differences were the net result of a complex set of mechanisms that both positively and negatively affected the abundance of different plant functional groups and species. These mechanisms will have included nutrient availability, foliar and root herbivory, and mycorrhizal colonization (*32*,

33). However, in contrast to the faunal-mediated mechanisms determining NEP and NPP, positive and negative responses within treatments clearly did not balance.

We have shown that a change in soil community composition markedly affects microbial and root biomass, decomposition rate, mycorrhizal colonization, and plant community composition. However, aboveground NPP and NEP were resistant to these changes. These findings demonstrate that the marked effects on ecosystem processes of changes in faunal size-class composition, observed in simple experimental systems (*14*, *15*), do not necessarily manifest themselves within complex communities. Although microcosm studies can never substitute for long-term field investigations, this study is useful to help predict the potential ecological impacts of a major shift in soil-faunal community composition.

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26. There was a significant change in grass species composition (time × treatment × plant species interaction; $F_{70,476} = 1.4$, $P < 0.05$). By day 85, *H. mollis* was consistently more abundant in the microfauna, and mesofauna, communities (time × treatment interaction; $F_{14,56} = 1.9$, $P < 0.05$). Values for the last sample event ($F_{2,8} = 18$, $P < 0.01$) were 4.5 ± 0.57 (microfauna), 9.6 ± 2.59 (mesofauna), and 1.9 ± 0.40 (macrofauna) [mean ± SE dry mass (g m^{-2})]. Significant changes in biomass of other grass species were not observed.
27. We detected no marked treatment differences in bulk density or pH of organic and mineral soil horizons. Equally, we observed no significant treatment differences ($P > 0.05$) in moisture, temperature, total and dissolved organic soil carbon, and total and dissolved organic and mineral nitrogen of these horizons.
28. Surface litter decomposition was significantly affected by faunal treatment after 42 days of litter exposure (time × treatment interaction; $F_{4,40} = 3.3$, $P < 0.05$). Values for the last sampling ($F_{2,20} = 20$, $P < 0.001$) were 31.6 + 2.74 (microfauna), 39.1 + 4.93 (mesofauna), and 14.0 + 3.44 (macrofauna) [back-transformed mean + SE (percentage litter mass remaining at 42 days)]. Cotton strip degradation (time × treatment interaction; $F_{4,234} = 2.4$, $P < 0.05$) was significantly affected by faunal treatment, and at the last sampling ($F_{2,135} = 9.0$, $P < 0.001$; strips inserted on day 207) cotton degradation rates (pooled across depth and removal day) were 23 ± 1.3 (microfauna), 25 ± 1.3 (mesofauna), and 27 ± 1.3 (macrofauna) [mean ± SE (cotton strips per year)].
29. Arbuscular mycorrhizal root colonization was significantly affected by faunal treatment ($F_{2,44} = 31$, $P < 0.001$) and in a consistent way (treatment × species interaction; $F_{6,44} = 0.46$, $P > 0.05$). Mean (±SE) percentages in the microfauna, mesofauna, and macrofauna communities were, respectively, 14 ± 1.1, 20 ± 2.0, and 6.9 ± 2.46 (*Agrostis capillaris* L.); 12 ± 1.6, 17 ± 2.5, and 6.6 ± 2.25 (*Anthoxanthum odoratum* L.); 13 ± 2.9, 21 ± 1.4, and 9.2 ± 2.21 (*Festuca rubra* L.); and 17 ± 1.9, 22 ± 2.8, and 7.1 ± 1.87 (*Poa pratensis* L.). Root density was markedly affected by faunal treatment ($F_{2,8} = 3.9$, $P = 0.065$). Mean (±SE) densities in the organic horizons were 34 ± 1.2 (microfauna), 22 ± 6.7 (mesofauna), and 16 ± 3.0 (macrofauna) (mg per g of dry soil).
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Supporting Online Material

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References

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