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Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment

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Abstract

A transplant experiment was carried out on the Moor House National Nature Reserve, Cumbria, UK, and two sites with different climatic characteristics were selected for determining how Enchytraeids, Diptera larvae and Tardigrades respond to changes in climate. The soil was a cambic stagnohumic gley, characterized by a high organic matter content and low pH. Vegetated soil cores were taken from near the summit of Great Dun Fell (GDF) and used for the transplant experiment. Cores were then placed back at GDF (845 m) and also transplanted to Sink Beck (SNK, 480 m), providing a mean annual temperature increase of 2.5°C. In order to discriminate between the effects of temperature and rainfall on the size and vertical distribution patterns of the fauna, a further series of lysimeters were established at SNK, and rainfall inputs were manipulated, intending to provide a total input equivalent to the ambient rainfall at the top site. At regular intervals, a number of cores were destructively sampled from each treatment (top site—GDF; lower site—SNK; enhanced rainfall inputs—SNK) and the vertical distribution of the soil fauna determined. Enchytraeidae, Tardigrada and Diptera were commonly found in soil samples at the Reserve and appeared sensitive to the imposed changes in temperature and moisture. Different species of enchytraeids responded differently: numbers of *Cognettia sphagnetorum* were correlated positively with temperature, whereas their vertical distribution was determined by moisture. *Cernosvitoviella atrata* was unable to avoid dry conditions which apparently caused severe mortality when exposed to the elevated temperatures; *Achaeta eiseni* was a more tolerant species, increasing in numbers with increasing temperature. Diptera larvae appeared to be dependent on the moisture status of the upper soil layers and their populations were reduced at higher temperatures and lower moisture contents. By contrast, tardigrades were able to survive adverse conditions by entering an anhydrobiotic stage, recovering when seasonal climate improved. General trends in soil faunal responses to climatological changes in the UK are predicted. © 1997 Elsevier Science B.V.

Keywords: Soil fauna; Climate change; Enchytraeids; Diptera larvae; Tardigrades

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1. Introduction

It is now widely accepted that increasing concentrations of CO_2 and other greenhouse gases will produce a warming of at least 1°C in the UK by the year 2050 (see, for example, Countryside Commission, 1995). However, it is not yet clear whether rainfall will increase or decrease at a regional level (Schneider, 1988 in Peters, 1992), but it is likely that higher temperatures will cause increased evapotranspiration in summer, resulting in greater water deficits in the east, with more frequent droughts (Countryside Commission, 1995).

The potential impacts of climate change on the soil biota have received considerably less attention than other ecosystem components, such as vegetation, and there are very few predictions concerning climate change responses of soil invertebrates. It has been argued that increasing temperatures may lead to a more rapid breakdown of organic matter in certain systems, and that this may have important effects on the soil heterotroph community (Tinker and Ineson, 1990). However, according to Whitford (1992) soil is thermally buffered and soil communities may be less sensitive to changes in atmospheric temperature than surface vegetation.

Several investigations have highlighted the similarity of the soil faunal populations in upland areas of the UK (such as Moor House in the northern Pennines) to those in subarctic and arctic systems (Cragg, 1961), with most soil groups paralleling those of Scandinavia. On a weight basis (live weight), the fauna in the Reserve is dominated by Oligochaetes, with lumbricids decreasing abruptly in numbers when the mineral content and soil pH decrease and Enchytraeids showing their greatest biomass in the bare peat (99%) but also in mixed moor (67%) and in moorlands with associated vegetation of *Juncus* (68%) (Cragg, 1961). In spite of the numerical abundance of Nematoda, Acarina and Collembola they never contributed more than 3% of the total biomass. Diptera larvae are very well represented, and they can become very abundant some years and their density in the following generation may depend upon the climatic conditions (Coulson and Whittaker, 1978).

The majority of these soil invertebrates occur in the surface horizons where they are most likely to be exposed to environmental change. Enchytraeids, which represent a replacement community for earthworms in these peaty soils, do not survive a soil water content of less than 10% of field capacity (Abrahamsen, 1971), and are mainly restricted to moist habitats. However, they can move deeper into the soil in response to moisture changes (Springett et al., 1970). Diptera larvae may be sensitive to changes in temperature and moisture, because of their inability to migrate to deeper horizons. Tardigrades or 'water bears', typical inhabitants of moss cushions, are previously unrecorded but present and they are similarly associated with wet and semi-aquatic environments which leads to consider them as a sensitive group to adverse climatic conditions.

To assess how these three taxa will respond to changes in the UK climate, vegetated soil cores were taken from a site near to the summit of Great Dun Fell (GDF, 845 m) and transplanted down to Sink Beck (SNK, 480 m), where the mean annual temperatures increase by 2.5°C. Half the number of cores were replaced at the summit and the other half were placed at the lower site, with destructive sampling at regular intervals. Additionally, a parallel series of cores were also established at the lower site, intending to discriminate between the effects of temperature and moisture using rainfall manipulations. These latter cores were sampled only towards the end of the experimental period.

2. Materials and methods

2.1. Site description

This study was conducted on the Moor House National Nature Reserve (NGR 710322) which was a principal UK ecosystem study site in the IBP tundra biome project (Heal and Perkins, 1978). The soils of the Reserve are described in detail by Hornung (1968), Heal and Perkins (1978) and Adamson et al. (1996).

Two sites were selected for establishment of the temperature transect experiment. The first was close to the summit of GDF at 845 m, and the second was near SNK, at 480 m, where the mean annual temperature is 2.5°C higher; both sites are within the Moor House National Nature Reserve (Fig. 1).

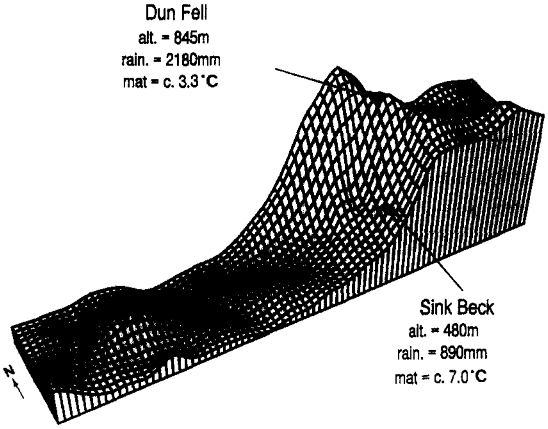

Fig. 1. Sampled sites: alt. = altitude, rain. = rainfall, mat. = mean annual temperature. Axes X and Y represent longitude and latitude, respectively.

2.2. Altitudinal setup

Intact undisturbed soil cores, 189, were taken using 15 cm diameter by 28 cm deep acrylic cylinders from a cambic stagnohumic gley soil with associated vegetation, near to the summit of GDF on 25 May, 1994. The vegetation was dominated by *Juncus squarrosus* L., with *Festuca ovina* L., *Deschampsia flexuosa* (L.) Trin. and *Polytrichum commune* L. Fifteen cores were used to assess the initial faunal populations, with the remainder being used in the transplant experiment. Cores, within the acrylic cylinders, were replaced at GDF (60 cores) and taken to SNK (60 cores) where they were re-buried, ensuring that the soil surface within the core was level with the surrounding soil.

2.3. Augmenting of rainfall inputs

The remaining 54 cores were used in the augmented rainfall experiment: 18 cores were placed at both the GDF and SNK sites for an additional sampling towards the end of the experiment (15 August 1994 and 22 August 1994); at Sink Beck, in addition to the 18 replicates left for the whole experimental period and receiving ambient rainfall, a further set of 18 cores received extra rainfall, intended to mimic the ambient rainfall at the GDF site. This was achieved by calculating the appropiate diameter of the collecting funnel from the rainfall data recorded during the previous year and directing the rainwater into the cores receiving additional inputs, via PVC tubing. These are referred to as the SNK-E treatments and were only sampled towards the end of the experiment (15 August 1994 and 22 August 1994).

To determine the output volumes a parallel series of lysimeters (six per treatment) were established at both sites. Intact soil cores were taken using 15 cm diameter by 28 cm depth clear acrylic cylinders and filled with a drainage bed at the bottom. A woven polypropylene matting was placed above to prevent bloking and a flexible PVC drainage pipe was connected to a 5.3l plastic bottle to collect the soil water leached.

2.4. Climatological monitoring

Temperature probes at two soil depths (2 and 10 cm) and at 0.5 cm above the soil surface were established at GDF and SNK. Each was constructed from thermistor beads (Betatherm 2252 Ω at 25°C; P/N 151–588: Farnell Components Ltd., Leeds, UK) soldered to round, screened, twin wire microphone cable and sleeved with adhesive-lined heat shrink sleeving. Data were logged using a Type DL2 automatic weather station (AWS; type WS01, Delta-T, Cambridge, UK).

2.5. Sampling

Fifteen replicates were taken from both sites every 2 weeks (four samplings), from 13 June 1994 to 25 July 1994, using a randomised block design. Cores were sliced horizontally into five 2-cm layers to a depth of 10 cm and a subsample (19 cm^2) of each layer was placed separately in a plastic bag and transported to the laboratory in a cool box. Invertebrates were extracted within 48 h using a modified wet funnel method (O'Connor, 1955), preserved in 70% alcohol, and counted. Enchytraeids were identified to species; only total numbers were recorded for Diptera larvae and tardigrades.

The enchytraeid *Cognettia sphagnetorum* was classified as either whole worms or regenerating tail fragments (fragments regenerating the head), which are known to be influenced by temperature (Standen, 1973).

At the end of the experiment nine replicates were collected from GDF, SNK and SNK-E during each one of the final sampling dates (15 August 1994 and 22 August 1994), sliced in the same way, and a subsample of 22 cm^2 per layer taken.

2.6. Statistical analyses

Total animal numbers per core were statistically analysed for treatment effects. This was achieved by logarithmic transformation of the total numbers of individuals of a particular taxa within each core, followed by ANOVA to quantify interactions between sampling date, treatment and depth.

The effect of climate on numbers and vertical distribution of each individual species or animal group was tested by regression analysis, with responses of all taxa being analysed by means of canonical correspondence analysis.

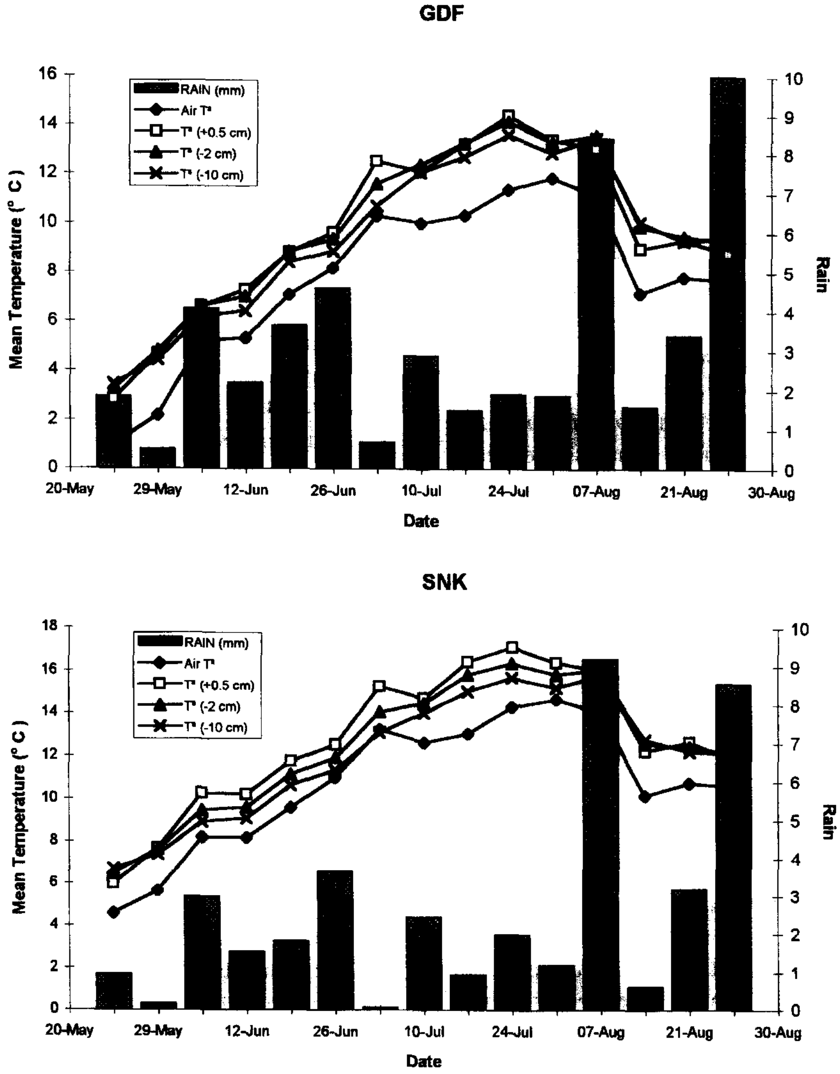

Fig. 2. Observed temperature profiles and rainfall inputs at GDF and SNK during the sampling period.

3. Results

3.1. *Climatic data*

The observed temperature profiles and rainfall inputs at the summit of GDF and at SNK are summarized in Fig. 2. The mean monthly temperature difference between GDF and SNK was 2.6°C with, at both sites, a dry period in July being coincidental with the highest temperatures.

A comparison between the rainfall input data and water volumes (cummulative values) collected in a parallel series of lysimeters is given in Fig. 3. At GDF (Fig. 3a) the volumes collected were low in comparison to rainfall inputs and may reflect the high evaporative loss due to strong winds at the summit. At SNK (non-enhanced, Fig. 3b) input values were slightly lower than for the top site, whereas in the SNK-E treatments (Fig. 3c) rainfall supplements increased the input to more than twice that for SNK, and 0.6 times more than GDF.

3.2. *Enchytraeids*

Three species of enchytraeids, *Cognettia sphagnetorum* (Vejdovsky), *Cernosvitoviella atrata* (Bretscher) and *Achaeta eiseni* Vejdovsky were recorded in the experimental treatments. *Mesenchytraeus* sp. Eisen was also found, but because of the low numbers was not included in the statistical analyses.

The vertical distribution of each taxon at GDF and SNK on the different sampling dates is summarized in Figs. 4–8. The results for SNK-E are presented in Table 1.

3.2.1. *Cognettia sphagnetorum*

In early summer, individuals of *Cognettia sphagnetorum* were concentrated in the upper two layers at both sites (90 and 70% of population in the top 4 cm of soil at GDF and SNK, respectively). In July, coincidental with rising temperatures, the population decreased in the top soil layers and increased in the deeper layers (Fig. 4). At GDF this increase occurred in the 2–4 cm and 4–6 cm layers, with the two remaining layers being unaffected. At SNK, all four deeper layers showed a parallel increase in numbers of *C. sphagnetorum* and 10% remained in the 0–2 cm layer in July.

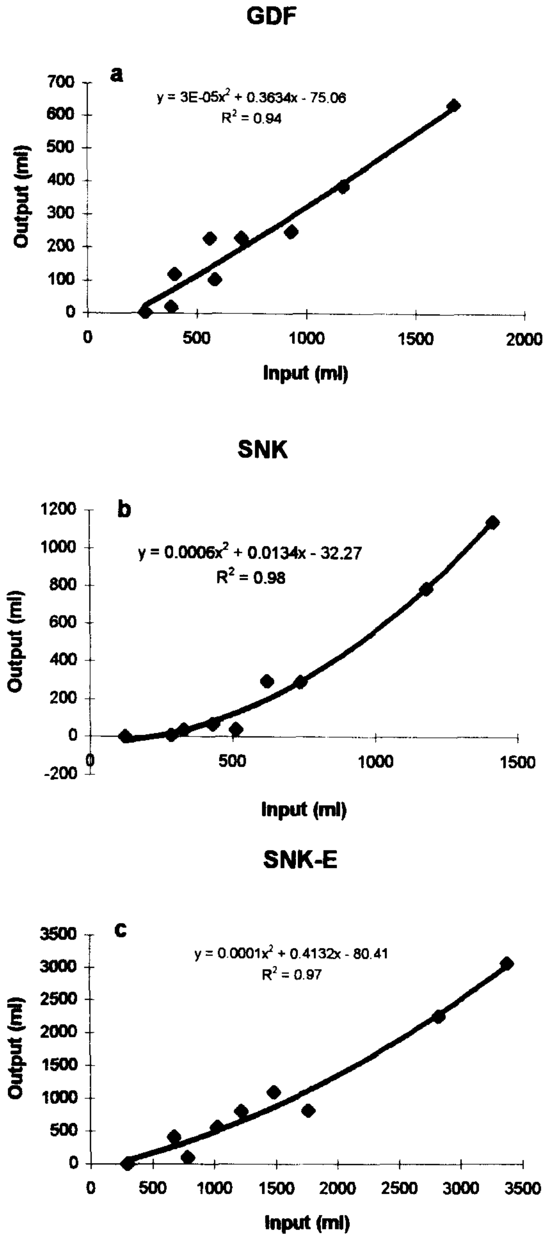

Fig. 3. Comparisons between the rainfall input values and water volumes collected in a parallel series of lysimeters at (a) GDF, (b) SNK and (c) SNK-E. Regression line (R^2, $P < 0.01$).

When total numbers per core are considered (Table 1), the most striking effect was the higher total number of enchytraeids recorded at SNK in comparison to GDF across the entire experiment. The differ-

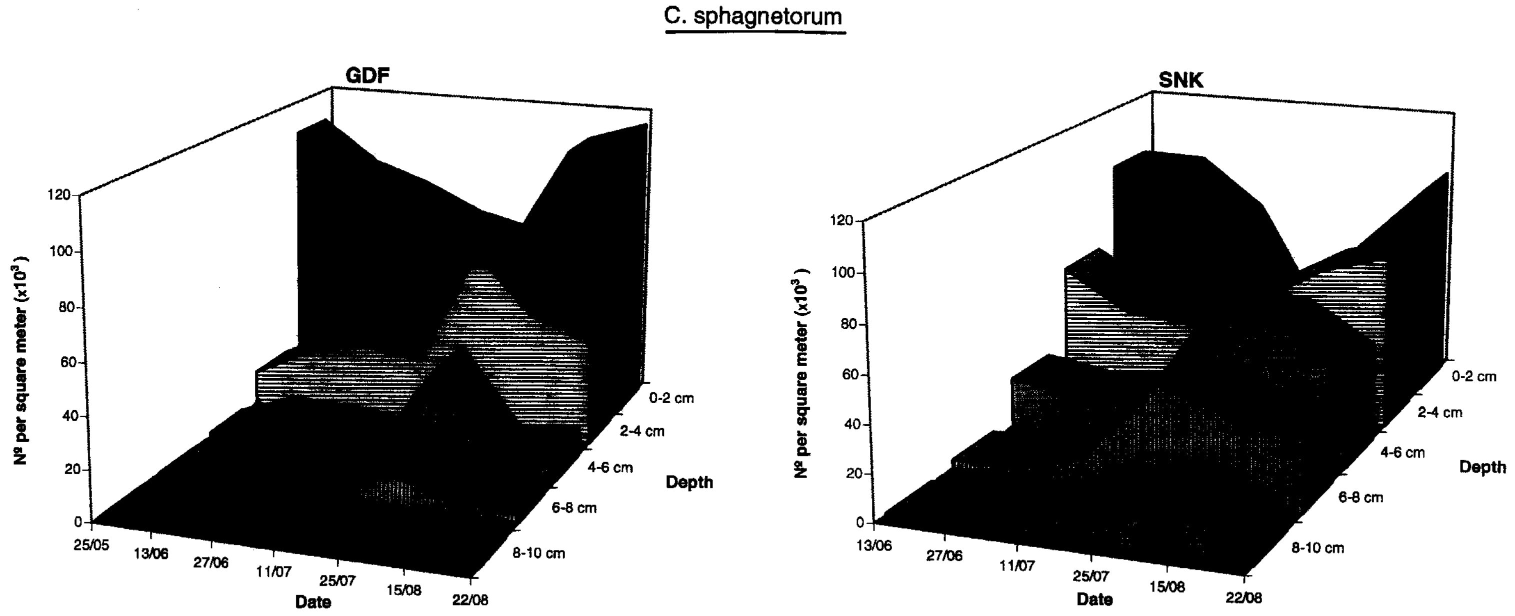

Fig. 4. Numbers and vertical distribution of *Cognettia sphagnetorum* at both sites during the sampling period in 1994.

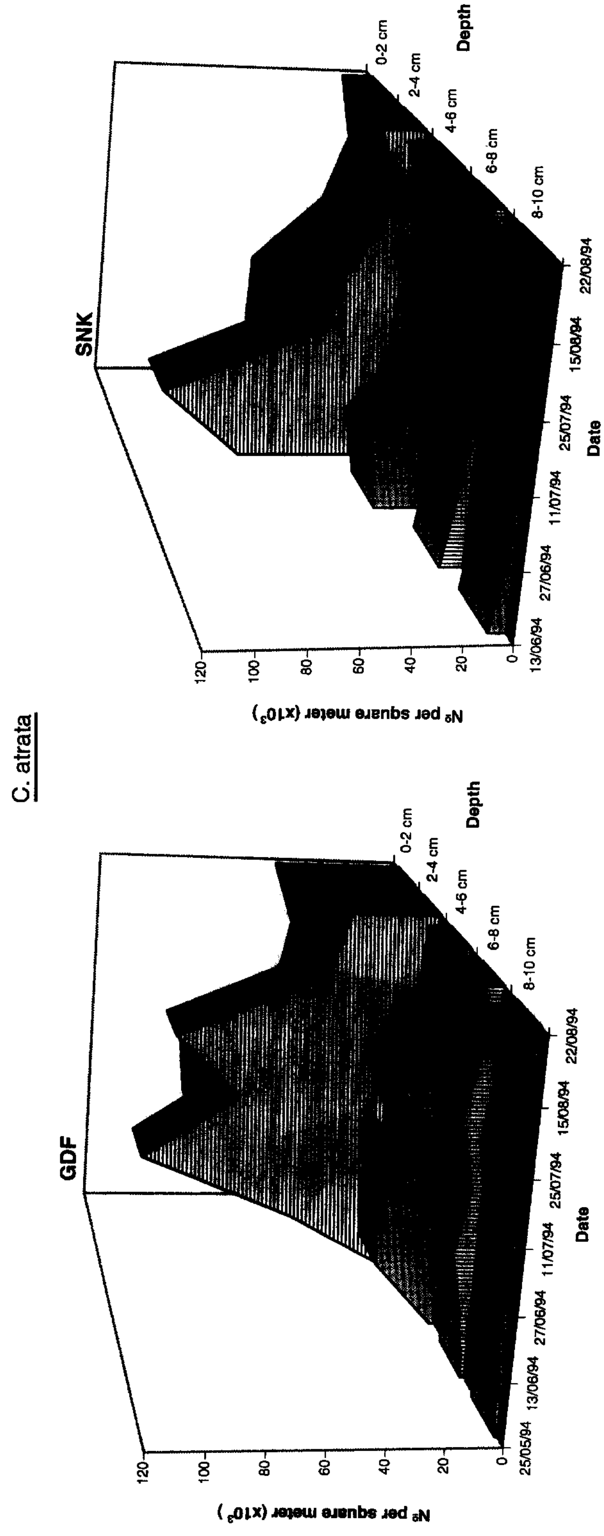

Fig. 5. Numbers and vertical distribution of *Pernosvitoviella atrata* at both sites during the sampling period in 1994.

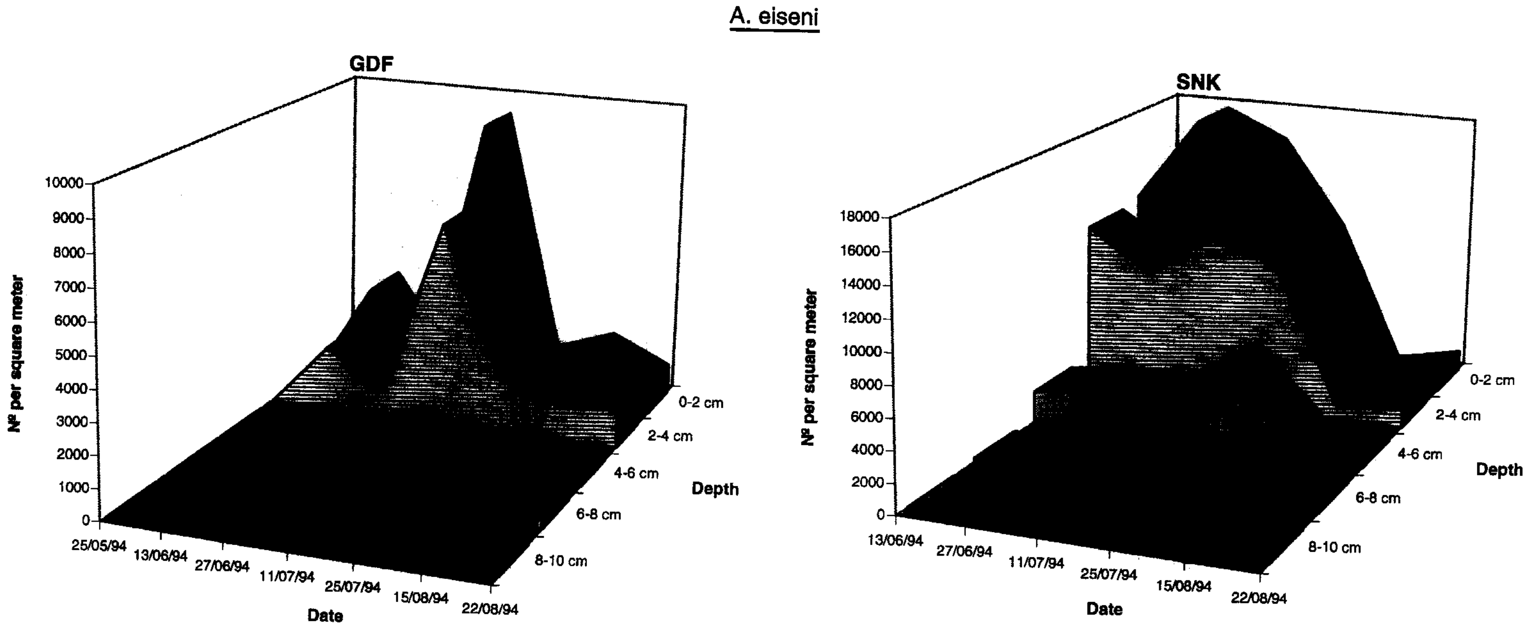

Fig. 6. Numbers and vertical distribution of *Achaeta eiseni* at both sites during the sampling period in 1994.

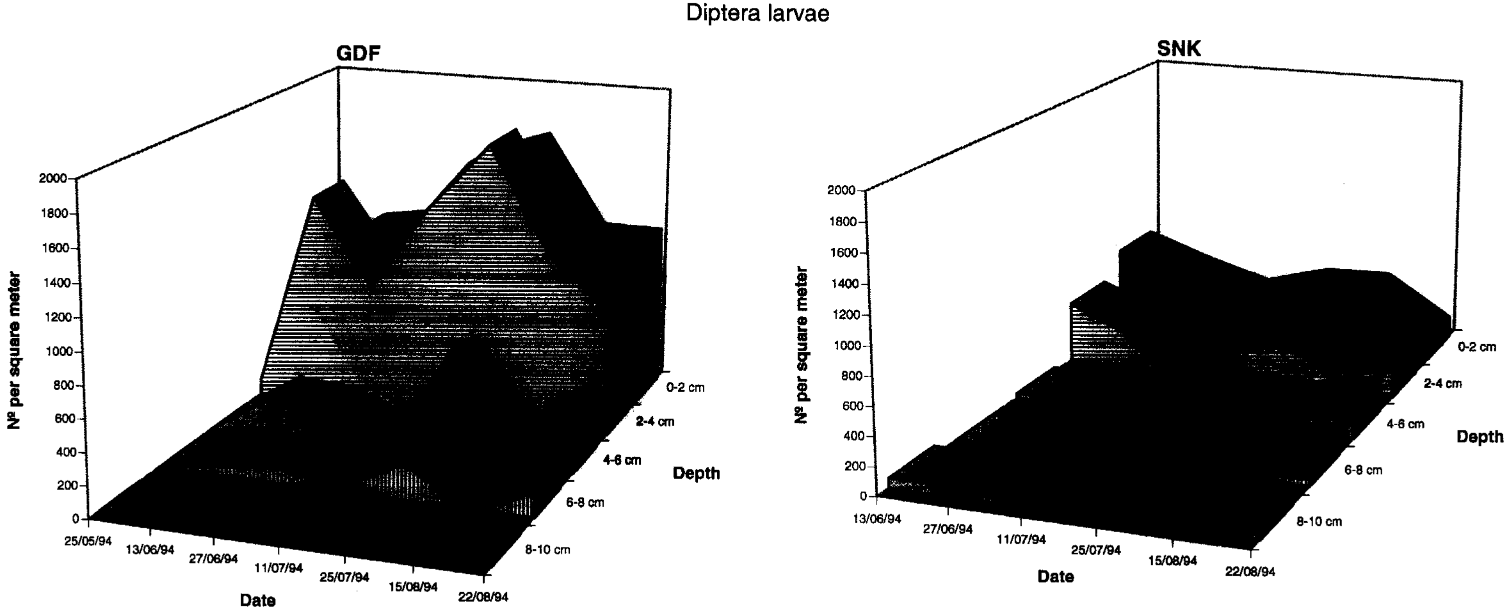

Fig. 7. Numbers and vertical distribution of Diptera larvae at both sites during the sampling period in 1994.

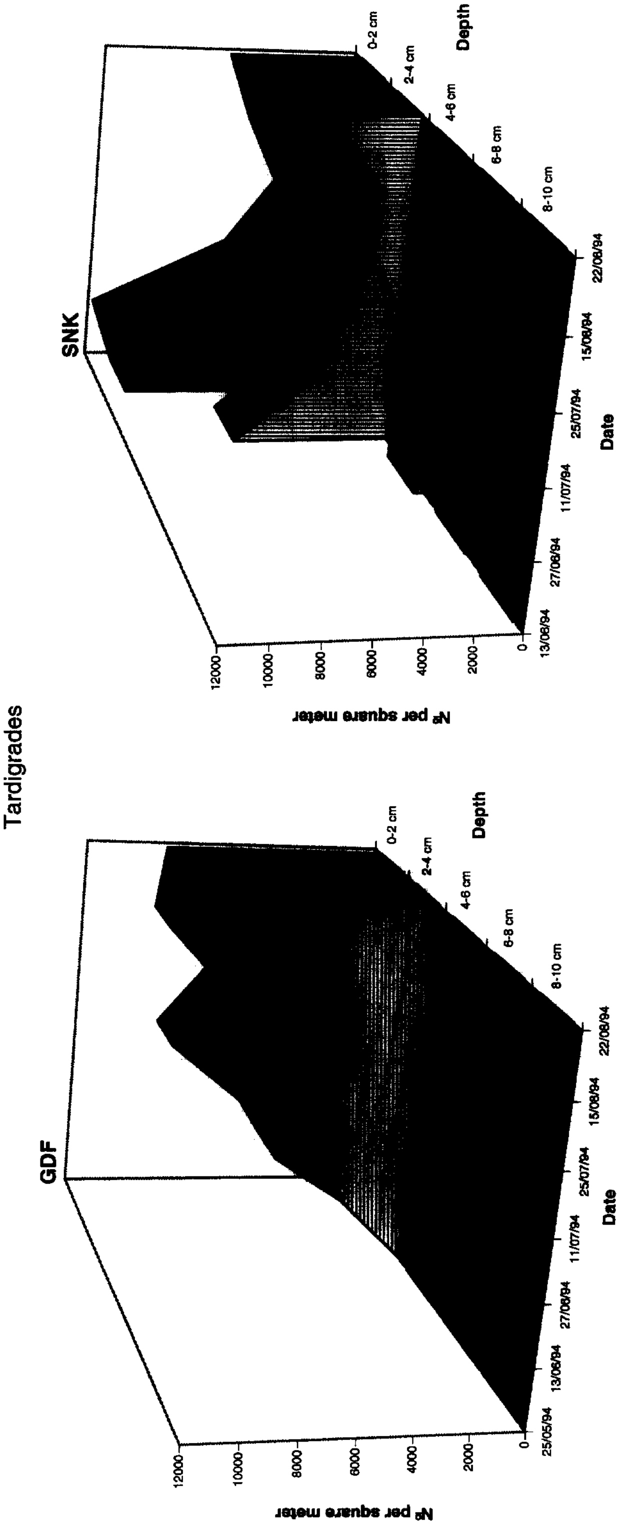

Fig. 8. Numbers and vertical distribution of tardigrades at both sites during the sampling period in 1994.

Table 1
Total numbers ($\times 10^3$ m^{-2}) of each taxa collected on the different sampling dates at each site, and significant results obtained from ANOVA with capital letters showing significant differences between sites (Tukey grouping)

	25 May 1994	13 June 1994	27 June 1994	11 July 1994	25 July 1994	15 August 1994	22 August 1994
C. sphagnetorum							
GDF	122	127A	126A	108A	195A	172A	173A
SNK		175B	154A	149B	196A	252B	254B
SNK-E						136C	229A
Site		$P < 0.01$	n.s.	$P < 0.05$	n.s.	$P < 0.01$	$P < 0.01$
Depth	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Site and Depth		$P < 0.05$	n.s.	n.s.	$P < 0.01$	n.s.	$P < 0.01$
C. atrata							
GDF	13	138A	227A	182A	189A	101A	104A
SNK		147B	194A	95B	54B	24AB	54A
SNK-E						13B	25A
Site		$P < 0.05$	n.s.	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.
Depth	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Site and Depth		n.s.	n.s.	n.s.	$P < 0.05$	n.s.	n.s.
A. eiseni							
GDF	0	5A	2A	17A	4A	3A	3AB
SNK		26B	29B	31B	26A	3A	3A
SNK-E						1B	0.5B
Site		$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.05$
Depth		$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Site and Depth		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Diptera larvae							
GDF	0.2	3A	2A	3A	4A	2A	2A
SNK		1A	1B	0.3B	1B	1B	1B
SNK-E						1B	1B
Site		n.s.	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.05$	$P < 0.01$
Depth	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Site and Depth		n.s.	n.s.	$P < 0.01$	n.s.	n.s.	n.s.
Tardigrades							
GDF	0.3	7A	10A	13A	10A	14A	14A
SNK		19A	16A	9B	5B	7A	11A
SNK-E						7A	8A
Site		n.s.	n.s.	$P < 0.01$	$P < 0.01$	n.s.	n.s.
Depth	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Site and Depth		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

ences were significantly different ($P < 0.05$), except for 27 June and 25 July. This increase in total numbers per core, and the decrease in number of individuals in the top soil layers, suggest vertical migration rather than mortality in response to the higher temperature and/or lower water content. Additionally, by the end of August, upward migration occurred in response to weather deterioration (Fig. 2), resulting in a recolonization of the upper layers at both sites accompanied by a decrease in numbers in the deeper layers (Fig. 4).

The number of tail fragments at the different sampling dates are given in Fig. 9. It can be seen that a higher number of tail fragments were recorded at both sites in July, when the highest temperatures were recorded, but more fragments were collected at SNK than at GDF over the whole experimental period, suggesting that increasing temperatures promoted reproduction.

In the SNK-E treatments the distribution pattern of *C. sphagnetorum* was similar to that for GDF but different from SNK treatments, with the majority of

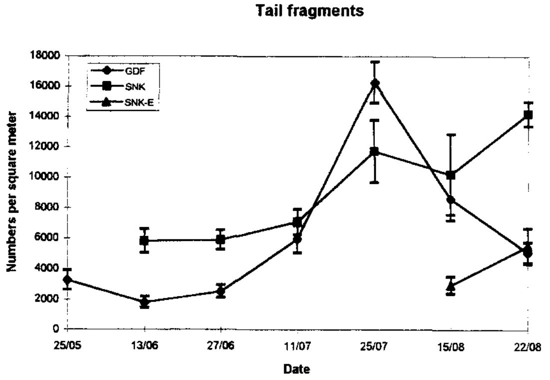

Fig. 9. Number of tail fragments per square metre for the three different treatments at the different sampling dates in 1994. Error bars represent standard errors.

the individuals concentrated in the first 2 cm (70% on 15 August and 81% on 22 August). Total numbers of individuals were significantly lower than the other two treatments on 15 August but were similar to GDF on 22 August (Table 1), which coincides with the low observed fragmentation rates (Fig. 9).

Total numbers of *Cognettia* showed a strong positive relationship with temperature at GDF (Table 2), but not at SNK where no clear dependence was observed. No significant relationships between rainfall and numbers were found for the GDF or SNK treatments.

3.2.2. *Cernosvitoviella atrata*

The 0–4 cm layer supported the main population of *C. atrata* (80%) and there was a clear maximum abundance in June at both sites (Fig. 5); at SNK this increase occurred in the 2–4 cm layer, although the difference in numbers of this species between layers was not statistically significant at this site. In July, the 0–2 cm layer showed a marked decrease in the abundance of *C. atrata*, more pronounced at SNK, which was significant from the end of July until mid-August (Table 1). No increase in numbers in the deeper layers (4–6, 6–8 and 8–10 cm) accompanied this observed decrease in the top layers (Fig. 5), and total numbers (Table 1) indicate that higher abundances occurred at GDF; this suggests that vertical migration of this species was insignificant at SNK.

There was no clear pattern in the vertical distribution in the SNK-E treatment; the population was equally distributed throughout the profile and showed the lowest total numbers, suggesting that high soil water content may had a negative effect on the population.

Cernosvitoviella populations showed a strong positive relationship with temperature at GDF, whereas at SNK this dependence was reversed. No significant relationships between rainfall and numbers were found for the GDF or SNK treatments (Table 2).

3.2.3. *Achaeta eiseni*

This species was represented less well than the other two enchytraeids at both sites. At GDF, a small peak in numbers occurred in the first 4 cm in mid-July (Fig. 6) whereas at the lower site (SNK), a popula-

Table 2
Results of the Regression Analysis. Correlation coefficients (r^2) for the total numbers of the different taxa and climatic factors at the two sites

Site	Species	Air *T*	*T*(+0.5 cm)	*T*(−2 cm)	*T*(−10 cm)	Rain (mm)
GDF	*C. sphagnetorum*	0.79 ($P < 0.01$)	0.77 ($P < 0.01$)	0.79 ($P < 0.01$)	0.79 ($P < 0.01$)	0.00 (n.s.)
	C. atrata	0.83 ($P < 0.01$)	0.82 ($P < 0.01$)	0.77 ($P < 0.01$)	0.74 ($P < 0.05$)	−0.08 (n.s.)
	A. eiseni	0.75 ($P < 0.05$)	0.76 ($P < 0.05$)	0.79 ($P < 0.01$)	0.81 ($P < 0.01$)	0.01 (n.s.)
	Diptera larvae	0.75 ($P < 0.05$)	0.72 ($P < 0.05$)	0.72 ($P < 0.05$)	0.72 ($P < 0.05$)	0.01 (n.s.)
	Tardigrades	0.91 ($P < 0.01$)	0.91 ($P < 0.01$)	0.90 ($P < 0.01$)	0.90 ($P < 0.01$)	0.00 (n.s.)
SNK	*C. sphagnetorum*	0.38 (n.s.)	0.34 (n.s.)	0.41 (n.s.)	0.45 (n.s.)	0.15 (n.s.)
	C. atrata	−0.86 ($P < 0.01$)	−0.81 ($P < 0.05$)	−0.83 ($P < 0.05$)	−0.84 ($P < 0.05$)	−0.02 (n.s.)
	A. eiseni	−0.08 (n.s.)	−0.07 (n.s.)	−0.11 (n.s.)	−0.15 (n.s.)	−0.44 (n.s.)
	Diptera larvae	−0.12 (n.s.)	−0.16 (n.s.)	−0.13 (n.s.)	−0.11 (n.s.)	0.04 (n.s.)
	Tardigrades	−0.38 (n.s.)	−0.36 (n.s.)	−0.31 (n.s.)	−0.26 (n.s.)	0.31 (n.s.)

Negative relationships are denoted by a negative sign. Significance levels in brackets. Air *T* = Air temperature, *T*(+0.5 cm) = temperature above 0.5 cm, *T*(−2 cm) = temperature at 2 cm depth, *T*(−10 cm) = temperature at 10 cm depth, Rain = Rainfall.

tion peak occurred in June and July in the upper 4 cm, coincidental with the higher temperatures. In July, the 4–6 cm layer had a higher number of individuals, although the differences between sampling strata were not significant (Fig. 6).

Total numbers of *A. eiseni* (Table 1) differed markedly in density between the two sites, with SNK supporting a higher population than GDF. This difference became statistically significant at the end of June and remained so until mid-July, leading to the conclusion that temperature could be controlling the changes in population size.

No clear conclusions can be drawn from the results for the SNK-E treatment due to the absence of any identifiable pattern in vertical distribution on either sampling date (Table 1). Only temperature appeared to explain the results from the top site, with higher temperatures having a positive effect on the population density of this species whereas at SNK no clear conclusions can be drawn (Table 2).

3.2.4. *Diptera larvae*

It can be seen that Diptera larvae at GDF were concentrated in the upper 4 cm and poorly represented in the deeper layers (Fig. 7) ($P < 0.05$), and at the end of July the 4–6 and 6–8 cm layers showed an increase in numbers coincidental with the summer peak of density in the upper layers. At SNK, abundances of Diptera larvae were lower in all soil layers during the whole sampling period, when compared to GDF.

Significant differences in total numbers of Diptera larvae between GDF and SNK were observed from the end of June to mid-August (Table 1), indicating that mortality rather than vertical migration was controlling population density in response to climatic changes.

In the SNK-E treatment low densities of Diptera larvae, similar to those in the SNK treatment, were recorded but they were not significantly different from those at GDF (Table 1). Temperature appeared

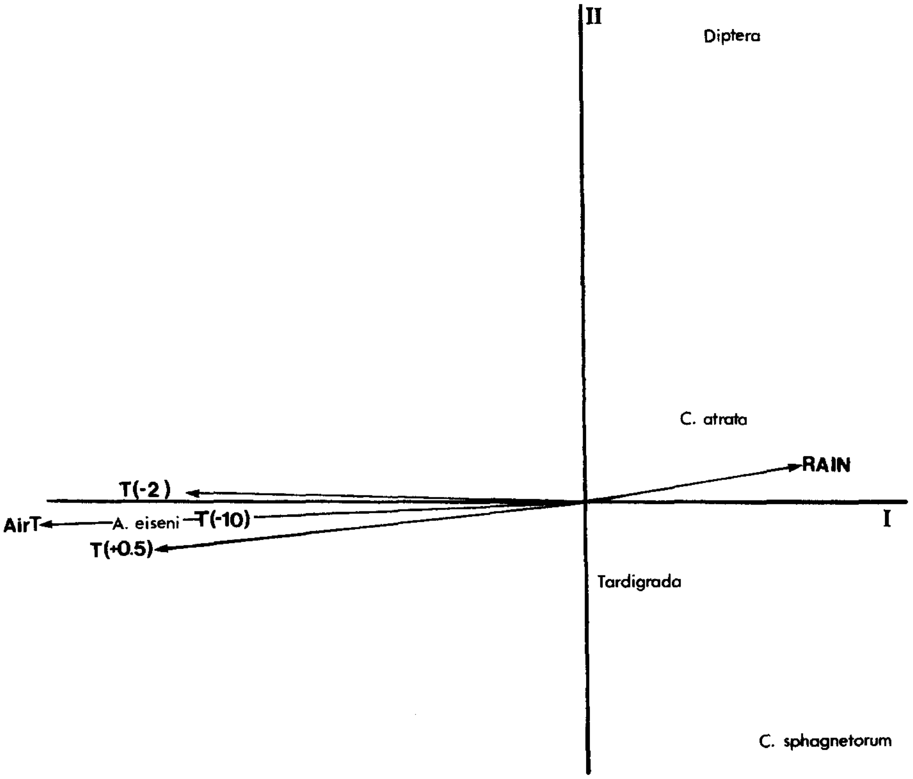

Fig. 10. Canonical correspondence analysis for the five taxonomical groups considered in relation to five climatic factors (AirT = Air temperature, $T(+0.5)$ = temperature at 0.5 cm above soil surface, $T(-2)$ = temperature at 2 cm soil depth, $T(-10)$ = temperature at -10 cm soil depth, and RAIN = rainfall).

to be the factor that explained the total numbers of Diptera larvae at the GDF site, with higher temperatures having a positive and significant relationship with the population density (Table 2).

3.2.5. *Tardigrades*

In the early summer (May and June) at GDF, and from June to mid-July at SNK, tardigrade populations were concentrated in the upper 2 cm layer ($P < 0.05$), whereas at the end of June at GDF, and a month later at SNK, the upper 4 cm of the soil contained significantly higher densities of tardigrades than the deeper layers ($P < 0.05$, Fig. 8). At the end of July, significantly lower numbers of tardigrades were recorded in the upper 4 cm at SNK compared to GDF and this decrease of numbers coincided with the recorded dry spell. In August the numbers rose again in response to the wetter conditions and lower temperatures (Figs. 8 and 2) so, by the end of August, no significant differences were detected in the vertical distribution of tardigrades between the three treatments (Table 1).

There were significantly higher total numbers of tardigrades at GDF than at SNK, across nearly all sampling dates (Table 1), except in June. The SNK-E treatment appeared to contain the lowest numbers of tardigrades, but no significant differences were detected between this and the other two treatments.

The total numbers of tardigrades were significantly and positively related with temperature at GDF (Table 2), whereas at SNK there was never any significant relationship with total numbers. No significant relationships between rainfall and numbers were found for the GDF or SNK treatments.

3.2.6. *Synecological responses*

Canonical correspondence analysis applied to the abundance data for the five taxa and climatic factors produced a first axis mainly explained by temperature (Fig. 10 and Table 3). The inertia percentage for the first axis was 91.8% and, after applying the Monte-Carlo test, was found to be significant at the 5% level.

Table 3
Interset correlation coefficients between the first two axes and the climatic factors

	Axis I	Axis II
Air *T*	−0.6991	−0.1678
T(+0.5 cm)	−0.6764	−0.1697
T(−2 cm)	−0.6358	−0.1466
T(−10 cm)	−0.6014	−0.1622
Rain (mm)	0.2957	0.1449

This axis clearly separates *A. eiseni* which appears to prefer high temperatures and low rainfall, in direct contrast to the other taxa.

4. Discussion

Soil moisture content is the resultant of temperature, rainfall, water-holding capacity and soil texture. Both enchytraeids and tardigrades are dependent on the free water in the soil for their existence and mobility, whereas Diptera larvae, like microarthropods, simply require a humid atmosphere (Andrén and Lagerlöf, 1983). Thus, individual species and higher taxa respond in distinct ways to changes in the environment, and the resulting communities are collections of species whose coexistence is dependent on physical, biological and historical variables (Graham and Grimm, 1990).

The results obtained, using canonical correspondence analysis, showed that the 'temperature–moisture' gradient determined invertebrate community composition. This technique facilitates a direct, one-step study of the relationships between species and environmental factors and is preferred to other ordination techniques, such as canonical correlation, principal component analysis and multiple regression, which are based on simple linear relationships (ter Braak, 1986). It has been shown here that *A. eiseni* is clearly favoured by higher temperatures, and adapted to decreases in moisture content, whereas other, hygrophilous, species showed the reverse tendency.

Our results showed that temperature and moisture played an important role in controlling: (i) total populations of soil invertebrates; and (ii) the vertical distribution of the populations, and that responses cannot be generalised but are species dependent. These responses are discussed more fully below.

4.1. *Enchytraeids*

Variation in size of enchytraeid populations is determined mainly by soil temperature and/or soil water content (Abrahamsen, 1971; Abrahamsen and Thompson, 1979; McColl, 1984) and summer droughts may result in severe reductions in total numbers (O'Connor, 1957) associated with increased adult and juvenile death rates and decreased cocoon survival, affecting the recovery of populations (Nielsen, 1955; Kasprzak, 1982). Enchytraeids mainly occur in the top layers of soils (Nielsen, 1955; Peachey, 1963; Springett, 1963) but they also occur in deeper layers where temporary increases in their numbers are attributed to vertical migration in response to adverse conditions (Springett et al., 1970).

A significant positive correlation was found between soil temperature and numbers at GDF for all enchytraeid species analysed (Table 2), indicating that temperature was the main factor influencing cocoon formation/hatching. Fragmentation rates are reported to be temperature dependent (Standen, 1973), which is also supported by our findings (see Fig. 9). Negative correlations between enchytraeid numbers and soil temperatures were recorded at SNK, which were significant for *C. atrata*, suggesting that there should be an optimum and when temperature reaches very high values severe reductions in the populations can be anticipated. In this sense, Edwards and Lofty (1971), in an electrically manipulated system, found that numbers decreased rapidly during spring in heated plots and that populations did not recover in autumn.

The low numbers of enchytraeids in the SNK-E treatment were somewhat surprising. Andrén and Lagerlöf (1983) and Healy (1987) have identified oxygen deficiency due to waterlogging as an important influence in enchytraeid survival, but Abrahamsen (1971) did not find reductions in *C. sphagnetorum* populations under excessive water regimes, which contrasts with our results.

From the above it may be concluded that temperature, and its effect on reproduction, is a key factor controlling population densities of enchytraeids with the response being highly species dependent. Under dry conditions it is likely that they can survive only in restricted favourable microsites (Lundkvist, 1982) or by vertical migration. Our results showed that *C. sphagnetorum* was able to move vertically to deeper layers, whereas *C. atrata* seemed unable to respond in the same way and, consequently, suffered greater mortality. In view of all this, temperature can be a limitant factor for populations and because Enchytraeids represent a species-poor group they could be susceptible to loss of species.

4.2. Diptera larvae

As geophilous forms, the Diptera larvae only spend part of their life in the soil and their abundance and dynamics depend on moisture regime due to their limited adaptation to terrestrial environments (Delettre and Lagerlöf, 1992). In our study, the upper 4 cm of the profile contained the main population, confirming with the findings of Chernov et al. (1977), Luxton (1982, 1983), Holliday et al. (1982) and Delettre and Lagerlöf (1992). They seemed to be very sensitive to temperature (see Fig. 7 and Table 2), and because of this superficial distribution, they are comparatively exposed to prevailing climatic conditions with only few species being able to withstand drought by downward migration or resistant stages.

4.3. Tardigrades

Temporal changes in tardigrade populations have been attributed either to food availability (Hallas and Yeates, 1972) or to climatic factors. Tardigrades are known to be able to enter a cryptobiotic state to avoid adverse conditions (Keilin, 1959; Crowe, 1975) with a revival time of 15–20 min (Crowe and Higgings, 1967). Because of these strategies, one can infer that tardigrades at SNK may have entered a dormant stage during the summer and increased their total numbers in August in response to wet conditions (see Table 1).

Despite this apparent climatic independence there are other studies which emphasise a strong dependence of tardigrades on moisture (Tilbrook, 1967; Morgan, 1977). The fact that the lowest numbers of tardigrades were recorded in the SNK-E treatment may be explained by oxygen deficiency as result of water excess, and Beasley (1981) explained the limited abundance of this group in Puerto Rico as a consequence of a continually moist environment.

There have been very few studies on the vertical migration of soil tardigrades (Kinchin, 1994; Büttner, 1989), and it is not clear whether tardigrade species maintain a relatively constant vertical distribution pattern or undergo significant migrations. Our findings indicated that vertical migration did not take place in response to changes in temperature and moisture content, which is in agreement with the observations of Hallas and Yeates (1972) and Leetham et al. (1982) who did not find a marked vertical penetration of tardigrades, concluding that they do not enter soil layers to any appreciable depth.

4.4. Proposed soil fauna scenario

Preliminary data showed that numbers of *C. sphagnetorum* remained relatively constant through the year suggesting that birth rates balances death rates whereas for the sexually reproducing species the maximum peaks are recorded during the summer, associated with higher soil temperatures (Springett, 1963). Soils at Moor House are frozen until the end of May and, despite the lack of information about overwintering for the different species, conclusions can be drawn in relation to the fauna under changing environments, since higher reproduction rates are essential for renewal of the populations.

Although we realize that the methodology adopted in the current work did not enable a factorial discrimination between temperature and moisture effects, the technique mimicked natural conditions and enabled some conclusions to be drawn on the impacts on the soil faunal populations.

Results from the canonical correspondence analysis showed that the 'temperature–moisture' gradient determined species composition at Moor House. Therefore, we can infer that climate change would result in new species associations in the soils investigated and increasing temperatures would result in increasing numbers of the more tolerant species (*A. eiseni*); migrations to other microhabitats or layers (*Cognettia*); dormancy and resistant states (tardigrades); or extinction (*Cernosvitoviella*, Diptera).

Vertical migration seems to be a successful strategy for avoiding adverse climatic conditions, but appendages and certain body shapes prevent penetration into deeper soil layers; in addition, readily-available organic matter is concentrated in the upper top 10 cm of the current soil, limiting the extent to which downward faunal movements can occur. Thus, if new climatic conditions persist then migration to the deeper layers may become an unsuitable strategy due to food exhaustion. In the short-term survival can also be ensured by entering dormancy states, but many species do not have this alternative strategy.

Many soil processes are affected by the activities of soil fauna, and any alterations in numbers, species composition, and distribution through the soil profile may have important implications for nutrient cycling, with particular impacts on organic matter turnover (Briones et al., submitted). Also, increasing temperatures result in changes in plant productivity which, in turn, may have important effects on the soil community. We conclude that assumptions that the soil fauna may respond little to predicted temperature changes (Whitford, 1992) are not substantiated by the current work.

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