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Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems

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Abstract

Soil microarthropod responses to long-term soil warming and increased fertilisation by addition of NKP or litter were assessed in three subarctic ecosystems. The experiment was carried out at three different field sites, where temperature and fertilisation manipulations had been running for 3–5 years (glade), 11 years (fellfield), and 12 years (heath) at the time of sampling. In the glade soil, warming led to decreases in Collembola and Gamasida, and increases in Oribatida, although effects were inconsistent between years. Actinedida densities were increased by fertilization, while Acaridida had higher densities in the treatment with both fertilisation and warming. In the fellfield, we found increased densities of Oribatida, Gamasida and Actinedida in the fertilised treatments, and some increases in Oribatida and decreases in Collembola and Gamasida in warming treatments. In the heath, there were increased densities of Collembola, Oribatida and Actinedida in the fertilised treatments, but we found no strong effects of warming. We suggest that the responses found in this study comply with the assumption that soil microarthropods are bottom-up controlled, and the observed changes are probably linked to changes in food availability more than direct climatic influences.

Keywords: Acari; Arctic-alpine; Climate change; Collembola; Field experiment; Leaf litter

1. Introduction

Several studies have addressed the possible consequences of global climate changes on the soil system, but only a few are concerned with long-term manipulations of the soil, and the possible direct or indirect effects on soil fauna. Most climate change models predict changes in soil moisture and temperature that will enhance N mineralisation and CO_2 emissions (Anderson, 1992; Nadelhoffer et al., 1992; Lloyd and Taylor, 1994; White et al., 1999). The rate of litter decomposition is influenced by temperature and moisture, as well as by biotic factors such as the community structure of the soil fauna (Swift et al., 1979; Seastedt, 1984; Verhoef and de Goede, 1985; Verhoef and Brussard, 1990; Davidson et al., 1998;

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Mebes and Filser, 1998). Soil biotic communities have been shown to be directly influenced by soil temperature and moisture (Coulson et al., 1996; Harte et al., 1996; Hodkinson et al., 1996; Sulkava and Huhta, 2003), and a temperature change may thus indirectly influence decomposition through top-down control by microarthropods of saprotrophic fungi and bacteria.

Climate change models predict that maximal warming, coupled with a reduction in the snow and sea-ice cover, will occur in the high latitudes of the Northern Hemisphere, and that the effects will take place more rapidly in higher latitudes compared to lower latitudes (IPCC, 2001). At heaths and fellfields near Abisko Research Station in northern Swedish Lapland, long-term field manipulations of microclimate have been performed since 1989. Focus has been mainly on plant/microbial communities and their interactions (Michelsen et al., 1996; Jonasson et al., 1999a,b; Schmidt et al., 1999), but recent work also included studies on diversity and density of Nematoda (Ruess et al., 1999a,b). Experimental increases of the soil temperature by 1–2 °C showed that warming may double the nematode population density, but causes decrease in the species diversity. Furthermore, effects were larger on high altitude sites most exposed to naturally occurring climatic stresses such as low temperatures, high wind-speed, and moisture limitations (Ruess et al., 1999b). Trophic structure and nematode species dominance changed significantly after eight growing seasons with warming and fertilisation. The observed effects were ascribed to physiological alterations or changing niche conditions such as predator-prey interactions or food resources (Ruess et al., 1999a). Annual net N and P mineralisation increased after soil warming and fertilisation, and also nutrient immobilisation in plants and microbes was enhanced (Jonasson et al., 1999b; Schmidt et al., 1999). While active fungal biomass and soil respiration (microbial activity) tended to be increased by warming in a low-altitude heath (Christensen et al., 1997; Ruess et al., 1999b), no such changes were found in a high-altitude fellfield (Jonasson et al., 1999b; Ruess et al., 1999b), possibly due to moisture limitations.

Similar to nematode communities, microarthropods may affect organic matter turnover, and may respond to changes in soil temperature and nutrient availability directly, and indirectly to changes in microbial biomass and activity following perturbations. In the present study, we investigated the effects of long-term temperature increases and/or fertiliser addition on soil microarthropod (springtails and mites) abundance in field manipulation experi–ments.

2. Materials and methods

2.1. Field sites and treatments

The experiments were carried out close to Abisko, northern Swedish Lapland (68°21′N, 18°40′E), at three different field sites. Site 1 was a mesic heath site at the border of the tree line, at 450 m elevation, southeast of Abisko Scientific Research Station, close to Mount Paddustieva. The plant cover was a species-rich dwarf shrub community dominated by *Cassiope tetragona*. The soil depth was 25–50 cm, with a 10–20 cm deep humus layer on top of the mineral soil. Climate records (1989–2002) from the nearby Abisko Scientific Research Station at 385 m elevation showed an annual mean temperature of 1.7 °C at 5 cm soil depth, with minimum and maximum temperatures of −9.3 and 12.5 °C, respectively. An experiment designed to simulate climate change effects was started at the location in 1989. Treatments consisted of temperature increase, fertilisation, a combination of the two, and an untreated control, set in a randomised block design with six replicates, each treatment plot measuring 1.2 m × 1.2 m. A 1.2–2.0 °C increase in mean summer soil temperature at 3–5 cm depth above an average temperature of 7.7 °C in control plots (Michelsen et al., 1996; Ruess et al., 1999b) was achieved by erecting ca. 0.7 m tall open top transparent polyethylene greenhouses every summer during the growing season (Havström et al., 1993; Jonasson et al., 1993). The fertilisation treatment consisted of applying N, P and K (10, 2.6 and 9 g m^{-2}, respectively) to each plot every year in June. The experiment was in its 13th year when sampling for the present study was conducted.

The second field site was a mesic fellfield located at the top of Mount Slåttatjåkka, at approximately 1150 m elevation. The plant cover in the area consisted mainly of mosses and lichens, with few vascular plants such as *C. tetragona*, *Salix herbacea* × *polaris* and *Vaccinium vitis-idaea*. The organic soil was shallow, with a depth of 0–5 cm (average, 2 cm) overlaying mineral soil or bedrock. The climate is sub-arctic montane with a growing season of approximately 3 months from late June to early September. Mount Slåttatjåkka has a permanent snow cover from mid-September to June. The average soil temperature (at 2–3 cm depth) recorded between August 2001 and August 2002 in a nearby field site was −1.8 °C, with a maximum of 16.6 °C, and a minimum of −18.3 °C. An experiment similar to the one described for site 1 was started at this site in June 1989. Treatments consisted of temperature increase, fertilisation, a combination of the two, and an untreated control, in a randomised block design with six replicates, each plot measuring 1.2 m × 1.2 m. The warming treatment resulted in a 1.2–1.3 °C increase in mean summer soil temperature at 2–4 cm depth, above an average temperature of 6.4 °C in control plots (Michelsen et al., 1996; Ruess et al., 1999b). The experimental treatments were terminated in August 1999. Hence, after 11 years of treatment, 1 year passed without further treatment prior to the sampling for the present study, and animal abundance at this site may, therefore, partly reflect recovery following perturbation.

The third field site was an open, hydric glade in a birch forest near Abisko, at 385 m elevation. Plant cover consisted mainly of dwarf shrubs, graminoids and mosses, in a wet, peaty environment. The climate is similar to that described for site 1. The average soil temperature (3 cm depth) recorded between August 2001 and August 2002 in a nearby field site was 1.5 °C, with a maximum of 15.5 °C, and a minimum of −12.9 °C. The experiment which started at the site in 1999 was designed to simulate climate change effects and the expansion of the birch forest into the open glade. Treatments consisted of temperature increase and/or fertilisation as outlined for sites 1 and 2. The temperature increase was achieved by erecting open top transparent polyethylene greenhouses every summer during the growing season. The fertilisation treatment consisted of applying 90 g dry weight (equal to 150 g fresh weight) m^{-2} of freshly fallen, dried birch leaves collected from the nearby birch forest. Leaves were applied to each plot every year in August, in an amount similar to the annual birch leaf litterfall in the adjacent birch forest. The experiment was in its 3rd–5th year when sampling for the present study was conducted. Due to cold water percolating the sloping terrain, the effects of the greenhouses on soil temperature were less marked at this site than at the heath and the fellfield sites. The mean growing season soil temperature at 3–5 cm depth increased by 0.6 °C above an average temperature of 9.8 °C in control plots, and the mean moss/litter surface temperature increased by 1.1 °C above an average temperature of 12.1 °C in control plots.

For more details about climate, vegetation and soil properties in the field sites, as well as further details about the treatments and the greenhouses, see Havström et al. (1993), Jonasson et al. (1993), Michelsen et al. (1996) and Ruess et al. (1999a,b).

2.2. Sampling and analysis of soil fauna

Soil was collected from each plot in the three field sites in July–August 2001; additional samplings were conducted at the glade in August 2002 and 2003. At the heath and glade, two samples measuring 3 cm Ø to a depth of 10 cm were extracted from each plot. At the fellfield, one sample measuring 5 cm Ø to a depth of 2–4 cm (representing the entire organic soil layer) was extracted from each plot within blocks 1–4. Blocks 5 and 6 could not be located due to missing plot tags. The soil cores were weighed (fresh weight), stored at 5 °C, and transported to the National Environmental Research Institute in Silkeborg, Denmark, where they were extracted within 1 week after sampling. Springtails (Collembola) and mites (Acari) were extracted into benzoic acid using a controlled temperature gradient extractor based on the principles by MacFadyen (1961) and Petersen (1978), over a period of 6 days. Collembola were identified to genus or species level, except Sminthuridae, which were not identified beyond family. Very small juveniles, and partly damaged specimens were pooled into a group named ‘‘unidentified Collembola’’. Taxonomic keys by Fjellberg (1980, 1998) were used. Acari were identified to superfamily or family level following the keys by Balogh (1972) and Krantz (1978), except Acaridida, which were not identified beyond order. Very small juveniles, and partly damaged specimens, were pooled into a group named ‘‘unidentified Acari’’. After counting and identification, the soil faunal data were pooled into five main groups: Collembola, Oribatida, Gamasida, Actinedida, and Acaridida. This grouping excluded the un-identified Acari. The soil cores were weighed after extraction for determination of dry weight. The numbers of soil animals in the main groups were calculated per gram dry soil, to correct for large variations in soil density. The numbers of soil animals were also calculated per m^2, to facilitate comparisons with other studies.

2.3. Statistical analyses

Treatment effects on the numbers of soil animals in the five main groups were analysed with MANOVA, separately for each field site. For the data from the glade, in which sequential sampling was done over 3 years, MANOVA analyses were performed separately for each year. The MANOVAs gave largely similar results for number of soil animals per g soil and per m^2 soil, and only results per g are generally reported. For the data from the heath and fellfield, treatment effects on the numbers of soil animals per g soil in the five main groups, and each identified taxon within the groups, were also analysed using three-way ANOVA with block, temperature and fertilisation as main factors. In addition, Tukey's test for comparison of treatment means was applied after a one-way ANOVA. For the data from the glade, treatment effects on the numbers of soil animals in the five main groups were additionally analysed using repeated measures ANOVA with block and treatments as main factors, and with year as the repeated time factor. Data with $P < 0.05$ were regarded as statistically significant, but tendencies towards significance ($P < 0.10$) are also reported. Levene's test was used to test for homogeneity of variance, and appropriate transformations were applied in cases with heteroscedasticity. Wherever transformations did not result in a homogeneous variance, data were removed from the analyses. However, this was only relevant for taxa where the abundance was very low, typically with only one occurrence of the taxon in all samples. Only data with significant differences, or a tendency towards significant differences in the MANOVA analyses are discussed. Statistical analyses were conducted using the GLM procedure (SAS Institute v8.02, 1999).

3. Results

3.1. Responses in the heath

In the heath (Fig. 1 and Table 1), there were significantly higher numbers of Collembola in the fertilised treatments; *Folsomia quadrioculata, Protaphorura* sp., and *Isotoma* sp. contributed most to the increase, *Protaphorura* sp. significantly so ($P < 0.05$). *Entomobrya* sp., which was not found in the control samples, tended to show higher numbers in warming and fertiliser treatments ($P < 0.1$), most strongly so in the combined warming and fertiliser (W + F) treatment ($P < 0.1$). The Oribatida also showed significantly higher numbers in the fertilised treatments, mainly due to a higher number of Oppioidea, but also due to the Camisiidae and Ceratozetoidea. None of the Gamasida or the Acaridida showed significant differences in the treatments. The Actinedida showed responses similar to the Collembola and Oribatida, with a tendency towards higher numbers in the fertilised treatments, mainly due to increases in Eupodoidea. Except for an increase in numbers of the un-identified Acari, there were no significant effects of warming on the microarthropods in the heath site.

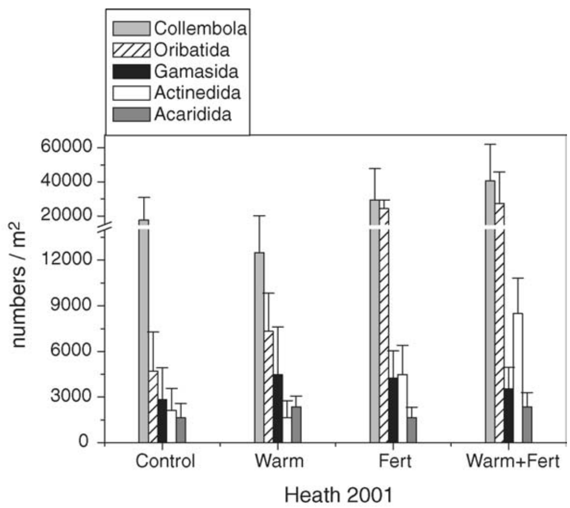

Fig. 1. Mean (+S.E.) number of Collembola (light grey), Oribatida (striped), Gamasida (black), Actinedida (white), and Acaridida (dark grey) per m^2, sampled in the subarctic heath in 2001, $n = 6$. Warm, warming treatment; Fert, fertiliser (NKP) addition.

Table 1
Main groups of soil fauna sampled in the sub-arctic heath in 2001

Taxon	MANOVA				3-Way ANOVA					Tukey's test			
	Block, 0.0057 Mean + S.E.	Warm, ns	Fert, 0.0651	W × F, ns	Model	Block	Warm	Fert	W × F	Con	Warm	Fert	W + F
	Con	Warm	Fert	Warm + Fert									
Collembola	1.91 + 1.45	1.22 + 0.72	4.25 + 2.49	4.67 + 1.97	0.001	0.001	ns	0.05	ns				
Folsomia quadrioculata	1.29 + 1.09	0.50 + 0.41	1.24 + 0.74	2.29 + 1.06	0.0005	0.0001	ns	0.1	0.05				
Protaphorura sp.	0.13 + 0.08	0.15 + 0.15	1.05 + 0.66	0.60 + 0.24	0.05	0.05	ns	0.05	ns				
Tetracanthella sp.	0.08 + 0.08	0.09 + 0.09	0.05 + 0.05	0.16 + 0.08	0.1	0.05	ns	ns	ns				
Isotoma sp.	0.22 + 0.11	0.27 + 0.15	1.13 + 0.71	0.58 + 0.25	0.05	0.05	ns	ns	ns				
Entomobrya sp.	0	0.05 + 0.03	0.05 + 0.05	0.16 + 0.06	0.1	ns	0.1	0.1	ns	b	ab	ab	a
Xenylla sp.	0.14 + 0.11	0.11 + 0.09	0.39 + 0.20	0.69 + 0.56	ns	0.1	ns	ns	ns				
Oribatida	0.80 + 0.40	1.00 + 0.37	3.89 + 1.07	3.50 + 1.74	ns	ns	ns	0.05	ns				
Camisiidae	0.11 + 0.08	0.17 + 0.08	0.25 + 0.12	0.72 + 0.46	0.1	0.1	ns	ns	ns				
Nothroidea	0.05 + 0.05	0	0	0	ns	ns	ns	ns	ns				
Oripodoidea	0.11 + 0.11	0	0.05 + 0.05	0.11 + 0.11	ns	ns	ns	ns	ns				
Damaeoidea	0.16 + 0.11	0.05 + 0.03	0.20 + 0.20	0.20 + 0.05	ns	ns	ns	ns	ns				
Ceratozetoidea	0.02 + 0.02	0	0.59 + 0.59	0.26 + 0.22	ns	ns	ns	ns	ns				
Oppioidea	0.31 + 0.18	0.54 + 0.20	2.60 + 0.89	2.02 + 1.37	ns	ns	ns	0.05	ns				
Gamasida	0.40 + 0.32	0.37 + 0.51	1.06 + 0.68	1.74 + 0.44	0.005	0.005	ns	ns	ns				
Zerconidae	0.24 + 0.19	0.44 + 0.35	0.54 + 0.28	0.35 + 0.18	0.01	0.005	ns	ns	ns				
Veigaioidea	0	0	0	0.04 + 0.04	ns	ns	ns	ns	ns				
Parasitoidea	0.08 + 0.06	0.07 + 0.05	0.14 + 0.06	0.05 + 0.05	ns	0.1	ns	ns	ns				
Actinedida	0.23 + 0.16	0.21 + 0.15	0.67 + 0.33	1.13 + 0.30	0.05	ns	ns	0.01	ns	b	b	ab	a
Raphignathoidea	0.05 + 0.05	0	0	0	ns	ns	ns	ns	ns				
Tydeoidea	0	0	0.03 + 0.03	0	ns	ns	ns	ns	ns				
Eupodoidea	0.23 + 0.16	0.21 + 0.15	0.64 + 0.32	1.13 + 0.30	0.05	ns	ns	0.01	ns	b	b	ab	a
Acaridida	0.24 + 0.21	0.38 + 0.24	0.33 + 0.26	0.15 + 0.31	0.05	0.01	ns	ns	ns				
Un-id. Collembola	0.14 + 0.14	0.06 + 0.06	0.36 + 0.21	0.29 + 0.11	ns	ns	ns	0.1	ns				
Un-id. Acari	0.11 + 0.07	0.21 + 0.09	0.15 + 0.09	0.28 + 0.11	0.0005	0.0001	0.05	ns	ns				

P-values ($P = x$) from the MANOVA analysis of the five main soil faunal groups. Warm, warming; Fert, fertiliser (NKP) addition; Warm + Fert (W + F), combination treatment with warming and fertiliser addition; Con, control. Mean + S.E.: mean number of specimens per g dry soil (+S.E.) for each treatment ($n = 6$). ANOVA: *P*-values ($P < x$) for the main factor effects (Warm, Fert), and interaction between main effects (W × F). Tukey's test: different letters denote a significant difference between treatments, only significant differences are included. Un-id., unidentified; ns, not significant; $P > 0.1$.

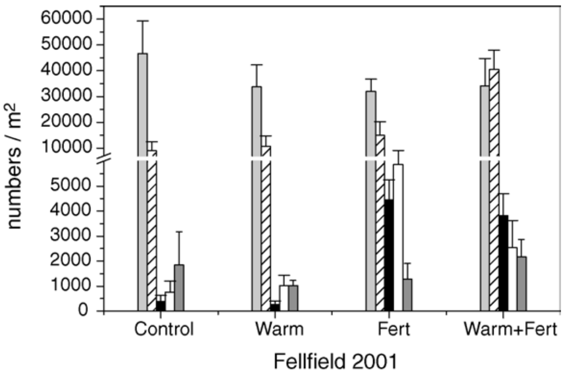

Fig. 2. Mean (+S.E.) number of Collembola (light grey), Oribatida (striped), Gamasida (black), Actinedida (white), and Acaridida (dark grey) per m^2, sampled in the fellfield in 2001, $n = 4$. Warm, warming treatment; Fert, fertiliser (NKP) addition.

3.2. Responses in the fellfield

In the fellfield (Fig. 2 and Table 2), there was a tendency towards lower numbers of Collembola in all treatments compared to the controls, with significant effects of warming on *F. quadrioculata*, and of fertiliser addition in *Tetracanthella* sp. The decreases were most pronounced in the combined warming and fertiliser (W + F) treatment, and strongest and significant for *F. quadrioculata* and *Tetracanthella* sp. *Protaphorura* sp. and *Friesea* sp. showed only slightly lower numbers in the warming treatment compared to the control. By contrast, the Oribatida had higher abundance ($P < 0.1$) in the fertilised treatment, significantly higher in the case of Oppioidea. The Ceratozetoidea showed four- to five-fold increases in the warmed plots. The numbers of Gamasida were strongly increased by fertilisation, with Zerconidae being the most responsive taxon, while warming reduced the abundance of Gamasida. There were higher numbers of Actinedida in the fertilised plots, while Acaridida did not show any significant changes.

3.3. Responses in the glade

In 2001 (Fig. 3a and Table 3a), there were no significant effects of the treatments on Collembola, Actinedida or Acaridida. In the case of Oribatida, there was a significant interaction effect, due to an increase by warming only in plots without fertilizer (litter) addition. The highest numbers of Oribatida were found in the warming treatment, mainly due to a higher number of Camisiidae. Gamasida also showed a significant interaction effect, with higher numbers in the combined W + F treatment, and lower numbers in the warming and fertiliser treatments. This was also the case for the Parasitoidea when analysed separately.

In 2002 (Fig. 3b and Table 3b), there was a tendency towards lower numbers of Collembola in the warming treatments ($P < 0.1$), while *Isotoma multisetis*, as well as other *Isotoma* species, were significantly more numerous in the fertilised treatment. There were no significant treatment effects on Oribatida as a group. However, the Oripodoidea, which was the most abundant taxon in the controls in all years, showed significantly lower numbers in the warming and W + F treatments. Gamasida also showed significantly lower numbers in response to warming, while the Parasitoidea responded positively to fertiliser addition. Actinedida showed significantly higher numbers in the fertilised and W + F treatments, while the Acaridida showed no significant treatment responses.

In 2003 (Fig. 3c and Table 3c), there were significant effects of the treatments only on Oribatida, which showed an interaction effect due to an increase by warming only in non-fertilised plots. Also, the Ceratozetoidea showed higher numbers in the fertilised treatments. Acaridida showed a tendency towards significantly higher numbers in the W + F treatment compared to the control, while none of the other groups responded significantly to the treatments.

When analysing the five main soil faunal groups at the glade across the 3 years (Table 3d), warming tended to influence both Collembola and Gamasida. However, the number of animals of all groups varied between years, as shown by significant year effects. Furthermore, for Oribatida, Gamasida, and Actinedida, effects of treatment differed between years, as shown by significant or near-significant year $\times$ warming effects.

4. Discussion

Few reports exist on soil faunal responses to in situ long-term temperature changes in the soil. Harte et al. (1996) investigated the effects of experimental

Table 2
Main groups of soil fauna sampled in the fellfield in 2001

Taxon	MANOVA				3-Way ANOVA					Tukey's test			
	Block, ns Mean + S.E.	Warm, 0.0188	Fert, 0.0043	W × F, ns	Model	Block	Warm	Fert	W × F	Con	Warm	Fert	W + F
	Con	Warm	Fert	Warm + Fert									
Collembola	25.75 + 6.56	13.28 + 3.74	13.25 + 1.80	10.19 + 3.15	ns	ns	ns	ns	ns	a	ab	ab	b
Folsomia quadrioculata	10.04 + 0.56	4.94 + 1.39	7.15 + 1.16	4.67 + 1.39	ns	ns	0.05	ns	ns	a	b	ab	b
Protaphorura sp.	0.19 + 0.09	0.09 + 0.05	0.42 + 0.24	0.61 + 0.25	ns	ns	ns	0.1	ns				
Tetracanthella sp.	10.54 + 4.91	4.91 + 1.86	2.61 + 0.54	1.34 + 0.86	0.1	ns	ns	0.05	ns	a	ab	ab	b
Friesea sp.	1.76 + 0.45	0.81 + 0.33	1.50 + 0.52	2.47 + 0.94	ns	ns	ns	ns	ns				
Isotoma sp.	2.71 + 1.69	2.35 + 0.85	1.23 + 0.30	0.70 + 0.15	ns	ns	ns	ns	ns				
Oribatida	4.44 + 0.50	4.31 + 1.50	6.31 + 2.24	13.96 + 4.07	ns	ns	ns	0.1	ns				
Camisiidae	1.68 + 0.70	1.90 + 1.03	2.26 + 2.18	1.22 + 0.63	0.05	0.05	ns	ns	ns				
Oppioidea	2.30 + 0.46	1.01 + 0.54	2.67 + 1.01	8.26 + 2.99	0.1	ns	ns	0.05	0.05	ab	b	ab	a
Oripodoidea	0	0.11 + 0.11	0.05 + 0.05	0.28 + 0.28	ns	ns	ns	ns	ns				
Phenopeloidea	0.18 + 0.18	0.05 + 0.05	0.29 + 0.29	0	ns	ns	ns	ns	ns				
Ceratozetoidea	0.29 + 0.29	1.19 + 0.51	0.75 + 0.45	3.89 + 1.20	0.1	ns	0.05	0.1	ns	b	ab	b	a
Eulohmannioidea	0	0	0	0.05 + 0.05	ns	ns	ns	ns	ns				
Gamasida	0.18 + 0.09	0.10 + 0.07	1.85 + 0.28	1.32 + 0.44	0.001	0.1	0.1	0.001	ns	b	b	a	a
Zerconidae	0.13 + 0.07	0.11 + 0.07	1.74 + 0.28	1.19 + 0.40	0.001	0.05	0.1	0.0001	ns	b	b	a	a
Parasitoidea	0	0	0.11 + 0.11	0.14 + 0.05	ns	ns	ns	0.1	ns				
Phytoseiidae	0	0.05 + 0.05	0.39 + 0.39	0	ns	ns	ns	ns	ns				
Uropodoidea	0.33 + 0.21	0.13 + 0.09	0.12 + 0.07	0.38 + 0.34	ns	ns	ns	ns	ns				
Actinedida	0.28 + 0.17	0.35 + 0.16	2.33 + 1.25	0.95 + 0.46	0.1	ns	ns	0.05	ns				
Tydeoidea	0	0.08 + 0.05	1.58 + 0.85	0.46 + 0.26	ns	ns	ns	ns	ns				
Eupodoidea	0.28 + 0.17	0.23 + 0.12	0.36 + 0.13	0.44 + 0.21	ns	ns	ns	ns	ns				
Raphignathoidea	0	0.16 + 0.09	0.33 + 0.19	0.58 + 0.21	ns	ns	ns	0.05	ns				
Acaridida	0.26 + 0.15	0.38 + 0.39	0.52 + 0.24	0.79 + 0.31	0.1	0.1	ns	ns	ns				
Un-id. Collembola	0.18 + 0.09	0.07 + 0.07	0.22 + 0.08	0.04 + 0.04	ns	ns	0.1	ns	ns				
Un-id. Acari	0.26 + 0.15	0.17 + 0.07	0.32 + 0.13	0.53 + 0.32	ns	0.1	ns	ns	ns				

P-values ($P = x$) from the MANOVA analysis of the five main soil fauna groups. Warm, warming; Fert, fertiliser (NKP) addition; Warm + Fert (W + F), combination treatment with warming and fertiliser addition; Con, control. Mean + S.E.: mean number of specimens per g dry soil (+S.E.) for each treatment ($n = 4$). ANOVA: *P*-values ($P < x$) for the main factor effects (Warm, Fert), and interaction between main effects (W × F). Tukey's test: different letters denote a significant difference between treatments, only significant differences are included. Un-id., unidentified; ns, not significant, $P > 0.1$.

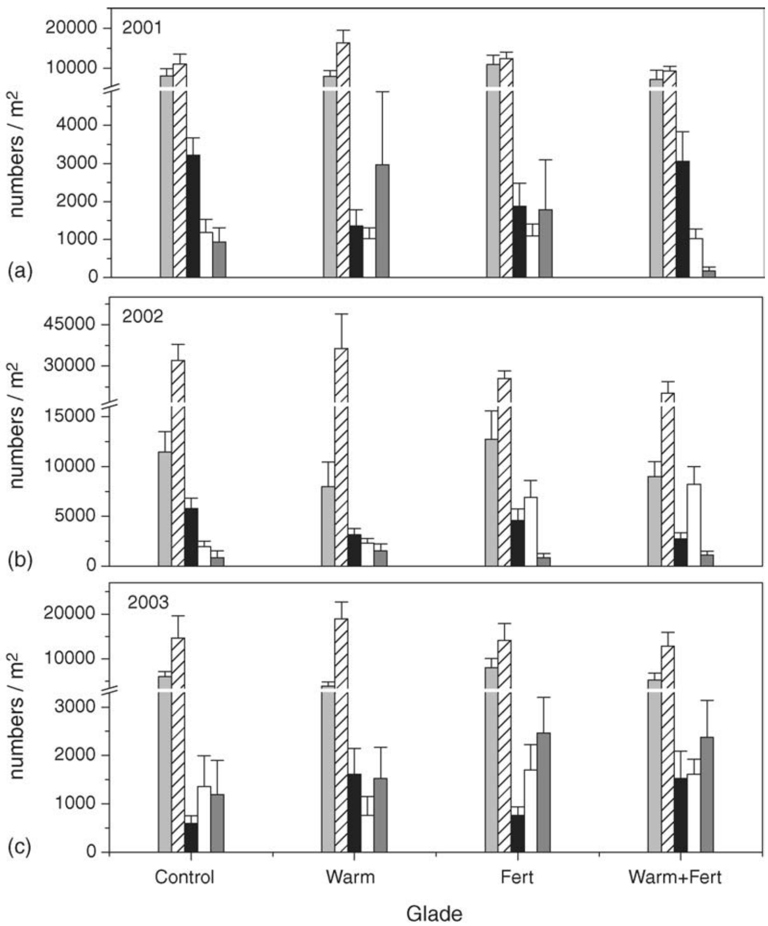

Fig. 3. Mean (+S.E.) number of Collembola (light grey), Oribatida (striped), Gamasida (black), Actinedida (white), and Acaridida (dark grey) per m^2, sampled in the open glade in 2001 (a), 2002 (b) and 2003 (c), $n = 6$. Warm, warming treatment; Fert, fertiliser (birch leaves) addition.

infrared radiation heating of a subalpine meadow, and found that heating increased the diversity and abundance of soil mesofauna if the summer was cool and wet, but decreased it in warm, dry summers. Coulson et al. (1996) found that in a polar semi-desert, the number of Collembola in temperature-manipulated plots after 3 years of warming by transparent plastic greenhouses during the growing season was significantly lower than in control plots. Ruess et al. (1999b) investigated the effects of increased summer temperatures and fertilisation on the nematode fauna and microorganisms, at the same field plots as those used in our study (heath and fellfield). Ruess et al. (1999b) found that nematode density doubled after eight growing seasons in plots with warming, increased by one-third in the fertilised plots, and doubled in plots with combined treatments. The bacterial feeding (and dominant) nematodes were increased almost two-fold by warming at both sites, and by fertilization at the fellfield. Numbers of fungal feeding nematodes doubled in the heath and increased up to six-fold in the fellfield in the warming treatments, and doubled in the fertilised treatments at the fellfield (Ruess et al., 1999b).

Sampling for the present study was conducted 13 years after the initiation of the experiments, and 5 years after the recording of the responses in the nematodes. Increased densities were evident in the fertilised treatments for Collembola, Oribatida and Actinedida at the heath, and for Oribatida, Gamasida and Actinedida at the fellfield. The increased numbers of Actinedida and Gamasida might be explained by

Table 3a
Main groups of soil fauna sampled in the glade in 2001

Taxon	MANOVA				3-Way ANOVA					Tukey's test			
	Block, ns Mean + S.E.	Warm, ns	Fert, ns	W × F, 0.0952	Model	Block	Warm	Fert	W × F	Con	Warm	Fert	W + F
	Con	Warm	Fert	Warm + Fert									
Collembola	0.99 + 0.17	1.07 + 0.20	1.39 + 0.30	1.00 + 0.34	ns	ns	ns	ns	ns				
Folsomia quadrioculata	0.60 + 0.14	0.56 + 0.18	0.97 + 0.32	0.53 + 0.19	ns	ns	ns	ns	ns				
Protaphorura sp.	0.09 + 0.02	0.13 + 0.07	0.20 + 0.07	0.02 + 0.01	ns	ns	ns	ns	ns				
Tetracanthella sp.	0.01 + 0.01	0.06 + 0.05	0.02 + 0.02	0.02 + 0.02	ns	ns	ns	ns	ns				
Isotoma sp.	0.16 + 0.05	0.14 + 0.03	0.17 + 0.04	0.13 + 0.05	ns	ns	ns	ns	ns				
Entomobrya sp.	0.07 + 0.03	0.10 + 0.10	0.03 + 0.03	0.12 + 0.11	ns	ns	ns	ns	ns				
Xenylla sp.	0	0.01 + 0.01	0.08 + 0.05	0.01 + 0.01	ns	ns	ns	ns	ns				
Sminthuridae	0.03 + 0.02	0.01 + 0.01	0	0.01 + 0.01	ns	ns	ns	ns	ns				
Oribatida	1.53 + 0.35	2.26 + 0.40	1.71 + 0.21	1.27 + 0.20	ns	ns	ns	ns	0.05	ab	a	ab	b
Camisiidae	0.47 + 0.20	1.26 + 0.34	0.62 + 0.13	0.48 + 0.10	ns	ns	ns	ns	0.05	b	a	ab	b
Ceratozetoidea	0.33 + 0.13	0.13 + 0.05	0.36 + 0.12	0.21 + 0.05	ns	ns	0.1	ns	ns				
Eulohmannioidea	0.05 + 0.02	0.01 + 0.01	0.05 + 0.02	0.02 + 0.01	ns	ns	0.1	ns	ns				
Oripodoidea	0.66 + 0.15	0.85 + 0.21	0.68 + 0.11	0.54 + 0.14	ns	ns	ns	ns	ns				
Gamasida	0.47 + 0.05	0.19 + 0.07	0.25 + 0.08	0.42 + 0.12	ns	ns	ns	ns	0.05				
Zerconidae	0.23 + 0.05	0.12 + 0.06	0.13 + 0.06	0.20 + 0.06	ns	ns	ns	ns	ns				
Veigaioidea	0.03 + 0.02	0.03 + 0.02	0.06 + 0.03	0.08 + 0.02	ns	ns	ns	0.1	ns				
Parasitoidea	0.13 + 0.03	0.05 + 0.02	0.06 + 0.02	0.12 + 0.04	0.1	ns	ns	ns	0.05				
Phytoseiidae	0	0	0.01 + 0.01	0	ns	ns	ns	ns	ns				
Actinedida	0.16 + 0.05	0.14 + 0.04	0.15 + 0.04	0.13 + 0.04	ns	ns	ns	ns	ns				
Trombidioidea	0.01 + 0.01	0	0	0.01 + 0.01	ns	ns	ns	ns	ns				
Cheyletoidea	0	0	0.01 + 0.01	0	ns	ns	ns	ns	ns				
Raphignathoidea	0	0.01 + 0.01	0	0	ns	ns	ns	ns	ns				
Tydeoidea	0	0.01 + 0.01	0	0	ns	ns	ns	ns	ns				
Eupodoidea	0.15 + 0.05	0.12 + 0.03	0.13 + 0.03	0.12 + 0.03	ns	ns	ns	ns	ns				
Acaridida	0.13 + 0.06	0.39 + 0.25	0.26 + 0.19	0.02 + 0.01	ns	ns	ns	ns	ns				
Un-id. Collembola	0.03 + 0.02	0.06 + 0.03	0.03 + 0.03	0.11 + 0.11	ns	ns	ns	ns	ns				
Un-id. Acari	0.12 + 0.05	0.34 + 0.19	0.24 + 0.19	0.02 + 0.01	ns	ns	ns	ns	ns				

P-values ($P = x$) from the MANOVA analysis of the five main soil fauna groups. Warm, warming; Fert, fertiliser (litter) addition; Warm + Fert (W + F), combination treatment with warming and fertiliser addition; Con, control. Mean + S.E.: mean number of specimens per g dry soil (+S.E.) for each treatment ($n = 6$). ANOVA: *P*-values ($P < x$) for the main factor effects (Warm, Fert), and interaction between main effects (W × F). Tukey's test: different letters denote a significant difference between treatments, only significant differences are included. Un-id., unidentified; ns, not significant; $P > 0.1$.

Table 3b
Main groups of soil fauna sampled in the glade in 2002

Taxon	MANOVA				3-Way ANOVA					Tukey's test			
	Block, ns Mean + S.E.	Warm, ns	Fert, 0.0005	W × F, ns	Model	Block	Warm	Fert	W × F	Con	Warm	Fert	W + F
	Control	Warm	Fert	Warm + Fert									
Collembola	1.82 + 0.32	1.19 + 0.35	1.89 + 0.46	1.46 + 0.25	ns	ns	0.1	ns	ns				
Folsomia quadrioculata	0.47 + 0.15	0.40 + 0.10	0.45 + 0.13	0.35 + 0.12	0.05	0.05	ns	ns	ns				
Protaphorura sp.	0.29 + 0.08	0.22 + 0.07	0.68 + 0.27	0.33 + 0.15	ns	ns	ns	ns	ns				
Tetracanthella sp.	0.15 + 0.05	0.14 + 0.10	0	0	ns	ns	ns	0.01	ns				
Isotoma sp.	0.08 + 0.04	0.18 + 0.10	0.36 + 0.05	0.32 + 0.11	0.1	ns	ns	0.05	ns				
Entomobrya sp.	0.67 + 0.24	0.11 + 0.03	0.07 + 0.03	0.11 + 0.07	ns	ns	ns	ns	ns				
Xenylla sp.	0.17 + 0.06	0.19 + 0.11	0.29 + 0.09	0.14 + 0.05	ns	ns	ns	ns	ns				
Isotoma multisetis	0	0	0.14 + 0.06	0.15 + 0.06	ns	ns	ns	0.05	ns	b	b	ab	a
Oribatida	5.85 + 0.67	5.78 + 2.20	4.00 + 0.46	3.64 + 0.87	ns	ns	ns	ns	ns				
Camisiidae	1.95 + 0.36	3.42 + 1.98	0.97 + 0.36	1.46 + 0.58	ns	ns	ns	ns	ns				
Carabodidae	0	0	0.01 + 0.01	0.07 + 0.04	ns	ns	ns	0.1	ns				
Ceratozetoidea	1.56 + 0.11	1.15 + 0.29	1.08 + 0.26	1.08 + 0.27	ns	ns	ns	ns	ns				
Eulohmannioidea	0.32 + 0.12	0.17 + 0.07	0	0.07 + 0.04	ns	ns	ns	ns	ns				
Oripodoidea	2.03 + 0.35	1.04 + 0.13	1.93 + 0.20	0.96 + 0.15	0.01	ns	0.0005	ns	ns	a	b	a	b
Gamasida	0.90 + 0.18	0.42 + 0.10	0.60 + 0.15	0.36 + 0.11	ns	ns	0.05	ns	ns				
Zerconidae	0.74 + 0.15	0.39 + 0.10	0.45 + 0.13	0.18 + 0.08	ns	ns	0.05	0.1	ns	a	ab	ab	b
Veigaioidea	0.14 + 0.05	0	0.06 + 0.03	0.01 + 0.01	ns	ns	0.05	ns	ns	b	a	ab	ab
Parasitoidea	0.03 + 0.02	0.03 + 0.02	0.08 + 0.04	0.13 + 0.04	ns	ns	ns	0.05	ns				
Phytoseiidae	0.04 + 0.03	0.10 + 0.05	0.17 + 0.07	0.12 + 0.04	ns	ns	ns	ns	ns				
Actinedida	0.32 + 0.09	0.38 + 0.08	1.13 + 0.28	1.35 + 0.29	0.005	ns	ns	0.005	ns	b	b	a	a
Bdelloidea	0	0	0.21 + 0.12	0.35 + 0.13	ns	ns	ns	ns	ns				
Cheyletoidea	0.06 + 0.04	0.04 + 0.03	0.15 + 0.10	0.21 + 0.08	ns	ns	ns	0.05	ns				
Raphignathoidea	0	0	0.18 + 0.08	0.25 + 0.10	ns	ns	ns	ns	ns				
Tydeoidea	0.09 + 0.04	0.06 + 0.03	0.21 + 0.10	0.11 + 0.06	ns	ns	ns	ns	ns				
Eupodoidea	0.18 + 0.07	0.28 + 0.09	0.37 + 0.14	0.43 + 0.12	ns	ns	ns	ns	ns				
Acaridida	0.14 + 0.11	0.25 + 0.11	0.14 + 0.07	0.18 + 0.06	ns	ns	ns	ns	ns				
Un-id. Collembola	0.04 + 0.02	0.06 + 0.03	0.10 + 0.08	0.07 + 0.05	ns	ns	ns	ns	ns				
Un-id. Acari	0.06 + 0.04	0.18 + 0.08	0.13 + 0.06	0.10 + 0.05	ns	ns	ns	ns	ns				

P-values ($P = x$) from the MANOVA analysis of the five main soil fauna groups. Warm, warming; Fert, fertiliser (litter) addition; Warm + Fert (W + F), combination treatment with warming and fertiliser addition; Con, control. Mean + S.E.: mean number of specimens per g dry soil (+S.E.) for each treatment ($n = 6$). ANOVA: *P*-values ($P < x$) for the main factor effects (Warm, Fert), and interaction between main effects (W × F). Tukey's test: different letters denote a significant difference between treatments, only significant differences are included. Un-id., unidentified; ns, not significant; $P > 0.1$.

Table 3c
Main groups of soil fauna sampled in the glade in 2003

Taxon	MANOVA				3-Way ANOVA					Tukey's test			
	Block, ns Mean + S.E.	Warm, ns	Fert, ns	W × F, 0.0645	Model	Block	Warm	Fert	W × F	Con	Warm	Fert	W + F
	Control	Warm	Fert	Warm + Fert									
Collembola	1.36 + 0.34	1.48 + 0.45	2.30 + 0.43	2.30 + 0.72	ns	ns	ns	ns	ns				
Folsomia quadrioculata	0.43 + 0.10	0.63 + 0.31	1.00 + 0.21	1.03 + 0.64	ns	ns	ns	ns	ns				
Protaphorura sp.	0.30 + 0.18	0.15 + 0.09	0.47 + 0.13	0.45 + 0.23	ns	ns	ns	ns	ns				
Tetracanthella sp.	0.03 + 0.03	0	0	0	ns	ns	ns	ns	ns				
Isotoma sp.	0.40 + 0.19	0.23 + 0.06	0.14 + 0.10	0.11 + 0.05	ns	ns	ns	0.1	ns				
Entomobrya sp.	0.18 + 0.09	0.19 + 0.08	0.20 + 0.13	0.18 + 0.15	ns	ns	ns	ns	ns				
Xenylla sp.	0.11 + 0.11	0.08 + 0.06	0.18 + 0.08	0.06 + 0.06	ns	ns	ns	ns	ns				
Oribatida	1.75 + 0.39	4.60 + 1.11	3.50 + 0.85	3.49 + 0.79	0.05	0.1	ns	0.1	0.1				
Camisiidae	0.74 + 0.29	3.06 + 0.91	1.73 + 0.75	1.47 + 0.36	0.1	ns	0.1	ns	0.05	b	a	ab	ab
Ceratozetoidea	0.25 + 0.08	0.51 + 0.27	1.98 + 1.16	1.43 + 0.48	ns	ns	ns	0.05	ns				
Eulohmannioidea	0.05 + 0.03	0.05 + 0.03	0.17 + 0.12	0.12 + 0.09	ns	ns	ns	ns	ns				
Oripodoidea	0.94 + 0.20	1.46 + 0.39	1.66 + 0.34	1.77 + 0.40	ns	ns	ns	ns	ns				
Gamasida	0.44 + 0.26	0.78 + 0.31	0.76 + 0.21	1.07 + 0.18	ns	ns	ns	ns	ns				
Zerconidae	0.40 + 0.16	0.28 + 0.12	0.21 + 0.07	0.29 + 0.10	ns	ns	ns	ns	ns				
Veigaioidea	0.05 + 0.03	0.08 + 0.04	0.11 + 0.04	0.20 + 0.15	ns	ns	ns	ns	ns				
Parasitoidea	0.07 + 0.03	0.02 + 0.02	0.12 + 0.07	0.07 + 0.03	ns	ns	ns	ns	ns				
Phytoseiidae	0	0	0.03 + 0.03	0	ns	ns	ns	ns	ns				
Actinedida	0.91 + 0.27	0.97 + 0.31	0.48 + 1.19	2.28 + 0.66	ns	ns	ns	ns	ns				
Trombidioidea	0.02 + 0.02	0	0	0	ns	0.1	ns	ns	ns				
Bdelloidea	0.07 + 0.03	0.07 + 0.04	0.07 + 0.05	0.06 + 0.04	ns	ns	ns	ns	ns				
Raphignathoidea	0.03 + 0.03	0	0	0.05 + 0.03	0.1	0.1	ns	ns	0.1				
Eupodoidea	0.25 + 0.15	0.41 + 0.20	0.31 + 0.11	0.46 + 0.06	ns	ns	ns	ns	ns				
Acaridida	0.25 + 0.11	0.21 + 0.06	0.12 + 0.08	0.08 + 0.05	ns	ns	ns	0.1	ns				
Un-id. Collembola	0	0	0.02 + 0.02	0.06 + 0.06	ns	ns	ns	ns	ns				
Un-id. Acari	0.18 + 0.11	0.37 + 0.26	0.46 + 0.15	0.61 + 0.14	ns	ns	ns	ns	ns				

P-values ($P = x$) from the MANOVA analysis of the five main soil fauna groups. Warm, warming; Fert, fertiliser (litter) addition; Warm + Fert (W + F), combination treatment with warming and fertiliser addition; Con, control. Mean + S.E.: mean number of specimens per g dry soil (+S.E.) for each treatment ($n = 6$). ANOVA: *P*-values ($P < x$) for the main factor effects (Warm, Fert), and interaction between main effects (W × F). Tukey's test: different letters denote a significant difference between treatments, only significant differences are included. Un-id., unidentified; ns, not significant; $P > 0.1$. MANOVA results for number of animals per m^2 showed tendencies ($P < 0.1$) towards warming and fertilization effects but no interaction.

Table 3d
Results from repeated measures ANOVA on the number of specimens per g dry soil in the main soil faunal groups in an open glade, 2001–2003

Group	Within-subject effects					Between-subject effects			
	Year	Year × Block	Year × Warm	Year × Fert	Year × Warm × Fert	Block	Warm	Fert	Warm × Fert
Collembola	0.0001	ns	ns	ns	ns	ns	0.1	ns	ns
Oribatida	0.0001	ns	0.1	ns	ns	ns	ns	ns	ns
Gamasida	0.05	ns	0.05	ns	ns	ns	0.1	ns	ns
Actinedida	0.0001	ns	0.1	ns	ns	ns	ns	ns	ns
Acaridida	0.01	ns	ns	0.1	0.1	ns	ns	ns	ns

Warm, warming treatment; Fert, fertiliser (birch leaves) addition. ns, not significant. $n = 6$.

their feeding habits. These mites are considered to be mainly predators (Krantz, 1978; Martikainen and Huhta, 1990; Smith et al., 1998; Scheu, 2002), so an increase in prey groups, such as Nematoda and Collembola, could facilitate higher numbers of predatory Actinedida and Gamasida. However, some species within the Actinedida are also often seen as detritivores, similar to Collembola and Oribatida (Behan and Hill, 1978; Krantz, 1978; Ineson et al., 1982; Seastedt, 1984; Norton, 1993; Maraun et al., 1998; Smith et al., 1998; Scheu, 2002). The higher numbers of detritivores in the fertilised treatments may reflect the increase in microbial biomass and active fungal biomass as described by Ruess et al. (1999b). The lack of fungal biomass responses at the fellfield (Ruess et al., 1999b), and the minimal responses found within the Collembola at the same site, support our assumption that changes in collembolan density are reflecting changes in fungal biomass. It may thus seem that the Collembola in the fellfield are more influenced by fungal responses than bacterial responses to the manipulations. However, as our sampling in the fellfield took place following 1 year with no treatment at the site, the lack of significant treatment responses in Collembola in this site may instead indicate that collembolan abundance in treated plots returned to normal level within 1 year following the termination of the experiment.

It is noteworthy that the strong increase in nematode density caused by warming at the heath (Ruess et al., 1999a,b) were not matched by similar increases in the Acari or Collembola at this site, although sampled 5 years later. However, in the climatically more harsh fellfield, the oribatid taxon Ceratozetoidea was increased while the dominant collembolan species *F. quadrioculata* was decreased by warming, and the Gamasida tended to be decreased by warming, suggesting a stronger effect of climatic changes on microarthropods in colder climates, as also observed by Hodkinson et al. (1998). The weak tendency towards increased numbers of some groups of microarthropods at the moister glade site because of warming in some but not all years is consistent with the study of Harte et al. (1996). These authors reported that in cool wet summers, microarthropods increased in numbers and diversity as a response to experimental heating, whereas in dry summers the opposite result was seen. It is also consistent with the conclusions of Hodkinson et al. (1998), who found that similar animal communities responded differently to warming on sites with different vegetation cover, and that arctic soil microarthropods were well adapted to surviving elevated summer temperatures, as long as moisture was not limited.

In general, the species diversity of soil fauna in the arctic and sub-arctic is lower than in temperate and tropical areas, and the species richness and abundance closely correlate with thermal and hydrological conditions (Thor, 1930; Dalenius, 1960, 1962; Chernov, 2002). The abundance of Acari and Collembola found in this study is similar to other studies of arctic and subarctic sites (Coulson et al., 1996, 2000; Sulkava and Huhta, 2003). The taxonomic diversity is difficult to compare to other studies, as most investigations on taxonomic diversity identify the individual soil animals to species level. However, the Oribatida taxa identified here are comparable to those found in studies by Dalenius (1960), although a lot more species were identified in his study. A study by Agrell (1941) identified 68 species of Collembola in the Abisko/Torneträsk area but these samples were taken from a large variety of habitats.

The results we report here comply with the general assumption that soil microarthropods in general are ‘‘bottom-up’’-controlled. Our data support this assumption by showing higher numbers of Acari and Collembola in treatments which previously have been demonstrated to have higher nematode abundances and higher microbial biomass. The numbers of Acari and Collembola may be influenced both by the number of nematodes, which act as prey and/or facilitate a higher decomposition rate, and by the species composition, biomass and activity of microorganisms, which also act as sources of food for many microarthropods. However, there is also a direct effect on the microarthropod abundance from the applied manipulations, as seen with the increased abundance at increased temperatures in sites where abundance is not limited by water availability. These effects are nevertheless much smaller than the temperature effects seen on nematodes at the same site (Ruess et al., 1999a,b), which indicates a higher sensitivity to temperature changes in the nematode community than in the microarthropod community. Changes in nematode abundance as a response to changes in microbial communities, and to temperature changes directly (Ruess et al., 1999a,b), may have been a cause of the changes seen in the number of nematode-feeding mites, especially within the Actinedida and Gamasida taxons. However, Martikainen and Huhta (1990) also observed that the oligophagous Zerconidae in a controlled mesocosm experiment significantly reduced the number of nematodes, without influencing decomposition and nutrient cycling. As pointed out in a recent review of soil food web structure by Scheu (2002), most soil animals are opportunistic regarding food sources, and will eat anything from bacteria to plant roots and other soil animals (dead or living), depending on what is available. On the other hand, other studies indicate that soil microarthropods may also be highly selective in their food preferences with little overlap between species (Jørgensen et al., 2003). In this study, we treat the Collembola as one group, and interpret the data based on the assumption that they are mainly detritivores. However, *Friesea* sp., which was found in the fellfield, was observed in the laboratory to prey directly on other living Collembola. We suggest that the effects of warming and fertilisation on the microarthropod communities observed in the present study are most likely caused by altered food web relations which, however, are difficult to specify.

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